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HUGH DINGLE

MIGRATION

The Biology of Life on the Move

SECOND EDITION



Migration

The Biology of Life on the Move

Migration

The Biology of Life on the Move

Second Edition

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Preface

It is now more than 15 years since the first edition of this book was published in 1996. As with most fields of science, the understanding of migration has advanced markedly in that interval with respect both to new data and to conceptual understanding. The time therefore seems overdue to provide an updated survey of the field with analysis of its tenets and assessment of its progress. This book is, then, more of a sequel than a second edition. Although portions of the First Edition are included within the text along with some figures, these are included to provide, usually, historical continuity. The overwhelming majority of the material in the text comes from research on migration that has been done since 1996, and I have made a conscious effort to refer back to earlier work only where it still obviously includes the best examples or is necessary to understand what has been learned since. Added stimulus to write this sequel is provided by the universality of movement among living organisms and its contribution to adaptation and life histories. Movement has been characterized as one of the ten great "inventions" of evolution (Lane 2009), and movement was the subject of a special feature in the Proceedings of the National Academy of Sciences (USA) (Nathan 2008). Migration is a very special and elaborate form of movement, and I shall emphasize both its special nature and its characteristics that make it distinct from other movements such as foraging, ranging, and commuting.

As with the first edition, this book is not taxon-limited, and it focuses on the similarities among migrants as well as on the differences that characterize the behavior in different taxa. There continue to be excellent books devoted to migration in specific groups. These include books on birds (Newton 2010), insects (Drake and Reynolds 2012), and salmon (Quinn 2005). At least one recent multi-authored work has considered migration across taxa (Milner-Gulland et al. 2011), but with a vertebrate and ecological modeling emphasis, whereas I place heavy emphasis here on the characteristics and evolution of migratory behavior as well as its ecology. Like its predecessor, this book is a further attempt to find common ground and to consider migration as a biological phenomenon rather than as a behavior in a taxon that I study. As before, I hope readers will inform me of errors, misinterpretations, or faulty logic they may find. I am grateful to those who corrected facts or interpretations in the 1996 edition, and where still relevant, these corrections have now been incorporated.

Once again I have written this book for students of migration and for those biologists who are generally interested in the functioning and adaptations of whole organisms. A reasonable background in biology should allow readers to understand the discussion, and it is my hope that the readership will include graduate students at all levels and even upper division undergraduates. Scientific terminology is necessary for a book such as this, but I have tried to define any unusual or highly specific terms. It is further my hope that, as I have endeavored to be as jargon-free as possible, the book will be intelligible to lay persons interested in conservation or natural history.

In writing this, my debts to others continue to accumulate. Much of the research for the book was done while I was an Honorary Research Consultant in the School of Integrative Biology at the University of Queensland in Brisbane, Australia, headed by Professor Scott O'Neill. Office space and logistical support were provided by Mark Blows and Myron Zalucki. After my retirement from the Department

of Entomology at the University of California, Davis, Sharon Lawler graciously provided me with office space in her laboratory complex in that department. In no particular order I am very grateful to the following for sending me papers, photographs, or figures, and/or for discussions and advice: Dustin Marshall, Brad Shaffer, Ron O'Dor, Peter Moyle, Jeremy Ringma, Tom Hahn, Marilyn Ramenofsky, Jamie Cornelius, Allison Shaw, Peter Armstrong, Sidney Gauthreaux, Marcel Holyoak, Alistair Drake, Myron Zalucki, Nann Fangue, Steve Reppert, Tom Sappington, David Arsenault, Scott Burgess, Chris Guglielmo, Scott MacDougall-Shackleton, Kathy Keatley-Garvey, Markus Lilje, Adam Riley, and Scott Carroll. Portions of the manuscript were read by Steve Reppert and Myron Zalucki with many useful suggestions. The figures and maps were drawn by Bao Sit and Ethan Mora, both students at the University of California, Davis. Arnold Duplantier guided me through problems with computer preparation of the manuscript, and Nancy Dullum once again cheerfully prepared the final typed version. Lucy Nash at Oxford University Press guided the book to publication and patiently answered my several questions. I continue to be amazed at how willingly friends and colleagues give time to assist me with this enterprise. It can truly be said that I cannot thank them enough.

H. D.
Davis, California
November 2013

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Introduction and plan of the book

Migration continues to draw attention from both biologists and the public because it is a fascinating behavior. In locusts, butterflies, birds, many fish, and large mammals many thousands or even millions of individuals move over what are often sizeable portions of the surface of our planet. The forces that drive these movements draw the curiosity of scientist and layman alike. Migration has been and continues to be the perpetual subject of television programs on natural history, coffee table books, and often the daily press to which can now be added the Internet. Descriptions of mass movements and notations of arrival and departure attract much of the attention the public devotes to matters of natural history.

The conspicuousness and prevalence of migration in the lives of organisms signals the importance of its role in life histories. By moving across space and time, migrants reduce the extremes of variation in their environments. The proximate and evolutionary adjustments of life histories to take advantage of suitable habitats that, relative to the size of the migrant, are often far apart is the focus of this book. Many books on migration have been written, but most are confined to a single taxon. In spite of increasing knowledge of its diversity, migration is still often viewed from the perspective of a single group, and indeed it is often defined in terms of properties within that group. Ornithologists and other vertebrate biologists have stressed migration as round-trip movement, even though such round-trips between "two worlds" (Greenberg and Marra 2005) are characteristic only of long-lived organisms such as vertebrates whose lifespans allow the time necessary for repeated journeys. The vast majority of migrants, with insects containing the prime examples, migrate only one way. A major point of this book is that by comparing across a spectrum of taxa, it is apparent that physiological and behavioral characteristics converge on a syndrome that defines migration and distinguishes it from other sorts of movements independent of pathway. The particular route followed is an outcome of migration important to the ecology of the migrant and the natural selection acting upon it, but it does not define migration. Other important aspects of the ecology concern the redistribution of the population that occurs with migration. The reason for writing this sequel is to update the consideration of the behavior and ecology of migration across taxa and to determine its common properties, its variability, and the way natural selection has molded the properties to fit the life histories of the organisms concerned. As with the first edition, I consider migration a property of both plants and animals.

Like its predecessor, this sequel is divided into four parts, each with a brief introductory section. In Part 1, I define migration, give examples, and place it in the spectrum of different types of movements, with emphasis on distinguishing between moving itself and its properties and the ecological consequences of movement of various types. I conclude with a chapter on methods for the study of migration and the new technologies that are providing insights into the frequently astonishing capabilities of migrants. Part 2 focuses on proximate mechanisms, including physiology, morphology, the constraints associated with them, and on how these constraints can be overcome by the interactions of migrants with winds and currents to facilitate transport. Among the most exciting of recent advances is the discovery and analysis of the extraordinary ability of migrants to use information from the sun, stars, polarized light, and magnetic fields to find their way over the Earth's surface.

The longest section of the book is Part 3 on the evolution of migratory life histories. Although this aspect of migration generally receives less attention than other aspects covered in Part 2, the evolutionary and ecological bases for migration—although more difficult to study than proximate factors—are important for understanding not only the role of migration in the lives of individuals, but also the impact of migrants on the communities in which they live. Migrants occupy a variety of habitats and have various ways of coping with this variation, and a common theme is that of changing habitats and the necessity for movement. The evolution of adaptation to migratory life histories involves the genetics of syndromes and the way in which natural selection acts upon them. The roles of migrants in their environments affect the interaction between migrants and humans, so the final section of the book, Part 4, is devoted to a brief consideration of the importance of migrants to pest and disease management and to conservation.

Like its predecessor, this book is not intended to be a comprehensive review. The large and ever-growing literature on the subject is well covered in several taxon-specific books and symposium volumes. I have tried here to focus on conceptual issues, especially as these might be illuminated by specific examples drawn from the diversity of organisms that migrate and from comparisons across that taxonomic diversity. Each chapter closes with a section I have called "Summing up," in which I attempt not only to summarize and draw conclusions, but also to speculate and reflect briefly on the major issues raised by the chapter subject matter. To conclude the book, there is a brief chapter in which I try to weave together some of the major threads and to offer some ideas on important future directions for research on the biology of migration.



Plate 1. The geolocator attached to an owl showing the exposed light sensor. Data from the geolocator are downloaded when the owl is recaptured upon return to its nesting area. Photo by David Arsenault. (See also Figure 4.6b.)





Plate 2. Two species of albatross in flight over the ocean. (Left) Black-footed Albatross at the Cordell Bank off Bodega Bay, California. (Right) Laysan Albatross off Half-moon Bay, California. Note the long wings of high aspect ratio typical of soaring, pelagic seabirds. Photos by Marcel Holyoak. (See also Figure 7.3.)



Plate 3. The Red or Common Crossbill (*Loxia curvirostra*); a bird captured in Russia for banding and study. Note the bill adapted for extracting seeds from conifer cones. Photo by Jamie Cornelius. (See also Figure 11.5.)



Plate 4. Two mating pairs of Soapberry Bugs *Jadera hematoloma* showing wing dimorphism. The upper pair are short-winged; the lower pair are long-winged. The matches are by chance and are not due to assortative mating. Photo by Scott Carroll. (See also Figure 13.1.)



Plate 5. The parthenogenic (summer) long-winged and wingless morphs of the Rose Aphid (*Macrosiphum rosae*). Note that in addition to wings the flight morph has a somewhat different morphology, especially of the head and thorax. Photo by Kathy Keatley Garvey. (See also Figure 14.3.)

PART 1

Migration and Methods for Its Study

Even to the most casual observer of nature, it is apparent that organisms make many different kinds of movement. Most of these are local in scale and are linked to the daily and other short-term activities contributing to growth, survival, and reproduction. But the observer who notes the arrival of geese in the autumn or the sudden appearance of a locust swarm in a crop recognizes that there is a different sort of movement that differs in scale. These movements reflect distinctive behavior and physiology and take organisms to a different habitat that can serve for either escape or colonization. The terminologies applied to different movements differ widely, often reflecting characteristics of the group or subdiscipline with which a biologist is most familiar. Thus, early on the term "migration" became associated with the conspicuous long-distance round-trip excursions of birds and other vertebrates and "dispersal" was applied to travels that were one-way and usually shorter. Unfortunately this ornithocentric view still leads to confounding of issues and to the failure of biologists working on different groups to appreciate or communicate common features of movement behavior, including migrations that were not to-and-fro but that included functions and physiologies that did not differ from those of round-trip journeys.

In the opening two chapters of this first section of the book, I deal with the issues of defining and characterizing different kinds of movement. Chapter 1 outlines a classification scheme to place migration in the context of the movements of various kinds and functions that occur across organisms. Starting from stasis and the simplest forms and rates of turning, I describe and define movements associated with resources and their acquisition in the course of local, short-term maintenance activities, for example those associated with food or mates. Inputs from resources directly influence the onset and cessation of these movements which include kineses, foraging, and other activities designated here as station keeping because broadly speaking they involve maintenance in a restricted area. Behaviors associated with search for a new home or home range, but still ceasing in the presence of the appropriate resource of a new station, are here called "ranging" because they usually incorporate a specifically exploratory component. This last is an assumption because we still know relatively little of the precise behavior that occurs during ranging; we know much more about start and finish than we do about what happens in between. Finally, I introduce migration as a behavior distinct from other movements because it is not a proximate response to resources, involves temporary suppression of inputs from resources, and serves not to keep an organism in its habitat, but to remove it to another.

Migration is examined in detail in Chapter 2. I emphasize the characteristics that define migration as so carefully worked out by J. S. Kennedy. The definition is based on experimental work with the Black Bean Aphid, *Aphis fabae*, but careful examination of a broad spectrum of migrants from aphids to whales reveals that all display a parallel set of behavioral and physiological responses that characterize their migrations. This migration syndrome is not based in a phylogenetically ancient genetic program, but is based in the modification for migration of traits evolved for a variety of purposes. I emphasize the distinction between migration as

an individual behavior on which natural selection acts and the outcomes of that behavior in migration pathways and the population processes of dispersal and aggregation.

The rich diversity of migratory patterns is illustrated more fully in Chapter 3. I discuss the familiar long-distance round-trip journeys of birds and large mammals, but show that even round-trips can have a multiplicity of forms from the trans-hemispheric flights across the Pacific of some shorebirds to the migrations to diapause sites by many insects that may cover only a few tens or hundreds of meters. Other patterns are less regular, as illustrated by the often spectacular patterns of the denizens of deserts and ephemeral wetlands. Diversity is also present in the patterns of organisms that migrate only once in a lifetime. Other migrants make round-trips that are divided by life-history stage or generation, with each stage or generation undertaking a different leg of the pathway. The point is made that it is not path followed but rather characteristics of behavior that determine whether migration is occurring. Although built from a similar blueprint, migration across taxa displays extraordinary diversity and richness.

Chapter 4 on methods for studying migration concludes Part I. Both old and new methods are described to show how each can contribute to our understanding of the behavior, ecology, and evolution of migration. Traditional methods of marking and banding still have much to contribute, but the rapid advancement of technology now allows a fuller understanding of details of migratory performance and the often astounding capabilities of migrants. The more recent contributions of radar, telemetry, and geolocators have resulted in advances of the field by the proverbial leaps and bounds. The technology of molecular genetics is now making major contributions to understanding the evolution of migration. Some aspects of migratory behavior are best studied with captive migrants or those reared under controlled conditions. These lead to the challenges of devising laboratory methods, with the challenges often producing ingenious devices and approaches, some of which I cover here. Overall the summary of methods is intended to provide enough understanding of how migration is studied to allow appreciation of the problems faced in gathering data on a behavior that occurs over space and time that is far from confined.

CHAPTER 1

A taxonomy of movement

Movement is an almost universal behavioral characteristic of living organisms; it makes major contributions to adaptation and the organization of life histories, and, as a consequence, to population and community dynamics. A recent book, for example, suggests that movement is one of the ten great "inventions" of evolution (Lane 2009), and a special feature in the *Proceedings of the National Academy of Sciences of the USA* was devoted to movement paradigms and ecology (Nathan 2008). This book addresses a special kind of movement known as *migration*, its particular defining characteristic traits, and the ecological consequences of those special traits. All the movements an organism makes throughout its life cycle sum to produce its lifetime track. Before embarking on a full discussion of migration and its evolution and ecology, I briefly define and describe the various important movements in lifetime tracks and include examples to indicate the adaptive roles they play in life cycles (Table 1.1). This taxonomy should serve to place migration in the context of overall lifetime tracks and indicate its significance relative to other forms of movement. Chapter 2 considers in greater detail the behavioral mechanisms that make migration such a special feature of life histories.

Most movements occur within a relatively circumscribed *home range* over which an organism travels to acquire the resources it needs for survival and reproduction. The sizes and durations of home ranges depend on the ecological conditions in the habitat and the sizes, feeding modes, breeding characteristics, and powers of movement and other traits of their residents (Roshier and Reid 2003). Most cover only a small area relative to the geographic range of the species, but some, like those of pelagic seabirds, may extend over considerable portions of the earth's surface. The kind of area within which home ranges occur and which provides the required resources for each phase of the life cycle is the *habitat* (Southwood 1981). Usually mobilized before resources decline and in contrast to other movement behaviors outlined in Table 1.1, migration takes an individual out of its current habitat to a new one with a new home range often at some distance elsewhere (Dingle 1996; Dingle and Drake 2007). This *pre-emption* is an important characteristic of migration. A second important and defining characteristic is suppression during migration of responses to inputs from resources that ordinarily would stop movement as detailed in Chapter 2, thus guaranteeing a move to a new habitat. The focus of this book is the specific characteristics of migratory behavior that lead to the ecological consequence of changed habitats.

The form of the lifetime track and its partitioning into its constituent elements is determined by natural selection and by the degree of behavioral flexibility conferred on the track in responding to environmental exigencies or stochasticity. As with home range, tracks are a function of factors such as the organism's size, life history traits and powers of movement plus its habitat and geographic range. All these factors will be discussed with respect to migration in this book. In turn, the dynamics of populations and communities are greatly influenced in both time and space by the lifetime tracks of the organisms that compose them. At the extreme of these influences migrant pests such as locusts can adversely impact whole biomes (Cheke and Tratalos 2007), and temperate avian communities around the world are profoundly influenced by the annual influx of breeding migrants from tropical or subtropical wintering areas. Before proceeding to a full analysis and

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Table 1.1 A taxonomy of movement behaviors contributing to lifetime tracks.

Movement	Characteristics	Examples
Movements home range or resource-directed		
Station keeping	Movements keeping organism in home range	
Kineses	Changes in rate of movement or turning	Moth in a pheromone "plume"
Taxes	Directed movement toward a stimulus source	Insect moving toward a light (positive phototaxis)
Foraging	Movement in search of resources; movement stops when resource encountered	Movement in search of food, mate nesting or oviposition site (animals); modular growth (plants, corals)
Commuting	Movement in search of resources on a regular short-term basis (usually daily or a few days); ceases when resource encountered	Albatross foraging; vertical migration in plankton
Territorial behavior	Patrolling territorial boundary; agonistic response to neighbors and/or intruders (stops when intruder leaves)	Many examples across taxa
Ranging	Movement over a habitat to explore it; ceases when suitable home range located	"Dispersal" of some mammals; "natal dispersal" of birds; parasite host seeking
Movements not directly responsive to resources or home range		
Migration	Undistracted movement to new habitat; cessation promoted by movement itself. Responses to resources or home range suspended or suppressed	Annual flights of birds to breeding grounds; flight of aphids to new hosts; movements to breed of diadromous fish; "dispersal" of some seeds
Movements not under control of organism		
Accidental displacement	Organism does not initiate movement. Movement stops when organism leaves transporting vehicle	Storm vagrancy
"Assisted migration" or assisted transport	Accidental or deliberate anthropogenic movement	Horticultural or weedy introductions; biological control species; conservation introductions

definition of migration in Chapter 2, I outline here and in Table 1.1 the different kinds of movements other than migration that, in their various ways and to varying degrees, contribute to lifetime tracks.

Station keeping

Activities and movements that keep an organism in a home range have been called *station keeping* (Hassel and Southwood 1978; Kennedy 1985), and this seems a useful term to include a number of behaviors that can also be described as "here and now" movements (Roshier and Reid 2003). These include an array of interactions with both biotic and abiotic environmental inputs all of which can be characterized as "vegetative functions," a term used by J. S. Kennedy (e.g., 1985) for activities that proximately exploit resources to promote growth and reproduction, in contrast to migration when growth and reproduction are temporarily suspended. These resources include not only food but also shelter, mates, nest sites, landmarks, enemy free space, microclimate and any other requirements for maintenance and survival of one's self and offspring. These are usually incorporated within the home range, but on occasion resource acquisition may require considerable forays with subsequent return to the home range (station) as with *commuting*. A salient feature of station keeping is that movements cease when a resource is located. A predator stops hunting when it kills its prey, a female cockatoo stops searching when it finds a suitable nest cavity in a tree, and a male moth stops flying and orienting to female sex pheromones when it locates a mate. As we shall see, cessation of movement in the presence of suitable resources is not characteristic of migration.

Among the simplest of station-keeping movements are *kineses*, defined as undirected responses in which the body's long axis shows no consistent relation to the direction of the stimulus and the direction of locomotion is random (Cardé 2008). Kineses can involve changes in the frequency of turning (klinokinesis) or in the rate of locomotion (orthokinesis); increased

turning and reduced movement will tend to keep an organism in its current location. The classic biology laboratory example of a planarian that slows down and increases its turning per unit distance causing it to avoid bright light and remain in shadow is a case in point. With the addition of a directed orientation, component kineses grade into *taxes* which are directed reactions in which the long axis is aligned with a stimulus and average movement is directed away from or toward that stimulus (Cardé 2008). Many larvae of bottom-dwelling marine invertebrates, for example, exhibit a positive phototaxis when they enter the plankton after hatching and a negative phototaxis when they settle out (Dingle 1996).

Some of the more interesting forms of taxes are the upwind orientations of insects to odor sources, as is the case with males of many species of moth responding to odor plumes of pheromones released by females. Moths (and any flying organisms) face two problems when attempting to locate an odor source. First, the odor gradient will lose concentration at increasing distance from the source, so flying up the gradient is not an option as gradients are only steep enough to follow within about 1 m of the source. The plume also consists of "puffs" interspersed with gaps that vary with wind velocity and shifts in direction of eddies (Murlis et al. 2000; Justus et al. 2002). Second, the moth cannot gauge its speed relative to the airflow by mechanosensory means because it is itself moving with the flow. Rather it must detect motion relative to the ground with an optomotor response to the pattern of visual inputs from the ground passing over the eye. Using an optomotor response, the moth turns upwind when it contacts the odor of the pheromone. It maintains contact with the odor by counterturning back and forth, often with metronomic consistency. When the odor is frequently contacted, the moth zigzags with high frequency and short excursions in each direction. If it loses contact for a brief period, excursions in each direction become longer, termed "casting", until contact is regained and zigzagging resumes (Kennedy 1983). Near the source, a gradient can be followed to the "calling" female. The whole process is given the cumbersome but descriptive term "odor-induced optomotor anemotaxis" (Cardé 2008; Cardé and Willis 2008). Similar mechanisms to locate odor sources occur in aquatic organisms orienting in currents (Atema 1996; Weissburg 2000) and by female mosquitoes which fly upwind when encountering CO_2 and follow body odor gradients in the immediate vicinity of the host (Takken et al. 1997; Dekker et al. 2005).

Kineses and taxes are often incorporated into *foraging* during which organisms seek resources by moving within a habitat. It has been defined as "reiterative . . . activity that is readily interrupted by an encounter with a resource of a particular kind" (Kennedy 1985) and usually takes place in habitats or habitat patches within the home range. Butterfly females of many species, for example, forage over often considerable areas seeking host plants on which to lay their eggs. These plants may be distributed in patches or as isolated individuals among patches or both. Zalucki and Lammers (2010) modeled the searching behavior of female Monarch Butterflies (*Danaus plexippus*) with simulations of habitats where the host plants (milkweeds, *Asclepias*) occurred scattered and in patches (Box 1.1).

The effect of searching behavior is shown by the examples in Figure 1.1. Figure 1.1A illustrates the effect of searching ability on ELP, the proportion (out of a theoretical maximum) of eggs laid over the lifespan of a female as the proportion of milkweed plants in suitable patch habitat increases. It is clear that good searchers, defined as having better than a random chance of finding resources, have a substantial advantage especially when patch density is low. The interactions between different levels of the density of single plants over the habitat and searching ability are illustrated in Figure 1.1B for a habitat that does not include any milkweed in patches. In this case a ten-fold increase in searching ability can more than double the proportion of eggs laid during a female lifetime so that good searchers have almost the equivalent success in a single plant habitat as they would if they remained in a patch. This would likely have a profound effect on fitness and suggests strong selection for searching ability. Although we know that insects can find host plants by odor (e.g., Finch and Collier 2000) and that habitat fragmentation can influence the ability to find resources (Merckz and Van Dyck 2007), we still have limited knowledge of searching abilities in real landscapes (Zalucki and Lammers 2010).

One of the important elements of plant biology receiving increasing emphasis has been the understanding of plant growth as a modular process

Box 1.1 Modeling butterfly search patterns

In the case where the host plants on which a butterfly lays its eggs occur either in patches or singly, Zalucki and Lammers (2010) considered the probability of a female finding a patch, $P\,(_{fPat})$, as based on the proportion of suitable patch habitat (A_{pat}) and on the searching ability of the particular female (S) so that:

$$P\,(_{fPat}) = A_{pat}{}^{S}$$

Once a patch is found, the butterfly lays ED_{pat} eggs for the day in it. If no patch is found, the female searches for single plants. The number of single plants found (F_{sin}) is influenced by the density of single plants outside the patches (A_{sin}), search ability S, and the time available for searching, t:

$$F_{sin} = t\,(A_{sin}/2 + A_{sin})^{S}$$

The number of single plants found determines the number of eggs laid on single milkweeds that day (ED_{sin}). The numbers of eggs laid on each day of life (ED) are then summed over the laying lifespan of the female and divided by the theoretical maximum number of eggs that that female could have laid during her lifetime (= 840 eggs based on field data of about a 14-day lifespan (L) and 60 eggs/day (ED_{pat})) to indicate a proportion of eggs laid over an individual lifespan:

$$ELP = \sum_{1}^{14} ED/ED_{pat}(L)$$

where the denominator $ED_{pat}(L)$ is 840 eggs as indicated.

(e.g., Lopez et al. 1994). Individual plants can be seen as populations of iterative units or modules, each with its own growth and development coupled to the demography of the whole plant. This approach allows growth analysis in relation to resource acquisition as an expression of foraging behavior. Clonal plants and other clonal organisms like corals, tunicates, bryozoans, and many algae provide useful insights into the relations among morphological structure, resource abundance and distribution, and consequent foraging strategies. This is illustrated in the phenotypically plastic red alga, *Asparagopsis armata*, where morphology varies under different conditions of color and intensity of light, a resource necessary for growth (Monro and Poore 2004, 2005). In high resource environments (high light) this alga produces "phalanx" phenotypes in which modules are close together because of frequent branching like a dense bush, whereas in low light it produces "guerilla" phenotypes with a stringy appearance and widely spaced modules leading to shade avoidance. Terrestrial plants show similar patterns under high and low light regimes. These foraging strategies are under both genetic and environmental control. There are also many further interesting parallels between the foraging behaviors of plants and animals that illustrate how natural selection has acted to produce equivalent solutions to similar problems, suggesting common biological processes (Lopez et al. 1994).

Whereas most foraging probably takes place more or less within a home range, this is not always the case. An example is the frequent matings by socially monogamous male birds with females outside their own territories. Such extra-pair copulations (EPCs, or EPFs if fertilizations occur) can be frequent, 58% in the case of the New World migrant Acadian Flycatcher (*Empidonax virescens*) (Hung et al. 2009). These excursions by male birds to procure matings outside the nesting pair may be designated *mate foraging* and may occur at some distance off the territory shared with the nominal nesting female mate. The Acadian Flycatcher tends to have linear territories along streams, for example, and males may cross territories to mate with females several hundred meters away (Woolfenden et al. 2005). Females accept EPCs on their territories but do not leave the territory to forage for them. In Hooded Warblers (*Wilsonia citrina*) in the northeastern USA, males may leave territories often and for long periods, but the foray rate into the territory of a given female was not a good predictor of whether extra-pair offspring were sired, probably because of mate choice by the female (Stutchbury et al. 2005). Mate foraging rates may vary considerably within and among species depending on species and habitat.

An impressive example of what may be called *extended foraging* (Kennedy 1985) occurs in the orthopteran Mormon Crickets (*Anabrus simplex*) and Old World locusts (*Schistocerca* and *Locusta*): the

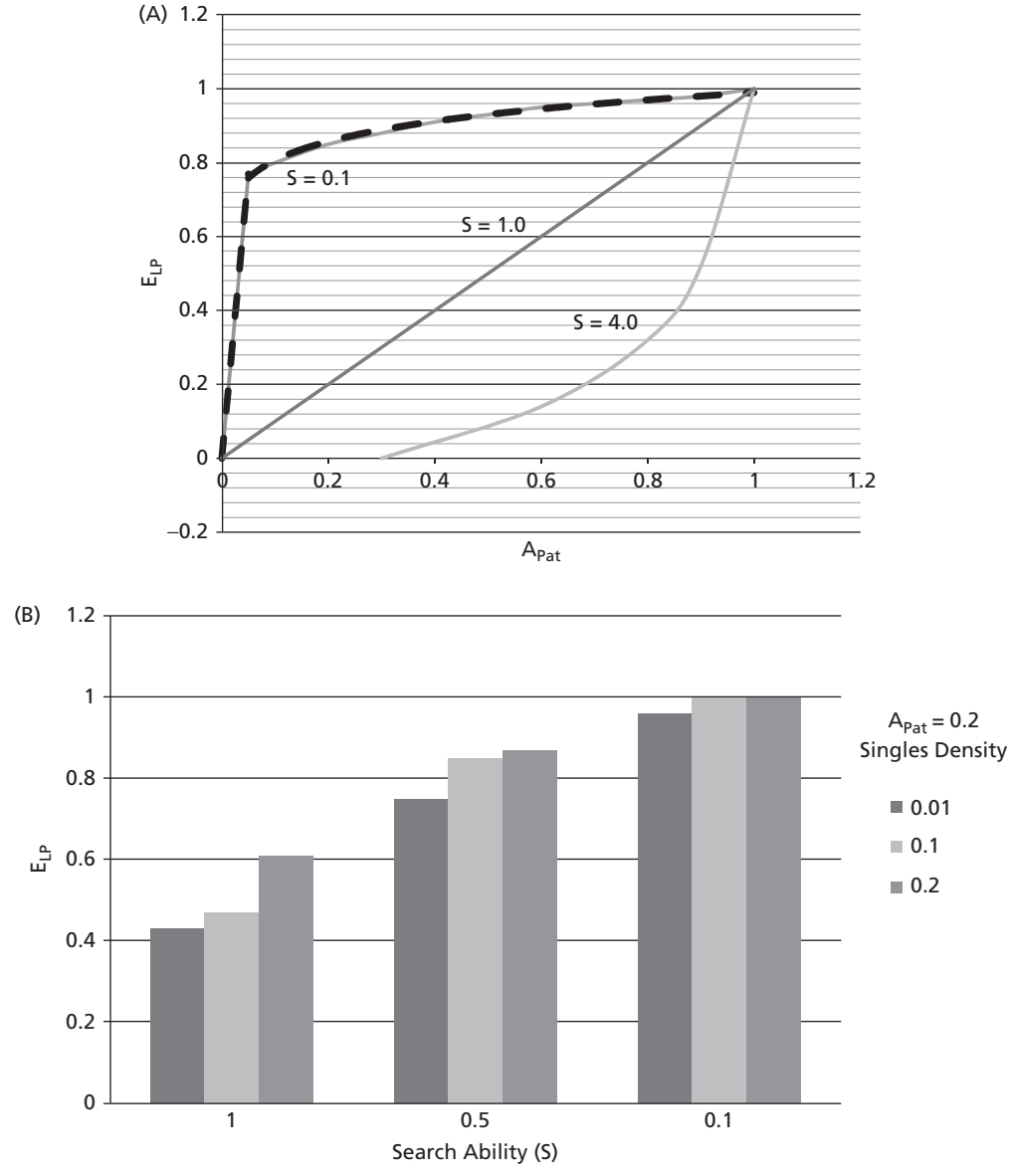


Figure 1.1 (A) The effect of search ability (S) by a Monarch Butterfly female on egg production (E_{LP}) as the proportion of suitable habitat (A_{pat}) increases. All milkweed plants are assumed to occur in patches. With random search $S = 1$, whereas for good searchers $S < 1$ (see Box 1.1). (B) The effect of search ability when $A_{pat} = 0.2$ and all milkweed plants occur singly rather than in patches. From Zalucki and Lammers (2010); used with permission from John Wiley & Sons.

latter are discussed extensively in Chapter 11. Mormon Crickets are large black wingless katydid-like insects (Tettigoniidae) that at high densities form huge "marching" bands comprising millions of insects that can extend for 10 km and cover 2 km per day (Simpson et al. 2006). They form these bands in shortages of two key nutrients in the diet—protein and salt—and are observed to feed selectively on high protein food sources such as seed heads and pods, and high salt sources such as soil impregnated with cattle urine, rather than stripping the vegetation as they go. One function of proteins—among

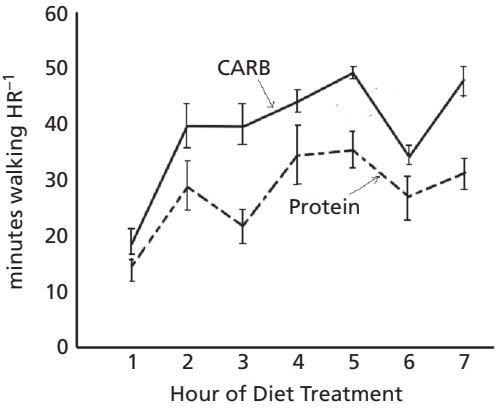


Figure 1.2 Walking activity of Mormon Crickets fed diets of 42% protein and 42% carbohydrate, respectively, for 7 h. Walking activity on protein is significantly less (analysis of variance, $P = 0.006$). The result for a mixed diet was similar to the protein diet ($P = 0.425$). Protein satiety thus inhibits locomotion. From Simpson et al. (2006); Copyright 2006 National Academy of Sciences of the USA.

other contributions to nutrition and growth—is to enhance immunocompetence (Srygley et al. 2009)—an important consideration at high population densities. When concentrations of crickets occur, depleting local nutrient sources, contacts among individuals activate movement and marching (Sword 2005). The crickets can acquire salt and protein through cannibalism, and, in effect, the bands are on a "forced march" to avoid being cannibalized by those closing on them from the rear (Simpson et al. 2006). There is a trade-off here because the large bands do protect their members from predation by heterospecific predators (Sword et al. 2005).

These large marching bands of Mormon crickets (and locusts) are often described as migratory (e.g., in the studies cited above), but because they are so obviously driven by the proximate quest for resources, they are best considered extended foraging rather than "true" migration which is not an immediate response to resource depletion but rather occurs prior to resource depletion (Chapter 2). Proximate responses to resources have been nicely demonstrated in Mormon crickets in experiments testing reactions of marching individuals to protein and salt. Simpson et al. (2006) placed two food sources of 42% and 21% protein and two sources with no protein in the path of marching crickets and found that many crickets (more at the higher concentration) stopped to feed on the protein diet whereas far fewer stopped for food with no protein present. Similarly water with an optimum salt concentration (0.25 M NaCl) induced many to stop. Furthermore, high concentrations of protein fed to crickets in the laboratory inhibited locomotion (Figure 1.2) which, as with the planarian above, will tend to keep an animal longer in its current location and in contact with the rich food source. These results are what would be predicted for foraging, i.e., movement should be reduced or cease when an appropriate resource is encountered (Table 1.1).

Some extensive foraging pathways occur as more or less round-trip excursions, which are most logically designated *commuting* (e.g., Kennedy 1985; R. O'Dor, personal communication) by analogy with the round-trips between work and home in urbanized human societies. Among the most impressive and important of these are the daily "vertical migrations" of many marine and freshwater organisms. These include the zoo- and phytoplankton, and also the fish and larger invertebrates that feed on them. Plankton communities are at the base of the food chain for marine animals and are therefore crucial to the growth and survival of those species at higher trophic levels, especially those predators that are exploited in commercial fisheries. As revealed by the decade-long Census of Marine Life program, throughout the world's oceans there are on the order of a billion tons of biomass that display large-scale (hundreds of meters) vertical movements on a daily basis in complex temperature and seasonally modified patterns (Vecchione et al. 2010; O'Dor et al. 2011), often forming several layers at varying depths (Figure 1.3). These movements are triggered by the proximate response to ambient light levels with the organisms descending to depth at sunrise and rising again at sunset. The best evolutionary explanations of these grand movements seem to be the avoidance of predation by rising to the surface at night—when predator vision will be limited at low light—and the exploitation of resources in different layers of the aquatic realm, or both (summarized in Dingle 1980). Phytoplankton can move vertically by regulating buoyancy or, if possessing flagella, actively swimming: their vertical movements appear to be responsive to light and nutrient gradients, enabling cells to move into regions con-

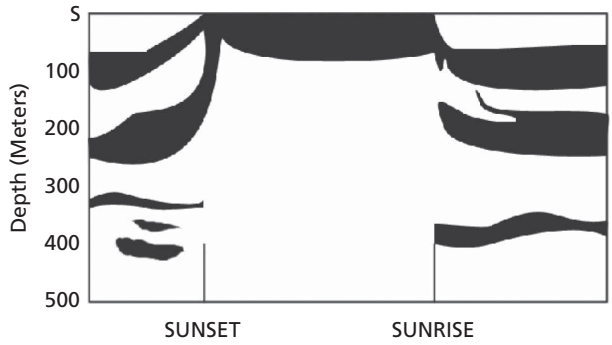


Figure 1.3 Drawing made from Deepwater Echo Integrating Marine Observatory System (DEIMOS) acoustic record in Monterey Bay, California, showing vertical movements of plankters and small fish. During the day the organisms are distributed in three layers centered at approximately 90, 200, and 350 m depth. They rise to <80 m at sunset and descend again at the following sunrise.

Source: <http:acoustics.washington.edu/DEIMOS/deimos_data.php>.

ducive to growth or to avoid deleterious conditions. Even minute animal plankters can move impressive vertical distances by swimming (Figure 1.3). On a far lesser scale, soil organisms in terrestrial habitats and above-ground organisms such as lepidopteran caterpillars may also exhibit diurnal–nocturnal daily commutes.

Other animals of both marine and terrestrial communities make longer-duration and often long-distance horizontal commutes. Albatrosses, shearwaters, and petrels, for example, nest on small islands and make extensive foraging excursions for food to feed their young, with parents alternating trips. Tracking of short-tailed and Sooty Shearwaters (*Puffinus tenuirostris* and *Puffinus griseus*) breeding on islands off New Zealand, Tasmania, and the southern coastline of Australia has revealed that they regularly forage along the edge of Antarctica over a period of several days before returning to the home colony (Weimerskirch and Cherel 1998; Klomp and Schultz 2000; Shaffer et al. 2009). New Zealand Sooty Shearwaters conduct both relatively short 1- or 2-day commutes of 800–1,500 km along the New Zealand shelf and long commutes of 4,500–12,700 km to areas of the polar frontal zone near Antarctica, both to the southeast and southwest of New Zealand for durations of 11–14 days. The use of two very different habitats for foraging evidently provides greater flexibility for maximizing resource acquisition (Shaffer et al. 2009). Wandering Albatrosses (*Diomedea exulans*) may make trips of up to 33 days for distances of 3,600–15,000 km when their mates are incubating and for 3 days and more than 300 km after the chicks are hatched (Jouventin and Weimerskirch 1990). A commute familiar in many rural areas in both Old and New Worlds is the daily excursion of winter flocks of corvids (crows, rooks, and magpies) from overnight roosts in the trees of towns and villages to feed in the surrounding agricultural areas. Similar commutes are also known from other terrestrial birds. Among mammals, hyenas (*Crocuta crocuta*) of the Serengeti Plains of East Africa may travel an average of 40 km to prey on the nearest populations of migratory grazers. By this commuting, clan sizes are maintained above the apparent carrying capacities of the family territories (Hofer and East 1993). Although consisting of round-trips like some (but not all) migration, these bird and mammal commutes and those of aquatic "vertical migrants" are clearly excursions to exploit resources in the form of food and refuge and are therefore a form of foraging.

Ranging

In addition to foraging outside the home range for mates or in the extended marches of locusts and Mormon Crickets, an organism may at certain times in its life cycle leave its home range to seek another one. There are two movement behaviors that accomplish this change, which I designate as *ranging* and migration. The definition and special characteristics of migration will be discussed in the next chapter. Ranging, like migration, occurs in a great variety of organisms and is characterized by a departure from the current habitat patch (emigration), the seeking of a new patch, and the occupation of an available *and* suitable patch so discovered (immigration). Following Jander (1975) and Bell (1991) I refer to this travel between resource patches as ranging because it involves "movement over an area so as to explore it" (*Webster's Collegiate Dictionary*,

10th edition). Ranging differs from migration in that responses to sensory inputs from resources or resource surrogates are not inhibited or suppressed, and the organism responds to those signaling a suitable habitat patch once it has been encountered. In this way ranging is similar to station-keeping behaviors and differs from migration. Ranging includes many of the movements described as "dispersal" in much of the movement literature such as "breeding dispersal" and "natal dispersal" (Dingle 1996); my reasons for preferring ranging over "dispersal" are detailed in Chapter 2.

In some cases ranging may, like commuting, cover considerable distances and grade into migration. Just such an instance has been analyzed in detail for the Australian Grey Teal (*Anas gracilis*) (Roshier et al. 2008a,b). This small duck is well adapted to using the often ephemeral wetlands of the driest of continents, and it moves widely and nomadically over the Australian region. Roshier and colleagues tracked individual teal in two differing drainage basins of Australia, the Murray–Darling River and the Lake Eyre, which differ in habitat predictability. The former is an area of eastern Australia that contains widely distributed permanent and temporary wetlands. By contrast, the Lake Eyre basin to the north and west of the Murray–Darling is a vast, internally draining desert basin characterized by infrequent, unpredictable floods and mostly ephemeral but highly productive wetlands (Chapter 11). Using satellite telemetry, Grey Teal were monitored for up to 879 days with 32 long-distance movements of more than 150 km identified. There was no relationship between flight distance and the recent occurrence of rainfall at the origin or destination of flights, the type of wetland (temporary or permanent), or the drainage basin of origin. Duration of stay at the destination did, however, increase with recent rainfall at the site from a mean of 29.1 to 95.3 days, a statistically significant difference that allowed time for breeding at the longer durations. A further interesting facet of the study was that many teal apparently responded at some point to distant environmental cues such as rainfall and flooding without prior knowledge and likely retained a memory of suitable breeding sites. How the appropriate time to travel is identified by the birds is still unknown.

A comparison of the flight pathways using fractal analysis suggested that there were two distinct movement patterns (Roshier et al. 2008b). Fractal analysis is based on the assumption that the fractal dimension describes movement independent of scale (Turchin 1998). Along a completely linear path the distance traveled, L, is equal to the displacement between start and finish, R. If L and R are related by a power law, $L^D = R$ and $D = 1$ for a straight path. With a curvy path, $D > 1$ up to a maximum of 2 in the case of Brownian motion. D thus provides a measure of the "sinuosity" or "tortuosity" of the movement path (see Turchin 1998 for calculation of D, and Bartumeus and Levin 2008 for additional theoretical analysis of movement pathways); in the extreme case of $D = 2$ the path fills a plane without ever crossing itself. In the case of the Grey Teal, pathways could be separated into two distinct patterns, one with D varying less than 0.2 and the other with D varying by more than 0.8 with no pathways intermediate. This suggests that pathways with high tortuosity may be ranging movements to explore for possible wetland breeding sites whereas those with low tortuosity (i.e., more straightened out), which also tended to bypass sites which seemed suitable, may well be migratory and based on prior knowledge of wetland conditions. The presumptive migratory flights occurred with greater frequency in the desert Lake Eyre basin of less predictable habitats, but both types of flight occurred in both regions. These Grey Teal movements, and likely those of other nomadic organisms, are particularly interesting and deserving of further study for the assessment of gradations between ranging and migration and of the relation between these types of movement and resource distributions within broad-scale habitats.

At the other end of the movement spectrum from migration, ranging may also grade into foraging. Fryxell et al. (2008) examined the movement patterns of free-ranging elk (*Cervus elephus*) that had been introduced into a new area. Over the course of 1–3 years these animals shifted from a "dispersive" to a "home-ranging" phase. The former was characterized by alternation between "decamped" (including what appeared to be foraging and social bonding) and exploratory modes (what I am calling ranging) with the result that they gradually occupied a wide area

by increasing the mean distance between individuals. During the home-ranging phase of movements, there was complex interplay between attraction to preferred habitats and memory of previous habitats across the home range movements. At fine scales, encountering high-quality food plants triggered area-restricted search while browsing interspersed with less sinuous paths when not browsing. A multiphasic structure to movement was fundamental at all spatial scales. Such should be the case with any organism capable of movement as it carries out its lifetime track, but the structure should vary according to the type of movement undertaken.

Accidental displacement

Movement, sometimes for considerable distances, can be "accidental" in the sense that no overt behavior on the part of the organism leads to the pathway in question. Migrants are among those that can be displaced in unpredictable fashion. The ornithological literature is replete with examples of birds being carried outside their usual ranges by storms or periods of prevailing winds in the "wrong" direction, sometimes appearing as "vagrants" at well-known "migrant traps" to the delight of local birdwatchers (e.g., Alerstam 1990). Many terrestrial insects are also blown off course (Dingle 1996). Spores, seeds, small insects and other organisms are no doubt on occasion simply plucked from their habitats by storms, high winds, or swift currents. These displacements differ from migration in two important ways: first, they are involuntary and there may even be devices such as holdfast organs or adhesive appendages evolved to prevent them; and second, they cease once the traveler is deposited by the transporting vehicle rather than as a consequence of specific behavioral and physiological responses to environmental inputs. By far the majority of such accidental travelers undoubtedly perish, but in rare instances these wayward waifs may colonize a completely new region. An example is the strong likelihood that the Old World desert locust (*Schistocerca gregaria*) colonized the New World after just such accidental displacement (Lovejoy et al. 2006). Thus in the right circumstances accidental displacement can assume considerable ecological and biogeographic importance (Taylor 1986a,b).

An interesting analysis of a likely accidental displacement with resulting colonization concerns the arrival of the Monarch Butterfly (*Danaus plexippus*) in Australia (Clarke and Zalucki 2004). The Monarch is native to the New World where it is a well-known migrant (see Chapter 3), and both it and its milkweed hosts have successfully established on many small islands across the Pacific, including Hawaii, Chuuk (Truk), Norfolk, Rennell, Samoa, Fiji, Vanuatu, and New Caledonia (Vane-Wright 1993; Clarke and Zalucki 2004; H. Dingle, personal observations), as a result of both natural and anthropogenic introductions. The butterfly was introduced and was well established in Vanuatu and New Caledonia by the 1860s, and its first appearance in Australia was in 1871 when it was noted in Queensland by butterfly collectors because of its novelty, being unrecorded until that time, although its milkweed host plants had been introduced into Australia some time before. In 1870 there were three major cyclones (hurricanes) that apparently crossed Vanuatu or New Caledonia and a few days later struck the coast of Queensland. It was at or near the locations where the cyclones came ashore that the first monarchs were observed. Shortly after its arrival the monarch spread rapidly and has evolved migration and the ability to orient its migratory flights appropriate to Australia, south in the spring and north in the autumn, albeit the travels are for shorter distances than those of the Northern Hemisphere migrants in the New World (Brower 1995; Dingle et al. 1999). This case and that of the desert locust above indicate the significant impact that occasional successful accidental invasion can have on a continental fauna.

Summing up

In studying movement it is important to recognize two distinct levels of analysis: the behavioral that concerns individuals and the ecological which concerns the consequences of individual movements to populations (Kennedy 1985; Dingle and Holyoak 2001; Nathan et al. 2008). From the behavioral perspective there are two broad types of movement (Table 1.1). The first concerns a range of movements associated with resources and frequently with home ranges. These are proximately triggered by inputs from those resources, including the shelter, food,

and mates required for growth, reproduction, and maintenance. A shortage stimulates movement until the resource in question is encountered, whereupon the movement ceases. Thus animals forage when they are hungry and mate forage when they are in breeding condition, but stop foraging when food or a mate is encountered and engage in feeding or courtship and mating.

Some movements that are proximately resource triggered extend beyond the home range. A young mammal or bird driven from its home range by social interactions ranges over the habitat until it encounters cues informing it of a new, suitable home range that it can occupy. These cues include greater access to, or abundance of, resources in the absence of competition from conspecifics (parents, sibs, or others) and the ability to optimize inbreeding or outbreeding. The successful occupation of a new home range will likely be a function of both resources and local variation in competition. Once the animal encounters and registers the necessary conditions, it stops ranging. An important ecological outcome is the spatial relationship among organisms produced by ranging. The same is true of commuting which involves foraging outside the home range but return to it. In the extended foraging of locusts and Mormon crickets, the spatial relationship among the participants both induces and maintains the marching and foraging behaviors of the population or swarm. In all the cases of non-migratory movement described, the behavior is both induced and terminated by the proximate response to resources.

As we shall see in detail in Chapter 2, response to proximate resources is not true of migration. It is a behavior that takes an individual out of its current home range, like ranging or commuting, but it also takes the organism out of its current habitat. Physiologically migration is characterized by a suppression or inhibition of responses to proximate stimuli emanating from resources required for vegetative functions. Movement is triggered not by a proximate lack of resources but rather by inputs that forecast a shortage of resources and/or by endogenous rhythms synchronized to changes in resource abundance. Migration ceases as a result of physiological changes brought about by the movement itself; until those changes occur, response to resources is suspended. The ecological consequence is movement to habitats different from those at the origin of a migratory journey and usually at some distance from it.

The different kinds of movement do not readily partition into easily distinguishable categories even, sometimes, in the case of extreme movement in the form of migration. Defining categories, however, should provide a useful guide for studying them. The present confusion of terminologies (see survey in Nathan et al. 2008) does not help matters in trying to understand movement behaviors. The framework in Nathan et al. (2008) may help, especially in emphasizing the analysis of the movement pathways of individuals (see also Turchin 1998). The patterns in these pathways allow formal distinctions between behavioral categories as described here (Table 1.1). The next challenge should be to go beyond statistical "brute analysis" to formulate and test hypotheses that connect pathways to the physiology, ecology, and evolution of the different movement behaviors and their interactions (Nathan 2008). Providing a classifying framework that includes behavior and ecology means that important questions can be asked that, in the absence of such a framework, would not be apparent. For example, what are the evolutionary consequences of having several movement behaviors (commuting, ranging, migrating) in the same population? And might they occur, say, in organisms as different as a host-seeking parasite and an ocean-crossing sea turtle?

In spite of indistinct boundaries between movement categories, distinguishing among them is important because natural selection will act differently on them and so influence the evolutionary trajectory of the behavioral repertoire. The degree of distinction between boundaries among categories will reflect the strength of selection in promoting the behaviors. It may be important in ecology, for example, to understand why selection might make types of movement distinct, and why, under other circumstances, it may render them overlapping. A combination of a useful behavioral taxonomy with powerful analytical methods for assessing pathways and steps should promote the understanding of how and why particular movement behaviors have evolved.

CHAPTER 2

Migration: definition and scope

What is migration?

The movement behaviors described in Chapter 1 all have proximate responses to resources as their focus. Migration is different. It involves suppression and thus postponement of responses to resources; this facilitates travel to different habitats before responses to resources again become evident. Migrants leave habitats where resources are deteriorating or their availability is otherwise reduced to colonize or take refuge in habitats where resources are available at least for maintenance. This relationship to resources drives the behavioral and life-history characteristics of migration. These characteristics take a variety of forms from the spectacular round-trip journeys of arctic terns flying from pole to pole to the migrations of a summer generation of young adult aphids seeking new host plants that may transit only a few hundred meters (Dingle 1996). Migrating animals are found in all major branches of the animal kingdom; their journeys take place in a variety of media; and they move by flying, swimming, walking, or drifting. The propagules of many plants and fungi have special devices to assure that they migrate by drift or soaring to new habitats before they germinate. Despite the variety, it is apparent that a single biological phenomenon incorporating specialized mobile behavior and transcending taxon, form, and environment is taking place. It should be equally apparent that migratory behavior can have a variety of outcomes in terms of population trajectories, degree of dispersal or aggregation, and roles in the life histories of the migrants (Gatehouse 1987, 1997; Dingle 1996; Dingle and Drake 2007; Reynolds et al. 2014).

If one looks across taxa and the natural history literature, it is evident that the term *migration* can evoke four different but overlapping concepts (Dingle and Drake 2007): (1) a type of locomotion that is notably persistent, undistracted, and straightened out; (2) a relocation of the organism that is on a much greater scale, and involves movement of much longer duration, than those arising from daily resource-directed activities such as foraging; (3) a seasonal to-and-fro movement of a population between regions where conditions are alternately favorable or unfavorable (including one region where breeding occurs)—the "two worlds" view deriving largely from bird migration (Greenberg and Marra 2005); and (4) movements leading to redistribution with a spatially extended population (Taylor 1986).

These viewpoints indicate significantly different perspectives on what migration entails and how it is defined. Types (1) and (2) relate to individual organisms whereas (3) and (4) explicitly concern populations. Type (1) describes a process (i.e., a behavior) whereas the remaining three types describe outcomes, for individuals or populations, of the locomotory behavior of individuals. Finally, types (2) and (3), but not (1) and (4), include a time or spatial scale. Much of the systemic confusion about the nature and definition of migration arises from a failure to distinguish between individual behavior and population outcomes. This process versus outcome distinction was at the heart of the debate among entomologists about whether migration should be defined for individuals ("behaviorally") or for populations ("ecologically") (summarized in Dingle 1996). One problem with the population perspective, which seems to have gone largely unrecognized, is that if one defines a trait such as migration in terms of populations, then natural selection should be acting on the population, i.e., group selection, which will be far too weak to produce the fine-tuned

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migratory syndromes observed, even if such group selection is occurring. A definition of a trait or syndrome should provide clear indication that it can respond to natural selection. With few exceptions, this means that the definition must be couched in terms of individuals. This is no less true of migration. At least among entomologists this view seems largely to have been accepted (Gatehouse 1997).

The definition of migration that I use in this book and that has guided my research is firmly rooted in the notion that migratory behavior is a characteristic of individuals and therefore responds to natural selection acting on individuals. This definition derives from the studies of J. S. Kennedy whose work is briefly summarized and his formal definition of migration given in Box 2.1. Any survey across migratory organisms reveals that, with appropriate modifications for differences in structure and physiology, the Kennedy definition is applicable regardless of taxon (Dingle 1996, 2006). As indicated by this definition, migration is seen as a distinct and specialized behavior whose broad characteristics are outlined in Box 2.2.

The first of these defining characteristics derives from frequent observation of migrants moving over longer periods and over longer distances than the movements commonly occurring during station keeping or ranging behaviors. At the extreme a small songbird or a Monarch Butterfly may move only tens of meters during breeding but cover thousands of kilometers during migration. Aphids such as the Black Bean Aphid are wingless and sedentary on a host while feeding and producing young, but are winged and capable of traveling from tens of meters to thousands of kilometers (aided by wind transport) when migrating. Second, migration pathways are straightened out, involving much reduced turning frequency when compared with station keeping, foraging, or ranging forays. In fractal terms (see Chapter 1) they exhibit less "tortuosity". Third, migrants do not respond initially to resources that arrest other movements,

Box 2.1 J. S. Kennedy's definition of migration

John Stodart Kennedy, FRS (1912–1993), was an entomologist and animal behaviorist who devoted most of his studies to the analysis of various kinds of insect movement (see Brady 1997, for a scientific biography). He defined migration based on several years of studying migratory flight in the Black Bean Aphid, *Aphis fabae*, using the controlled conditions of a laboratory flight chamber that allowed observations of the free flight of individual aphids (Figure 4.11). Kennedy noted that the behavior of aphids changed over the course of migratory flight. At take-off, they were sensitive to blue light in wavelengths predominant in the sky. After take-off, aphids settled into a cruising phase which in the field would result in straightening out of the direction of travel. Finally after flying for extended periods aphids became ever more responsive to stimuli involved in settling on a new host plant, including a change from blue to yellow light sensitivity (yellow wavelengths are the predominant reflection from the young host plant leaves preferred by the aphids). With an ingenious series of experiments Kennedy further demonstrated that migratory flight behavior and settling behavior inhibited each other and that each would "rebound" following a period of inhibition by the other. This had the important consequence that responses to host plants and subsequent settling behavior were actually prevented at take-off, but were then primed and made stronger by the ensuing flight. (For a full description of Kennedy's aphid experiments and their results see Dingle 1996). These behavioral characteristics led to Kennedy's definition of migration (Kennedy 1985):

> Migratory behavior is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.

Note the flexibility in migratory behavior embodied in the words "some temporary inhibition" and note that the definition allows repeated entry into, and departure from, the migratory state. Note also that wind- or current-aided migration is not "passive" even in tiny migrants, because there is active embarkation (and disembarkation, see also Dingle 1996) on the transporting vehicle. With a few modifications discussed in the main text (and see Table 2.1), this is the definition of migration I have followed and that I use in this book.

Box 2.2 Characteristics of migration as a distinct and specialized behavior

1. Persistent movement of longer duration than occurs during station keeping or ranging.
2. Straightened-out movement relative to the turning frequency of station keeping or exploratory ranging.
3. Initial suppression or inhibition of responses to stimuli that arrest other movement but with the subsequent enhancement of these responses.
4. Activity patterns particular to departure and arrival.
5. Use of surrogate cues such as photoperiod or population density to abandon habitats before they deteriorate, i.e., migration is pre-emptive.
6. Specific patterns of energy and internal resource allocation to support movement.

Sources: Dingle (1996); Dingle and Drake (2007).

for example foraging, but these responses are enhanced as migration progresses, or as David Quammen (2010) has put it, migrants ". . . maintain a fervid attentiveness to the greater mission . . ." and are "undistracted by temptations." This characteristic has the important consequence that migrants will not stop too soon if they encounter favorable, but soon-to-deteriorate, resources, but they will be especially responsive when they arrive at their ecologically and temporally suitable destination (Kennedy 1985). Fourth, as a consequence of these characteristics, there will be activity patterns particular to departure and arrival. There are likely, in other words, to be specific take-off and settling (arrival) behaviors. Fifth, because deteriorating conditions are likely to increase the difficulty of preparing for migration by, for example, increasing energy stores, migrants usually respond to surrogate cues that predict habitat or resource detrioration to anticipate migration. Migration is thus pre-emptive and not a direct response to proximate resources. It is, of course, ultimately a response to resource fluctuation. Finally, there are specific patterns of energy and internal resource allocation to support movement as opposed to, for example, reproduction (birds, or insects) or germination (plant seeds). Adjustments of biochemical pathways and temporary morphological changes like gut shrinkage and seeds that may require passage in vertebrate guts are among the patterns observed (Chapter 6). Although these traits are subject to thresholds and may not occur in a particular migrant, all are common to some migrants, occur across taxa, and are properties of individuals and subject to individual selection. Furthermore identification of these traits explicitly addresses what the targets of natural selection acting on migration might be.

In defining migration in a way that applies across organismal diversity, I have been accused of ". . . an effort to force migratory behavior into preconceived pigeonholes . . ." and thus of missing much of the "richness and elegance" of the phenomenon (Able 1997). I would argue in response that the definition proposed is analogous to a definition of animal winged flight. Birds, bats, and insects (and in the past pterosaurs) all fly (and migrate!), and all have wings, but the wings are quite different morphologically (Palmer 2011). Bird wings are modifications of the forearm with the hand diminished and have added feathers; bat wings are based on the elongated digits of the hand and a stretched membrane; pterosaur wing membranes were supported by a single elongate wing finger; and insect wings are outpocketings of the dorsal thoracic cuticle. Yet all wings are convergent in modifications for increased lift, reduced drag, and production of power by flapping, and all produce movement through the air that we define as flight, with no loss of richness or elegance (compare a pterosaur with a bumblebee!). Like flight, migration can be distinguished by a distinctive set of convergent characteristics whose evolutionary origins and functional aspects may differ across the taxonomic spectrum (Dingle 1996 and Table 2.1). As with flight, migration systems will indeed evolve as a result of both common and diverse sets of factors of varying importance in different taxa. With a definition focusing on testable criteria addressing behavioral and related characteristics of the organism that produce the migration phenomenon, one can seek the factors and selective forces that are at work.

A full understanding of migration and its implications, however, requires attention not only to the behavior, as we have defined it, but also to the context in which the behavior occurs. Like other biological phenomena, migration can be viewed at a series

Table 2.1 Comparisons among divergent taxa in behavior and other traits that indicate convergent migratory syndromes[a].

Trait	Hemiptera	Birds	Lepidoptera	Fish
Suppress maintenance	Yes	Yes	Yes	Yes
Orientation	?	Yes	Yes	Yes
Use winds/ currents	Yes	Yes	Yes	Yes
Fat deposition	Yes	Yes	Yes	Yes
Hormonal mediation	Yes	Yes	Yes	Yes
Wing (tail) shape	Yes	Yes	Yes	Yes
Body shape	Yes	Yes	?	Yes
Mouthparts	Yes	Yes	No?	No?
Fecundity	Yes	Yes	?	Yes

[a] Details with respect to each trait are discussed in subsequent chapters.
Source: Dingle (2006).

of organizational levels from the molecular to the evolutionary. We can describe events occurring at one level, such as the behavior of the individual migrant, in terms of lower-level attributes such as metabolic pathways, but we must seek explanations for them by identifying their functions and outcomes at higher levels. The hierarchy is in fact closed, as the highest level, natural selection, acts directly on the lowest, genes underlying the migratory adaptations (Rogers 1983; Dingle and Drake 2007).

Figure 2.1 expresses this hierarchical view of migration in a holistic conceptual model of what can be termed the "migration system" (Drake et al. 1995; Dingle and Drake 2007). The model incorporates both components and process (changes in linkages between components) and explicitly includes the environment in which the migrant population exists as well as the responses and adaptations of the migrant to it. In other words it includes both the behavioral process and the ecological outcome. There are four components of the model that express the relation between migratory behavior, its place in the environment, and its response to the natural selection imposed. First, a *migration arena* comprises both biotic and abiotic elements of the environment in which the migrant lives and to which it is adapted. More than one habitat may be included if the migrant moves between breeding and refuging areas. Second, a *migration syndrome* comprises a suite of traits promoting migratory activity including locomotory capabilities, a set of responses (or inhibited non-responses) to environmental cues that schedule and steer locomotor activity, and sets of morphological and life-history traits that add to the fitness of the migrants. Table 2.1 gives a brief comparison across four taxa that include migrants, indicating that in spite of different phylogenetic histories, migration syndromes share common characteristics derived from traits evolved for a variety of purposes (Dingle 2006). Migrant species in all the taxa included in the Table use fat for fuel and have wings (or tails in fish) with high aspect ratio (longer and narrower wings, lunate tails), for example. Third, a *genetic complex* or genome underlies the syndrome and contributes through direct gene influences and via the strength and direction of genetic correlations among traits (van Noordwijk et al. 2006; Pulido 2007; Roff and Fairbairn 2007). Fourth, there is a *population trajectory* (or its long-term average, the *population pathway*) comprising the route followed by the migrants, the timing of travel along it, the points where migration temporarily ceases (e.g., stopovers in birds), and the times when these points are occupied for breeding, refuging, and other key life stages. The model thus incorporates the ultimate (selective) and proximate (the arena) factors acting on migration, the response to natural selection in the phenotype and genotype of migrants (the syndrome and its genetic complex), and the population outcomes and consequences in terms of both selection and current conditions (the trajectory and pathway).

Conceiving migration as per Figure 2.1 leads to some important conclusions about the behavior and how to investigate its characteristics and its significance in the lives of migrants. A definition of a trait or syndrome in biology should provide clear indication that it can respond to natural selection. With few exceptions this means couching the definition in terms of individuals. Migration is no exception, and because of its characteristics undergoing selection, it can be distinguished from other sorts of movement. Migration is also important for its outcomes with the behaviors of many individuals producing population outcomes that produce selection acting back on individuals (behavior, syndromes),

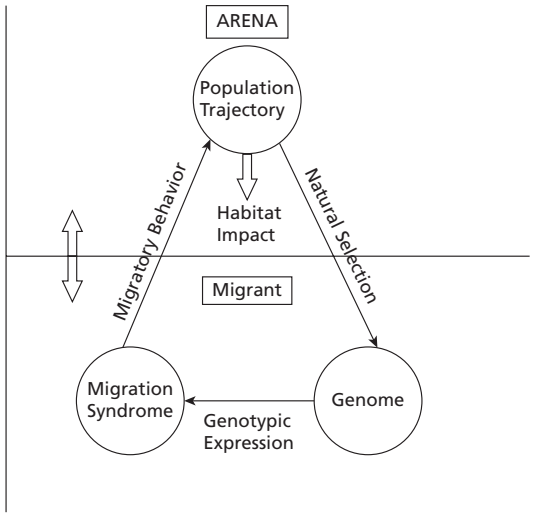


Figure 2.1 A holistic view of migration. Upper: the arena in which a migratory life cycle (the population trajectory) takes place. The life cycle impacts habitats through processes such as exhaustion of resources, and the arena habitats impact the migrant through natural selection acting on the genome. Lower: the individual migrant whose genome produces the migration syndrome including appropriate response to the environment and migratory behavior under the influence of natural selection. The phenotypic syndrome steers individuals and their genes to different destinations along varying trajectories with interactions between the migrants and the arena as indicated by the double-headed arrow. Redrawn with modification from Dingle and Drake (2007).

but it can also be *described* in terms of population outcomes (dynamics, pathways, displacements) (Gatehouse 1987). To fully understand migration, it is necessary to consider the whole migration system outlined in Figure 2.1.

A further advantage of the definition of migration used here (Box 2.1) is that it provides an empirical method for distinguishing migration from other movements and invites investigation of contributing organizational levels and precision in determining the action of natural selection (Dingle and Drake 2007). There are specific hypotheses that one can test to make the distinctions. As an example (not unique), Salewski and Bruderer (2007) say that "By definition, migration is a round trip" involving seasonal movement between breeding and non-breeding areas. They then add that the long-distance foraging expeditions of albatrosses (a seasonal round trip between breeding and non-breeding areas!) are not included, but give no criteria for exclusion. The criteria are in fact straightforward; foraging albatrosses, for example, do not inhibit response to resources, and they do not exhibit dedicated, straightened out movement while foraging on the feeding grounds. Contrast this behavior with that of migrating Great Snipes (*Gallinago media*) that make long, fast, straight, non-stop flights not only over desert and ocean, but importantly also over extensive areas of suitable habitat (Klaassen et al. 2011). At a different scale, juveniles of the Hawaiian waterfall climbing gobioid fish, *Sicyopterus stimpsoni*, migrate upstream in waters with organic cues. Once they start climbing waterfalls, however, performance does not differ in waters of varying organic content, suggesting an all-or-nothing commitment once migration and climbing commence (Leonard et al. 2012). Round-trips do not define bird or fish migration; they describe an outcome of a syndrome of specific behavioral, metabolic, and life-history traits (lifespans of sufficient length). The Kennedy definition clearly allows hypotheses about migratory behavior to be falsified. Thus it can be modified, improved, or replaced, but proposed alternatives must clearly distinguish individual migrants and migration from other movements and provide clear means, at least implicitly, by which empirical observation and experiment can make the distinctions. No other definition of migration is as complete, and it is the best characterization of migration across taxa until its specific tenets are invalidated by suitable test. It is unfortunate that tests and analyses of migration as an explicit *behavioral* syndrome are all too rare.

A final observation is that there are several different kinds and degrees of migration, and these will be extensively treated in this book. Some "classic" examples of migration may be extreme cases and the exception rather than the rule. Investigating migratory adaptations that seem less complete than these, or facultative rather than obligatory, may prove especially revealing. Gradations between migration and other movements should provide interesting insights into how natural selection acts on potential trade-offs between migration and alternative strategies. Precision of definition cannot conceal the fact that migration is part of a continuum of movement

strategies and tactics. The degree of distinctiveness of boundaries should provide especially interesting insights into the evolution of migration and accompanying adaptive complexes.

Migratory behavior

One of the difficulties in attempting to analyze and compare migratory behavior among organisms is that the physiological and behavioral patterns that define it (Box 2.1) are severely understudied despite the fact that the need to do so has been clear for at least 40 years. This is especially true with regard to the inhibition of responses to resources (Gatehouse 1997). In carefully recorded observations of migrants, however, some of the major characteristics do appear in examples from across the spectrum of migratory taxa using a variety of means of locomotion. Comparisons reveal similarities in performance in the face of variation in life-history stage or the coordinates or distances of the routes traveled. I describe some further examples here that illustrate and underscore the characteristics that determine the behavior of migrating individuals and the outcomes in terms of population movements.

In the butterfly literature there are frequent reports of streams of large numbers of individuals moving across the countryside in a steady, undeviating, and unidirectional stream (e.g., Dingle et al. 2000 and references therein). I observed such a stream of Caper Whites (*Belenois java*) in Brisbane, Australia on October 30, 2007. The Caper White is a large (55 mm wing span) white butterfly with conspicuous black and white spotted wing tips and is a well-known migrant, with immense numbers on the move unidirectionally in the spring and autumn (Braby 2005). Starting around 14:00, I observed from the 5th floor of an apartment building a stream of butterflies about 50 m wide flying steadily and without interruption along the Brisbane River from ENE to WSW, a direction that would take them inland to presumptive spring breeding areas. Minute-by-minute counts of the butterflies streaming in a 50 m wide band past my observation post led to an estimate of 48,000–52,000 passing in each hour for a period of about 2.5 h. They were probably somewhat wind-aided as there was a following wind out of the east and ENE of about 10 knots. The route crossed many flower-rich gardens along the river, but no butterfly even hesitated at profusely flowering bushes, although there were butterflies of other species nectaring at them. Thus these butterflies were displaying three distinct characteristics of migratory behavior (Box 2.2): (1) persistent and (2) straightened-out movement that was (3) undistracted by stimuli from resources (nectar-rich flowers) that would ordinarily stop movement.

An example of the components of migratory behavior from birds is that of New World *Catharus* thrushes (Cochran and Wikelski 2005). At a stopover site in Illinois, radio transmitters were attached to Hermit (*C. guttatus*) and Swainson's (C. *ustulatus*) Thrushes during spring migration through the Mississippi Valley to Canada, allowing the birds to be followed on their subsequent journeys north. During time spent in stopover habitats, they established more or less circular foraging areas of about 100 m diameter during daylight hours within which they moved and stopped frequently. Birds with sufficient fat took off in the evening between 20:00 and 24:00 on days when maximum daily shaded air temperature was >21°C and surface winds were <10 km/h. Migration thus occurred at night when the birds would otherwise be sleeping, a resource-mobilizing activity. These nocturnal flights covered more or less straight-line distances of 100 km or more at altitudes of 400–1,500 m with birds maintaining a constant heading, even in the face of cross-winds that could exceed 10 km/h. Many species of bird are known to migrate when there are tailwinds and to choose altitudes with optimum winds (Chapter 5 and summarized in Dingle 1996), but it is unclear whether these thrushes do so. Landing responses may be triggered when there is a sudden temperature fall of as little as 1.7°C. Birds also prefer landing at the end of a night's migration in areas where it has just rained, often altering course to do so, possibly cuing on lightning flashes which can be visible for up to 100 km at the altitudes the birds are flying. There thus seem to be specific take-off and landing behaviors, a lengthy undistracted straightened-out flight at night when there are no responses to resources, a restoration of responses to resources after a period of migrating, and the allocation of energy (fat) to support long-distance movement. These thrushes thus exhibit a characteristic syndrome of migratory traits.

The problem of "dispersal"

> To disperse is to separate and become further apart.
> L. R. Taylor (1986a)

If migration suffers from a confusion of definition, no word has contributed more to that confusion than the term "dispersal." The term is most often used for presumptively one-way movements and applied to individuals moving to breeding locations away from the place where they were born (now usually specified as "natal dispersal") or between two successive breeding locations or social groups ("breeding dispersal") (Clobert et al. 2001). Thus in Howard's classic use for small mammals, it is ". . . the permanent movement an individual makes from its birthsite to the place where it reproduces or would have reproduced had it survived and found a mate . . ." (Howard 1960). Other definitions are variations on this theme and may also include specific reference to gene flow (e.g., Ronce 2007). The reason the term was used, apparently, was that migration was thought of, as it often still is, as a round-trip movement. Since small mammals were evidently not making round-trips, a different term was needed, and because young were obviously moving away from their natal sites, they were apparently scattering or dispersing.

Howard distinguished two distinct types of movement undertaken by his young field mice (*Peromyscus maniculatus*). One type, which Howard called "environmental dispersal," was defined as a density-dependent process with movement away from the natal site in response to ejection by parents and/or from a territory or in response to a lack of mates. Because of "homing behavior" (*sic*), settlement was relatively nearby. This movement is most similar to what I have called ranging (Table 1.1). The second type of movement, called "innate dispersal," was independent of density and the organism was ". . . predisposed at birth to disperse beyond [the] parental home range [and] *ignore available and suitable niches* . . ." (italics mine), a description that certainly matches the pre-emptive undistracted movement of migrants. Innate dispersers would leave suitable field habitats, proceed on a lengthy unidirectional course across tracts of woodland, and finally settle when eventually another field habitat was reached. This is the sort of behavior one might expect of a migrant. Other species of *Peromyscus* such as the Brush Mouse (*P. boylii*) also display movement variation some of which is described as longer (cross-country) and straightened out and would seem to fit a migration paradigm (see Karen Mabry's New Mexico State University web site). The "decision rules" for habitat selection discussed by Mabry and Stamps (2007) make sense for their apparently ranging Brush Mice (their "dispersers"); it would be interesting to consider in addition the possible modification of rules for mice displaying the qualitatively different behavior of migration (Howard's innate dispersal).

For some time, descriptions of the behavior and physiology of small mammals have indicated that some of these animals deposit fat prior to departure, ignore inputs from favorable resources, and otherwise show signs of being migrants (Gaines and McClenaghan 1980). In addition to mice, radio-tracked "long-distance dispersers" among red squirrels (*Tamiasciurus hudsonicus*) and flying squirrels (*Pteromys volans*), for example, apparently bypass favorable habitats before settling (M. Andruskiw and V. Selonen, cited by Stamps et al. 2007). As these observations indicate, the assertion by Dufty and Belthoff (2001) that ". . . dispersal movements are rarely as persistent or as unidirectional as migratory movements . . ." is simply not true. That assertion also misses the point, namely that in the case of movements usually called "dispersal," there are two kinds of behavior that can be distinguished—ranging and migration—either of which can lead to dispersal. Far from suggesting that "dispersal" has lost utility, as Dufty and Belthoff allege, I suggest that dispersal has great utility indeed—but as an ecological outcome of behavior, not as a designation of the behavior itself.

Stamps et al. (2007) recognize the fact that at the onset of movement (their "dispersal") there may be an interval when individuals do not respond to favorable resources, which they refer to as the "refractory period." As one example, they cite the studies of J. S. Kennedy on the migration of *Aphis fabae*, the Black Bean Aphid. They model the refractory period as a time-dependent delay in response (as might be expected in ranging) with a concave "acceptance threshold" that might link refractory periods with habitat selection. However, in his experiments Kennedy explicitly

showed that the period during which aphids did not respond to resources was primarily travel dependent, with only slight involvement of time dependency, and was modulated by the central nervous system as a consequence of reciprocal inhibition and rebound between flight and settling that indicates migration (see Box 2.1 and Dingle 1996). The implication from Kennedy's studies is that in migrants the time course of the acceptance threshold should be concave or even a step function with refractoriness at first slowly and then rapidly changing to response as a function of behavioral activity (movement, but not fatigue) rather than time. Experiments to evaluate the shape of the acceptance threshold curve could be an interesting contribution toward understanding the nature of the difference between migration and ranging (and perhaps other behaviors such as extended foraging).

Behavioral differences between ranging and migrating notwithstanding, the real problem with the term "dispersal" as it is usually used is that it confuses the behavior of individuals with the population processes that result from that behavior. The original meaning of dispersal included a component of scattering or spreading, which, in biological terms, translates to an increase in the mean distance between individuals (Southwood 1981; Kennedy 1985; Taylor 1986a). The movement of individuals may or may not result in dispersal of the population. Whether the movement be station keeping (Table 1.1), ranging, or migrating, it can also lead to convergence whether by aggregation or congregation (Box 2.3), a point made in some detail by Turchin (1998). Insects, birds, or parachuting spiders all migrate with the aid of winds and may be concentrated by converging winds or dispersed by changing wind directions (Chapter 5). Aggregation and dispersal may occur in different parts of a migrant life cycle; in the ladybird beetle, *Hippodamia convergens*, concentrations occur following migration to favorable montane diapause sites, but dispersal is prevalent when migrating to fields of new crops in the spring (Hagen 1962). In phoretic mites, behaviors of both transporting host and mite can lead to benefits that would be reduced or even eliminated with population dispersal (Houck and O'Connor 1991). Many classical to-and-fro migrations act specifically to prevent population dispersal because they facilitate return to particular regions or sites where a population aggregates for overwintering, diapausing, or breeding.

Box 2.3 Population outcomes of movement in which individuals are displaced in space over time

Population redistribution—the population-level consequence of movement by individuals. It occurs in two forms:

1. *Dispersal*—redistribution leading to spatial spread (increase in mean distance between individuals). May be caused by physical scattering (e.g., by wind) or by repulsion or avoidance of conspecifics.
2. *Aggregation*—redistribution leading to concentration or non-uniform spatial distribution (decrease in mean distance among individuals). There are three broad mechanisms leading to aggregation:
   - (i) *Habitat choice*—attraction to a particular resource or location.
   - (ii) *Physical concentration*—aggregation caused by converging winds, currents, or geography (e.g., valleys, ridges, shorelines).
   - (iii) *Congregation*—aggregation as a result of positive *behavioral* responses to conspecifics; a coming together.

Dispersion—the static spatial pattern of a population.

Population trajectory (Figure 2.1)—the route followed by a population and its timing (whether migration may be one-way or round-trip).

Population pathway—the long-term average of the population trajectory.

Lifetime track—the movement trajectory of an individual over its lifetime (the time series of its successive locations).

Sources: Southwood (1981); Kennedy (1985); Turchin (1998); Dingle and Drake (2007).

Aggregation is as important as dispersal as a population outcome resulting from individual movements. The convergence of individuals may occur as a by-product of habitat choice or concentration by physical forces such as wind or landform configuration, or by the behavioral process of mutual attraction (as dispersal may also be caused by repulsion) (Box 2.3). The outstanding example of mutual attraction leading to congregation is the

formation of the gigantic swarms of the Desert Locust, *Schistocerca gregaria*, as discussed in Chapter 11. If these locusts dispersed rather than congregated, they would not have nearly the economic impact that they do. The swarms of migrating locusts themselves often aggregate due to travel on winds converging on the Inter-Tropical Convergence Zone. Gregarious movement can be key to understanding the population dynamics of other organisms as well as locusts; it is important because of implicit positive feedbacks that are capable of amplifying subtle gradients and behavioral responses to produce extreme variations in population density (Turchin 1998).

Box 2.3 summarizes the various ecological outcomes of movement behavior, including ranging and migration. Following Turchin (1998), who also distinguished individual movements from population consequences, I use the general term *population redistribution* for the process at the population level resulting from movements at the individual level. Such movements can cause the population to spread (dispersal) or converge (aggregation), or there may be no net change in the *dispersion* which is the static spatial pattern of the population. It is worth noting that many studies of ranging ("dispersal" or "natal dispersal") result in no change in dispersion, for example in the case of the occupation of vacant territories in many species of bird. In addition to the spatial patterns among its constituent individuals, an entire population or a significant portion of it may change location as a unit as a consequence of the movement of the individuals within it, as is the case with many species of migrating bird. Dingle and Drake (2007) called this the *population trajectory* and its long-term average the *population pathway* (Figure 2.1). An individual also has a trajectory and a pathway, both of which are included in its lifetime track; these do not define the movements that produce them but are important autecological outcomes of those movements. The type of behavior is *defined* by processes internal to the organism but can be *described* in terms of its ecological outcomes (Gatehouse 1987).

With respect to population dynamics, the most understudied of the processes that produce aggregation is congregation, the convergence produced by mutual attraction among members of a population (Turchin 1998). Mechanisms of habitat choice are by comparison relatively well studied, for example the role played by natal experience (Davis 2008). The social dynamics of congregations is a frequent subject as the huge literature on the behavioral aspects of herds, flocks, and schools indicates, but the mechanisms of attraction are less well known. The role of movement behavior in the coming together, whether that movement is ranging, migration, or some form of station keeping, offers many possible insights, as indeed the studies of locust attraction have demonstrated (Pener and Simpson 2009). The dynamics of locust swarms is a significant population consequence of individual movement. A potentially useful modeling approach to the population dynamics of aggregation using modified diffusion equations has been outlined by Turchin (1998).

The use of "dispersal" to indicate presumptively one-way movement is one manifestation of attempts to define migration ecologically. These all suffer because they do not distinguish between the mechanisms producing a behavior that are the objects of natural selection and the outcomes that are a consequence of the behavior. But ecological definitions do illustrate two important points. The first is that it is necessary to distinguish hierarchical levels when discussing migration. Ecology and behavior (and physiology) must be kept distinct, but both are important to a full understanding of migration because it is ecology that determines its evolutionary course through natural selection acting on individual behavior (Figure 2.1; Gatehouse 1987; Dingle and Drake 2007). Thus the evolution, genetics, ecology, and physiology of migration are all critical elements of this book. The second point is that the issues are not merely semantic. What migrants actually do, the ways in which they do it, and the outcomes of their actions are biologically fundamental. It matters to be able to distinguish between a migrant and a ranger or forager because the outcomes of these behaviors can be quite different, and natural selection may act on them in different ways. Similarly, it might be desirable to know whether an organism far out of its normal range (a "vagrant"), is an off-course migrant, or simply the victim of accidental (or human) transport. Without a behavioral definition of migration that is not possible, even in

principle, because there is no specific hypothesis to test for making the distinction. Important, too, is the redistribution of populations in space and time, whether they are dispersing or aggregating, for that continuum of processes has profound implications for the ecology of populations and the fitness of individuals. The reason for adopting Kennedy's definition for this book (Box 2.1) is that it makes very clear the issues to consider for a full understanding of migration as a biological phenomenon, and perhaps, especially, of its relation to other important movements.

Summing up

Migration is an important event in the life histories of organisms, and it occurs across taxa. Historically studies of migration have tended to focus on a particular group, with definitions circumscribed by the characteristics of the taxon in question. Thus round-trips were seen as defining migration in long-lived animals such as birds and mammals without recognizing that many other organisms show very similar behavior but in their short lifespans make only one-way migrations. The commonalities of function and behavior that characterize migration in a variety of organisms were obscured by focus on the differences in ecological outcome. With attention to the behavioral and physiological characteristics, we can address the task of finding a definition of migration that encompasses that spectrum, and which provides a guidepost for future studies. It is my contention that such a definition should focus on behavior and its accompanying physiology, not on the ecological outcome. Ecological consequences are crucial for determining how natural selection influences a behavior, but not for defining it.

A survey of a broad array of organisms suggests that there are six characteristics of migration distinguishing it from other forms of movement. These are: (1) it is persistent; (2) it is straightened out relative to other movements; (3) it is undistracted by resources that would ordinarily halt it (responses to resources are inhibited); (4) it is triggered by surrogate cues and is pre-emptive; (5) there are distinct arriving and departing behaviors; and (6) energy and internal resources are re-allocated to sustain it. Given the flexibility of organisms and the vicissitudes of the environment, it is important to realize that not all migrants will display all of these characteristics all of the time, but most will display most of them at least part of the time during which they are migrating, even though there are different kinds and degrees of migration. These characteristics contribute to a migratory syndrome which is not genetically fixed, but rather involves the modification of already existing traits that may have evolved originally for other purposes. A definition that incorporates the important characteristics of migration is that of J. S. Kennedy (1985), which stresses that migrants inhibit or suppress inputs from resources that terminate other types of movement and that migratory behavior itself primes later responses to those same inputs (Box 2.1). An advantage of the definition is that it provides hypotheses to determine whether a given individual is a migrant. Much research is needed on the behavioral characteristics of migration, especially with respect to response to resources, within the guidelines the definition provides, and on the transitions between migration and other movements.

There have been various attempts to define migration ecologically, but from the perspective advocated here the difficulty they present is a confusion of behavior with ecological outcome. Such is the case with the term "dispersal," which is commonly used to describe presumptively one-way movements that could in my terminology be either ranging or migration. From a population and outcome perspective, dispersal means a scattering or spreading of the constituent elements of a group or population; in biological terms this means an increase in the mean distance between individuals. In other words, dispersal is better considered a population phenomenon, not a characteristic of individuals. Not only does considering "dispersal" a behavior rather than an outcome confound individual movement with population processes, it draws attention away from the important redistributions that involve aggregation and congregation. Migration and other movements can lead to all three outcomes or to no population redistribution at all.

A full understanding of migration and other movements nevertheless should include ecology. Outcomes are important because the pathways of

migrants in the arena of habitats they cross provide the selection on individuals that molds the migratory behavior and the accompanying physiology and morphology. Consideration of the role of natural selection takes us beyond the strictly ecological viewpoint, however. Migration, like other biological phenomena, can be viewed as a series of organizational levels from the molecular (the genome) to the evolutionary, and whereas we can define traits occurring at one level—such as the behavior of the individual migrant in terms of lower level attributes—we must seek explanations for them by identifying their functions and consequences at higher levels. The hierarchy of perspectives is in fact closed, as the highest level, natural selection, acts directly on the lowest, genes underlying the migratory adaptations. The definition of migration that I advocate provides the foundation for the analysis of the framework that supports and connects these hierarchical levels of migratory systems.

CHAPTER 3

Patterns in migratory journeys

Migration is a behavior of great variety not only for insects, as noted by C. B. Williams (1958), but also in numerous organisms across a diversity of taxonomic groups. Nowhere is this variety more evident than in the pathways followed by migrants on their journeys. This chapter examines the diverse ways a similar behavioral organization can be modified by environmental contingencies and natural selection to serve a multiformity of ecological requirements. The pathways are a function of the ecologies, sizes, lifespans, and physiological capacities of the migrants that follow them. Outlined are a number of different pathways and their spatial and temporal elements. These illustrate the richness of the patterns generated in the life cycles of organisms by the synergisms between migratory behavior, environmental variation, and geography, and set the stage for a more detailed examination of both proximate and ultimate factors in migration in the remainder of this book.

To-and-fro migrations

Long distance annual to-and-fro migrations are the ones with which we are most likely to be familiar. These include the great seasonal movements that bring songbirds back to temperate zone forests and gardens often in spectacular numbers, the kettles of hawks soaring along ridge lines or over narrow isthmuses, the pods of great whales swimming past our coasts, or the gardener-friendly ladybird beetles flying from mountain refuges to lowland fields and flower beds. Many to-and-fro migrations are on a large scale covering major portions of our planet; others are on a much smaller scale—in the case of many insects, for example, over distances of only a few hundreds or thousands of meters. All involve breeding at one end of the migratory pathway and most include refuging at the other to escape seasonal harshness in the breeding area. As with all types of migratory journey, great variety is evident, but all exhibit characteristics that define them as migratory behavior (Chapter 2, Table 2.1).

Among the grander of to-and-fro migratory journeys are those that include crossings of large stretches of open ocean. The Arctic Tern (*Sterna paradisaea*) has a circumpolar breeding distribution in the Northern Hemisphere, nesting along the northern rims of both Old and New World continents and on Arctic and sub-Arctic islands. In the autumn they depart on the longest migratory journey known for any bird to feeding areas in the Antarctic at the edge of the pack ice (Alerstam 1990; Dingle 1996; Egevang et al. 2010). Birds breeding in northern Europe and Siberia and its islands migrate along the western borders of Europe to the Cape of Good Hope at the southern tip of Africa from whence they enter the prevailing westerly winds of the southern oceans to fly to the margins of the pack ice. Terns breeding on the northeastern coastlines and islands of North America, Greenland, and Iceland first fly eastward across the North Atlantic to coastal Europe, a transoceanic journey of up to 3,000 km for the westernmost breeders. They then join the stream flying south along the African west coast. Terns from Arctic Canada west of Hudson's Bay, Alaska, and the Bering Strait migrate to and from the Antarctic along the Pacific coasts of both the New World continents. The routes by and large follow the nutrient-rich waters provided by the cold currents of the western edges of these continents. The journey is annual when birds reach maturity, but many juvenile birds remain in Antarctic regions for more than a year before making their first return

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journey north, so that the migration cycle is not exclusively annual.

Arctic terns do make long overwater flights in the North Atlantic, but theirs are by no means the longest. An interesting terrestrial overwater migrant is the Amur Falcon (*Falco amurensis*). This species breeds in northeast Asia from southeast of Lake Baikal through Mongolia and northeast China. In the autumn it undertakes an 11,000 km migration to southern Africa crossing the Indian Ocean from southwest India to East Africa before proceeding south to wintering areas from Malawi to the Transvaal and west to Botswana (Ferguson-Lees and Christie 2001; Dingle 2008). In the northern spring they return to their breeding grounds over apparently the same route.

But the most impressive over-ocean migratory flights, confirmed with birds bearing attached satellite transmitters, are those of Bar-tailed Godwits (*Limosa lapponica*) across the Central Pacific from Alaska to Australasia (Wilson et al. 2007; Gill et al. 2009). Two populations of these godwits spend the northern winter in Australasia. Birds in northwestern Australia are of the subspecies *L. l. menzbieri* and breed in northeastern Siberia. This subspecies migrates in both directions between Siberia and Australia via staging areas in the western Yellow Sea and a direct flight of 5,400–6,200 km across the South China Sea and the Indonesian islands. The eastern subspecies, *L. l. baueri*, winters in southeastern Australia and New Zealand. Its northward migration takes the birds apparently across the Coral Sea and the Western Pacific to staging areas in the eastern Yellow Sea and Japan, a distance of 8,200–8,500 km, before a final transit across the remaining 4,000 km to breeding grounds in western Alaska. The timing of departure and arrival only a few days apart strongly suggests that flights from eastern Asia to Australia and vice versa are nonstop or very close to it.

As impressive as these flights are between Australasia and eastern Asia, they pale in comparison to the southward migration of *L. l. baueri* from Alaska to Australia and New Zealand (Gill et al. 2009). Seven birds were captured on the breeding grounds in Alaska, and 16 more were captured on the wintering areas in New Zealand. The larger females were implanted with battery-powered transmitters in the coelomic cavity whereas the smaller males carried lighter solar-powered models on the lower back. The transmitters functioned long enough for nine birds, seven females and two males, to be tracked over two years. The seven females on their southward migration flew non-stop for between 8,117 and 11,680 km over the Central Pacific to islands in and around the Coral Sea: the longest flights took birds directly to New Zealand (Figure 3.1). The female making the longest recorded flight arrived in New Zealand 8.1 days after departing from Alaska. The transmitter of a second female stopped recording after 6.1 days and 9,621 km, but she was subsequently identified in New Zealand by her coded leg tag. Another female's transmitter stopped in the vicinity of the Solomon Islands after more than 10,000 km of flight, but she, too, was subsequently observed in New Zealand. The two smaller males flew directly to the Gilbert Islands (7,008–7,390 km), and one was tracked on to New Zealand after this stopover in the Gilberts.

Several aspects of the godwits' behavior seem to be adaptive and to facilitate the long transoceanic flight. Before departure the birds gather in the Yukon–Kuskokwim Delta where the intertidal fauna is among the richest in the world in terms of biomass, allowing the high intake rates of feeding godwits to store energy for the long flight. The area also appears to have fewer predators than other staging areas in Alaska, and the long overwater journey allows predator- and parasite-free transport. By contrast, a coastal Asian route supports several predators capable of taking godwits and a diverse pathogen fauna. The birds take off from Alaska into following winds (Chapter 5), and long-term observations of autumn low pressure systems over southern Alaska indicate that following winds generally occur around the time of departure. Indeed plots of winds over the Pacific suggest that, on both sides of the Equator, there are likely to be favorable tailwinds—in the Southern Hemisphere generated by the southeast trades and austral westerlies (see Dingle 1996 for a survey of global wind patterns). Possible landing sites are scarce in the Central Pacific, but even when present the godwits ignore them as predicted for focused migratory flight. Hawaii, for example, is near the mean flight path, but 35 years of records have yielded only 40 individuals. These results led Gill et al. (2009) to

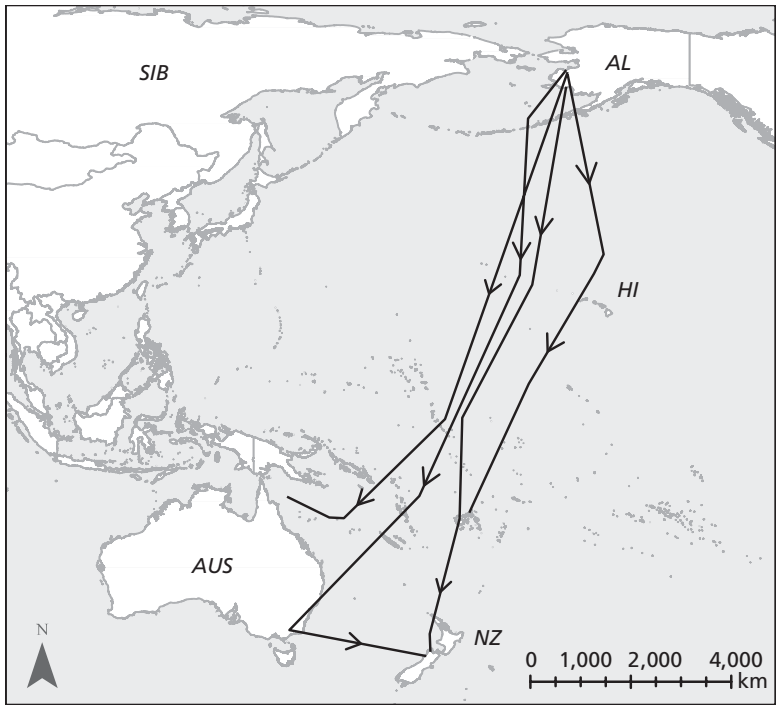


Figure 3.1 Examples of the autumn migration flights of the Bar-tailed Godwit (*Limosa limosa baueri*) breeding in Alaska. Four autumn flights from Alaska to Australasia are indicated. Flights to Australia and New Zealand can be as long as 11,000 km most of which is covered without stopping. From data in Gill et al. (2009).

suggest that the Central Pacific is a migration corridor, rather than a barrier, that allows the godwits to minimize migration time and total energy expenditure while traveling through predator- and parasite-free space.

If the Central Pacific is a migration corridor for *L. l. baueri* in the autumn, why do these godwits use the Asian route in the spring, flying via Japan and the eastern Yellow Sea? Gill et al. (2009) suggest two probable reasons for the continental route. First, godwits may "overload" with energy storage at a final stopover site to give themselves an advantage in initiating breeding at their final destination in western Alaska. Second, on the trans-Pacific route there are no "emergency" landing sites for the last 4,000 km of the flight should the birds run short of fuel or encounter severe early spring weather. The overall pathway is thus a circular one: south across the open Central Pacific in the autumn with a return via coastal eastern Asia and Japan in the spring.

Not all to-and-fro bird migration pathways show the extreme length of those of Arctic Terns and Bar-tailed Godwits. Several species that breed on the Australian island of Tasmania fly across the short expanse of Bass Strait (400 km) to winter on the Australian mainland (Dingle 2004; Peter 2011). Included are three small parrots, the Swift Parrot (*Lathamus discolor*), the Blue-winged Parrot (*Neophema chrysostoma*), and the very rare (only 150 or so individuals) Orange-bellied Parrot (*N. chrysogaster*) (Griffioen and Clarke 2002; Pizzey and Knight 2007; Saunders and Heinsohn 2008). Even though trips are short, they still function to keep the birds in the most favorable environments throughout the year. The two *Neophema* species are so-called grass parrots feeding on the seeds of grasses and small seeded forbs. The Blue-winged Parrot is a species primarily of drier areas and grassy woodlands and in the southern winter ranges north into northern New South Wales and northeastern South Australia. The Orange-bellied Parrot is limited to damp coastal and subcoastal areas, wintering in a few salt marshes, dunes, and beaches of the coast of Victoria. The Swift Parrot is a forest and woodland species that feeds on lerp and nectar. It visits more than half of foraging sites repeatedly with coastal and subcoastal habitats as far north as Southeast Queensland providing important drought refuge habitats (Figure 3.2). The

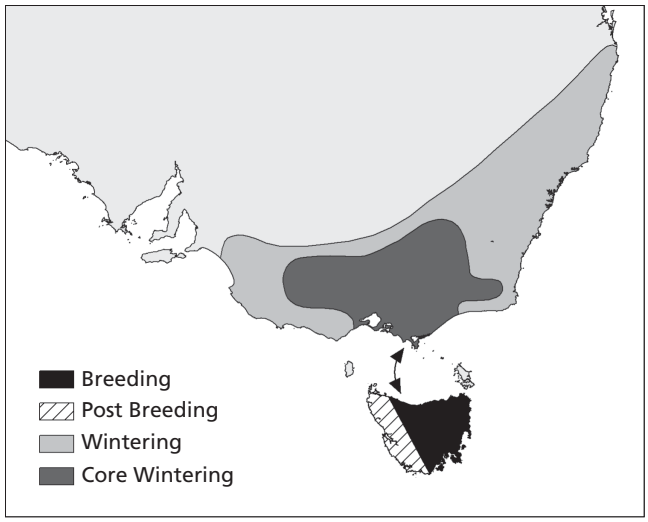


Figure 3.2 Migration of the Swift Parrot in southeastern Australia. The birds breed in Tasmania and winter on the mainland roughly from Adelaide in the west to Brisbane in the northeast, with greatest concentrations toward the center of the wintering range. From Dingle (1996).

use of particular foraging areas is strongly influenced by the degree of aggressive competition with other nectar and lerp foragers. When competitors are not aggressive, for example some honeyeaters (Meliphagidae), sites are frequently visited, but the presence of aggressive competitors such as similar-sized lorikeets tends to exclude Swift Parrots (Saunders and Heinsohn 2008).

In spite of claims to the contrary (e.g., Holland et al. 2006), many insect species make round-trip migrations. Often these are migrations to seasonal refuging sites with a return trip to breeding habitats when conditions are again favorable. In Sweden, for example, the milkweed bug *Lygaeus equestris* migrates for distances of as little as a few hundred meters to winter diapause sites in the crevices of limestone outcroppings or the protected doorways of old Viking lighthouses (summarized in Dingle 1996). In the Midwestern USA the Boxelder Bug, *Boisea trivittata*, behaves similarly, often invading houses as migrants seek sheltered spots at the bases of walls and foundations.

Among the more impressive of insect migrations to seasonal refuges is that of the Bogong Moth, *Agrotis infusa*, in southeastern Australia <http://www.csiro.au/resources/BogongMoths>. The moths emerge in the spring from pupae in the ground and feed on nectar, building up fat reserves that may reach 60% of body weight, and this high fat content made them a favorite food item among local aborigines. As the weather becomes warmer and habitats drier, the sexually immature moths migrate by night to the high country areas (about 1,200 m above sea level) of the Snowy Mountains in southern New South Wales and the Victorian Alps. There they spend the summer aestivating in crevices and caves (Figure 3.3). Under favorable weather conditions with abundant food, these moths may reach plague numbers. In the mid-1970s, for example, the moths passed through Canberra in such abundance that when they invaded brightly lit buildings they

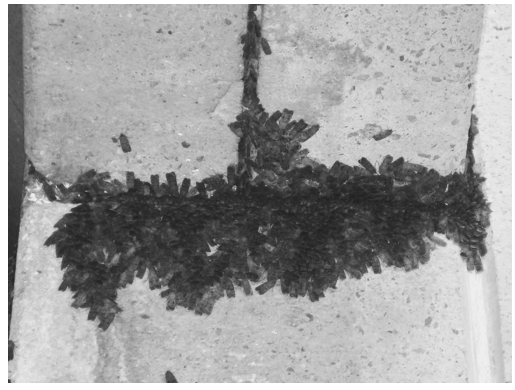


Figure 3.3 A cluster of summer aestivating Australian Bogong Moths in the corner of a building. These moths migrate in the spring to high altitude refuges in the Australian Alps where they aestivate over the summer (in nature in caves or among rocks) before returning to lower altitudes closer to the coast to breed. From Wikipedia; released under the GNU Free Documentation License.

caused the machinery of elevators (lifts) to fail. In 1988 another mass migration invaded the newly constructed Parliament House necessitating the redesign of air intakes and a reduction in the intensity of lighting. After spending the summer aestivating, the moths migrate in the autumn back to the lowland areas where they again feed on nectar and now breed. The populations overwinter as larvae, pupate in the late winter, and emerge as adults in the spring to repeat the migration cycle.

Not all to-and-fro migrations take place by flight. Among crustaceans, there are several species of terrestrial crab that must migrate back to the sea to breed. Perhaps the most famous of these is the red crab, *Gecarcoidea natalis*, of Christmas Island in the Indian Ocean just south of the Indonesian island of Sumatra. Some millions of these crabs leave their burrows in the forest and migrate up to 5 km over five to seven days to mate and deposit eggs in the ocean (Hicks 1985; Adamczewska and Morris 1998). This requires them to maintain locomotion for as much as 12 h a day. Radio tracking reveals that the mean walking speed of the crabs is near their maximum aerobic speed, but the locomotion may be interspersed with pauses of minutes and sometimes hours. The migrating crabs, however, can sustain locomotion aerobically for up to 12 h per day compared with their performance between migrations when just 10 min of aerobic exercise is possible before the muscles become anaerobic. There is thus a major shift to a specialized migratory physiology. This shift to maximal aerobic performance is facilitated by a switch in gene expression in the leg muscles causing the upregulation of proteins that increase the fatigue resistance of muscle fibers (Postel et al. 2010 and Chapter 14).

The migration is triggered by the onset of the wet season with specific movements timed to synchronize with the lunar and hence tidal cycle (Adamczewska and Morris 2001). Once underway, the crabs travel in straight lines to the ocean shore but not necessarily the nearest one, implying a still unknown navigational mechanism. When they arrive at the sea, males excavate burrows on the lowest shore terraces and mate with females in or near these burrows. Males return to the inland forested areas after mating, but females lay their eggs and remain in the burrows. Spawning is fixed by the lunar cycle and occurs 17–18 days after mating in the days just before the new moon and highest tides. At the end of incubation the females with their fully developed embryos move to the coastal cliffs where they cast their eggs into the ocean. The females then return inland. The larvae meanwhile develop over three to four weeks in the sea before metamorphosing into juvenile crabs, returning to land, and moving inland to complete the migratory cycle.

In addition to migration to the sea by terrestrial animals such as the red crabs, there are many aquatic species that migrate between the sea and freshwater (diadromy). The best known and most studied of these aquatic migrations are those of several species of salmonids which take place between freshwater breeding habitats and the ocean where fish mature over one or more years (Quinn 2005). (This is anadromy; the opposite cycle, as seen in eels, where breeding is in the ocean and maturation is in fresh water, is termed catadromy.) Pacific salmon (*Oncorhynchus* spp.) breed in streams and rivers on both sides of the Pacific, spawn only once (semelparity), and then die. In their migration and death they contribute significant amounts of protein and other nutrients both to the freshwater habitats and to the neighboring terrestrial communities (witness the many films of bears catching the migrating fish). This is an example of the "trophic" effects of migrants on communities (Holdo et al. 2011) and of the flow of resources between ecosystems or "ecosystem subsidy" (Moore and Schindler 2010). Two other genera of salmonids, the Atlantic Salmon and several species of trout (*Salmo* and the Rainbow Trout *Oncorhynchus mykiss*) and the lake trout and char (*Salvelinus*), are repeat spawners (iteroparity). There are many variations on the themes of semelparity and iteroparity, depending on species and populations. There may, for example, be some maturation in lakes before migration to the sea, and there are landlocked populations of both Atlantic and Pacific salmon.

Diadromous migrations are also known among many species of molluscs and decapod crustaceans. Several neritid snails in both the tropical Atlantic and the tropical Pacific live in freshwater streams, but newly hatched larvae are carried downstream and spend the larval period in the ocean before migrating back into streams (Resh et al. 1992; Blanco

and Scatena 2005, 2006, 2007). The migration of the Caribbean neritid, *Neritinea virginia*, has been studied extensively by Blanco and Scatena in streams at the northeast corner of Puerto Rico. The migrations occur in streams that are connected to the ocean essentially throughout the year and can be massive (500–3,000 snails/m^2). Most migrations of many individual snails were timed to rainy periods, but with no seasonality apparent, when streams had relatively high discharge rates. They could occur as often as once every 15 days. There was strong habitat selection by migrating individuals for specific fast-flowing or deep water areas of stream channels which also may function as flow refugia. These habitats were more stable than nearby shallower areas that were subject to scouring during high flows. The selection of the deeper, swifter stream channels was especially evident in smaller snails (<7 mm); larger snails with larger drag forces acting on them were more likely to occur in side channels with lower velocities and less turbulent flow. Habitat preferences are thus a function of snail size and the hydraulic characteristics of the stream. In areas that were still forested and protected the snails could migrate up quite steep gradients. They thus contrasted with other diadromous invertebrates and small fish occurring in tropical streams whose migrations were limited by steep gradients, waterfalls or dams (Fievet et al. 2001; Joy and Death 2001; Resh 2005).

Modifications of the to-and-fro pattern

Many species of migrant display a to-and-fro pattern in their movements, but with modifications of the basic scheme. One of the more interesting of these species is the African Black Oystercatcher, *Haematopus moquini*, studied by Hockey et al. (2003) who followed 85 tagged birds. This shorebird breeds along the coast of southern Africa from about Lüderitz in southern Namibia around the Cape of Good Hope to Port Edward on the Kwazulu/Natal coast of South Africa. Young birds take three (females) or four (males) years to mature sexually and breeding usually occurs when adults reach the age of six years. There is thus a lengthy period between fledging and first breeding.

Migration in this oystercatcher occurs in a portion of post-fledging juveniles and occurs but once in a lifetime. The species occurs in eastern and western populations with a dividing line roughly halfway along the southern coast between Cape Town and Port Edward. Juveniles of the eastern population tend to be smaller at both hatching and fledging than western juveniles and lack the energy capacity for long-distance migratory travel. Some 71% of these juveniles move over distances of ≤500 km, with half of these moving <150 km. These distances are within the breeding range of the oystercatchers and likely constitute widely dispersed foraging movements of these juveniles. About 40% of the juveniles of the western population also move for <150 km during the interval between fledging and sexual maturity.

Western birds, however, showed a distinctly bimodal distribution of movement distances in contrast to those of the eastern population. Less than 2% of the birds were found moving between 150 and 1,000 km, whereas almost 60% moved around 2,000 km and up to 2,800 km, to lagoons on the coast of Namibia well north of the limit of the breeding range at Lüderitz. The evidence indicated that these longer movements were migratory as the birds bypassed apparently suitable resources and eventually returned to their point of origin. These migrants averaged 21% heavier at hatching and 15% heavier at fledging than the short distance birds, suggesting that they were energetically more capable of the longer flights. The really interesting difference between these birds and those of species displaying more usual to-and-fro patterns is that these migrants remained on the coast in the non-breeding range for 2–3 years (cf. also juvenile Arctic Terns). They then returned to their natal sites to breed and never migrated again. Migration in this species is thus a once-in-a-lifetime event.

A different modification of the basic to-and-fro scheme is displayed by the New World Monarch Butterfly (*Danaus plexippus*) which spreads its migratory round-trip over several generations. The migration of the Monarch has been studied for many years by F. A. Urquhart (1987) and more recently by Lincoln Brower and his students and colleagues (summarized in Brower 1995, 1996). This butterfly belongs to the tropical and subtropical subfamily Danainae and is unique among the 157 or so species in undertaking extraordinary migratory journeys for distances up to about 3,000 km. The longest journey occurs in the autumn in the population

that breeds in eastern North America and is necessitated because this species cannot overwinter in the temperate zone, even in diapause. Monarchs, however, are highly variable in migratory behavior, with populations in tropical Central and South America, the West Indies, Hawaii and other Pacific islands (where it is introduced) being sedentary, and populations in western North America and (also introduced) Australia moving for shorter distances (usually) than eastern North American butterflies (Malcolm and Zalucki 1993; Dingle et al. 2005).

Monarchs specialize on milkweeds (Asclepiadaceae), and their migratory patterns have evolved to exploit the often abundant but seasonal milkweed food supply. Going back to the 19th century (Edwards 1878; Scudder 1881) there has been a debate about the migration pathway of the monarch population in eastern North America. Was the pathway a single round-trip with a flight south in the autumn with a return to northern breeding areas in the spring by the same individuals (the single sweep hypothesis), or was there a return northward in steps with breeding by successive generations at higher latitudes (the brood recolonization hypothesis)? It now appears that brood recolonization explains most of the northward migration, but the situation is more complicated than a simple stepwise northward progression. In the autumn these eastern Monarchs do indeed make a single journey south; their reproduction is suppressed by short days and cool temperatures (Barker and Herman 1976). The bulk of the population migrates in more or less distinct streams through Texas (Calvert and Wagner 1999) and along the Gulf Coast to overwinter in specific sites and spectacular aggregations of millions of butterflies in the fir (*Abies religiosa*) forests in the mountains of the Transvolcanic Range in central Mexico (Figure 3.4). A few butterflies cluster at sites in peninsular Florida and some apparently reach Cuba (Dockx et al. 2004). The overwintering sites in Mexico evidently have the cool climate conditions necessary for the survival of the butterfly aggregations over the winter (Chapter 6). In late February and early March the butterflies in the Mexican aggregations become more active, mating occurs, and the monarchs begin moving northward.

Most of the individuals departing from the wintering clusters do not reinvade the original habitats in the northwestern USA and southern Canada. Rather they stop in coastal and subcoastal regions around the Gulf of Mexico extending only as far north as southern Missouri and Kentucky (Figure 3.4). Here their offspring feed on the early spring milkweed emerging in this region. These offspring then migrate farther north after they become adults to produce offspring on northern milkweeds as the southern species of *Asclepias* are dying back. This was demonstrated by chemically identifying the cardenolides in the milkweeds that the caterpillars ate. Milkweed cardenolides are species specific, allowing butterflies to be "fingerprinted" according to food plant fed on as larvae. Butterflies overwintering in Mexico all have cardenolides from northern milkweeds, especially the most common species, *A. syriaca*, indicating a single sweep south in the autumn. By contrast, most butterflies entering areas north of Missouri and Kentucky in the early summer leave fingerprints characteristic of the Gulf Coast and southern milkweeds, *A. viridis* and *A. humistrata*, thus demonstrating a two-generation northward movement (brood recolonization).

This is still not the whole story, however. Using stable hydrogen isotopes (see Chapter 4) Miller et al. (2012) provide evidence that about 25% of the Monarchs captured in late spring and early summer in the Great Lakes region of eastern North America displayed a natal origin in the upper Midwest, consistent with a single-sweep northward migration from Mexico. Thus single-sweep and brood recolonization are both true, although with the latter hypothesis applying to most migrants. But evidently brood recolonization is not a straightforward two-generation process. Further studies with stable isotopes indicate that Monarchs turning up east of the Appalachian Mountains in mid-to-late summer are descendants of butterflies that matured earlier on milkweeds in the Great Lakes region (Miller et al. 2011). Here brood recolonization appears to be a three-step process (Figure 3.4).

Migration patterns in the Monarchs of western North America are also variable (Dingle et al. 2005). For years it was thought that all western Monarchs migrated to coastal central and southern California to overwinter at several well-known sites like

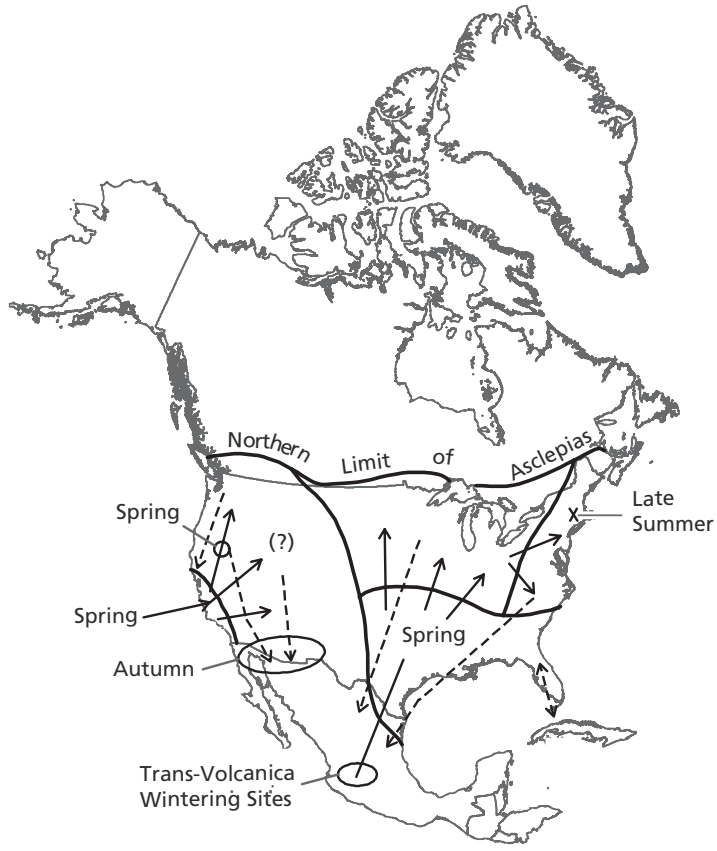


Figure 3.4 Migration of the Monarch Butterfly in North America. The butterflies of the eastern population winter in the Transvolcanic Range of central Mexico. In the spring most migrate to the southeastern tier of the USA where they breed on early milkweeds (but a few apparently migrate directly back to the Midwest). Subsequent generations breed in the Midwest and then in the Northeast before the autumn generation migrates back to Mexico (with a few migrating to Florida and Cuba). The western population wintering on the coast of California migrates inland in the spring and northward as far as southern Canada. In the autumn there are two and possibly three migration routes south. One well-known route goes to California, but a second proceeds down the Colorado River Valley to Mexico, and a possible third traverses eastern Utah and Arizona to Mexico. Wintering areas for the latter two sets of butterflies are unknown. Solid arrows indicate spring migration and dashed arrows migration routes in the autumn.

Pacific Grove and Pismo Beach followed by a return migration to inland breeding areas in the spring (see Figure 3.5 in Dingle 1996). Recent work, however, has shown the migration pattern to be considerably more complex. Certain California coastal and subcoastal milkweeds, such as *A. californica* in the south and *A. cordifolia* in the north, may start sprouting as early as January and some overwintering butterflies breed on these, with their offspring migrating inland and over Sierra Nevada passes to breed on later-growing milkweeds such as *A. fascicularis* and *A. speciosa*. Records from northern Oregon and Washington State reveal that other butterflies migrate directly inland to begin breeding so that both single-sweep and brood recolonization pathways are present. Plots of Monarch distributions in late summer and autumn reveal three possible southward pathways (Dingle et al. 2005 and Figure 3.4). The first brings butterflies to coastal California, as long known. The second route follows the east slope of the Sierra Nevada to southern Nevada and hence along the valley of the Colorado River and on into

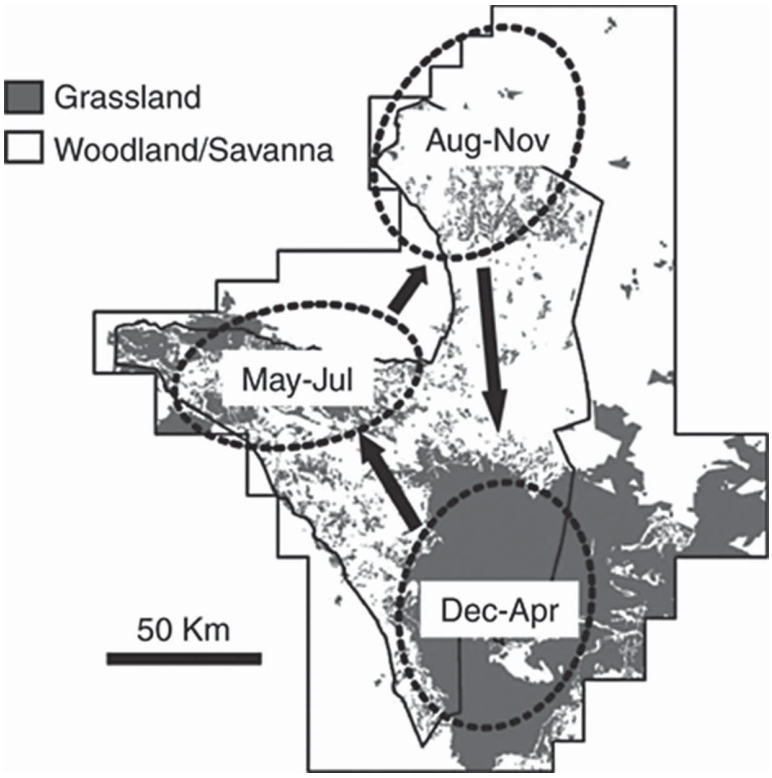


Figure 3.5 Wildebeest migration in the Serengeti Region of East Africa (inner polygon is the boundary of the Serengeti National Park whose northern edge is the Kenya/Tanzania border). Movement is, first, from rainy season breeding areas in grasslands of the southeast to wet areas near Lake Victoria. This is followed by movement to the northeast to meet the earliest rains. The final movement is back to the grasslands of the southeast. From Holdo et al. (2011); used with permission from Oxford University Press.

Mexico. The third route is less certain because of a paucity of records, but seems to follow a path east of the Great Salt Lake and west of the Wasatch mountains in Utah and then through eastern Arizona before butterflies cross into Mexico. The destinations of Monarchs entering Mexico on these routes are completely unknown, but the pattern raises speculation that there may be gene exchange between eastern and western butterflies as a result of population mixing in Mexico. In any case there is little genetic differentiation among Monarch populations (Shephard et al. 2002 and references therein). The pattern of monarch migrations in Australia is similar to those of western North America with overwintering sites near Sydney, Brisbane, and Adelaide, and summer movement inland with some breeding in the overwintering areas, especially in the subtropical areas around Brisbane. The overall migratory pattern of the monarch thus includes single generation round-trips, multi-generation round-trips, or mixtures of quasi-residents and migrants over the range (western North America and Australia). In tropical areas of the Caribbean and South America, the monarchs are fully resident.

Still another modification of the to-and-fro pattern of migration is exhibited by three ungulates in the Serengeti–Mara region of East Africa: the wildebeest (*Connochaetes taurinus*), the zebra (*Equus burchelli*), and the Thompson's gazelle (*Gazella thompsoni*). These migrations feature a circular pattern driven by a marked seasonal rainfall gradient from SE to NW interacting with soil fertility and plant nutrition (Figure 3.5) (Dingle 1996; Holdo et al. 2009, 2011). The migrations take place over a total area of about 25,000 km^2. The herds of these migratory grazers spend the wet months of December through April in the grassy plains of the southeastern Serengeti where their preferred food of short grass is green and high in nutrient content. Most calving takes place at this time. As the grass dries out in May and June the animals undergo a behavioral change, especially the wildebeest, forming

into large herds that migrate northwestward to the wetter scrublands near Lake Victoria, sometimes passing through areas of territorial bulls that do not migrate. In the wildebeest this movement may occur in spectacular fashion with single files of animals extending for miles with zebras and gazelles mixed in. Near the end of July and early August as the dry season approaches its end, the herds move northeastward to spend the next two to three months in the northern part of the region, the Mara of northern Tanzania and Kenya, where rains arrive as the Inter-Tropical Convergence Zone (ITCZ) of wind systems moves in from the north. In November and December there is a return movement to the southeast and the breeding area, more or less behind the rain front. The migration of these ungulates can considerably modify the behavior and ecology of other animals in the Serengeti–Mara ecosystem. Serengeti lions (*Panthera leo*), for example, time reproduction to coincide with the arrival of migrant wildebeest with lions in the north and south of the region, producing offspring roughly six months out of phase with each other.

There is variation among both individuals and populations in the tendency of these ungulates to migrate. Old bull wildebeest may remain territorial throughout the year if there is a water source, and some green vegetation persists in wetter areas. These males can presumably mate quickly with females on return migration and so gain reproductive advantage. The populations in the nearby but less seasonal Ngorongoro Crater are largely sedentary, but there may be some facultative movement out of the crater in dry years. It is apparent that the presence of sedentary populations requires a water source and at least some food in the form of green vegetation throughout the year. The variability present in this migration system is thus a response to the resource pattern in both space and time.

Similarly, a response to resource pattern is evident in the migratory circuits of oceangoing fishes such as the herring (*Clupea herengus*), the cod (*Gadus morhua*), and the plaice (*Pleuronectes platessa*) (Dingle 1996) and at least five species of Australian bird (Griffioen and Clarke 2002). The different populations of each species of fish again display considerable variation. In the herring, for example, some populations breed off Norway in the spring whereas others breed on the Dogger Bank in the North Sea in the autumn. The basic pattern for all three fish species is movement between spawning sites, feeding areas, and wintering areas. Juveniles may also spend time in a nursery area, into which eggs and young larvae have drifted on currents, before entering the primary migration circuit upon reaching maturity. The movement along regular circuits allows these migratory fishes to exploit an extensive but widely distributed resource base. The Australian birds which include two cuckoos, a woodswallow, and two songlarks, are all insectivorous species. The circuits followed by these birds involve breeding in southeastern Australia, northward movement to wintering areas in Queensland, then a turn westward for a return migration west of the northward movement. Since the interior of Australia is hot and dry in the autumn but cooler in the spring, the more or less circular migration route may be driven by temperature, presumably as it affects insect abundance. Thus the movements of the wildebeest and other ungulates, the three oceangoing fish, and the Australian birds all display resource-driven circular pathways, superimposed in the case of the terrestrial migrants, on a north–south pattern.

Nomadic and opportunistic migrations

Species that live in arid regions are subject to often extreme fluctuations of resources—what has been described as a "boom and bust" ecology (Robin et al. 2009). The organisms that are adapted to exploit the most extreme boom and bust variations are those that depend on dry country wetlands which may vary between many years of being bone dry to brief filling with torrential rainfall when they can be very productive indeed (e.g., Puckridge et al. 1998; Roshier et al. 2001; Kingsford and Norman 2002). The bird that perhaps most epitomizes a nomadic migratory habit of ephemeral wetland use is the banded stilt (*Cladorhynchus leucocephalus*) of Australia (see also Dingle 1996). The species was first described in 1816 from a skin collected between 1800 and 1804, but the first observation of breeding did not occur until 1930 in spite of the fact that the bird is fairly common and conspicuous across much of southern and western Australia (Pizzey and Knight

2007). In 1930 some 40,000 nests were found at Lake Grace in the state of Western Australia and about 27,000 nests at Lake Callabonna in South Australia. These are somewhat remote desert salt pans that are usually dry, but fill to form large shallow lakes after heavy rains. Since 1930 other "big bang" breeding events have been recorded at interior Australian lakes which can remain dry for years or even decades. When these lakes fill they produce dense populations of brine shrimp which are the primary food of chicks and thus key to the nomadic life cycle of the stilt.

During non-breeding periods, which can extend for several years, the stilts congregate in large numbers at salt lakes and salt marshes such as the salt works north of Adelaide and the Coorong along the coast of South Australia. There was even a small breeding attempt at the Coorong in 2006. Stilts may also range widely over several hundred kilometers in search of suitable habitat. Migration to breeding sites is triggered by heavy rainfall that fills the large shallow salt lakes where massive breeding occurs. Lakes with fishes or other breeding birds do not attract stilts, perhaps because of competition for the brine shrimp food supply (Robinson and Minton 1989). The stilts arrive at breeding sites not long after the lake basins fill, but how they find them remains a mystery. There is some speculation that movement may be triggered by widespread weather systems that cause interior rainfall. Perhaps, too, there are "exploratory" flights of the sort seen by Roshier et al. (2008) in Grey Teal (see Chapter 1), but so far we lack tracking data on banded stilts, although such studies are beginning.

Over the last several years large breeding events have been recorded mostly on lakes in interior South Australia. In 1980, at Lake Barlee 179,000 nests produced about 500,000 eggs. Lake drying, a major hazard for stilt breeding, killed about half the eggs and chicks, but still left some 250,000 chicks to set out from the colonies. Breeding on islands in Lake Torrens in 1989 provided considerable data on breeding and its relation to the nomadic migratory cycle in this species. Heavy rainfall in March in the nearby Flinders Ranges caused run-off that formed a salt lake 200 km × 30 km in area but only half a meter deep. By the middle of April, four weeks after the heaviest rains, the first nesting colony of several thousand pairs was established on islands to be followed quickly by more colonies. Pairing and mating had occurred apparently en route, so egg-laying began shortly after arrival. Overall about 100,000 birds nested.

In April/May 2010 a small breeding event occurred on Lake Eyre, South Australia, the largest of Australia's interior salt pan lakes <www.shorebird-network.net/PDFs/Lake-Torrens.pdf>; another had occurred there in 2000. The 2010 breeding was estimated to produce between 6,000 and 7,500 chicks. At the same time a colony of 140,000–150,000 stilts produced up to 200,000 chicks once again, as in 1989, on islands in Lake Torrens <http://worldwaders.posterous.com/largest-recorded-breeding-event-of . . . >. Some idea of the frequency of banded stilt breeding is evidenced by the fact that these birds are known to have bred in South Australia only seven times in 70 years.

Once breeding begins, it is rapid. Arriving mated pairs scrape out a nesting hollow to which they may add a few sticks and grass stems. The three or four eggs are large and produce large, very precocious young in 19–21 days. After hatching the chicks leave the nest as soon as they dry and after two days proceed singly or in small groups accompanied by some adults. At Lake Torrens in 2010 chicks proceeded to the water at a rate of 50–350 chicks per hour with only a few preyed upon by neighboring gulls. Once in the water they immediately begin feeding and form into large "crèches" accompanied by some adults and swim in a moving line, feeding as they go, sometimes creating pathways through the dense concentrations of brine shrimp that are visible from the air, and traveling as far as 100 km from the hatching site. Following the post-hatching departure of the chicks from the nest, adults immediately begin nesting again. In 1989 at Lake Torrens initial nesting began on April 15 and chicks from the second had hatched by mid-June so that two complete nesting cycles were compressed into 12 weeks. Apparently more broods can sometimes be produced, but heavy predation (95% by gulls on the second brood at Lake Torrens) and lake drying impose high costs that bring the breeding cycle to a close. But the rapid production of huge numbers of

offspring is clearly an adaptation to the nomadic lifestyle that exploits the very rich but highly episodic wetland resources.

A number of other Australian waterbirds exploit ephemeral wetlands in a similar, if not quite so dramatic, fashion (Dingle 2004). We have noted the dual movement patterns of Grey Teal occupying drier or more mesic habitats (Chapter 1 and Roshier et al. 2008). A pattern possibly similar to the Grey Teal is followed by the Australian Pelican (*Pelecanus conspicallatus*) which uses both coastal and subcoastal breeding sites and inland ephemeral lakes, the latter with huge breeding events much like the Banded Stilt (Reid 2009 and Chapter 11). The Freckled Duck (*Stictonetta naevosa*) is dependent on lignum, a dense matted vine, for nesting especially when it overhangs water. This situation occurs only after the infrequent heavy rains and flooding, so its life cycle resembles the Banded Stilt in less extreme form. Because of the prevalence of long dry periods interrupted only infrequently with rainfall-produced wetlands, most Australian waterbirds and shorebirds are more or less nomadic and opportunistic in their migration and breeding patterns, in contrast to the much more seasonally regular breeding and migration in their Northern Hemisphere counterparts.

Nomadic bird migrations are not limited to waterbirds. A good example of their occurrence in landbirds is the Red-billed Quelea (*Quelea quelea*) of Africa. This seed-feeding species depends for breeding on the emergence of fresh grasses following the rains that accompany the movement of the ITCZ wind patterns north and south of the Equator (Dingle 1996; Cheke and Tratalos 2007). The rainfall is erratic, varying in amount and occurrence across years. Queleas are major pests because huge flocks can descend on grain and decimate the crop. Although the migrations are nomadic, varied, and complex, they are also seasonal, depending as they do on seasonal rainfall. The mass movements are truly migratory because the birds lay down fat deposits in amounts proportional to distances traveled (Ward and Jones 1977), although how this is regulated is unknown; they make long, straight flights and orient in directions consistent with their migration routes (Dallimer and Jones 2002); and they fly over areas apparently suitable at the time but which may not be later when breeding occurs (Cheke and Tratalos 2007).

We can take the dry season as the starting point for the general pattern of quelea migrations. At this time they feed on the fallen seeds of several species of animal grasses and congregate in huge roosts which ebb and flow in size and location depending on seed abundance. With the arrival of sufficient rains (60–70 mm within 10 days) the remaining seeds sprout, denying the birds their food source. There can be some movement ahead of the rains and some temporary feeding on swarms of termites triggered by early rainfall, but eventually the birds must depart on an "early-rains migration," laying down fat as they do so. This migration passes over or through the advancing rain front, followed by a flight of a further 300 km or more to a final destination of ripe grass seeds and abundant insect larvae for feeding young. Birds that have completed prenuptial molt and have mature gonads now breed, but many birds are evidently still not ready for breeding. These non-breeders move along the zone of ripening grass behind the rain front and eventually breed when they gain suitable condition, often in large colonies. The rapid quelea breeding cycle, which is only five to six weeks, means that the early breeders are now finished and migrate to catch up to the rain front, leaving fledglings to complete maturation on their own. Once the adults reach suitable seeding grasses, they breed again. Such itinerant breeding and migration can thus involve two or even more nesting episodes up to 700 km apart during a suitably lengthy rainy season.

A variation on this theme is shown by birds in southern Africa (subspecies *Q. q. lathamii*). These birds occur as a large metapopulation, consisting of subpopulations linked by movement and in which between-subpopulation mixing has important consequences for population processes (summarized by Hanski 1999). The subpopulations of quelea are separated by a migratory divide that traverses Botswana and Zimbabwe at an angle of about 27° running from southwest to northeast (Cheke and Tratalos 2007 and see section on Biogeographic Patterns in this chapter). The divide separates the birds into two populations which spend their dry seasons either north or south of the divide (Figure 3.6). The dry season separation does not translate into

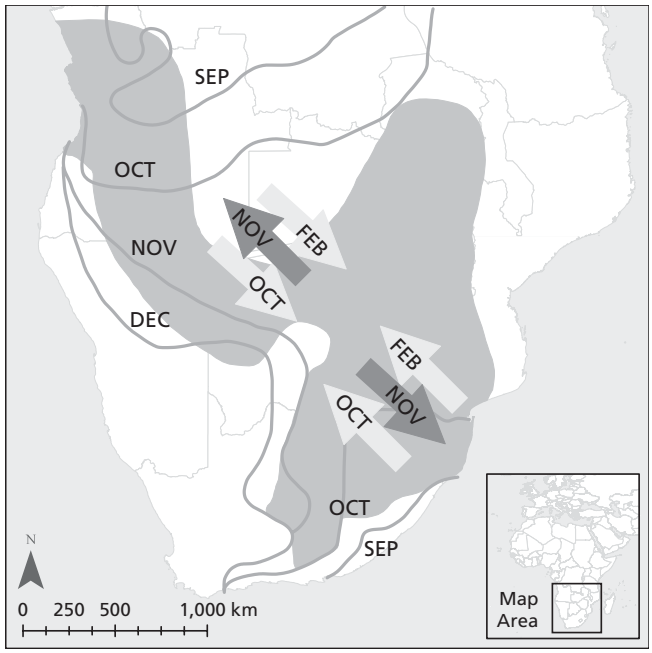


Figure 3.6 Probable directions and times of Red-billed Quelea migrations in southern Africa. Shaded area is the birds' geographical range and isolines indicate the usual start of the rainy season. Movements are initially (October) ahead of the rain fronts, taking birds to the center of the region. When the rain fronts meet, the birds move back over them (November) to the northwest or southeast; the direction of movement depends on which side of the migratory divide the birds originated. They then breed and return toward the center of the region in February. Adapted from Cheke and Tratalos (2007) after Dallimer et al. (2003).

genetically differentiated populations, however, as revealed by both morphology and DNA microsatellites (Jones et al. 2002; Dallimer et al. 2003). Genetic mixing presumably takes place when birds from the two subpopulations overlap while breeding during the wet season at locations that vary over the years.

The variation in migration routes and breeding sites is illustrated by the three seasons from 1965 to 1968 (Figure 3.7). In 1965–1966 breeding began in Mozambique in December, moved to the South Africa/Mozambique border in January, and by February was located in eastern Botswana where it continued into March, facilitated by 249 mm of rain which fell in February. In the next year breeding began near Pretoria in South Africa in December following heavy rain, and then moved to eastern and northern Botswana. In 1967–1968 there was drought throughout the region with sufficient rain to allow extensive breeding only in Mozambique with widely scattered small colonies elsewhere. Similarly in 1999–2000, 224 breeding episodes were recorded in Botswana whereas in 2004–2005 there were none. The opportunistic patterns of migration and breeding in quelea populations have evidently evolved as adaptations to the erratic spatiotemporal patterns in the occurrence and amounts of rainfall.

Species such as the Red-billed Quelea that move among sequentially energy-rich patches of habitat have been designated "rich-patch" fugitives (Ford et al. 1993). Several species in Australia, for example the Regent Honeyeater (*Anthochaera* (*Xanthomyza*) *phrygia*) which is largely dependent on nectar from sequentially flowering trees (Geering and French 1998), also fit the rich-patch fugitive pattern (or perhaps better "rich-patch exploiter"—see Chapter 11).

A number of other species of bird and insect take advantage of erratically distributed resources in space and time. Some of these will be discussed extensively in Chapter 11 where I consider migration under ephemeral circumstances in greater detail.

One-way migrations

One-way migrations are those in which there is no apparent circuitry in the pattern of movements, either by individuals or populations. This does not necessarily mean that a given area is abandoned completely by migrants because there may be immigration by individuals originating elsewhere even as those reared locally are emigrating. It is also the case that individuals may migrate only unidirectionally, but the population may complete a circuit.

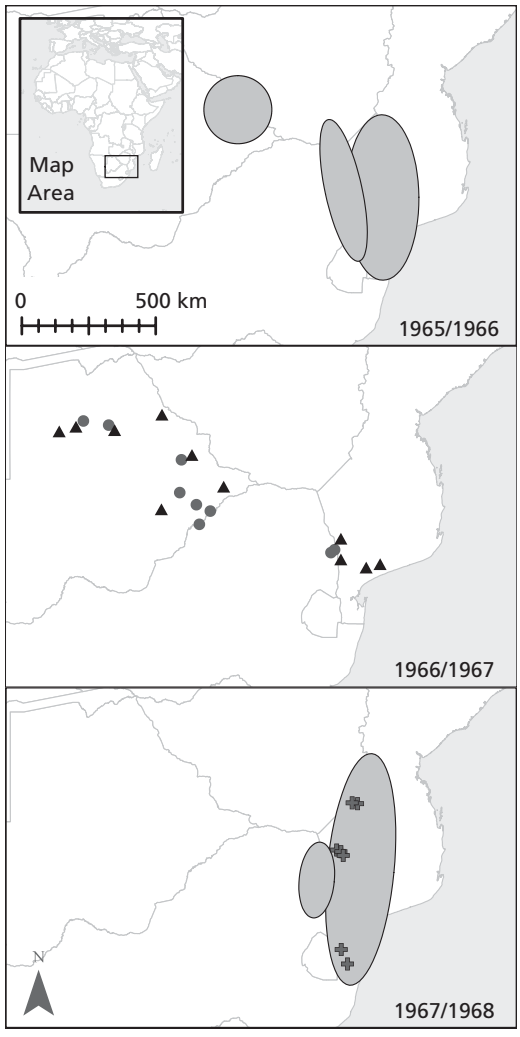


Figure 3.7 Breeding patterns of the Red-billed Quelea in southern Africa for three successive years. Ellipses indicate different breeding areas at various times, and symbols indicate breeding sites at times different from each other or from main breeding within an area. Breeding takes place between December and April at times and places where there has been recent adequate rainfall. Based on maps in Cheke and Tratalos (2007).

Late spring Monarch Butterflies, for example, make individual one-way movements northward, but the overall pattern is for the population to return, at least more or less, to the location or area prevailing at some arbitrary point at the "beginning" of the cycle such as the sites of overwintering aggregations (Figure 3.4). In this section I consider cases where an overall pattern of cyclicity in return movement is not evident.

Such a pattern of individual one-way migrations without apparent population route cyclicity is known for many insects (Dingle 1996). In several species of aphid (Homoptera) there is a succession of generations on a spring and summer host plant maintained through live-bearing parthenogenic females. Initially wingless young are produced through one or more generations on a host. Depending on aphid species, as females age, as host plants senesce, or both, young are produced with wings. These winged offspring then migrate to a new host plant and produce young there after shedding their wings. In the autumn some species produce sexual young under the influence of short days (called holocycly) which migrate to an often different host plant where they mate and produce zygotic eggs. The young hatched from these eggs migrate back to the original host the following spring. In other cases sexual offspring are not produced, and it is the parthenogenic females that overwinter in sheltered spots (anholocycly). The mild climate Milkweed-oleander Aphid (*Aphis nerii*), for example, winters just below the soil surface on the perennial root systems of milkweed plants (personal observations). Many true bugs (Heteroptera), such as several cotton strainers (*Dysdercus*) and water striders (*Gerris*, *Aquarius*), migrate to new host plants (cotton strainers) or different ponds or streams (water striders) after adult eclosion to reproduce at the new site (Dingle 1996). Females of several species of both groups histolyze the flight muscles upon arrival at a suitable breeding location and convert the proteins so acquired into yolk proteins for egg production (Nair and Prabhu 1985). Males may or may not histolyze. The tendency to migrate before beginning oviposition was termed the "oögenesis–flight syndrome" by C. G. Johnson (1969) and seems to be generally true of migrating insects.

Several species of moth are known to migrate one-way pre-reproductively, including those that are wide-ranging pests of various crops (Gatehouse 1997). One such is the European corn borer, *Ostrinea nubilalis*, in the Midwestern USA whose nocturnal migratory flights were analyzed in the laboratory using a tethered flight apparatus (Dorhout et al. 2008). The round-about flight mills used allowed

the authors to analyze flight distance, duration, and speed as a function of age and whether or not individuals were mated. For unmated females both propensity to fly and the duration of flights were highest on the first night after eclosion and declined markedly thereafter, suggesting an obligatory migratory flight by unmated females. In these experiments the median flight duration on the first night was about 2 h, but some females flew during the full 8 h of the night. Because not all females made long flights, on a population basis these moths may be only partially migratory. After the first night females mated, and flight behavior thereafter (tested from two to five days) was both reduced relative to the first night and unaffected by mating. Males, in contrast to unmated females, flew little the first night and about the same as females after that, whether or not they were mated. These male flights probably represent foraging rather than migration, including foraging for mates.

The corn borers may also engage in specific foraging, commuting and ranging behaviors. Males use pheromone plumes in foraging for females (see Chapter 1), and mated females forage for oviposition sites on corn plants. Both sexes seek water droplets for drinking. At least part of the population, especially males and young females, aggregates at grassy sites during the day and commutes to cornfield and other habitats at night. Although the same individuals may not return to the same sites the following night, there is a daily flux of moths in and out of these aggregation sites. Dorhout and colleagues also speculate that the moths engage in ranging movements to find appropriate aggregation sites or to find cornfields after emerging from fields rotated to other crops (Sappington 2005). The one-way pre-reproductive migration of females thus appears to be part of a collection of movements that help to co-ordinate the life histories of corn borers.

In addition to freshwater insect migrants, for example water striders, many freshwater taxa display broad geographic ranges, so that even those that are sessile or otherwise with limited mobility must move from site to site (Bilton et al. 2001). Many of the smaller of these are transported by other animals such as on the legs or feathers of birds. There is evidence that many of these aquatic organisms facilitate this transport to a degree that may constitute one-way migration. A feature of some freshwater bryozoans, for example, is the formation of encapsulated dormant buds—the statoblasts—within the colony, and these serve as propagules (Wood 1991). Some of these are buoyant, so-called floatoblasts, bearing a band of gas-filled chambers. The floatoblasts of *Cristatella mucedo* possess an outer ring of marginal hooks and spines that make these floating propagules more likely to become entangled in fur and feathers. There is some evidence that drying speeds up release of the organism within the statoblast (Wood 1991) so that conditions during, say the flight of a duck, could prime the "settling" of the propagule when the bird reached a different pond. Various crustaceans possess sticky surfaces, knobs, spines, or capsules (ephippia) that also seem to be adaptations for transport (Fryer 1996; Dole-Olivier et al. 2000). In at least some bryozoans the release of many transportable propagules seems to coincide with the peak time of waterfowl migration (Okamura and Hatton-Ellis 1995). Some bryozoans increase statoblast production when the colony becomes large enough to deplete local resources, thus pre-empting total resource collapse. All these bits of evidence suggest migration rather than simply "passive" displacement. Most studies of spread or "dispersal" of aquatic invertebrates have focused on ecological and population dynamic outcomes of movement. Analyses of the physiology and behavior of the different steps in the movement process with a view to determining whether the action of natural selection produces ranging or true migration could be highly illuminating with respect to processes governing aquatic systems.

Migration with the aid of devices

The presence of spines in bryozoans to facilitate movement by attaching to bird feathers is an example of migration with a device that allows the organism to embark on a transporting vehicle which can be a mobile animal, winds, or currents. The journeys undertaken fall roughly into four categories and may be examples of ranging or of migration, depending on organism and circumstances. First, there is travel promoted by spinning a silken thread that is then used for transport by the wind, a method

usually referred to as "ballooning." This method is used by some lepidopteran larvae and by numerous species of spiders and mites (Bell et al. 2005). Second, there are seeds that are attached to fluffy "parachutes" or pappi (singular pappus) which, like silk threads, function for wind transport; the milkweeds (Asclepiadaceae) and many composites (Asteraceae) such as common dandelion (*Taraxicum officinale*) are well-known examples. Third, there are seeds with fleshy arals, embedded in a fleshy fruit, or bearing a fleshy attachment such as an eliasome, all to facilitate animal transport. Arals and fruits ensure that seeds are swallowed by vertebrates, which then regurgitate them or pass them through the gut, in most cases depositing them some distance from the parent plant (Howe and Wesley 1988). To the extent that seeds have evolved special adaptations for transport such as hard coats to prevent damage by chewing or where passage through a gut promotes germination, they can be considered possible true migrants inhibiting premature settling and germination in unsuitable locations. Finally, there is transport by phoresy, or the superficial attachment to a mobile animal so that the migrant is itself transported. This mode of transport is common in pseudoscorpions (Zeh and Zeh 1992) and mites (Houck and O'Conner 1991), and these tiny animals are frequently found attached to flies and beetles (Reynolds et al., 2014).

Migrants that use ballooning or attachment to another organism are subject to constraints that keep them small. Seeds and arachnids that become airborne are prisoners of the drag forces required for take-off, and those that attach are restricted by adhesive strength. Phoretic pseudoscorpions and mites are presumably also small so that they will not be detected by the organisms carrying them and removed, and can be easily transported. Seeds transported in the guts of vertebrates are less constrained by size and some can be quite large. All that is required is that they may be handled by the trophic apparatus and gut of the transporting animal. Indeed there is speculation that many trees with large fruits were especially adapted for propagule transport by the "Pleistocene megafauna", and now face extinction or severe limitation because of the extinction of their vertebrate associates. A possible example is the Kentucky Coffee Tree (*Gymnocladus dioicus:* Fabaceae) (Zaya and Howe 2009).

An example of spider ballooning is provided by the small European species *Erigone atra* studied by de Meester and Bonte (2010) under controlled conditions in wind-tunnel experiments. Like other spiders, take-off behavior involves climbing to a high point on a tall plant or fence post and the standing on "tip-toe" to launch the thread on which the spider will be carried (Bell et al. 2005). Two kinds of movement were observed. The first, called "short-distance dispersal" by de Meester and Bonte, involved spinning out the silk drag line which was then anchored at the point of take-off; the spider then "repelled" to its landing spot. In females this movement increased in frequency with an increase in female density experienced during development. In males it increased under combined high male/low female densities experienced by the male spiders. The repelling behavior thus seemed to involve exploring for a new home range, as would be expected from ranging (Table 1.1). By contrast, ballooning (called by the authors "long-distance dispersal") was more likely to occur if silk threads from previously departing spiders were present on the take-off platforms. These threads would signal both density of departing spiders and a high probability that wind conditions were suitable for take-off and travel. Thus the response to the presence of these threads would seem to be part of specialized behavior involved in a (facultative) migration. Observations that spiders may reel in their drag lines when ready for landing (Dingle 1996) further imply that ballooning in at least some instances may represent migration. Labeling the two types of drag line departure as "short- and long-distance dispersal" tends to obscure what may be differentiated specialized behavioral processes evolved for different purposes and having different outcomes. It may be further noted that the wind currents chosen for take-off may actually concentrate the spiders in a new location, of advantage in e.g., finding mates, for example, rather than dispersing them, i.e., increasing the distance between individuals!

Biogeographic patterns

The location and configuration of the land masses on the surface of earth exert profound influences on migration routes. These influences are a consequence

of weather systems (see Chapter 5) and of ocean or mountain barriers. In North America, for example, major flyways for birds occur between the Pacific Coast and the Sierra Nevada and Rocky Mountain chains, in the Mississippi Valley, and in the east between the Atlantic and the Appalachians. Snow Geese (*Chen caerulescens*) and Sandhill Cranes (*Grus canadensis*) breeding in Alaska migrate to wintering grounds in the central valley of California following the west coast flyway, while those from the vicinity of Hudson's Bay westward through the Northern Territories winter from New Mexico to the Gulf Coast of Texas and Louisiana after flying down the central flyway that follows the Mississippi Valley (Sibley 2000). Many other species of waterfowl and numerous other birds from hawks and shorebirds to small passerines show similar divisions in their migration routes.

The Mississippi Valley route is especially important for insects (reviewed by Johnson 1995) of which several are major agricultural pests, making an analysis of routes followed and subsequent population dynamics upon arrival of particular interest. In the spring, warm air masses from the Gulf of Mexico move northward up the Mississippi and provide following winds that aid in transporting migrating insects (Chapter 5). Two economically significant Homopterans that arrive in the upper Midwest after migrating from probable overwintering source areas (for example, Texas and neighboring states) are the Potato Leafhopper, *Empoasca fabiae*, and Aster Leafhopper, *Macrosteles fascifrons*. Both species are vectors of plant diseases that affect many susceptible crops. Backtracking of the insect pathways along transporting weather fronts (Dingle 1996) reveals that even these very small insects can move long distances in a short time. Potato leafhoppers arriving in Michigan on June 1, 1989 were backtracked to a probable source in eastern Texas, eastern Oklahoma, Arkansas, or Louisiana with travel time between 36 h and three days depending on whether the leafhoppers flew continuously or only at night. The distance traveled was thus on the order of 1,500–1,700 km. Other insects that migrate north along the Mississippi flyway include tiny aphids and several species of moth.

After one or more generations at northern latitudes, the descendants of spring and early summer migrants return southward. Potato Leafhoppers' movements are concurrent with northerly winds that follow on the passage of a cold front, even though it is westerly winds that prevail at the time. This suggests that the insects are selecting the appropriate winds, as now seems evident from many orientation studies (Chapters 5 and 8). There is direct evidence of return south from a mark–release–recapture experiment on the Black Cutworm (Silver-Y) moth, *Agrotis ipsilon*, demonstrating southward migration from central Iowa to southern Texas during September (Showers et al. 1993). This occurred on northerly winds following passage of cold fronts even though there were opportunities for northward passage on southerly winds. Once again the insects evidently selected winds that would take them in the appropriate direction.

The occurrence of major geographic barriers between northern breeding and southern wintering areas have produced in some birds the interesting phenomenon of migratory divides (Bensch et al. 1999, 2009; Ruegg and Smith 2002; Irwin and Irwin 2005; Ruegg 2007; Irwin 2009; and see previous discussion of queleas). These divides are more or less narrow regions of contact between populations that migrate in different directions and over different routes. These alternative pathways are generally the result of major geographic barriers that lie between breeding and wintering ranges, although for some divides, like that occurring in the Red-billed Quelea of southern Africa, barriers appear to be lacking (Cheke and Tratalos 2007).

Three extensively analyzed migratory divides are those of the Willow Warbler (*Phylloscopus trochilus*), breeding in Scandinavia (Bensch et al. 1999, 2009), the closely related Greenish Warbler (*P. trochiloides*), breeding from eastern Europe across northern Asia (Irwin and Irwin 2005), and Swainson's Thrush (*Catharus ustulatus*), breeding from Alaska across Canada and in the mountains and along the coast of western North America (Ruegg 2007) (Figure 3.8). The divide for the Willow Warbler occurs along a line that runs through central Sweden and Norway from north of Stockholm in the east in a NNW direction to the Norwegian coast. Genetic, morphological, and stable isotope (see Chapter 4) evidence shows that north of this line the warblers migrate through eastern Europe, Turkey and around the



Figure 3.8 Migratory divides in three species of bird: (A) Willow Warbler breeding in Sweden; (B) Greenish Warbler breeding in central Siberia, and (C) Swainson's Thrush breeding in western North America. Dashed lines indicate the separation of the breeding populations which take the separate migration routes and winter in separate areas. In each case the divides are the result of geographic features, the Alps and Mediterranean for Willow Warblers, the Himalayas and Tibetan Plateau for Greenish Warblers, and the Rocky Mountains for Swainson's Thrushes. Modified and with additional data from a map in Irwin and Irwin (2005).

eastern Mediterranean to wintering grounds in eastern and southern Africa. Birds breeding south of the divide migrate southwestward through Spain and Gibralter to wintering areas in West Africa. The two populations thus take migratory routes that pass around the major barrier formed by the Alps, the Mediterranean Sea, and the Sahara Desert. The divide is apparently maintained in the face of gene flow because hybrids between the two populations are selected against as a result of taking intermediate directions that would take them across the barrier. An interesting aspect of this divide is that populations of the Willow Warbler are continuous with presumptive gene flow around the Baltic forming a ring, and populations along the southern coast in Germany, Poland, and the Baltic States do migrate across the Alps and central Mediterranean. Bensch et al. (2009; see also Irwin 2009) speculate that these birds have long evolved adaptations to this route whereas hybrids resulting from gene flow across the divide will not have done so and will therefore be selected against. Eastern and western Willow Warblers must have met recently in central Scandinavia, following spread north after the last glaciation, and so may be forming incipient species across the divide. This seems to be an early developing example of species formation at the section of a ring where two genetically distinct populations, otherwise connected by gene flow around the ring, come into contact (Mayr 1963; Irwin et al. 2001).

The Greenish Warbler also seems to be a case of speciation in a ring resulting at least indirectly from the evolution of different migration routes followed by contact along a divide (Irwin et al. 2001; Irwin and Irwin 2005). As in the case of the Willow Warbler, populations of the Greenish Warbler spread northward following retreat of glaciers. This spread was evident on the two sides of a geographical barrier formed by the Gobi, Taklamakan, and Tibetan Plateau deserts and the high Himalayan, Tian Shan, and Kunlun Shan mountains. East of a migratory divide through central Siberia, the birds migrate from their breeding grounds to winter in Southeast Asia, whereas west of the divide migrants winter in forests of the Indian subcontinent. The two Greenish Warbler populations have evolved different songs and display very limited interbreeding along the contact zone. Because the two populations have essentially the same ecological requirements, Irwin et al. (2001) suggest that the barriers to gene flow may have evolved by sexual selection on song types that differed between the two separated populations. In any event the limited interbreeding along the zone of contact indicates that the two forms of Greenish Warbler are behaving as two species, but they are connected by continuous gene flow among populations breeding south through central Asia in the west and through China in the east and connected in a band across the southern foothills of the Himalayas (Figure 3.8). This seems to be a more

advanced example of speciation at the northern extremes of a ring than is the case of the Willow Warbler in Scandinavia.

The migratory divide in Swainson's Thrushes coincides with a marked discontinuity in genetics and morphology that suggests secondary contact between populations isolated in eastern and western refugia during the last glaciation (Ruegg and Smith 2002; Ruegg 2007). Like the Old World warblers, the two populations (or subspecies) of Swainson's Thrush have evolved two distinct migration routes to separate wintering areas. The western population, *C. u. ustulatus*), which breeds primarily in riparian habitats west of the Coast Range, Cascade, and Sierra Nevada mountains, migrates along a western flyway to winter in southern Mexico and Central America. The eastern subspecies, *C. u. swainsoni*, which breeds in boreal and coniferous forests from Alaska to Newfoundland and in inland western mountains, migrates along the Mississippi Valley and eastern flyways and across the Caribbean Sea to winter from Panama to central Argentina along the east slope of the Andes. There is a zone of contact with some hybridization between populations in coastal and interior climatic regions throughout the Pacific Northwest of the USA and Canada. The region of hybridization is best explained as a "tension zone" with restricted gene flow (Barton and Hewitt 1985) that results from limited movement (ranging) of thrushes into the zone because of breeding habitat differences and selection against hybrids that is ecologically mediated (Ruegg 2007). This is not a case of ring species formation because nowhere along the ranges of the two subspecies is there a connection involving breeding by a continuous chain of intermediate populations.

On a still larger scale than flyways and migratory divides are the annual movements of many species of migratory land and freshwater birds within and between continents. These migrations involve huge numbers of birds—more than two billion individuals, for example, between Europe and Africa (Hahn, S., et al. 2009). What is particularly interesting, however, is that very little of this migration occurs across the Equator between the Northern and Southern Hemispheres (Dingle 2008). Considering those parts of Africa and South America south of the trans-Equatorial tropical forest belt, only 42 and 28 species, respectively, reach the "truly" southern or temperate areas of those two continents. This in spite of the fact that the pool of migrants consists of some 130 species that winter south of the Sahara in Africa (Fry 1992) and an even larger pool that migrates out of North America to winter farther south (De Graaf and Rappole 1995). No migrants that are breeding endemics in southern Africa or temperate South America winter north of the Equator, most probably because they are filtered out by suitable wintering habitats well before they reach Northern Hemisphere areas (Dingle 2008).

This paucity of migrants from the Northern to the Southern Hemispheres is particularly apparent in Australasia which includes Australia and New Guinea (Dingle 2004 and Table 3.1). From a pool of nearly 200 Asian breeding migrants only 14 reach as far as the Wallacean Islands (the Indonesian islands east of Wallace's Line). Of the four raptors represented, all reach only Wallacea and 98% of these are Chinese Sparrowhawks (Germi et al. 2009) of which a few may reach the western tip of New Guinea. These raptors reach Wallacea by two wind-aided "island-hopping" routes, one via Java and Bali with

Table 3.1 Land bird migrants breeding in Asia and wintering in Australasia/Wallacea.

Common name	Scientific name
Chinese Sparrowhawk (Wallacea)	*Accipiter soloensis*
Japanese Sparrowhawk (Wallacea)	*Accipiter gularis*
Grey-faced Buzzard (Wallacea)	*Butastur indicus*
Peregrine Falcon (Wallacea)	*Falco peregrinus calidus*
Oriental Cuckoo	*Cuculus saturatus*
White-throated Needletail	*Hirundapus caudacutus*
Fork-tailed Swift	*Apus pacificus*
Eastern Yellow Wagtail	*Matacilla tschutschensis*
Grey Wagtail (New Guinea)	*Motacilla cinerea*
Barn Swallow	*Hirundo rustica*
Red-rumped Swallow	*Hirundo daurica*
Gray's Warbler (northwest New Guinea)	*Locustella fasciolata*
Oriental Reed-warbler	*Acrocephalus orientalis*
Grey-spotted Flycatcher (west New Guinea)	*Muscicapa griseisticta*

Sources: Dingle (2004); Germi et al. (2009).

wintering east as far as Flores and the second south from the Philippines via Sangihe and neighboring islands to northern Sulewesi and Halmahera (Chapter 5 and Figure 5.2). A mere three species migrate beyond the northern periphery of Australia. The Oriental Cuckoo penetrates along the east coast as far as the New South Wales border with Queensland, the Fork-tailed Swift ranges over much of the continent, and the White-throated Needletail occurs east of the Great Dividing Range as far south as Tasmania. The two swifts and the two swallows are members of the strong flying highly migratory aerial predator guild (Dingle 2008). The Grey Wagtail is common in New Guinea, but rare in northern Australia, and the Yellow Wagtail regularly reaches northern areas but is rare to uncommon. The Barn Swallow is mostly confined to northwest Australia and the Red-rumped Swallow is very rare in tropical North Queensland. Gray's Warbler and Grey-spotted Flycatcher reach only western New Guinea and the Oriental Reed Warbler is also very rare and occurs only in the far north central region (the "Top End" and adjacent areas). Thus for most of the few species that do reach Australasia, it is only a small representation of the total southward migrating population that does so.

From Australasia to Asia there are no migrants. This might be expected of the unique avifauna that evolved in Australasia, but it is true even of those species that have close relatives in Asia (Table 3.2). All the species or their relatives are migrants on both continents, and the Australian forms presumably are descended from Asian migrants that reached Australia—a probable example of "migratory dosing" as described by Bildstein and Zalles (2005). Once they arrived in Australasia they developed migration systems restricted to that region with movements to northern Australia, New Guinea and occasionally the (primarily) easternmost Wallacean islands. Thus the region east of Wallace's line not only has its special diversity of species but also its own largely self-contained bird migration system (Dingle 2004).

Why are there so few migrants in either direction between Asia and Australasia? Four broad reasons for differences in species diversity, including migrant diversity, have been proposed (Dingle 2008). The first is area, which is based on the assumption

Table 3.2 Intra-Australasian migrant land birds with the same, sister, or similar species in Asia.

Common name	Scientific name
Black Kite	*Milvus migrans*
Shining Bronze-cuckoo	*Chrysococcyx lucidus*
Little Bronze-cuckoo	*Chrysococcyx minutellus*
Pallid Cuckoo	*Cuculus pallidus*
Brush Cuckoo	*Cacomantis variolosus*
Australian Koel	*Eudynamys cyanocephalus*
Dollarbird	*Eurystomus orientalis*
Rainbow Bee-eater	*Merops ornatus*
Spangled Drongo	*Dicrurus bactreatus*
Australian Reed-warbler	*Acrocephalus australis*

Sources: Dingle (2004); Clements (2007).

that larger areas will have more available ecological niches and therefore support more species (Chown and Gaston 2000). This seems an unlikely contributor to species reduction in this case because there is no marked decline in the area available for wintering going in either direction (in contrast to the reduction in areas as one proceeds south in South America, for example). The second possible factor is distance with, presumably, longer distances being more demanding and therefore with fewer species traversing them. Again this seems an unlikely causative impact because distances between Asia and Australasia are no greater than those traversed by many small land bird migrants over the Sahara between Europe and central Africa or over the Atlantic and Caribbean en route between North and South America (Dingle 1996).

The two remaining possible causative factors, barriers and habitats, do seem probable influences on passage between Asia and Australasia (Dingle 2004, 2008). With respect to barriers, there are several lengthy water crossings between the two continents over the Sunda Shelf (on which lie Borneo, Sumatra, Java, Bali, and adjacent islands) and over the Wallacean islands. Many migrant birds do make major water crossings, but these are usually substantially wind-aided, as in the case of the godwits described earlier in this chapter. For birds flying on a predominantly north–south axis in mainland Asia, crossing

to Australasia would require a prominent "left turn" followed by a "right turn" if any continued to mainland Australia. In this part of the world the route would be hindered by wind patterns, as north or south of the Equator autumn migrants would be flying into easterly trade winds or experiencing the still air of the "doldrums" over the Equator itself. An evolutionary shift in migration pathway requiring an extension of journeys, two orthogonal changes in direction, and long flights over water against prevailing winds seems unlikely. Migrants proceeding or returning to Asia, even though there might be some wind assistance, would still face a conspicuously "dog-legged" route and overwater crossings. Selection for such a route would need to be compelling. Colonization of Australasia by Asian species in the past was probably made much easier because changes in sea level during Pleistocene glaciations repeatedly connected the islands of the Sunda Shelf and, within Australasia, portions of the continental shelf, thus reducing the distance of overwater crossings considerably (Johnson 2004).

Habitats influencing travel en route and at destinations are likely to be even more important than barriers in determining migratory patterns (Dingle 2008). Asian migrants tend to predominate in more climatically exposed "unbuffered" forest edge or woodland habitats (Chesser and Levey 1998; Hockey 2005 and Chapter 9) or in the wetter of more open areas. Such areas are common in Southeast Asia and on the Sunda Shelf islands, so migrants need not continue farther to find suitable wintering habitat. Habitats thus act as a filter, removing migrants as they move southward. Furthermore the dense rainforests of New Guinea and the much drier northern areas of southern New Guinea and Australia provide very little suitable habitat for the Asian species. These same drier habitats are, however, quite suitable for Australian species that migrate north for the winter, with the result that there is little natural selection favoring departure from Australasia.

Summing up

The examples in this chapter reveal the enormous variety of migration behaviors and the often awesome performances of the migrants. In spite of its diversity, however, a common thread weaves through the tapestry and reveals that migration is defined neither by its magnitude nor by the particulars of its routes. Rather its defining characteristics of active embarkation, enhanced locomotion, and temporary suppression of maintenance, trophic, and reproductive activities are evident throughout no matter the size of the migrant or the pathway followed. Migrants vary in size from tiny mites to the larger mammals, and pathways can be classic round-trips of Bogong Moths or long-lived lived birds or the one-way paths of minute aphids or bryozoan propagules. Nor can migration be distinguished on the basis of active versus passive movements because, even when migrants are borne ballooning on the wind or in the gut or on the body of an unwitting host, they got there through precise behavioral or physiological embarkation mechanisms that assured their transport. In spite of the detail in the variety, the common thread of pre-emptive specialized behavior to leave an old home well behind and travel to a new is woven throughout the migration phenomenon. In the tiny and short-lived the journey occurs only once; in the large and long-lived it may repeat tens of times throughout the lifespan.

Migration can involve enormous numbers of organisms—for example the 2.1 billion birds estimated to travel from Europe to Africa (Hahn, S., et al. 2009), although even this number pales in comparison to the numbers of migrating insects. Large dragonflies may number 4–6 billion migrants at a time (Holland et al. 2006), and, in the case of small insects, the early work of Glick (1939), using an airplane-borne net for aerial sampling, demonstrated that the numbers were vast even over a minute portion of the earth's surface. The populations of winged migrants of many species often follow more or less defined routes or flyways in both Old and New Worlds and various barriers and ecological features can have profound effects on the distribution of migrants, such as the self-contained bird migration system of Australasia and the various migratory divides separating migrant populations following different routes.

Equal in importance to migratory behavior itself in all the examples outlined is its ecological outcome. In classic to-and-fro migrants—for instance the bar-tailed godwits migrating between Alaska

and Australasia, the swift parrots traveling only between Tasmania and the Australian mainland, or the Christmas Island red crabs moving between forest and sea—the journey supplies a predictable safe haven with available food at one end of the route and a productive breeding ground at the other. Other versions of round-trip migration may include stops at one or more sites to exploit temporary resources, as in Serengeti Wildebeest, and can occur across several generations as in the Monarch Butterfly of North America. The seemingly erratic migrations of the Banded Stilt and other denizens of Australia's arid interior also have their ecological logic, allowing exuberant reproduction in those years and places where itinerant rains or floods briefly soak the landscape and cause creeks to run and lake basins to fill. The various one-way migrations allow exploitation of successively available food resources during the course of a season and escape from areas where resources are collapsing. The ecological requirements of each species select for the timing of migration and the particular pattern of each migratory cycle. Underlying each is a physiological syndrome producing a similar well-defined behavior. The ultimate outcomes of that behavior and the source of natural selection upon it are survival and reproduction, i.e., fitness, in an environment that varies over space and time shaped by the planet's geography, climate, and seasons.

Thus the examples in this chapter reflect the fact that migration is a characteristic behavior with specific physiological properties molded by natural selection to yield specific life-history and ecological outcomes. It is the properties that must be considered when defining migration and the outcomes that must be considered when determining the ecological and evolutionary significance.

CHAPTER 4

Methods for studying migration

The development of methods to track and study migrating organisms has a long history. Initially counts and relatively simple marking techniques predominated and indeed are still in use today, often supplemented by increasingly sophisticated trapping. Where the major advances have come, however, is in the recent rapid developments in technology. These have been in identifying natural markers such as genes and isotopes (Webster et al. 2002), in miniaturization of devices that can be attached to migrants, in the collection of data transmitted or stored by the devices, and in the development of computers capable of analyzing the huge amounts of data on location, direction, and rates of movement (Bridge et al. 2011). These devices are now providing often startling insights into the details of migratory pathways and the performance of the migrants. At a different level, new technologies are allowing extensive measurements of migrants under laboratory conditions, yielding new understanding of physiological performance and orientational and navigational capabilities. As some interesting recent results have shown, however, there is still much that can be learned from relatively simple methods of marking and counting, especially if they are done systematically.

In the following sections I briefly describe some of the means used to study migration. Several methods were outlined extensively in Dingle (1996), so here I focus on updates and developments since 1996. As with the earlier work, the discussion is divided into field and laboratory methods. Field techniques are used to determine what migrants are doing under natural conditions; laboratory methods may be necessary to answer questions about orientation capability, physiological performance, and life-history adaptations to migration. Because it occurs over broad scales of time and space, migration is one of the most difficult behaviors to study. All the methods have trade-offs between advantages and disadvantages. The design and use of methods to maximize the information gained concerning migration thus present formidable challenges to the ingenuity of investigators. The big gains in knowledge, however, are testament to success.

Field methods

Direct observations and counts

One of the commonest methods for studying migration in the field involves counting migrants as they move past a lookout. This technique is especially prevalent for observing and counting migratory birds, but it has also been used for insects such as butterflies and dragonflies and occasionally for other organisms (Dingle 1996 for a summary). Most often observers take advantage of topography in the form of ridges, coastlines, peninsulas, islands, and isthmuses that funnel large numbers of migrants. Even man-made features have been used, for instance the Empire State Building in New York City (De Candido 2007). In the autumn of 2005 (August to mid-November) more than 17,000 nocturnal migrants passed the observation deck and demonstrated that migrating birds successfully avoided this obstacle, or, in the case of some flycatchers, even perched for intervals and sallied for night-flying insects. Another interesting observation was that Peregrine Falcons (*Falco peregrinus*) hunted passing migrants at night. More usually, however, observations are made at locations such as the Kittatinny Ridge at Hawk Mountain, Pennsylvania, the Isthmus of Panama where 500,000 raptors may

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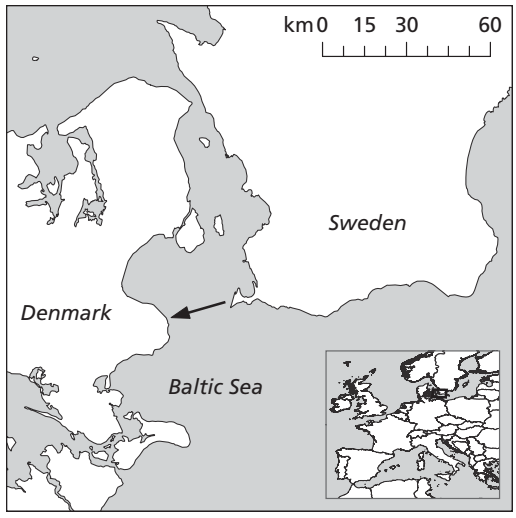


Figure 4.1 Falsterbo peninsula and the route followed by Red Admiral butterflies during southward migration (arrow). The route is the shortest distance between Falsterbo, Sweden and Denmark. Once across the water, the butterflies again turn south. Data from Brattström et al. (2008).

pass over the city of Balboa in a single autumn (Dingle 1996), and the Falsterbo Peninsula at the southwestern most tip of Sweden where some 1.8 million birds of the 25 most numerous species have been observed to pass by (Alerstam 1990). At locations such as Hawk Mountain and Falsterbo (Figure 4.1), observations have been ongoing for long periods (since the 1940s at Falsterbo) and have provided much long-term data on the timing of migration and the species and numbers of birds involved.

Falsterbo is also a good place to study butterfly migration, and Brattström et al. (2008) have used the concentrations of the Red Admiral (*Vanessa atalanta*) there to examine the potential influences of wind and weather on these migrants. The Red Admiral is perhaps the most conspicuous migrant butterfly in Europe, shows a regular pattern of migration from south to north and return, and is the most abundant migratory butterfly at Falsterbo. Two observers recorded butterflies migrating out over the sea between August 1 and October 25 during the hours from dawn to 14:00 over three autumn seasons (2004–2006). The approximate direction of departure of each individual was noted from the vanishing bearing estimated to the nearest 45°. Weather data were obtained from a station a short distance from the observation site.

There were three interesting observations about the migration of Red Admirals at Falsterbo from this study. First, there was a considerable difference in the timing of migration between years. In 2005, a cool year, the median date of passage was August 31, whereas in the warmer year of 2006 (2°C per day on average) the median date of passage was September 24. Given the difference between years, variation in the timing of migration is likely due to temperature. Second, the mean daily flight directions in the two years were 265° in 2005 and 255° in 2006, or almost due west, with very little variation (Figure 4.1). This is interesting because flying due west means covering the shortest overwater distance between Falsterbo and the coast of Denmark (24 km), even though the passage of migration is in general to the south. An unresolved question is whether the butterflies can detect the coast of Denmark, are channeled by topographic features of Falsterbo, or use some other means to orient to the west. Also, do they turn south once they reach Denmark? Third, the probability of migration was highest when a northeasterly wind of low speed occurred on days with a clear sky. This means the passage over water was largely wind-aided (see Chapter 5). Red Admirals, like other migrating butterflies, are strong flyers usually traveling within a few meters of the Earth's surface, as was the case here. Many migrating butterflies have been observed flying independently of wind direction as long as velocity was not too high, so it is noteworthy here that favorable winds seem to be selected for the sea crossing. The butterflies at Falsterbo were not observed flying at high altitudes, although at other locations with longer water crossings they may do so (Mikkola 2003a,b). The Red Admirals at Falsterbo thus seem attuned to local conditions.

In addition to direct observations and counts of migrants, field data can be used for indirect assessments of migration. An outstanding example is the analysis of atlas and bird count data to determine migration patterns in eastern Australia by Griffioen and Clarke (2002). Atlases are a method frequently used to accumulate information about ranges, relative

Table 4.1 Relative sizes of the quarterly population sums for three species in eastern Australia.

Species	Quarter			
	Pre-breeding	Breeding	Post-breeding	Wintering
Dollarbird (migrant)	3.71	11.47	5.78	0.20
Budgerigar (migrant)	12.21	9.21	7.57	12.55
Noisy Miner (sedentary)	12.64	11.71	10.82	13.22

Note especially the contrast between the strongly migratory Dollarbird and the non-migratory Noisy Miner. Full explanation in text. Source: Griffioen and Clarke (2002).

densities, and seasonal changes in bird populations, and two have been produced covering bird distributions continent-wide over Australia (Blakers et al. 1984; Barrett et al. 2003). There are also some more local atlases for different regions. These atlases take observations and counts of hundreds or thousands of observers (the "reporting rate"), collate them, and map them usually by season. These counts usually extend over several years, but the databases are generally combined as if all surveys were conducted within one theoretical year. Griffioen and Clarke (2002) converted all reporting rates to presence/absence data so that all databases conformed. They divided eastern Australia into 200 × 200 km grid squares and divided the year into four three-month seasons (quarters), based on the time of breeding of each species (see Table 4.1). The relative population sizes of each species were calculated by summing over the grid squares for each three-month quarter. Variations in quarterly sums between seasons indicate the size of the population change for a species and may indicate the movement of the species into and out of the area. A limitation of the method is that only large-scale movements (>200 km) can be detected, but in spite of this limitation many insights into Australian bird migration emerged.

Three examples of the results are shown in Table 4.1. The Dollarbird (*Eurystomus orientalis*) is a migrant that largely departs Australia to winter in New Guinea. This is shown here by the very low population sum (0.20) for wintering in Australia, indicating that almost no birds are present at this time compared to the high value for breeding (11.47) when eastern Australia is well populated with nesting Dollarbirds. The values for the Budgerigar (*Melopsittacus undulatus*) are less distinct, although differences are still statistically significant. In this case the degree of similarity between seasons may reflect partial migration. The atlas data show that budgie populations are resident in the north, and that they breed there during the summer monsoon as well as in the southeast in the spring (Wyndham 1982). The Noisy Miner (*Manorina melanocephala*) is resident throughout its range in eastern Australia, as reflected in the very similar and not statistically different population sums in Table 4.1.

Griffioen and Clarke (2002) estimated the directional patterns of migrations by calculating "centroid vectors." The centroids in this case are the geographic centers of species' ranges at a particular season. The vector between the map coordinates of two season centroids was calculated using simple trigonometry, and shifts in centroids indicated shifts in range with the direction of the shift and hence migration indicated by the vector (Figure 4.2). From these estimates and the seasonal differences in population sums (Table 4.1), Griffioen and Clarke found strong evidence of migratory movements in 101 of the 407 species they examined and suggestive evidence in a further 45 species. These results further yielded 19 distinctive patterns of migration in the birds of eastern Australia from a simple crossing of Bass Strait from Tasmania to the mainland (as in the Swift Parrot in Figure 3.2) to more elaborate patterns of directional slope, changes in direction, and circular pathways. The patterns for the Dollarbird and the Budgerigar are illustrated in Figure 4.3. These same patterns are displayed by five additional species in the case of the Dollarbird and a further 13 species in the case of the Budgerigar.

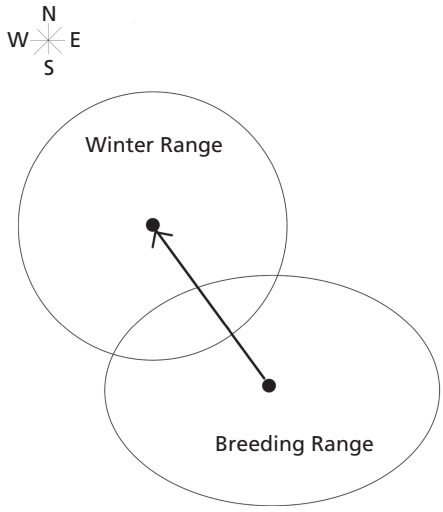


Figure 4.2 The method used to determine migratory pathways from the Australian bird atlas. The lines enclose the breeding range and wintering range of a species with the centroids of the ranges represented by dots. The arrow connecting the two dots is the overall migration route. Adapted from Griffioen and Clarke (2002).

In addition to the atlases and censuses, the world's museums and collections are repositories for enormous amounts of long-term and distributional data on migrants (and other organisms) based on the specimens in their possession (Baker 2011; Lister and Climate Change Research Group 2011). Dingle et al. (2005) took advantage of such data to plot the movements of Monarch Butterflies in western North America (see Figure 3.4). The date and location of monarch specimens from several museums and private collections were recorded from the label accompanying each specimen, and locations were then plotted by month on a map of western North America roughly west of the continental divide. As with the atlas data for Australian birds, all observations were compressed into one theoretical year. The "classic" model of Monarch migration in the American west had presumed that butterflies from throughout the region migrate in the autumn to wintering aggregations along the coast of California and a multi-generational return inland in the spring, with the western population being distinct from the migratory Monarchs of eastern North America. The western museum data of Dingle et al. (2005), however, indicated at least two and probably three autumn migration routes in the west (Figure 3.4). The

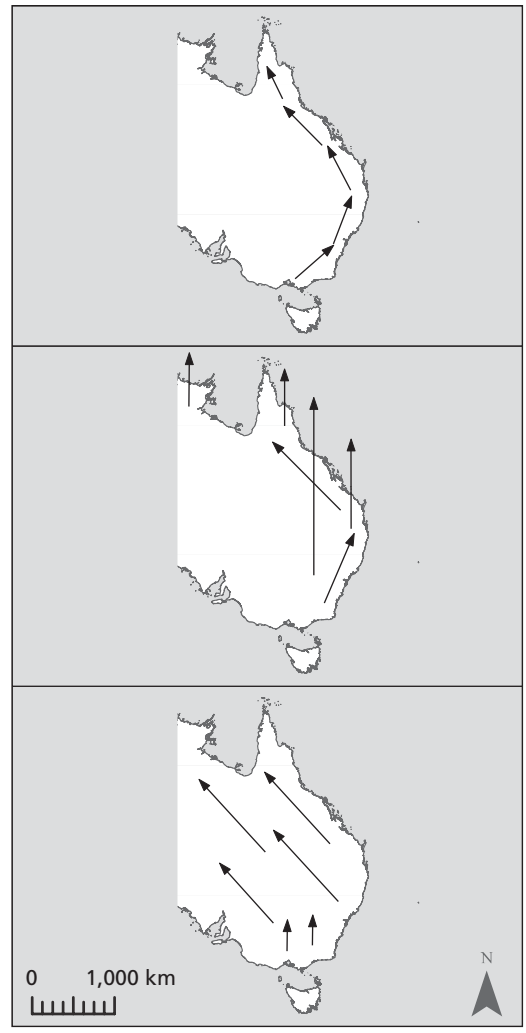


Figure 4.3 Autumn migration routes for Yellow-faced Honeyeater (upper), Dollarbird (middle), and Budgerigar (lower) in eastern Australia. The Yellow-faced Honeyeater breeds primarily in the southeast and migrates up the coast, making an orthogonal turn at the New South Wales/Queensland border, and winters mostly within Australia. The Dollarbird breeds throughout eastern Australia and migrates mostly to New Guinea for the winter. The Budgerigar has breeding populations in the southeast, and they migrate northwest to winter (and breed again?) in the northern monsoonal region. Adapted from maps and data in Griffioen and Clarke (2002).

recent progress in digitizing museum records and making them available online promises more opportunity for the use of museum data to analyze migration and other problems of biodiversity (Baker 2011).

Natural markers

Natural markers of several kinds have been used to identify migrants, to distinguish migrants from resident populations in the same area, to determine the source of migrants, to determine "connectivity" between populations in two areas at opposite ends of a migration route, or any combination of these (Webster et al. 2002). The best markers allow identification of individuals such as the markings and patterns on flukes, heads, or bodies of migrating whales. These have been used successfully to identify individuals and to map their routes over long distances, often with the help of extensive photographic libraries (Lockyer and Brown 1981; Bigg et al. 1986; Ford 1991). In large terrestrial mammals such as rhinoceros or tapir, it may be possible to identify and track individuals by their individually identifiable footprints (Unger 2006). Usually, however, it is only populations that are distinguished. Plumage details separate Grey Plovers into subspecies, for example, allowing birds of a given wintering region to be identified as to source breeding areas (Minton and Serra 2001 and Chapter 3). Contra Dingle (1996), however, subspecific differences do not separate Tasmanian silvereyes from northern subspecies. Song dialects also separate migratory from resident bird populations as in the White Crowned Sparrow (*Zonotrichia leucophrys*) (Baptista and Petrinovich 1984). Birds wintering in the central valley of California, for example, can be identified by their songs as migrants that breed in Alaska. Chemicals present from food eaten can also sometimes be used, as in the milkweed-specific cardenolides of Monarch Butterflies (Chapter 3).

One of the most successful of recent developments has been the identification of the source of populations through the presence of biogeochemical markers, especially stable isotopes in body tissues (Hobson 2003, 2005; Rubenstein and Hobson 2004). These markers are particularly useful for studying migration and other movements because they do not require the external marking, re-sighting, or recapturing of individuals. Stable isotope measurements in tissues reflect the values of the isotopes in food webs and provide information on both diet and location of feeding. To obtain reliable information, isotope "signatures" from many individuals are needed because of the variance in the measurements introduced by many factors; as a consequence they provide evidence of movement patterns relevant only to populations and not individuals. A number of isotopes from different tissues have proved useful (Box 4.1).

Stable isotopes have been used to map the connectivity patterns and routes of several migrants. In the demonstration that Monarch Butterflies east of the Appalachians in North America have their natal origins in the Midwestern region cited in Chapter 3 (Miller et al. 2011), the authors used isotopes of carbon ($\delta^{13}C$) and hydrogen (δD) to determine origins. Also from these isotopes, there is evidence that most Monarchs in the wintering sites in the Transvolcanic Range of Mexico come from the Midwest (Wassenaar and Hobson 1998), and that there is some southward migratory travel to Cuba (Dockx et al. 2004). In Europe the studies of migratory Willow Warblers across the migratory divide in Sweden (Chapter 3 and Bensch et al. 2009) relied primarily on nitrogen ($\delta^{15}N$), in addition to genetic and morphological features, to demonstrate separate wintering areas in Africa, because this isotope is more informative across the east–west moisture gradient in Africa than is hydrogen (Rubenstein and Hobson 2004). Hydrogen (δD) values are most useful for studying avian migration in the Neotropical system because there is strong latitudinal geographical structure (Figure 4.4), whereas in the Eurasia–Africa system $\delta^{13}C$ and $\delta^{15}N$ have proved more informative for bird migration because of the aforementioned east–west moisture gradient across tropical Africa. Stable isotopes of hydrogen (δD) have been useful in mapping the seasonal migrations of Red Admiral butterflies across Europe (Brattström et al. 2010).

Genes are also useful natural markers. With the development of the techniques of electrophoresis and the rapidly evolving technology of molecular genetics such as next generation sequencing (NGS) and restriction site-associated DNA (RAD) sequencing that allow relatively cheap sampling of large sections of the genome (Davey et al. 2011), they are becoming increasingly useful for determining the geographic origins of migrants and their routes of travel. To test hypotheses about genetic population

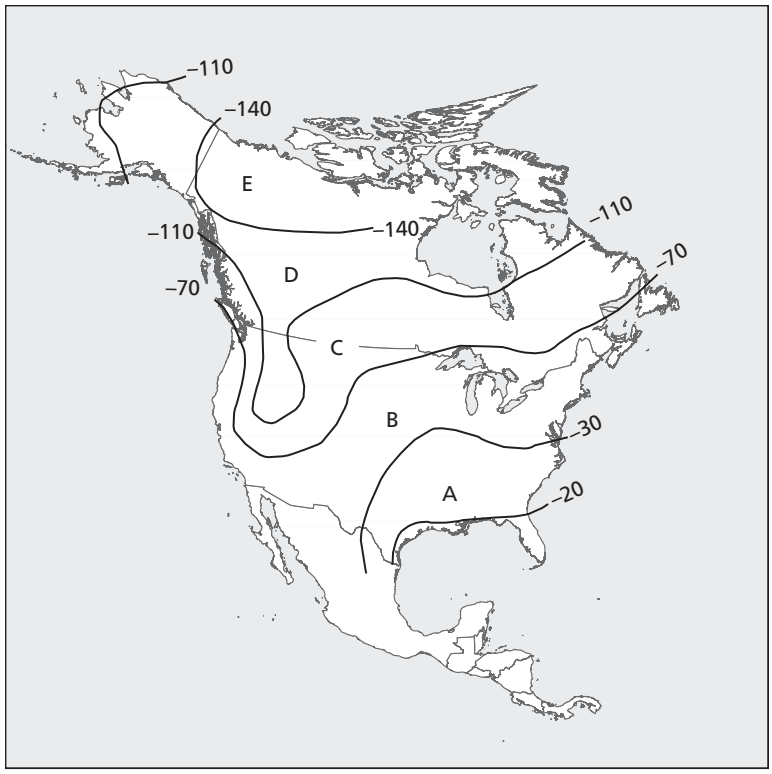


Figure 4.4 The distribution of values for stable isotopes of deuterium across North America with isolines of equal value indicated. Analysis of deuterium isotopes in, for example, bird feathers or insect wings can indicate approximately where the organisms have been consuming food (i.e., within one of the bands labeled A–E) and so acquiring deuterium of the value present in the environment. From a map and data in Hobson and Wassenaar (1997).

structure and the origin of Australian populations, Shephard et al. (2002) used allozyme electrophoresis (seven enzymes) applied to Monarch Butterflies from Australia, Hawaii, and North America. Contrary to predictions based on the assumption of reduced genetic variability in founding butterflies, the Australian and Hawaiian monarchs had less population structure relative to North America. The Australian butterflies also could not be assigned to a definitive source. The high degree of resemblance among Australian populations, however, did suggest a single colonization event, a notion further supported by Clark and Zalucki (2004) as detailed in Chapter 1.

Bensch et al. (2009) analyzed DNA markers in the Willow Warbler populations that surround the Baltic Sea and meet at a migratory divide in central Sweden (see also Chapter 3 and discussion of isotopes). They used 12 microsatellite loci and two markers derived from amplified fragment length polymorphisms (AFLPs). Microsatellites are neutral markers with high mutation rates and provide a great deal of information per locus (up to 30 or so alleles). AFLPs (and SNPs or single nucleotide polymorphisms) are less variable and are subject to selection. They may therefore reveal differences in the selection acting on different populations. There was no evidence of neutral genetic differentiation around the Baltic Sea or across the divide, suggesting that the birds formed one panmictic population during the last glaciation rather than two allopatric populations that met as the climate ameliorated. In contrast there was a sharp discontinuity across the zone of contact in Sweden in AFLPs, suggesting that selection acted on the frequency of the AFLP loci as the species spread around the Baltic. The result was different gene frequencies at the ends of the two distributions when they met in central Sweden. This hypothesis suggests that the terminal forms of the Willow Warbler have diverged over the last 10,000 years as supported also by the lack of differentiation in the neutral markers. This further

suggests that the separate migration routes to East and West Africa have evolved in the same 10,000 year span.

Differentiation of migration behavior has also occurred in Swainson's Flycatchers (*Myiarchus swainsoni*) in South America (Joseph et al. 2003; Joseph 2005). Joseph and colleagues used base pairs of mitochondrial ATPase genes to examine different subspecies of this flycatcher. There are two migratory subspecies, *M. s. swainsoni*, and *M. s. ferocior*, and two non-migratory subspecies, *M. s. pelzelni* and *M. s. phaeonotus*. The genetic evidence suggests that *M. s. swainsoni* is an evolutionarily old member of the *Myiarchus* radiation and should probably be considered a separate species with a relatively long history of migration. The other three subspecies are closely related, and the genes likely reflect a recent and rapid population expansion and a recent evolution of migration in *M. s. ferocior* that is independent of that in *M. s. swainsoni*. Studies of Swainson's Thrush (*Catharus ustulatus*) using mtDNA by Ruegg and Smith (2002) have shown similar separate pathways for the evolution of migration within a species, with Alaskan and eastern North American breeding birds forming one population and birds west of the Rocky Mountains another (see also Chapter 3). Analysis of genomes has thus provided considerable insight into the evolution of migration as well as serving as markers to identify separate populations. Another variant of genetic markers in migrant genomes is the use of genomes specific to parasites that might be carried by migrants (e.g., Webster et al. 2002). Needless to say, modern genetics offers some exciting opportunities for elucidating the biology of migrants.

Tagging and trapping

A great deal of information on migratory origins, destinations, and routes has been obtained over the last several decades by marking and recapturing migrants. Tags of various sorts have been applied to organisms as diverse as butterflies and tuna and have been later recovered to reveal the origin of animals captured at a destination and at least the straight line between the origin and the destination (recovery point) (summarized in Dingle 1996). Trapping can further be used effectively to positively identify organisms that are observed by another means, such as radar (see sections that follow), that do not allow certain identification of species, as is often the case with high-flying moths or other insects (Chapman et al. 2003). There are various mass-marking techniques, such as fin clipping in fish or applying colored dusts in insects, which may be applied if there is access to large numbers of individuals (Dingle 1996).

A technique that has been used for many years with birds is leg banding (ringing). This involves clamping a numbered lightweight metal band around the leg of a bird on which is an address to which the band should be sent if the bird is found dead, or to which the band number and information on location, date, and condition can be sent if it is captured and released. Long-term banding studies have been carried out in North America and Europe, especially, and from these a great deal of information has been accumulated not only on migration routes but also in some cases on important conservation issues such as population trends.

In spite of much success, however, there are some major constraints on mark-and-recapture methods. One, which applies to any system involving capture, is that whatever the trapping technique, it may be a biased sample of the population. Juveniles, say, may be more subject to capture than adults, or trapped individuals may be less healthy. Environmental conditions may alter trapability and so cause misestimates of population trends. On the Mettnau Peninsula of Lake Constance in southern Germany, for example, mist-netting of migrating birds is affected by weather and changes in vegetation structure around the nets as shrubs and trees grow around the net lanes and probably reduce trapability. The result was an overestimate of population declines (Hochachka and Fiedler 2008). The problem of trapability in some cases can be avoided by attaching visible leg flags that are color-coded as to origin and visible without capturing the birds. These have been successfully used in shorebirds to supplement information from tracking data (Gill et al. 2009).

Perhaps a more serious constraint is that in order to be most effective, mark-and-recapture methods require very large sample sizes of marked individuals and a large contingent of observers who are likely to make and report captures (Dingle 1996, and

references therein). Bird banding and the tagging of Monarch Butterflies have been successful because both criteria are often met. An example is the European Lapwing (*Vanellus vanellus*): almost half a million birds were banded and some 9,500 recovered. Even though only 2% of the total is represented in the recoveries, there is a large enough sample to determine routes and breeding areas of lapwings across northern Europe. At the opposite extreme is the situation in terrestrial Australia, an area the size of lower 48 states of the USA but with only about 21 million people (in 2010) and most of the population concentrated in coastal major cities on an arc from Brisbane to Adelaide. Even very large-scale banding efforts concentrating on a single migrant species such as the Yellow-faced Honeyeater (*Lichenostomus chrysops*) have failed to produce much information (Purchase 1985).

With banding there is also a bias toward large and visible species (Hobson 2003). In data collected by the Patuxent Wildlife Research Center <http://www.pwrc.usgs.gov>, of almost three million Canada Geese (*Branta canadensis*) banded about 600,000 or 20% of bands were recovered, whereas for four warbler species (Parulinae) there were recoveries for only a tiny fraction of banded birds (0.02–0.09%). Similarly tagging works well for large marine fish such as tuna (also commercially important) and sharks, but is impracticable for thousands of smaller species. The problem of small size is even more acute for insects, where, with the exception of the easily identifiable Monarch Butterfly, more indirect methods focusing on population movements must be employed. In a well-organized Monarch program, tags are applied to the wings and an extensive network of observers and the general public report recoveries so that monarch migration routes can be mapped. Between 1992 and 2010, for example, there were more than 15,000 recoveries of monarchs tagged in North America <http://www.monarchwatch.org> in one of the most successful of mark/recovery programs.

Tracking migrants

A limitation of standard mark-and-recapture methods such as banding is that one knows the origin of the migrant at the place it was marked or banded and the place of recovery, but not the route followed to the recovery point. An indirect method to determine at least the approximate route is backtracking. For aquatic or aerial migrants this requires knowledge of movement characteristics such as speed and altitude or depth of travel and knowledge of wind or current speed over the period of migration. Using this sort of information a number of backtracks have been constructed, especially for insects arriving en mass in a major fallout. Complications reducing accuracy of backtracks include varying wind speeds near storms, at different altitudes, or along coastlines. Summaries of the method are given in Scott and Achtemeier (1987) and Dingle (1996).

Obviously it would be much more satisfactory to track migrants during their entire journeys, and rapidly advancing technologies are now allowing this to be accomplished with great success (Bridge et al. 2011). One of these technologies is satellite telemetry. A standard satellite application is the Argos system <http://www.argos-system.org>. The Argos instrument flies aboard Polar Orbiting Environmental Satellites (POAS) of the National Oceanic and Atmospheric Administration (NOAA) of the USA and MetOp of the European Organization for the Exploitation of Meteorological Satellites (Eumesat). These satellites are 850 km high and make polar revolutions of the Earth in about 100 min and so allow frequent contact with transmitters beaming information to them. The information is transmitted to the satellites from a "platform" or Platform Transmitter Terminal (PTT) attached to the migrant and powered by a battery or more recently by solar power which allows a much lighter-weight device (Berthold et al. 2001). The information is then forwarded via receiving stations to processing centers in either Washington DC, USA or Toulouse, France from whence the data are accessed by the users, in this case the biologists tracking the migrants.

Satellite tracking has proven to be very useful for tracking large migrant birds in particular. Two examples are the White Stork (*Ciconia ciconia*) tracked from eastern Europe to wintering grounds in East Africa by Berthold et al. (2001) and Eleonora's Falcon (*Falco eleonorae*) tracked by Mellone et al. (2011) from wintering grounds in Madagascar back to the Mediterranean region. It had been known from many years of banding and recovery records that

the storks flew along the Nile in Egypt and had a major staging and resting area in the eastern Sudan on the way to wintering grounds farther south in eastern Africa. Berthold and colleagues followed birds whose transmitters were attached in Germany, Poland, and Israel and found that there were staging areas not only in eastern Sudan but also western Sudan and Chad. One stork was even tracked as far as Nigeria before it flew back over Northern Cameroon to Chad. This added to speculation that there might be some gene exchange between eastern and western stork populations. Thus satellite tracking added information that revised understanding of migration routes derived from banding alone. Telemetry tracking of Eleonora's Falcon revealed that when crossing the Mozambique Channel between Madagascar and mainland Africa the birds showed variable routes from year to year. They changed their migration routes in response to weather conditions, in particular by selecting winds blowing toward Africa and avoiding low pressure systems (Figure 4.5). Falcons have pointed wings that are

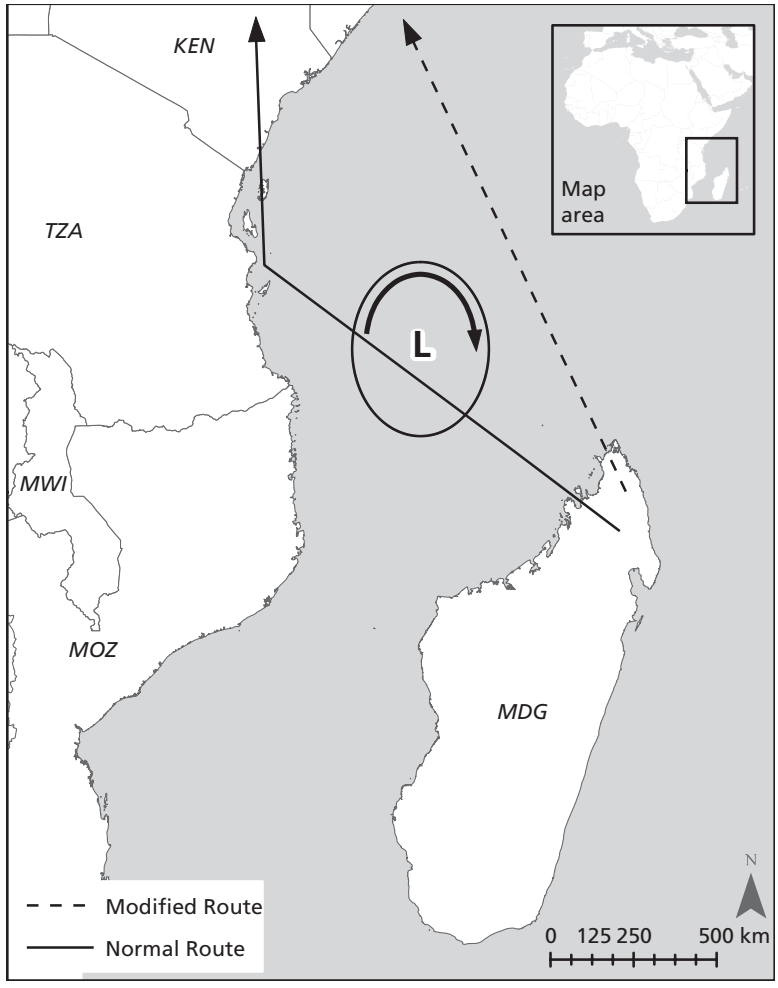


Figure 4.5 Northward migration of Eleonora's Falcon between Madagascar and the African mainland. The most direct route is taken except when it is blocked by a low pressure cell (solid line). In the latter case the birds take an alternate but somewhat longer route (dashed line). Redrawn and modified from information in a map in Mellone et al. (2010).

not long enough for extensive soaring (see Chapter 7), but their powerful although energetically relatively costly flight allows species of the genus to regularly cross stretches of water, for example the Amur Falcon (*F. amurensis*) which crosses the Indian Ocean between India and Africa (Chapter 3). The satellite tracking revealed the efficiency of Eleonora's Falcon in optimizing its trans-ocean route by selection of suitable weather conditions. An earlier satellite tracking study had revealed considerable variation in routes over the African mainland (Geschweng et al. 2008).

Before the advent of satellite telemetry it had still been possible to track migrants using radio telemetry. William Cochran and his students and colleagues have used radio telemetry to track migrating Swainson's (*Cotharus ustulalus*) and Hermit (*C. guttatus*) Thrushes between Illinois and Canada (Cochran and Wikelski 2005). They glued a transmitter to the back of a thrush and tracked the bird with an antenna mounted on a vehicle. Later models could transmit heart rate and wing beat and respiration frequencies, allowing the assessment of physiological performance at all stages along the route. The thrushes migrated at night for up to 850 km and followed six relatively simple "rules of thumb" during their flights and to determine stopovers. These were: (1) migrate when sufficiently fat, (2) migrate when daily maximum air temperature exceeds 21°C, (3) migrate when surface wind speed at takeoff is <10 km/h irrespective of direction, (4) maintain constant heading based on a sun-calibrated magnetic compass, (5) land when hit a cold front or when body reserves reach near levels of the previous morning, and (6) adjust flying efforts to wind direction but don't compensate for wind drift. The birds foraged during the day over areas of about 100 m radius, and interestingly would alter migration routes to fly toward thunderstorms (and their lightning flashes) presumably to take advantage of moist areas when foraging during a stopover. The data also allowed the calculation that it would take about 18 nocturnal flights to travel from Panama to Canada during the April/May spring migration.

Technological advances in miniaturization now permit the attachment of transmitters to large insects such as dragonflies (Naef-Daenzer et al. 2005). Wikelski et al. (2006) attached miniature radio transmitters weighing only about 300 mg to the ventral surface of the thorax of 14 individuals of the Common Green Darner (*Anax junius*), one of several dragonfly species worldwide that are known to migrate (Russell et al. 1998). The transmitters did not seem to impair dragonfly flight and in any case were considerably smaller and lighter than many insects that these dragonflies are known to carry about after capturing them as prey. The dragonflies were tracked for up to 12 days during autumn migration over central and southern New Jersey using ground vehicles and at intervals with slow flying Cessna airplanes. They were observed to migrate only during the day and would do so on average every 2.9 days with an average distance of 11.9 km/day (maximum 200 km) and an average direction toward the south (186 ± 52°) as expected for the season. Flights on stopover days between bouts of migration were not oriented but were omnidirectional, as is typical of foraging flights, to replenish energy (fat) stores for further long distance flight. The dragonflies further tended to migrate after passage of a cold front so that winds were from the north, but migratory flights were limited to days when wind velocity was low (~13 km/h). Interestingly if the darners flew out over the ocean, they reversed direction (like many songbirds and small hawks) before turning westward and then south again over land. This behavior and the tendency to fly with gentle following winds are similar to the decision rules that are followed by the thrushes tracked by Cochran and Wikelski (2005). The signals from the miniature transmitters on these dragonflies are strong enough to be picked up by orbiting satellites, offering exciting possibilities for the tracking of migratory insects.

One of the most exciting developments in tracking migrants over long distances and for long periods is the invention of geolocators by Vsevolod Afanasyev and engineers at the British Antarctic Survey (Afanasyev 2004; <www.birdtracker.co.uk>; <www.antarctica.ac.uk>). The geolocators are miniature devices that can be attached to a bird usually by a leg-loop or body harness (Figure 4.6) or directly to a leg band of a large bird; they are so small (<1.5 g) and have so little drag that they can be carried easily even by songbirds or, as in the figure, a tiny owl (Bridge et al. 2011; Stutchbury et al. 2011). The devices consist of a light sensor and

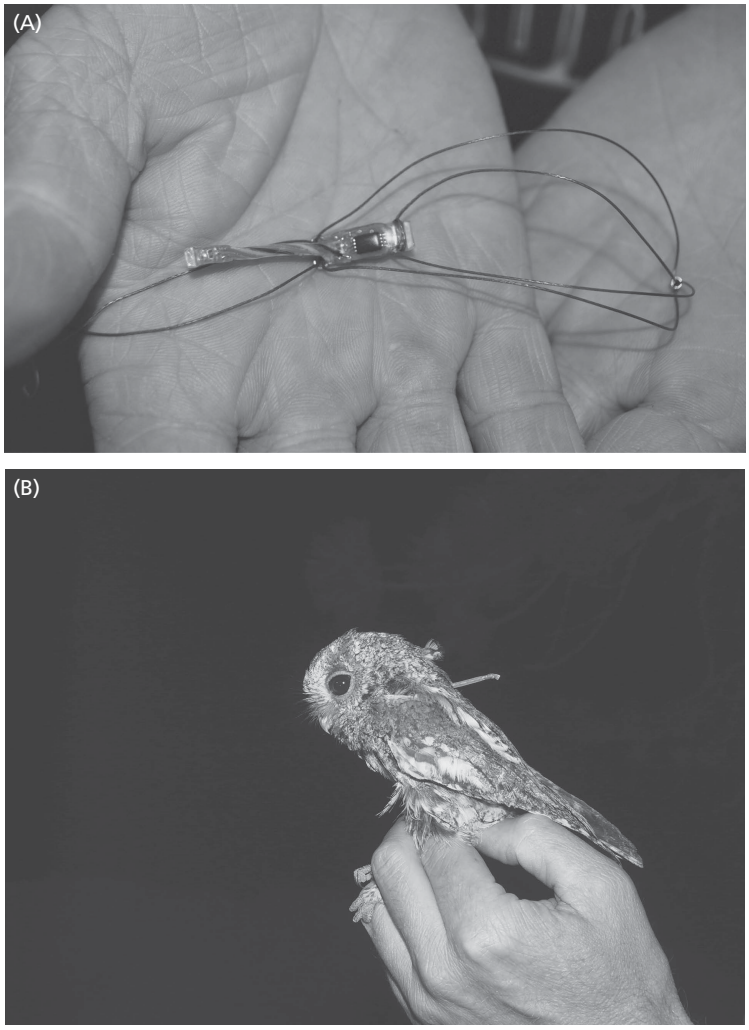


Figure 4.6 (A) A geolocator and its harness used in the study of migration routes of Flammulated Owls (*Otus flammeolus*) which migrate from the Sierra Nevada of California to central Mexico. Photo by David H. Johnson. (B) The geolocator attached to an owl showing the exposed light sensor. Data from the geolocator are downloaded when the owl is recaptured upon return to its nesting area. Photo by David Arsenault. (See also Plate 1.)

the electronics to record and store light-level information. Thus these data loggers work worldwide wherever there is dawn and dusk (and thus do not provide information during the constant daylight of an arctic summer). By calculating the length of day, which indicates latitude, and the time of solar noon, which indicates longitude, a bird or other organism carrying the geolocator can be positioned accurately to within ±150 km, with the level of uncertainty caused mostly by periods of cloud cover. If temperature data are recorded, even greater accuracy is possible. The loggers are not as accurate as GPS- or ARGOS-based systems, but they are small, cheap, and record for many years. They do require that the animal be recaptured to download and analyze the data. The British Antarctic Survey has used these devices to track thousands of seabirds from relatively small petrels to the great albatrosses.

Geolocators have been used successfully to gain information on smaller avian migrants as well as seabirds. They were used to test hypotheses about connectivity and the influence of physiological condition and molt on the timing of migration in the Wood Thrush (*Hylocichla mustelina*) (Stutchbury et al. 2009, 2011). The thrushes were tracked from northern Pennsylvania to wintering sites in a



Figure 4.7 Migration routes of a Ruddy Turnstone from the wintering area in Australia to breeding grounds in Siberia as determined by downloading data from an attached geolocator. Solid line 2009; dashed line 2010. Numbers indicate stopping points en route. Redrawn with permission from Birdlife Australia from a map in *Wingspan* 2011; 21(2): 32.

narrow band in Honduras and Nicaragua. The relatively small area occupied in winter indicated high connectivity of the breeding and wintering populations. With respect to timing, late-nesting thrushes delayed feather molt and migrated south later than earlier breeders. Birds in poorer condition, e.g., with lower triglyceride levels, entered the tropics significantly later in October. Because stopover durations were highly variable, however, neither late molt nor poorer condition resulted in late arrival in the winter territories.

Ruddy Turnstones (*Arenaria interpres*), relatively small shorebird migrants, were tracked with geolocators from wintering areas on the south coast of Victoria (Australia) to breeding grounds in Siberia and return (Minton et al. 2011; Anonymous 2011). Considerable variation in routes occurred at both population and individual levels (see also Chapter 12). On the flight from Siberia to Australia some birds returned via northern China where they fed on the rich mudflats of the Yellow Sea, whereas others made their way via stopovers on the atolls of the Central Pacific. At the individual level, one bird migrated north via Taiwan and south via Kiribati in 2009 and north via Hainan and south via the Marshall Islands and Vanuatu in 2010 (Figure 4.7). Researchers in the cases of both the Wood Thrushes and turnstones were able to take advantage of known breeding and wintering locations to re-acquire the geolocators for data downloads.

Radar

One of the most successful tools for studying migration, especially when it comes to the movements of large numbers of individuals, is radar (Dingle 1996; Drake and Reynolds 2012). Its history in migration studies extends back to the early days of World War II when units used in the UK to detect German aircraft also recorded the passage of unidentified targets or "angels" later shown to be birds and even insects. After the war radar was applied

to ornithological work by David Lack and others who showed that there was a vast amount of bird movement between the British Isles and the continent often triggered by severe winter weather. These early days of bird studies are nicely covered in Eastwood's (1967) book *Radar Ornithology*. Insect studies began later in the 1960s with radar monitoring of the large number of moths and grasshoppers migrating over East Africa by Schaeffer (1976). Since then radar studies have proceeded apace on both birds and insects, and have contributed to a much greater understanding of migration in these two taxa, especially with respect to the relationships between migration and meteorological conditions (see Chapter 5). Drake and Reynolds (2012) provide an up-to-date and thorough survey of both radar technology and the many ways in which radar may be used to track migrants.

Briefly, the principles of radar (from RAdio Detection And Ranging) are straightforward, although with much sophisticated electronics and hardware. Radar is one form of echo-ranging systems that function by transmitting a pulse that is reflected back from the object to be identified. Radars require (1) a transmitter of radio waves, (2) a sensitive receiver to detect returning echos (usually transmitter and receiver are combined in a directional antenna), and (3) a cathode ray tube (CRT) consisting of a screen and phosphor much like a television screen. The CRT is often a circular plan position indicator (PPI) whose center is the radar position and with concentric rings to indicate the "scale" of the "map". The latter may be an actual outline map of the particular geographic area around the radar site projected on to the screen (as with most television weather radars). Radar beams can be in the form of broad "fan beams" or narrow "pencil beams"; the former are used to monitor several objects simultaneously (as with airport radars) whereas the latter are designed to follow individual targets, although a pencil beam can be used for many targets if it sweeps in a circle above the radar. Radar beams of different wavelengths (3 cm, 10 cm, and 20–30 cm) are used depending on the objects to be identified; shorter wavelengths, for example, characterize smaller objects. Various patterns displayed on the PPI by groups of objects of varying size, shape, and direction of travel are illustrated in Dingle (1996).

Until recently most radar studies of migrating insects relied on traditional pencil beam radars and focused on pest species. The principal results are summarized in the next chapter in Box 5.1. The older radars were expensive, large, not very mobile, and labor intensive to operate, and so were not suitable for long-term monitoring. A significant advance in long-term studies of insect migration is the advent of Vertical Looking Radar or VLR (Chapman et al. 2003, 2011). The VLRs are relatively small devices that, unlike scanning radars, do not require special siting; this means that they can be placed where migration of interest occurs, as on a rooftop at the Rothamsted Experiment Station in the UK, or in an unobstructed area remote from a home research laboratory, as in Thargomindah in far southwest Queensland, Australia (Figure 4.8). Observations of migrating insects in particular are made with a design with which echoes are recorded electronically and continuously as targets fly through a stationary upward-pointing beam. The beam is nutated, a conical scan motion similar to that of a spinning top that has started to wobble. This produces information about the target's movement, heading, size, and shape, and often permits probable identification of species. Certainty of species identification usually relies on supplementary trap catches using various airborne traps or ground-based trapping networks.

VLRs have one further significant advantage over other radars. They can operate automatically under microcomputer control and so can record migratory activity over long periods. Datasets extending over several years with millions of individual traverses are now available from the UK and Australia, and in Australia are routinely drawn upon by the Australian Plague Locust Commission to guide control strategies during locust outbreaks (Drake et al. 2001; Deveson et al. 2005; Chapman et al. 2011).

A second recent development in radar technology is the harmonic radar. This device relies on a rectifier, incorporated into a tag attached to an animal, which produces an echo half the length of a transmitted wave reaching the transponder. A receiver operating at the harmonic wavelength detects the echo coming back from the target. Because the transponders are passive, requiring no power supply, they are very light weight and can be

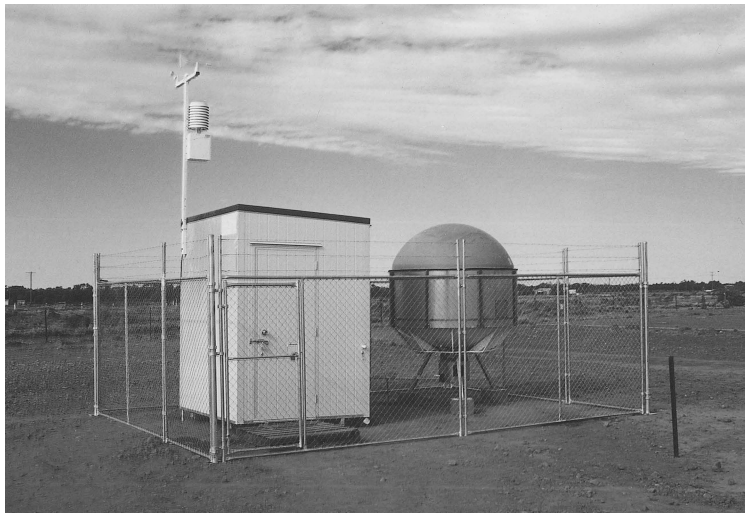


Figure 4.8 The entomological radar at Thargomindah, Queensland, Australia, that can record passage of migrating insects remotely and on a continuous basis (see some results in Figure 15.1). On the right is the radar itself, and on the left the small building that houses the computer equipment that controls the radar and transmits the results to a remote laboratory in Canberra. Photo by V. A. Drake.

attached to medium-sized insects. They are, however, range-restricted and provide no identification information. The latter means that only one or two animals can be tracked at a time. The original use of the principle was as a hand-held direction finder (Masconzoni and Wallin 1986) with use limited to species largely confined to walking. Harmonic radars can now be used to track flying insects, but because of the constraints, only for short distances. They have been useful in tracking moth movements in a pheromone plume (Riley et al. 1998) or honeybees orienting in response to waggle dances (Riley et al. 2005).

Radar has further been used to monitor and track bird migrations at both local and continental scales (Gauthreaux et al. 2003, 2008). Gauthreaux and colleagues have especially made use of Doppler weather surveillance radar with a national network in the USA of 155 stations equipped with the WSR-88D radar (Weather Surveillance Radar-1988, Doppler) also known as Next Generation Weather Radar (NEXRAD) (Gauthreaux et al. 2008). This network is operated by the National Weather Service and supports activities of the Federal Aviation Administration, military bases, the Department of Transportation and other users. Data from the network of WSR-88D radars are recorded on magnetic tape and archived at the National Climatic Data Center (NCDC) from which they can be disseminated to various users, including those researching bird migration. It is thus possible to survey records from the radars for bird movements and densities at different locations and across seasons.

The WSR-88D sends out a beam ~1° in width and at angles of 0.5–19.5° above horizontal. At a distance of 30 km the beam width is 486 m, so precise altitudinal estimates are not possible—only a relatively broad range of altitudes. Echoes are received not only from weather systems but also from objects in the atmosphere, be they dust particles, birds, or insects; because the radar is Doppler, movement can be distinguished as entering or leaving the radar beam and the direction of entry or departure determined. Dust particles and very small insects can be distinguished because their movements are unpatterned or follow wind patterns and speeds. Large insects and birds are distinguished by flight speeds. Insects have modal airspeeds of about 2 or 3 m/s (highest 7 m/s) (Feng et al. 2004), whereas birds fly at airspeeds >8 m/s (Bruderer and Boldt 2001). Foraging birds can be distinguished from migrants because their movements lack directionality (Table 1.1), and in any case they usually fly too low to be detected by the radar beam; migrants show distinct directionality. In addition to failure to detect low-flying birds, a further limitation is that the radar images cannot be used during periods of precipitation. Nevertheless, under clear conditions

and properly interpreted, these weather radars can yield an enormous amount of information on the density, speed, and direction of migration and, when combined with independently recorded wind speed and direction, on the relation between migration and winds. The recent development of a small radar beacon or transponder that can be detected as a bright spot by weather radar opens up the possibility of detection of individual migrants as soon as these can be made small enough to attach to birds (Bridge et al. 2011).

Gauthreaux et al. (2003) used the WSR-88D radar network to assess the geographic variation in magnitude and direction of spring migration across the lower 48 states of the USA. The patterns present in the space from 0 to 754 m altitude from May 4 to 9, 2000 are illustrated in Figure 4.9. Three patterns are apparent. First, there are many more migrants east of the Rocky Mountains than there are to the west, which matches many years of ground observations. Second, there is a major movement of migrating birds from southeast Texas northward just to the west of the Mississippi River Valley and another along the east coast. In the east this includes major landfalls of migrants in New Jersey, southeast Massachusetts, and especially Long Island, New York (601 birds/km^3). Third, there is a bifurcation of migration routes approximately at the junction of the Ohio and Mississippi Rivers at the southern edge of Illinois, with one stream of migrants moving to the northwest and another to the northeast. Birds decreased in density at higher altitudes (not shown), but the overall direction patterns remained the same.



Figure 4.9 Map of spring migration of North American birds for May 4–9, 2000 in one altitudinal zone (0–754 m) as recorded by WSR-88D Doppler weather surveillance radar units across the USA. Arrows indicate the direction of flight and numbers indicate the number of birds per cubic kilometer. Note the large flights along the east coast and the bifurcation of the pathway in the upper Mississippi Valley. Redrawn from Figure 4A in Gauthreaux et al. (2003) with kind permission from Springer Science + Business Media B.V.

At a more local scale, Diehl et al. (2003) assessed bird migration in the vicinity of the US Great Lakes using WSR-88D stations around the lakes. Birds took off after sunset to proceed on migration and crossed the lakes in large numbers. At some locations, for instance at the two ends of Lake Erie, there was some tendency to fly around the lakes instead of directly across. There was also a tendency to "pile up" at prominent features like the Point Pelee and Long Point peninsulas on the north shore of Lake Erie during fall migration. Birds also tended to increase altitude toward dawn—a "dawn ascent", when over water before—then descending to the nearest land if they were within about 28 km of shore, even if this descent meant reorientation. The behavioral responses to the lakes influenced the distribution of birds stopping over in the adjacent terrestrial landscapes. Radar observation thus made a significant contribution to understanding migration patterns in the vicinity of major landscape features such as the Great Lakes.

Tracking underwater animals

Determining the movements and tracks of aquatic animals presents special problems. This is especially true of animals that live in the oceans because not only are they under water and therefore invisible to surface observers most of the time, but they also traverse huge distances unimpeded or unguided by topographic features that might serve as specific locations for observations (Block et al. 2010). Older methods of tagging, such as fin clipping, tend to be limited to large concentrated populations at both tagging and recovery, for example those of salmon raised in hatcheries and recovered as they enter their home rivers on return migration. Transmitting devices are limited by the necessity to transmit through water. In recent years, however, the ingenuity of investigators and developments in technology have overcome many of the limitations in tagging and transmission to provide great quantities of fascinating data on the migratory movements of marine organisms in particular (McIntyre 2010).

Over the last several years the Census of Marine Life Program has been carrying out extensive studies on life in the oceans of the world (McIntyre 2010; O'Dor et al. 2011). A large-scale field program of the Census, Tagging of Pacific Predators (TOPP), carried out long-term observations of the movements and migrations of large marine animals in the Pacific using various tagging procedures (Block et al. 2010, 2011). Archival tags were similar to the data loggers previously described. These were programmed to record not only location based on diel light levels, so providing data on map location, but were also set to measure water and body temperature, pressure, and salinity, thus providing information on the physiology and depth of movements as well as the tracks of the migrating animal. They had the same limitation as geolocators, namely that the tags had to be recovered to obtain the stored data; they were therefore limited primarily to use in exploited species that were likely to be caught again, such as tuna. They were also used to some extent on animals that returned predictably to colonies, such as pinnipeds.

The TOPP program investigators also used tags that transmitted data to the ARGOS satellite system. The antenna of the satellite transmitter must be out of water to communicate with the orbiting satellites, so initially the technology was used mostly with air-breathing vertebrates that surfaced regularly. This transmission problem was solved ingeniously by the invention of the pop-up satellite archival tag (PSAT) that could be used for fish and sharks that remained perpetually submerged. These tags combine data storage with satellite transmission; they are externally attached via a tether and are programmed to pop off at a predetermined time. After release they float to the surface where they transmit stored data to the researchers via the ARGOS system. A further advance has been the development of a GPS tag that can be used with marine species and provides a location estimate via ARGOS. These tags provide precise location data to within 10 m, compared to 1–10 km with standard ARGOS tags, and they provide better resolution of time because they acquire information on position every few minutes rather than only 8–10 positions a day as ARGOS does. The use of GPS required the development of a special "Fastloc" system to indicate location because the ARGOS satellites can be accessed only briefly by diving animals. Good descriptions of the pop-up tags are available on the Wikipedia web site with links to more detailed

specifications <http://en.wikipedia.org/wiki/Pop-up_satellite_archival_tag>. The TOPP program deployed more than 4,000 tags on 23 species in the North Pacific. The results revealed movements over the entire North Pacific, multispecific "hotspots" with concentrations of migrants, and several major north–south migrations among other aspects of the movement ecology and behavior of these major marine predators (see Chapter 9). Tags have further been effectively used in combination with genetic data to examine aspects of population structure and philopatry in marine migrants (Jorgensen et al. 2010).

Marine animals can also be tracked with ultrasonic tags (Klimley 1993, 2013). Klimley placed these tags on sharks by diving with a transmitter attached to a pole spear and inserting a dart into the musculature between the first and second dorsal fins. A monofilament line connected the dart to the free-floating transmitter. The ultrasounds were beamed to a radio-acoustic positioning system consisting of three sonobuoys in a triangular array so that the shark could be located. Because of the need for buoys or a boat to carry an observer with headphones to pick up the acoustic signals, ultrasonic systems are more limited in their use for tracking migrants. They have, however, been very useful in tracking local movements, including those of migrants when feeding or orienting within an area between migratory excursions.

Acoustic systems are now in use to monitor the activities of marine animals constantly within certain areas. One such is the Deepwater Echo Integrating Marine Observatory System (DEIMOS) <http://acoustics.washington.edu/DEIMOS/deimos_data.php>. This system is located in Monterey Bay, California, and samples the water column from the seafloor to the surface once every 5 s, and indicates the movements of many organisms from plankton to fish (see Figure 1.3). The data are stored and eventually analyzed at the University of Washington in Seattle which makes the outputs available online via their Echosounder Online feature. It is thus possible to observe migrations and commutes on one's own computer! High-resolution upward-looking sonar such as Simrad even makes it possible to monitor activity in the water column over the Mid-Atlantic Ridge (O'Dor et al. 2011). These acoustic systems do not allow tracking of individual migrants, but they have the potential to provide considerable data on the movement of migrants into and out of the locations where they are functioning and have been especially useful in detecting other important movements such as the vertical commutes of plankton.

Laboratory methods

Many questions concerning migration are difficult or impossible to answer using field methods alone and require some sort of laboratory assessment of migratory performance. In particular, studies of physiology, behavioral physiology, orientation capability, genetics, and the relation of migration to reproductive performance and other aspects of life histories are likely to depend on some combination of controlled environments, laboratory measurements, and experimental manipulations. Successful analyses depend on adequate indexing of migratory performance such as speed and endurance or response to manipulation of orientation cues. To test and assess performance, a number of techniques have been used, all with various advantages and disadvantages with regard to measuring "true" migratory ability.

Laboratory studies are usually limited to relatively small organisms for reasons of practicality, expense, and sample size. Insects are the organisms most frequently studied in the laboratory because their small size allows rearing in numbers in growth chambers or other types of controlled conditions. Pest insects are frequent subjects because their economic importance justifies the expense of appropriate equipment and labor required for rearing and testing, although many studies have used non-pest species that are interesting behaviorally or ecologically. Insects migrate by flying, so the usual analysis requires apparatus that adequately indexes migratory flight and contrasts it to flight for other purposes such as foraging. One method is simple tethering of insects and lifting them off the substrate to trigger the flight reflex. Flight duration can then be measured on the insect in place either in still air or with wind directed at the head to stimulate wind receptors; longer flights, especially those with "fat tail" distributions (Dingle and Drake 2007), are assumed



Figure 4.10 Side view of a harness for moth tethered flight. The moth (a Black Cutworm) is attached at the thorax and flight is automatically recorded via the clasp at the upper left which connects to a computer. Photo by David Dorhout.

to be migratory. Species of several families, both terrestrial and aquatic, have been tested in this way (Dingle 1996).

Tethering involves attachment of the insect at the thorax to a flexible thread or a small inflexible arm of wood, metal, or plastic. If the attachment device is joined to a long lever arm in turn joined to a pivot, the insect can fly in a circle allowing flight distance to be measured. Such a "flight mill" has been used with several insects, including European Corn Borers (*Ostrinia nubilalis*: Lepidoptera) by Dorhout et al. (2008). They tethered adult moths to a flight mill using a harness constructed of garden ties (Figure 4.10). Two ties were glued together but separated at one end which was bent to form a Y-shape. The Y was then shaped to form a U that was fitted around the thorax and glued while still allowing natural wing motion. The harness with its attached moth was then joined to a mill arm of aluminum about 25 cm long. This allowed the moth to fly in a circular horizontal plane. The revolutions were sensed by an infrared eye mounted on the central post and interfaced to a computer where the number of revolutions was recorded and the data stored (Beerwinkle et al. 1995). Twelve flight mills could operate simultaneously. They were housed in a walk-in environmental chamber maintaining constant conditions (light:dark 16:8, 24°C, 80% relative humidity). Some of the results of these flight mill tests of migratory performance were discussed in Chapter 3.

Although tethered flight has been shown in most tested insects to correspond to take-off timing and flight duration of migrants in the field, it is still desirable to study migrants in "free" flight. Among other considerations, flight speed—and therefore estimates of distance flown per unit time—is likely to be greater when measurements are on unrestrained insects (Taylor et al. 2010). A highly sophisticated flight chamber was designed in the 1950s by J. S. Kennedy to study migration behavior in free-flying aphids, *Aphis fabae* (Kennedy and Booth 1963a; Figure 4.11). This was a large box with top lighting to attract aphids taking off and a controlled wind stream from above that could be adjusted to hold a flying aphid in the air by matching downward wind speed to upward flight speed of the aphid. A vertical lever arm with a platform at its top, to which a leaf or other experimental surface could be attached, could be twisted to force the aphid into flight. Aphids would fly in this chamber for up to several hours allowing analysis of flight duration and strength, and the reciprocal interaction of flight with landing responses. A summary is presented in Dingle (1996) (and see Chapter 2). A modified version of the Kennedy flight chamber with the bottom wider than the top was used by David and Hardie (1988) for studies of flight in both sexual and asexual forms of *A. fabae.* Their version produced an increase in wind speed as the aphid approached the top, so dampening the change in height associated

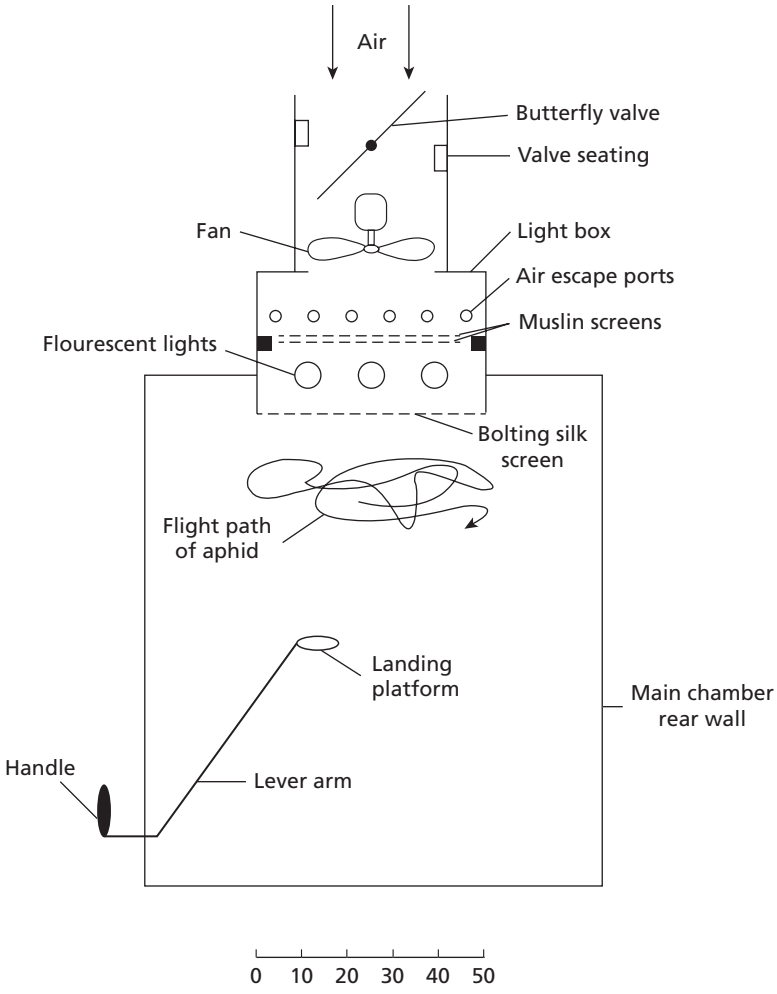


Figure 4.11 The Kennedy flight chamber used for studies of aphid migration. The lever arm can be twisted to shake the aphid off the platform. Free flight is maintained by wind from the top of the chamber, and the wind speed is varied with the butterfly valve whose setting thus indicates the wind speed balancing the aphid's rate of climb. From Dingle (1996) after Kennedy and Booth (1963a).

with change in climbing speed. Blackmer and Byrne (1993) have used a similar "vertical wind tunnel" arrangement to examine the influences of time of day, sex, age, and host quality on the flights of Sweet Potato Whiteflies (*Bemisia tabaci*).

Hardie and colleagues (Hardie and Young 1997; Storer et al. 1999) used a horizontal wind tunnel in combination with video cameras to analyze aphid flight tracks in three dimensions. They mounted two video cameras at the side of a glass-walled wind tunnel in such a way that their fields of view only partially overlapped but the convergence point of focus was the same. With a black background and overhead lighting the image of the flying aphid was clearly visible. A landing platform of yellow paper attractive to the aphids (Kennedy et al. 1961) was provided to record landing responses including the relation between landing and wind speed and direction. The cameras were connected via a mixer to a videocassette recorder and monitor screen. Mixing the signals produced superimposed images from the two cameras, and a series of calculations produced the tracks of the aphid in three dimensions. Turning rates, flight duration, turn bias, and sinuosity (three-dimensional turning angle per unit distance) were all analyzed using the apparatus. Among other aspects of behavior, flight parameters on approach to the landing platform differed depending on the presence of wind. Approach trajectory, for example,

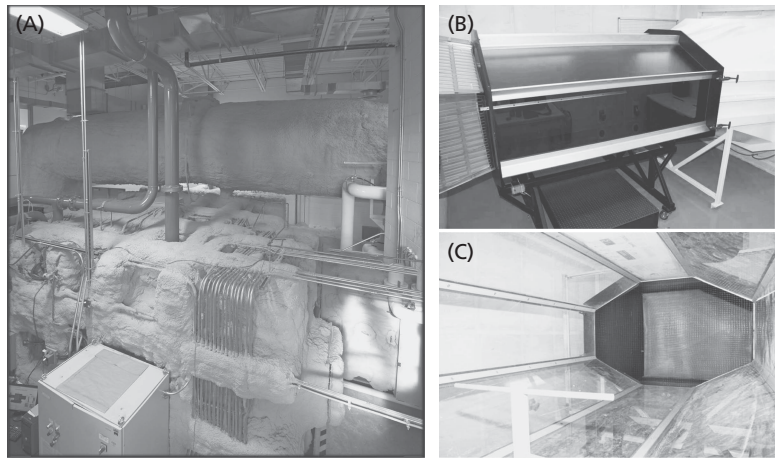


Figure 4.12 ((A) The University of Western Ontario wind tunnel, outside view. The control box can be seen in the lower part of the photograph mounted on the outside of a room with an airlock. The large pipe through which air circulates around in the wind tunnel is in the background. Inside the airlocked room is the working chamber in which the bird flies and may be observed. (B) The exterior of the working chamber attached at each end to the circulating airflow. (C) The interior of the working chamber. Note the platform from which the bird takes off to fly into the wind. The chamber is also used without the platform to prevent flight from being interrupted by landings. Photo A by Mitch Zimmer; Photo B by Fernando Aguirre. Photos courtesy of Chris Guglielmo.

was upwind if wind was present, even if it meant changing direction from the flight path in the absence of the landing platform.

Wind tunnels have also been used to examine the flight characteristics of migrant birds, although at much greater expense because considerably larger tunnels with more powerful wind generation are required. A good example is the wind tunnel at the University of Western Ontario in Canada (Figure 4.12). In this apparatus a transparent "working section" inside which the bird flies is located within a large observation chamber (a room with an airlock) that allows investigators to view and film the flying bird through the transparent panels of the working section. The wind stream enters the working section through a honeycomb baffle so that the airflow is laminar, exits at the opposite end, and passes through a tubular loop that includes a motor and fan located above the chamber. Airflow is thus circular from the fan down through the working section and back up to the fan. Birds are trained to launch from a perch inside the working section and fly in the wind stream. To visualize the airflow over the bird, olive oil is misted into the working section, and a laser sheet flashes at a high rate to determine the direction of movement of the droplets and hence the airflow. Images show the pattern of air flow over the body and the wing tips and the wing tip vortices and other air flow variables (particle image velocimetry or PIV).

The observation chamber in which the working section, observer, and recording equipment reside is entered via an air lock. In this room, air pressure is maintained that is contiguous with the "altitude" present inside the wind tunnel. Temperature, air pressure, and humidity as well as wind velocity can be manipulated to simulate different altitudes and atmospheric conditions, including the passage of weather fronts, to observe the birds' behavior under the various conditions they are likely to experience on a migratory flight. Altitudes up to 7 km above sea level can be simulated. Other wind tunnels for observations on avian migrants are located at the University of Montana and Lund University in Sweden (Pennycuick et al. 1997 and <http://www4.lu.se/animal-flight-lab>).

Wind tunnels are of great utility for analyzing energetics and flight dynamics. Another major aspect

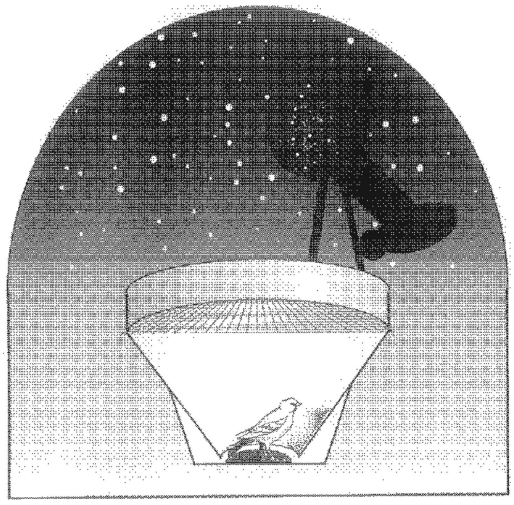


Figure 4.13 The Emlen funnel cage. A bird is placed in a circular cage with an ink pad on the bottom and paper-covered sloping walls. The cage is covered with a screen and placed in a planetarium (as here) or exposed to the sky (real or artificial). As the bird attempts to fly, the traces of the inked feet on the walls indicate the direction of orientation. In recent versions correction paper on the sides records bird tracks instead of paper recording ink streaks, and in some cases recording tracks from the cages has been computerized. From Dingle (1996) after Emlen (1975).

of bird migration is the ability of migrants to orient and the nature of the cues involved. The device that has made investigations of orientation relatively amenable under controlled experimental conditions is the Emlen funnel cage (Emlen and Emlen 1966; Dingle 1996) (Figure 4.13). The device consists of a circular cage the sides of which are paper, rolled and stapled into the shape of a funnel with its constricted end downward. A bird is placed in the bottom of the funnel, and the entire cage is covered with a screen or clear plastic to prevent escape. The bird hops upward and its footprints are recorded on the paper either because the bottom of the cage is an inkpad or the paper is typewriter correcting paper that records scratches on its surface (e.g., Funnell and Munro 2007). The bird can see only directly overhead which means that the "sky" can be manipulated (as in the planetarium "sky" in Figure 4.13). When the bird hops upward it slides back down the paper walls leaving marks whose distribution can be analyzed to determine the direction of orientation and whose density gives a measure of activity. The cage can also be placed in the midst of Helmholtz coils to distort the magnetic field while sky patterns or natural sky are simultaneously visible, providing sophisticated analysis of the combinations of cues used by the birds (see Chapter 8). The fact that the bird is confined to a small space at the bottom of the cage avoids problems of parallax that would be present if the bird could hop back and forth in a large cage with therefore different viewing angles of an experimental sky. Emlen funnels have provided a remarkable amount of information on the orientation capabilities of smaller migratory species.

Various tunnel and channel devices that generate water currents rather than air currents have been in use for some time to measure the swimming performance of fish. Attempts to assess the bioenergetics of swimming led to the development of two popular designs that are still in extensive use (Cech 1990; Castro-Santos 2011). The first of these is the Brett respirometer (Brett 1964; Brett and Groves 1979). In this device, fish are confined in an acrylic tubular chamber and water flow through it is regulated by a centrifugal pump. A long straight section at the upstream end helps to keep flow characteristics uniform throughout the cross-section of the swim chamber. In the Blazka-type respirometer there are two coaxial tubes with fish located in a swim chamber in the internal tube and an axial pump driving water flow in the enveloping tube. The system can be modified with plastic grids at either end to facilitate laminar flow (Nendick et al. 2009). These devices have been used to measure aspects of performance such as metabolic rate, swimming speed, and the relation between speed and fatigue (Castro-Santos 2011).

In addition to physiological measures, there has been a great deal of interest in designing "fishways" to permit passage of migrating species past dams and other obstructions. Different flumes have been designed that allow control of stream velocities and habitat characteristics to determine the performance of fish under various conditions (Figure 4.14). Passage through the flume as current velocities are changed is then monitored by video or telemetry arrays placed strategically to provide measures of fish swimming performance. Circular chambers

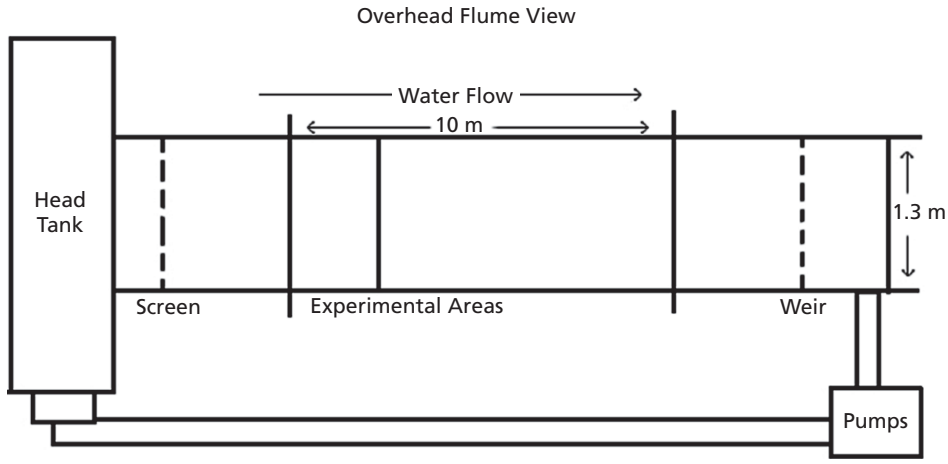


Figure 4.14 Diagram of a large outdoor flume used for studying fish swimming behaviors. The flume can be covered by a canopy and water flow can be regulated by the pumps. The "experimental areas" are used to vary bottom conditions (e.g., rocky or sandy) or to add vegetation of varying types or densities. Modified from a diagram provided by Nann Fangue.

have also been used to test performance. In these a usual design is a trough rotated at the swimming speed of the fish so that the test fish remains stationary relative to the observer (Beamish 1978).

The various chambers are used to measure performance without necessarily any reference to migration (although usually studies involve commercially important migratory species). A simple test used by salmon biologists sampling from streams is the "bucket test." Fish (smolts usually) are poured from one bucket to another; those that attempt to swim up the flow are assumed to be pre-migratory residents whereas those going with the flow are assumed to be migrants ready to head downstream. Snyder (1988) tried to address the question of spring upstream migration of sticklebacks (*Gasterosteus aculeatus*) with a tank in which fish were introduced in the center and could swim up- or downstream through a series of partitions allowing current flow through openings. Distance moved was measured by the number of partitions traversed, with the assumption that migrants would move upstream while non-migrants would either move downstream as the course of least resistance or would show no preference. Different sorts of apparatus, including the ones discussed here, are illustrated in Beamish (1978) and Castro-Santos (2011).

Summing up

Because migration usually takes place over large distances relative to the size of the migrant, it is one of the most difficult of behaviors to study. Yet with considerable ingenuity, biologists have made often remarkable progress in understanding the migration process. Both traditional and new methods have contributed to the exciting and interesting advances. For decades ornithologists have been observing migrants passing by major geographic features such as peninsulas and mountain ridges. This method has been extended to insects, with the extensive observations of butterflies at the Falsterbo Peninsula in southern Sweden being an excellent case in point. Birds have also been counted from the top of the Empire State Building in New York with some surprising observations of their behavior in transit. Counts and surveys in the form of atlas data have recently come into their own for assessing bird migration. The data are melded into a single "theoretical year" from which seasonal movements and the pathways followed can be estimated. In thinly populated Australia where banding has limited utility, analysis of atlas data has provided unique insights into the migratory pathways followed by species of arid and semi-arid environments. Similarly, compressing data from museum records into

a single theoretical year has revealed previously unknown routes for the migration of western populations of the Monarch Butterfly. These various studies demonstrate that traditional methods of investigating migration are still very useful. In some cases natural "migrant traps" can be used as sites to capture birds for measurement and marking to provide further information.

Rapid advances in technology have revolutionized our understanding of the pathways followed both by individual migrants and by populations of migrants. Two examples are the use of marker genes (DNA) and of stable isotopes acquired from the environment in which the migrants live. Both methods have been very useful to determine "connectivity"—whether populations in the breeding range are the same as those in the wintering range of the species. In migrants such as the Monarch Butterfly, isotopes have further helped to define the movement and spread of the populations in eastern North America. Genes have further been of great use in identifying "migratory divides" that separate populations of the same species and in providing insights into a possible mechanism of speciation. Both genes and isotopes are nice examples of how advances in one field of science can lead to important advances in another.

Another good example is provided by the gains in the miniaturization of electronic transmitting and recording devices and in the linking of those devices to satellite technology. Geolocators have opened a new window into the capabilities of migrating birds, for example. Recognition of the astonishing performances of shorebird and other migrants in crossing wide oceans non-stop is directly due to our recent ability to attach miniature data loggers to the legs of these birds to document their incredibly long-distance travel. The devices even allow us to document the movements of small shorebirds and songbirds. Similarly, they have been used to follow the tracks of marine migrants and to record depths and vertical movements during travel. Relatively "old-fashioned" radio telemetry told us much, but satellite telemetry making use of the ARGOS system now allows tracking of individual migrants, both terrestrial and marine, over far greater portions of the Earth's surface. We now know facts never guessed at with respect to the travels of migrants from storks to sharks. Given that the technology is now available, we may soon be able to track individual insects with satellite systems.

Although radars have yet to be miniaturized, vertical-looking radars are now relatively portable and can be located remotely to continuously record the passage of migrants with computer data storage and analysis. No longer are we limited by the large size, limited mobility, and expense of radar equipment, and radars can now be used for long-term monitoring of migrant passage by siting VLRs at suitable locations. The data are promoting reassessments of our views of the ability of insects to orient, for example. Their sophisticated capabilities are just beginning to be understood, and one hopes that VLRs will come into even greater use. Investigators are also taking advantage of the continent-wide Doppler weather radars. These continually record bird movements as a by-product of weather surveillance, and the data are archived. With appropriately designed algorithms to identify bird targets, information on the size, timing, speed, and direction of bird movements is obtained, providing a record of the passage of migrants over a continent-wide region. The relation of migration to wind and weather patterns, to the association with particular geographic features, and to time of day or season can be assessed on a large scale. Radar studies of both birds and insects have shown that these migrants use winds aloft for assistance during the course of their journeys.

For many questions concerning the dynamics of migration, laboratory analysis is required. A major issue with laboratory studies is whether they accurately reflect performance in the field, because of necessity the experimental subjects are constrained in some way. Insects have been the most amenable to laboratory studies, mostly because of their small size, and their apparent indifference to being tethered while flying. For small insects such as aphids and whiteflies, it has been possible to design "flight chambers" that allow these migrants to fly freely while being kept more or less in place by clever manipulations of wind speed and lighting. Studies using these flight chambers have led to profound insights into the nature of migration and its interaction with reproductive behavior and maintenance functions, for example

foraging. Recent technological advances are now allowing assessment of the performance of birds in free flight using specially designed wind tunnels with laminar wind flow. Several of these are now in use in Europe and America and are providing valuable insights into the relation between energy use, speed, and power in flight, among other aspects of migration. Combined with newer technologies, older methods such as the Emlen funnel are still providing valuable and often surprising information on the orientation abilities of migrant birds. Likewise methods developed many years ago and refined since are still providing information about the metabolism and swimming abilities of migrant fish, although much remains to be explored concerning migratory performance per se. Overall we can expect technology and innovation to continue to provide some remarkable results and perspectives with respect to migrant organisms.

PART 2

Proximate Factors in Migration

The chapters in this section consider the proximate mechanisms that influence migratory behavior and pathways. Chapter 5 outlines some of the ways migrants take advantage of perturbations of air and water to facilitate their journeys. The winds and currents considered range from those of a planetary scale acting over thousands of kilometers to those of nanoscale acting over distances of ≤10 m on small organisms. Following brief introductions to weather and ocean circulation patterns, I give several examples of migrants that use winds or currents to aid them on their journeys. Natural selection has molded migrants in ways that allow them to select wind and water patterns of appropriate direction and speed to produce migrations of impressive sophistication and performance. Waterfowl, moths, and eels are but some of the migrants to enhance both the timing and routes of their journeys. Methods like radar have produced major advances in our understanding of the use of atmospheric conditions, and new tracking methods have provided much insight into the interactions between oceanic migrants and current systems.

I consider aspects of the physiological basis of migration in Chapter 6. Because migration often takes place over large spatial scales, it can be energetically demanding. It is also pre-emptive so it is an advantage for migrants to anticipate environmental change with a reliable cue like photoperiod. But this cue interacts with internal cues like endogenous circannual rhythms. Fueling migration requires the remobilization of resources internally, and this physiological transformation is mediated by hormones. These and their function in migration are best understood in insects and in vertebrates and in both groups, hormones are adapted from other functions (hormone "capture"). The physiology of migration can vary across the range of a species, and migration must interact with other functions like molt in birds, diapause in insects, and reproduction in both groups and in fish. Finally, I examine the fuels for migration, especially fat, the most efficient fuel by far in providing the energy necessary for migratory journeys.

Migrants are subject to a number of constraints on their performance, including aspects of both morphology and energetics. These are discussed in Chapter 7. Mechanisms and the medium can both impose constraints. The size of migrating spiders, for example, is constrained by the properties of their ballooning threads. Seeds may also be limited in size by their mechanisms of transport, whether by vertebrates or wind carried by parachute. The wings of birds and butterflies are constrained by other functions. The optimal wing shape for a migrating bird is long and narrow, but this is not a good shape for maneuvering through vegetation. Similarly swimming is more efficient in fusiform fish, but flattening is more advantageous in reeds or on reefs. I consider at some length the power requirements for migration, and the modifications to optimize its production. I conclude by considering some of the special problems faced by migrants such as the Sahara crossing by European breeding birds and the long overwintering period of Monarch Butterflies in Mexico. The flexibility of migrants is also noted, with many able to circumvent constraints.

Chapter 8 addresses orientation and navigation by migrants. These are the most intensely studied of migration phenomena. The recent development

of sophisticated techniques in neurobiology, genetics, and chronobiology has provided sometimes startling insights into the orientation capabilities of migrants. The Sun, the stars, polarized light, and the Earth's magnetic fields all provide information used by migrants to reach their destinations. These often interact with internal rhythms to provide bi-coordinate systems of navigation. Recent advances concerning insects are especially exciting in this regard as are data concerning localization in the brains of birds. We are learning more about the interactions between systems; the role of the eye of birds in both vision and magnetoreception is an example. I discuss the general conclusion that migrants use not just one cue, but rather use a hierarchy of cues with one backing up another to coordinate navigation, orientation, and timing to pursue their migratory tactics.

CHAPTER 5

Migration, winds, and currents

Our planet is a diverse place, and much of this diversity is a result of weather and climate. Because migrants move widely over the planet's surface, they experience a range of climatic vagaries, and indeed it is the variation in climate and seasons that provides most of the ultimate basis for migratory journeys. Therefore to fully understand migration, it is necessary to understand how migratory behavior may be influenced by conditions in the atmosphere and in the oceans (Shamoun-Baranes et al. 2010). Migrants that fly, swim, or drift can expect contact with winds or currents that often influence their pathways in major ways. This is true for large active swimmers or flyers as well as for small insects or minute spores or plankton. The influences of weather and current patterns on migration extend over spatial scales from large global events to nanoscale changes in the microclimate. They are a major component of the "energy landscape" (Shepard et al. 2013) that extends across habitat types and spatial scales.

This chapter discusses the responses of migrants to a variety of atmospheric and oceanic events that are briefly defined and described in Box 5.1, which is based on a more extensive discussion in Dingle (1996). We proceed from large to small, beginning with *planetary-scale* phenomena and working down to events at such a reduced level that they may be appropriately designated *nanoscale*. In between are phenomena that range from *synoptic scale*, which includes the patterns depicted in the usual weather maps and television radar images covering a portion of the Earth's surface, through *mesoscale* to *microscale* patterns. These are summarized with examples in Table 5.1. Migration is analyzed both in the air and in the oceans with examples of short- and long-term behaviors that allow organisms to adjust to winds and currents in some surprising ways with often astonishing capabilities. Like the meteorological and oceanographic events that affect them, migratory patterns can take place over a range of scales.

Depending on the direction and strength of wind or current flow, a migrant may benefit or be hindered by the movement of the medium in which it is traveling. The degree of benefit or cost further depends on the capabilities of the migrant (Åkesson and Hedenström 2007). Wind speeds, for example, are of the same order of magnitude as the flight speeds of birds, but they are likely to exceed, often by a considerable margin, the flight speeds of insects. As a result, there should be differences in how migratory performance is influenced in the two taxa (Alerstam et al. 2011 and below). The optimal travel speed (minimum energy cost per unit distance) depends on the marginal gain in speed over the Earth's surface ("ground speed" in terrestrial migrants) with increased speed in the medium ("air speed" in flying migrants). With a direct following wind, ground speed will be more or less the sum of flight and wind speeds, and it will be optimal to slow down. With a direct headwind, ground speed will be negatively affected, and it will be optimal to speed up. Crosswinds pose a more interesting problem. In general with cross flows, it will be optimal to speed up as the angle between track and heading vectors increases, but whether birds, the taxon capable of such adjustments, actually do match theory is not known (Åkesson and Hedenström 2007). There is evidence in raptors that adults show more wind-drift compensation than juveniles, but the cause (experience or prior knowledge of wintering areas) is uncertain (Thorup et al. 2003). Further, as a rule of thumb, migrants should increase compensation for drift as they near their goal (Liechti 2006).

Migration. Second Edition. Hugh Dingle. © Hugh Dingle 2014. Published 2014 by Oxford University Press.

Box 5.1 Definitions of terms used in describing atmospheric and oceanic conditions that influence the behavior and pathways of migrants[a]

Obliquity of the Ecliptic

The 23.5° tilt of the axis of the Earth. The consequence is the annual variation of the seasons as the Northern and Southern Hemispheres tilt toward or away from the sun during the Earth's path in its solar orbit. The general global atmospheric effect is rising warm air in the tropics and sinking cold air at the poles.

Troposphere

The lowest 12,000 m (approximately) of the atmosphere. Temperature lapses at about 6.25°C/km as altitude increases. At about 12,000 m ozone begins to form and temperature rises again. This temperature inversion is the tropopause.

Coriolis force (or effect)

Describes the tendency for air masses to drift to the right (east) in the Northern Hemisphere and to the left (also east) in the Southern Hemisphere. This drift results because air leaving the Equator increases in relative speed as the diameter of the Earth beneath decreases. This tendency to drift largely accounts for the prevailing westerly winds in the temperate zones of both hemispheres.

Jet streams

Winds channeled into rapidly moving tubes of air at mid-latitudes. High-level jets may move at speeds of 150–250 km/h, and their paths influence the paths of weather fronts. There are usually two and sometimes three high-level jets in each hemisphere. Low-level jets at slower speeds also occur.

Trade winds

Winds blowing more or less steadily from the east at latitudes around 20–30°. They result from high-level air moving from the Equator toward the poles being deflected downward by a subtropical jet.

Inter-Tropical Convergence Zone (ITCZ)

The merging and mixing of warm air masses from north and south in the vicinity of the Equator. As the warm air rises, it cools and loses moisture as rainfall, stimulating new plant growth. Except for local storms, winds are usually calm (the "doldrums" of the sailing ship era). The ITCZ moves north and south with the seasons.

Monsoon

Seasonal rain caused by rising air over warm land masses that sucks in moist air from neighboring oceans. It is iconic for India and Southeast Asia, but it also occurs in summer in northern Australia and the southwestern USA.

Pressure cells

Regions of high and low air pressure in the atmosphere. Air flows from high to low pressure but is slowed by friction at and near the Earth's surface, resulting in greater wind velocities higher in the atmosphere (the Ekman spiral). In the Northern Hemisphere air moves clockwise around a high and counterclockwise around a low (the Coriolis effect at work); in the Southern Hemisphere the opposite is true.

Thermals

Large "bubbles" of warm air rising above warmer patches of land or sea. They rise until encountering the capping temperature inversion at the tropopause (causing the anvil shape of thunderstorms). The displaced cooler air descends, often as gusty storm outflows.

Currents

Water movements which, in the ocean, are usually driven by prevailing winds. For example, immediately north and south of the Equator the prevailing winds drive surface waters westward as the North and South Equatorial Currents. Currents decrease in velocity from surface to depths (reverse Ekman spirals).

Gyres

The flow of oceanic currents around the periphery of the ocean basins. The flow is clockwise in the Northern Hemisphere (e.g., the North Atlantic Gyre) and counterclockwise in the Southern Hemisphere as a result of the Coriolis effect.

Upwellings

The rise of cold, usually nutrient-rich, water generally along a coastline. Upwellings are caused by the driving of warmer surface water offshore by winds from land to be replaced by the deeper colder water.

Gulf Stream

A major current of warm water flowing from west to east across the North Atlantic. Trade winds from the east drive warm water into the Gulf of Mexico where it "piles up." This water then flows ("downhill") through the narrow strait between Florida and Cuba forming a stream that flows clockwise across the Atlantic to warm Europe.

Box 5.1 *Continued*

Tidal stream (or current)

A current flow generated by rising and falling tides. Flow is toward shore on rising tide and away from shore on falling tide. Coastline configurations can cause tidal streams to flow along shore.

[a]See Dingle (1996) for greater detail.

Departures from any point on the migratory route will also likely involve interaction between winds and fuel loads (Weber et al. 1998; Åkesson and Hedenström 2000, 2007). For example, winds will change the utility of fuel loads which in turn influence flight distance. Tailwinds (or facilitating currents in marine species) might be expected to induce departure on migration before fuel loads required for still air are reached. Similarly fuel loads may be less than optimal if long periods of headwinds delay departure much beyond the usual time of its occurrence, especially if there is the option of stopping over farther along on the route. Thus one would expect migration routes to evolve to enhance the use of favorable winds both en route and at the optimal times of departure from breeding, nonbreeding, and stopover sites. With the various considerations of time, speed, capability, and fueling in mind, we can examine what we know about migratory behavior under various wind and current conditions.

Table 5.1 Scales of atmospheric and oceanic events that influence migration.

Size	Horizontal dimension	Examples
Planetary scale	10,000 km	Jet streams, trade winds; equatorial oceanic currents
Synoptic scale	1,000 km	Warm and cold fronts; coastal currents
Mesoscale	100 km	Sea breezes; tidal-stream currents
Microscale	1 km	Thermals; estuary currents
Nanoscale Nanoscale	<10 m	Air or water moving over a surface

Source: Dingle (1996).

Migration in the atmosphere

There is one important way of increasing migration speed through increased flight speed without affecting [rate of energy expenditure]—and that is to obtain a free ride with the winds!

Thomas Alerstam (2003), p. 257

Planetary-scale bird migration in the Western Pacific

Many years of observations in the Western Pacific region indicated that many species of bird, and especially shorebirds, were making long-distance migratory flights between breeding grounds in Alaska and northeastern Siberia and wintering grounds either on Pacific islands or in Australasia (e.g., the Bar-tailed Godwit discussed in Chapter 3). The Pacific Golden Plover (*Pluvialis fulva*) migrates between Alaska and Hawaii, exhibiting considerable site fidelity at both ends of the journey, allowing identification of individually tagged birds (Johnson et al. 2004). One individual made the trip in a minimum of 70 h with a minimum flight speed of 56 km/h, and the time was likely less and the speed greater than actually recorded because of uncertainties in exact departure and arrival times. Pacific Golden Plovers are also recorded in large numbers in the Mariana Islands along with 45 other species of plovers and sandpipers that were less abundant (Stinson et al. 1997). These latter birds were probably en route between both Siberia and Alaska and wintering grounds in Australia and New Zealand. The long overwater crossings demand considerable energy expenditure so that the birds should, at least in theory, take advantage of any wind assistance they can access. Indeed Landsberg (1948) suggested that atmospheric pressure patterns in the vicinity of

the Arctic would generate wind regimes that would assist shorebirds on their migration routes.

The advent of satellite transmitter and geolocator technology has allowed tracking of migratory birds not just at starting, ending, and stopover points, but also more or less continuously en route (see Chapter 4). Thus, we now know that even relatively small species such as the Ruddy Turnstone (*Arenaria interpres*) make very long distance non-stop flights (Minton et al. 2011 and Figure 4.6). It seems likely that birds making long migratory trips across the Pacific would seek whatever assistance they could get from favorable winds. This notion was tested by Gill et al. (2005, 2009) via assessing the wind conditions concurrent with the departure of Bar-tailed Godwits from western Alaska on their trans-Pacific autumn migration to Australasia (Chapter 3). High and low pressure centers regularly pass over Alaska in the autumn and potentially generate winds supporting departure of the godwits (Liechti 2006). Gill and colleagues compared weather conditions between 30 August and 7 October, the period during which godwits departed, on days when the birds began journeys south with days on which no godwits left. To make sure birds were in true migratory mode, as opposed to making local flights, they examined track directions of godwits relative to wind direction at a distance of 100 km from the departure site. Winds can vary with altitude, and the altitude at which these godwits migrated could not be determined from the geolocators. It was assumed they were flying at about 1,500 m above sea level, which is consistent with known altitudes of migration of other shorebirds and with the fact that wind direction between ground and this height is relatively constant. Wind directions on both departure and non-departure days were further compared with a 29-year pattern over the northern Pacific for the same period of the annual cycle.

The godwits timed their departures from Alaska to coincide with weather systems that produced following tailwinds. The mean track of the nine godwits was 193° (south = 180°), and that of the direction in which the wind was blowing was 174°, significantly correlated ($r = 0.88$, $P < 0.001$). Considering the various assumptions concerning flight altitude, the correlation is remarkably good. Wind speeds averaged 8.3 ± 6.1 m/s for the nine godwits, strongly suggesting wind assistance for take-off on migration. On the eight days when birds departed, sea level air pressure was conspicuously depressed over the northern Gulf of Alaska, east of the point of take-off (Figure 5.1). The counterclockwise pattern of wind flow around these lows would provide the following winds apparently used by the godwits to support the commencement of migration. This strong wind assistance probably outweighs any advantages there might be to following a route along the (longer) coast of Asia that would allow stopovers and hence reduced fuel loads (see Chapter 6 for discussion of

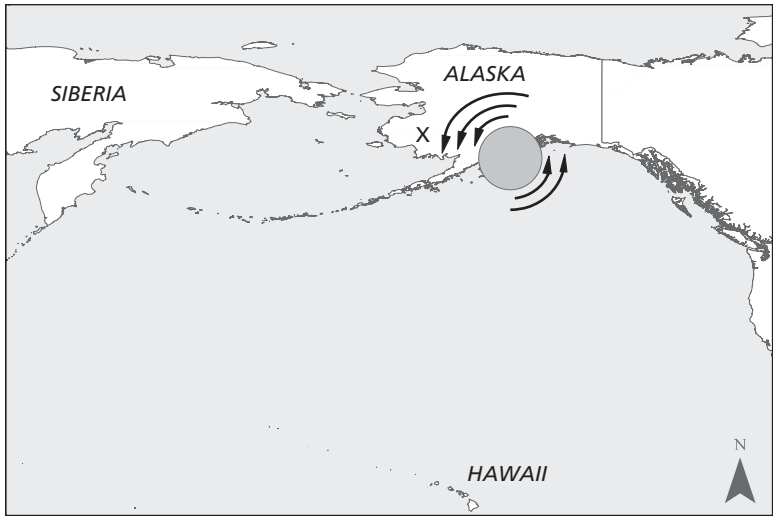


Figure 5.1 The position of a major low-pressure cell in Alaska when Bar-tailed Godwits depart for their autumn migration across the Pacific. The place from which the birds take off is indicated by the "X." Note that because of rotation around the cell, the birds will be taking off with a following wind. Modified from maps and data in Gill et al. (2005).

fueling). Furthermore the coast of Asia lacks the steering trough present off the coast of Alaska that directs winds southward; thus there would be less predictability in directions of wind flow. Once en route from Alaska the godwits could still be assisted by winds as circulation around the sub-Arctic low-pressure cells reaches a fair way south (Liechti 2006). In the equatorial latitudes winds are generally benign (the "doldrums"), and once birds cross into the Southern Hemisphere they enter a region of south-east trade winds and prevailing austral westerlies. These latter would tend to direct the migrants toward their eventual landfall in Australasia (Gill et al. 2005). The general pattern of winds seems to support the notion of the Western Pacific as a corridor favoring migrants rather than a barrier hindering them (Gill et al. 2009 and Chapter 3).

Departure on return migration to breeding grounds in the northern spring also appears to be aided by winds (Battley 1997). The departure behavior of Bar-tailed Godwits and Red Knots (*Calidris canutus*) was monitored at Farewell Spit at the northwest tip of New Zealand's South Island. Most flocks left in the evening on a rising tide and on average with a light tailwind. Most departures occurred after the passage of a low-pressure system or at the approach of a high-pressure system. In either case, winds rotating around these cells would be timed to produce favorable southerly winds aiding flight northward. Some departures, however, did occur with headwinds up to 12 km/h, especially if take-offs had been delayed for some days by strong winds. In a more recent study of 45 individually tagged godwits departing from New Zealand, Conklin and Battley (2011) noted that the birds showed little variation in March departure date and generally maximized wind assistance. When departures were off-schedule, however, early departures with favorable winds were more likely to occur than were late departures as a result of unfavorable winds. This observation suggests that although there is strong selection for individually optimized departure date, there is enough flexibility to take advantage of favorable winds. These godwits seem to attain the necessary fuel loads well in advance of departure, allowing for this flexibility.

These New Zealand data are consistent with previous observations of both shorebird and passerine migration in the western North Atlantic where major departures from eastern Canada over the Atlantic to the Caribbean and South America occur under expected following wind conditions, most notably at the leading edge of a high, following passage of a low pressure cell (Richardson 1990; Dingle 1996). For shorebirds migrating along the west coasts of the Americas, dynamic modeling suggests that winds are the most important factor influencing fitness, exceeding stopover resources or predation pressure (Clark and Butler 1999).

Unlike shorebirds, passerines and raptors from eastern Asia do not reach Australasia, with very few exceptions (Dingle 2004 and Chapter 3). For raptors, at least, the autumn migration flights split into two routes (Bildstein and Zalles 2005; Germi et al. 2009). The first of these is overland from Siberia, Mongolia, and Manchuria through China, Indo-China, and the Malay Peninsula to wintering areas on Sunda Shelf islands. On this western, mainland route the migration is apparently supported in the autumn by northerly winds (Bildstein and Zalles 2005). The second route proceeds through the Korean Peninsula to Japan, the Ryukus, Taiwan, and the Philippines to the Sunda Shelf islands and the northern Moluccas and the northern peninsula of Sulewesi, a route that includes several water crossings up to 300 km. Germi et al. (2009) observed the passage of more than 230,000 Chinese Sparrowhawks (*Accipiter soloensis*) over Sangihe Island which lies midway between Mindanao, at the southern end of the Philippines, and Sulewesi and Halmahera in Wallacea (Figure 5.2). These Accipiters are strong flyers, relying less on soaring than larger raptors, and so less impeded by water crossings; they made up 98% of the raptors migrating over Sangihe.

On this route via Taiwan and the Philippines water crossings are much shorter, and tailwinds are less important than is the case of the long water crossings made by shorebirds. In both spring and autumn, migrations via Sangihe occurred in the face of monsoon headwinds, and Germi and colleagues speculate that in these strong flying insectivorous raptors slow progress may be supported when necessary by feeding stopovers on larger islands, and indeed the sparrowhawks were observed preying on larger dragonflies and cicadas during stopovers in passage through Sangihe. Monsoon winds are relatively light in the vicinity of Sangihe so they do

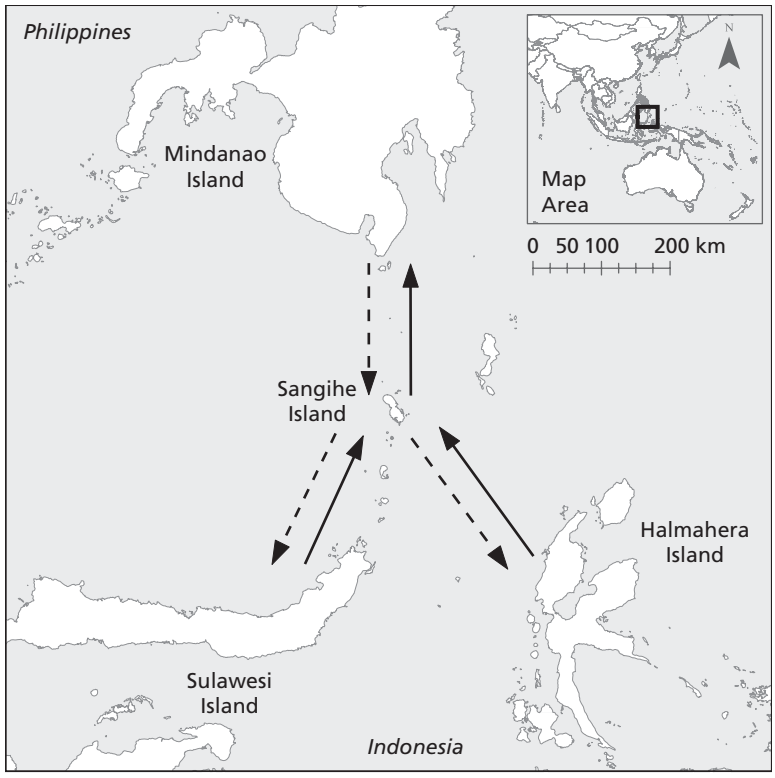


Figure 5.2 Pathways of migrating sparrowhawks over the island of Sangihe. Dashed lines are autumn migration, solid lines migration in the spring. Most of the birds winter on Sulewesi, but a few do so on Halmahera. Sparrowhawks are among the few Asian breeding birds that reach Wallacea to winter. Data from Germi et al. (2009).

not seem to impose a major impediment. Delaying migration to avoid headwinds would also mean flying through a band of storms and precipitation that forms along the boundary between the northeast and southwest monsoons. Crosswinds do influence migration frequency. More migrants fly during crosswinds in the spring when the route covers more closely spaced islands with less risk of being blown over wider stretches of open water, than in fall when the risk of deviations is greater. While over land, the migration is assisted by soaring in rising thermals and gliding.

Synoptic-scale migrations

Migrants traveling between Northern Europe and the Mediterranean region to sub-Saharan Africa face some formidable barriers (Figure 5.3). In Central Europe is the mountain massif formed by the Alps and associated ranges. If traveling to Africa, migrants must cross the Mediterranean Sea and, if they continue beyond the North African littoral, the large expanse of the Sahara Desert. In Central Europe winds can add to the difficulties faced. In the case of birds, winds on this portion of the journey commonly range from 50% to 100% of usual airspeeds and opposing winds predominate (Liechti and Bruderer 1998). At the eastern and western ends of the Mediterranean, however, not only are water crossings much shorter, but head- and tailwinds occur in roughly equal frequencies allowing migrants significant opportunities to select favorable winds. Furthermore, because winds vary with altitude and the diurnal cycle, birds can gain about 30–40% extra speed by selecting the right time, in this case night, and the right altitude (Liechti and Bruderer 1998). The potential gain in flight speed is such that selecting favorable winds should outweigh adjusting departure times to fat (fuel) accumulation rates.

For birds breeding in Europe, migration routes to the southwest via Spain and Gibraltar and southeast via the Bosporus and the Levant do indeed seem to prevail (Erni et al. 2005). Erni and



Figure 5.3 Migratory routes taken in the autumn by most European breeding birds that winter in Africa to avoid crossing the Alps or the Mediterranean. Winds in Europe at this time are mostly headwinds, while over land at each end of the Mediterranean head- and tailwinds balance out. Birds can gain airspeed by selecting altitudes where favorable winds occur. Soaring raptors benefit from the updrafts that occur over the warmer land.

colleagues assessed the potential survival of passerines migrating in the autumn from Europe to Africa with computer simulations. They assumed that wind conditions selected for migration were those occurring at about 1,500 m above sea level. Under these conditions survival rates were greater for the southeast passage via the Levant than for the southwest route. If migrants in the simulations were allowed to choose from among four altitudes, survival rates were similar and high, but on the southwest route they depended on refueling opportunities in northwest Africa. On the southeast route, refueling possibilities are virtually absent in the eastern Mediterranean and the Egyptian desert, but the frequent favorable wind conditions mitigate the unfavorable refueling chances. The general conclusion is that both autumn migration routes are significantly supported by wind assistance and would be unlikely without it (Erni et al. 2005).

For purposes of analyzing the influence of winds on migration, one can separate the possible wind effect into four components: wind at departure, wind en route, wind at different altitudes, and variation in wind direction and velocity. These are not mutually exclusive, but separation facilitates their assessment. The first component, wind at departure, was examined by Åkesson and Hedenström (2000) for a group of passerine migrants departing from southern Sweden. Their study considered four species of nocturnal migrants, seven thrush nightingales (*Luscinia luscinia*), a Eurasian robin (*Erithacus rubecula*), ten song thrushes (*Turdus philomelos*), and one Eurasian blackbird (*T. merula*). The birds were captured on migration at the Ottenby Bird Observatory located at the southernmost point of the island of Öland, a long, narrow island in the Baltic very close to the east coast of southern Sweden. Radio transmitters were attached to the birds which were then tracked, vanishing bearings noted, and the tailwind component (velocity and direction) and the track were compared.

The overall departure direction of the seven birds (five thrushes, two thrush nightingales) whose exact departure time could be determined was 206°

or just west of south (south = 180° clockwise from north = 0°). There was a strong association between departure track direction and the wind direction at the time of departure with the birds leaving when there was a tailwind. Considering all the birds whose departures were noted, the tailwind component on departure days was 0.88 m/s on average, whereas, on days when no birds left, wind speeds averaged –2.99 m/s. The minus sign denotes headwinds, so on average birds departed with tailwinds. A direct comparison of winds on the day of departure with winds the day before departure confirmed the tailwind choice. Four birds did depart with headwinds, but two of these experienced headwinds for several days before departure. Their leaving is consistent with theories concerning the optimal timing of migration as outlined at the beginning this chapter.

The relation between winds en route and spring migration was examined by Green (2004) for flocks of Brent (or Brant) Geese (*Branta bernicola*) and waders traveling from the Wadden Sea between the coasts of Germany and Denmark to breeding grounds in Arctic Russia between the Kola and Taymyr Peninsulas, the latter at about 40°E (Figure 5.4). The birds were tracked by radar as they flew over Lund, Sweden. Ground speeds exceeded air speeds for most flocks, suggesting an effect of wind on flock movements (ground speed equals airspeed plus added wind speed). Further, most flocks were flying at altitudes between 1,000 and 3,000 m although 18% of flocks were below 1,000 m. Waders were generally recorded at higher altitudes than the geese with no flocks of the latter recorded above 1,000 m. It was evident from the radar tracks that, at the altitudes at which the migrants were flying, tailwinds predominated and increased the air speed of the flocks. The majority of the winds in the altitudinal profile (100–4,000 m above ground level) through which the birds flew were crosswinds. Thus the birds were able to select flight altitudes where tailwinds predominated and assisted their passage. This was especially true for the higher-flying shorebirds. Winds over southern Sweden are highly correlated with those over the Wadden Sea, strongly suggesting that, if the birds select good tailwinds at take-off, these are likely to continue for a major portion of their migratory transit, although for just how far is not known. The altitudes at which waders fly, as noted here and in numerous other studies, may also indicate that waders are particularly prone to use winds at higher altitudes, more so than other birds. Winds at different seasons may not be equally favorable, which may in part account for different spring and autumn routes followed, as we saw in the Western Pacific.

Further confirmation that migrating birds adjust flight altitudes to optimize use of favorable winds is provided by Dokter et al. (2011) for the autumn flights of passerines over Western Europe. They tracked migrants over France and Belgium using the network of OPERA weather radar sites (Operational Programme for the Exchange of weather RAdar information). A conspicuous aspect of their observations was that bird density profiles often consisted of multiple layers, and these were explained by differences in wind conditions present at the different radar sites. Decisions on whether or not to depart on migration are not necessarily based on local weather at the time of take-off (Erni et al. 2002), and in fact migration patterns may depend on conditions that determine situations farther along the migratory flyway. Thus at any particular point a layer of birds can be observed at one altitude with a second layer at a different altitude, reflecting the fact that favorable winds occurred at these altitudes at two different departure sites. The ability to co-ordinate observations from a number of sites offers considerable promise for both understanding and predicting migrations in relation to weather and other factors.

As the Dokter et al. (2011) study shows, migrants may encounter varying wind and weather conditions along their routes. This may influence both flight and stopover patterns in birds as shown by Shamoun-Baranes et al. (2010) in a simulation study of the flight paths of Red Knots (*Calidris canutus*) on their migration from Mauretania to the Wadden Sea. These shorebirds sometimes make a non-stop flight to the Wadden Sea, but on other occasions will use a site on the Bay of Biscay coast of France as an emergency stopover. Shamoun-Baranes and colleagues found that in some years the knots made a non-stop flight in about two days, whereas in other years up to eight transit days occurred with no apparent interannual pattern. They then simulated the flights



Figure 5.4 The pathway for Brent Geese and many shorebirds from the Wadden Sea to Arctic Russia (long arrow). The arrow in the circle indicates the prevailing wind direction at the altitudes at which the birds were flying when detected by radar located at Lund, Sweden. Modified from a map and data in Green (2004).

for different years and altitudes up to about 3,000 m above sea level. For the three altitudes up to 1,500 m (110, 770, and 1,500 m) the annual numbers of knots observed on the coast of France were positively and significantly correlated with mean flight times. The implicit assumption was that decisions to use the emergency stopover were based on winds en route. This seems reasonable because wind conditions in France are highly auto-correlated in space and time with winds farther along. Thus these authors concluded that in years with little wind assistance, longer flight times, and increased energy expenditure, the knots made increased use of the Bay of Biscay site. Further evidence in support was provided by the fact that the birds staging here were lighter than birds from the coast of Germany, suggesting reduced energy stores necessitating use of the French site to refuel.

Winds en route vary not only in velocity, but also in direction. Klassen et al. (2011) examined the response to crosswinds by two species of migrating raptors, Ospreys (*Pandion haliatus*) and Marsh Harriers (*Circus aeruginosus*), traveling from southern Sweden to West Africa and tracked by satellite telemetry. Winds strongly influenced flight speeds: for every meter per second of tailwind daily movement increased by 15.3 and 13.8 km for ospreys and harriers respectively. For every meter per second of crosswind the rates of daily movement perpendicular to the flight path increased on average only by 6.7 and 6.5 km. The birds drifted partially with crosswinds, allowing about 47% drift (combining data from both autumn and spring migrations). Response to crosswinds varied during migration, however, as the birds sometimes drifted, sometimes compensated, and sometimes overcompensated. At the onset of migration the birds frequently drifted, rarely overcompensating, whereas toward the end of migration overcompensation was frequent. The birds also tended to overcompensate when crossing barriers such as the Alps, the Mediterranean, or the Sahara. Furthermore, Marsh Harriers, but not Ospreys, responded to wind directions differently. For example, on departure in autumn, harriers

compensated for westerly winds, but drifted with easterlies; in southern Spain the opposite response occurred. These raptors thus modulate their response to crosswinds depending on where they are and on how long they have been migrating. We saw in Chapter 3 that Eleonora's Falcons migrating back to their breeding grounds from Madagascar will actually alter the over-ocean route to Africa by selecting favorable winds and avoiding areas of low pressure (Mellone et al. 2011 and Figure 4.5). In the cases of all these raptors, the migrants must have good navigational skills because they do not use exactly the same routes from year to year (Klassen et al. 2011 and see Chapter 8).

Insects are much weaker flyers than birds, and it might be expected that they would also migrate with wind assistance. This is indeed the case with the Red Admiral butterfly (*Vanessa atalanta*) in the Western Palearctic as we saw in Chapter 4 (Figure 4.1) regarding observations on the Falsterbo Peninsula in southern Sweden (Brattström et al. 2008). Here the butterflies cross the Baltic in the autumn to Denmark. Days on which the butterflies were observed migrating were characterized by light northeasterly winds and clear skies. These are the winds that would aid the WSW passage across the water between Falsterbo and Denmark which is the shortest sea-crossing route. Synoptic winds are also used in the autumn by Red Admirals migrating from Finland (Mikkola 2003a) and by Monarch Butterflies in North America (Calvert 2001).

The closely related Painted Lady butterfly (*V. cardui*) is also a migrant in Europe, arriving in spring from wintering areas in North Africa (Stefanescu et al. 2007). Stefanescu and colleagues tested the hypothesis that Painted Ladies arriving in spring in northeastern Spain were influenced by synoptic-scale wind currents blowing from North Africa. They monitored peaks in the numbers of arriving butterflies in the vicinity of Barcelona between the beginning of March and the end of June over a period of 10 years from 1997 to 2006. Winds from North Africa often bring with them quantities of dust that are assessed with the Dust REgional Atmospheric Model (DREAM). Using this model and backtracks at 1,500 m above sea level, they compared butterfly abundance with the prevailing winds. There was an association between peaks of migration and the occurrence of winds blowing from North Africa in 16 of 21 cases, a statistically significant association of winds and migration. There was thus a strong link between major northward migration arrivals and winds blowing in the appropriate direction. The results from *Vanessa* spp. indicate that these butterflies are aided by winds during both spring and fall migration.

Long-term studies of pest insects in North America and eastern Asia have revealed that many species are wind-assisted on both spring and autumn migrations (Johnson 1995; Kisimoto and Sogawa 1995; Gatehouse 1997; Zhu et al. 2000). In North America at least four major insect orders (Orthoptera, Homoptera, Coleoptera, and Lepidoptera) and at least nine families from these orders are involved in these migrations. In the spring, insects are transported on poleward-moving tropical air masses, especially up the Mississippi Valley, and even tiny insects like aphids can migrate for more than 1,000 km on these systems (Dingle 1996). In the autumn, equatorward airflows transport insects to the south (Showers et al. 1993; Johnson 1995). In eastern Asia attention has focused mostly on the Brown and White-backed Planthoppers (*Nilaparvata lugens* and *Sogatella furcifera*) which are major pests of rice, and the Oriental Armyworm (*Mythimna separata*) (Chen et al. 1995; Kisimoto and Sogawa 1995). In all three species, mass migrations occur with appropriate wind directions in both spring and autumn, interestingly in both cases often on the winds moving in a clockwise direction around a high-pressure cell. In the autumn this would mean as a high approaches and in the spring after the passage of a high. In the case of the armyworm, three generations breed successively northward in the spring, with two more breeding events following southward movement in the autumn.

Intensive studies using vertical looking radar (VLR) have revealed a great deal about the relation between wind and migration for insects flying over southern England (Chapman et al. 2008a,b, 2010, 2011). One of the insects studied was the noctuid Silver-Y Moth, *Autographa gamma* (known as the Black Cutworm Moth in North America), a nocturnal migrant which arrives in the UK in the spring, breeds through several generations over the summer, and returns south to overwintering grounds

in the Mediterranean region in the autumn (Hill and Gatehouse 1993). Chapman et al. (2008a) first analyzed the autumn migration of the Silver-Y after confirming with aerial netting that this species was the most abundant moth at the altitude observed.

Observations of 42 mass autumn migration events revealed that in more than 90% of the cases the moths were displaced southward by winds blowing from the north. The insects concentrated at altitudes of maximum wind speed, and these were not related to temperature. There was a significant degree of common orientation, probably using a turbulence cue (Reynolds et al. 2010) although sensory mechanisms are still unresolved (Alerstam et al. 2011). Furthermore, when there were crosswinds producing a drift angle of >20°, the moths corrected for crosswind drift in the expected direction. By adding their own speed (about 5 m/s) to the wind speed and compensating for crosswinds, the moths were able to migrate up to 650 km per night in the seasonally appropriate direction. On nights when winds were not generally northerly, the moths did not migrate. This ability not only to select appropriate winds but also to compensate for drift implies that these insects must have a compass sense, and for several reasons a magnetic compass seems most likely (see Chapter 8).

The ability to select favorable high-altitude winds was not limited to the Silver-Y. The night-flying noctuid, *Noctua pronuba*, and hawkmoths (Sphingidae), and day-flying butterflies also do this and are capable of correcting for crosswind drift (Chapman et al. 2010). Furthermore there is a seasonal switch in compass orientation such that the insects select northerly winds in the autumn and southerly winds in the spring (Chapman et al. 2008b), with the mechanism likely the seasonal change in daylength as noted for pierine butterflies by Baker (1968). Simulation studies (Chapman et al. 2010) comparing movements of inert wind-carried dust particles with trajectories of insects selecting winds and compensating for drift, revealed that the insects would fly farther and with less scatter than simple passive drift. A further interesting aspect was that these moths and butterflies were able to attain migration speeds exceeding those of passerine birds (Åkesson and Hedenström 2007; Alerstam et al. 2011). Summarized in Box 5.2 are results from various radar studies regarding the performance of migrating insects with reference to atmospheric conditions.

Box 5.2 Principal findings from scanning radars concerning winds and insect migration

1. Migration occurs day (beginning mid-morning) or night (beginning with mass take-off at dusk).
2. Flights occur regularly up to a few hundred meters and even up to 1 km above ground level.
3. Movement almost always is approximately downwind.
4. In the convective daytime atmosphere (mixed, thermally driven, up- and downdrafts) insects are concentrated in rising plumes of air.
5. In night-time stable atmospheres, insects are distributed nearly uniformly in the horizontal and usually form layers at specific heights in response to temperature or wind profiles.
6. In stable atmospheres large insects tend to exhibit mutual alignment, often different from the track direction.
7. Line concentrations and changes of direction often occur when stable atmospheres are disrupted (e.g., by storm outflows or sea breezes).

Source: Chapman et al. (2011).

Comparisons between passerine bird and noctuid moth migration are extensively discussed by Alerstam et al. (2011). Their data were based on the VLR observations of Silver-Y Moths over southern England and on passerine flights over an ornithological radar at Lund in southern Sweden during both autumn and spring migrations. Identified passerines included several species of Old World warblers (Phylloscopidae and Sylviidae), thrushes and chats (Turdidae), and flycatchers (Muscicapidae). As already noted, moth ground speed was even greater than that for birds in the spring (15.7 versus 13.1 m/s), although the speeds were similar in the autumn. The moths flew at lower altitudes than the birds (200–800 versus 400 to 1,400–3,600 m above ground level) because of temperature constraints, but this meant that moths concentrated in the fast, warm airstreams associated with

Table 5.2 Comparison of migratory performances in noctuid moths and passerine birds during migrations over Western Europe.

Characteristic	Noctuid moths	Passerine birds	Both moths and birds
Speed	Slow flyers with air speeds circa 4 m/s	Fast flyers with air speeds 10–14 m/s	Similar ground speeds (moths somewhat greater in spring)
Wind selection	Strongly select winds in preferred direction	Weak or no wind selection (but may select at take-off)	–
Orientation	Orientation primarily downwind with some crosswind correction toward preferred direction	Orientation primarily in preferred direction with partial compensation for wind drift	Similar track directions. Similar range of angles between track and direction
Tailwind assistance	Strong tailwind assistance	Weak or no tailwind assistance (may even be headwinds)	–

Source: Alerstam et al. (2011).

temperature inversions (Reynolds et al. 2010). Passerines, being warm-blooded, are more flexible and can fly in colder airstreams that may provide physiological and aerodynamic benefits. Moths were more restricted in times of migration because of their need for downwind travel; passerines were in full control of their migratory direction and generally flew in winds, including headwinds, that were slower than their airspeeds. In spite of differences in tactics, the tracks were similar, and both groups proceeded in well-defined and seasonally appropriate directions. The comparisons are summarized in Table 5.2.

Meso- and microscale effects

Sea breezes and breezes that can arise in association with large lakes are good examples of mesoscale events that can influence migration. They can affect organisms both large and small. An example of small organisms comes from the study of Greene et al. (2008) on transport of seeds by sea breezes arising along the Jalisco coast of Mexico. Sea breezes arise when land areas heat up, causing warm air to rise and be replaced by cooler air from the ocean. In this region of coastal Mexico the lower relative humidity of early afternoon causes increase in rates of abscission in the five species of plants studied that depend on wind transport of their seeds. This adaptation to low humidity assures that seeds will be primarily transported inland on the sea breeze that arises around midday. The night land breeze would transport seeds toward the sea, as indeed occurred in the few cases where abscission occurred at night. Furthermore seed abscission was also correlated with wind speed when humidity was held constant. Thus dual adaptation to wind and humidity promotes landward migration in these wind-transported seeds.

The effect of sea breezes on large, soaring, migrating birds was studied in Israel by Leshem and Yom-Tov (1998). Migrants such as raptors, storks, and pelicans generally follow three north–south routes through Israel following valleys, generated by parallel mountain ranges, and the coast between mountains and the sea. The various mountain ranges provide complex soaring conditions, but there is a general tendency toward deflection by sea and land breezes. In the autumn, for example, the coastal or western route migrants are usually deflected toward the west. Then between 10:00 and 11:00 the sea breeze from the Mediterranean comes into play and the migrants are deflected back toward the east. A similar deflection occurs in tracks of birds flying on the eastern route. The shifts in the axis of migration allow the migrants to take advantage of good soaring conditions arising over mountains as the day progresses. Migrant soaring birds also tend to align along sea breeze fronts (Alpert et al. 2000). This is a simplified description of complex conditions, but in any case the influence of sea breezes on the migrants is apparent. Further examples of movements on sea and lake breezes are given in Dingle (1996).

Large bird migrants such as raptors and storks take advantage of tailwinds to assist in their migrations

(Maransky et al. 1997; Liechti and Schaller 1999), and an equally important atmospheric factor may be thermal updrafts on which these birds can soar. In contrast to flapping flight, soaring does not lead to much increase in metabolic costs (Mandel et al. 2008). The ability to track migrants by satellite has allowed assessment of just how much the use of atmospheric conditions generated by thermal energy contributes to migratory performance along entire migration routes.

Chevalier et al. (2010) tracked 16 Black Storks (*Ciconia nigra*) over their entire spring and autumn migration periods from 1998 to 2006 and compared performance to meteorological conditions. Daily travel distances varied along the route from West Africa to northern Central Europe, but the daily distances had no relation to tailwinds or crosswinds. There was a significant negative relationship, not surprisingly, with headwinds. Hourly flight speed was significantly correlated with high thermal energy values with the result that daily migration distances were higher in Africa than on the cooler flight path in Europe. The highest speeds occurred on the two sides of the Strait of Gibraltar, 588 km per day on the African side and 493 km per day on the European side, suggesting perhaps higher values of turbulent kinetic energy (TKE) in Africa produced by local conditions such as sea or land breezes. The greater flight distances in Africa relative to Europe probably resulted from the recorded flights being at higher altitudes with higher thermal energy and the consequent ability to glide "downhill" for great distances. The greater migration speeds and hence shorter travel times per unit distance in Africa also mean that costs would be less for this part of the journey.

A common and frequently soaring raptor in North America is the Turkey Vulture (*Cathartes aura*), and it, too, relies on higher values of TKE to assist it along the migration routes (Mandel et al. 2008). These birds were tracked from breeding areas in the Northern USA to wintering areas in Florida or Oklahoma. The distance traveled by the vultures was most strongly affected by TKE with higher values (and hence more thermal updrafts) resulting in greater distance traveled. Other raptors that migrate along the Appalachian chain of mountains in eastern North America clearly benefit from the organizing effects on TKE generated by the mountain ridges. One of these is the Kittatinny Ridge (Hawk Mountain) in southeastern Pennsylvania. A second notable observation for the vultures was that high values of TKE strongly reduced deviations in bearing; in other words, when readily available uplift in the form of thermals is present, the birds are much more able to fly in their preferred direction. With infrequent thermals, the vultures must deviate from the preferred direction to find suitable energy to assist them in their efforts. The use of TKE means that the energetic cost of long-distance flight is only a little more than that of short-distance flight. Similar observations have been made for albatrosses which epitomize energy-efficient, long-distance, even circumplanetary, travel (Weimerskirch et al. 2000 and see Figure 7.3).

Turbulent kinetic energy also influences the flight behavior of tiny migrating arthropods such as aphids and spiders (Reynolds et al. 2006, 2007, 2009). Spiders rely on silk "draglines" to become airborne and for subsequent transport. Numerical simulations (Reynolds et al. 2006) suggest that these draglines are flexible and can become contorted by both stretching and twisting. These flexible, extendible draglines enable the spiders to rise in the air column and follow the flow of air, promoting relatively long-distance travel. Take-offs decrease markedly when wind speeds exceed ~3 m/s (Suter 1999). The reason is that at these speeds hazards increase, and there is less likelihood of rising thermals (Reynolds et al. 2007). Modeling predicts that travel is likely to be most effective when atmospheric conditions are "non-ideally convective", which occurs in warm temperatures, a light breeze, and with rising thermals. The modeling suggests that spider ballooning is constrained to these conditions, but the theory derived remains to be experimentally tested (Reynolds et al. 2007).

In spite of their small size and apparent fragility, aphids are active flyers when they migrate. Kennedy and Fosbrooke (1973) emphasized the behavioral component of aphid migration (summarized in Dingle 1996) and proposed that aphids' lift was unlikely to be constant. Rather, they suggested, aphids were likely to fly upward in updrafts to enhance migration and downward in downdrafts to promote post-migratory landing. Reynolds and Reynolds (2009) addressed the issue by combining

models of particle trajectories in atmospheric turbulent flow with the characteristics of aphid migratory behavior. They compared the results of their models with known densities of aphids with height above ground level. The observed density profiles can be reproduced in numerical simulations if it is assumed that aphid flight produces just enough lift to make the insects neutrally buoyant in updrafts and to cease producing lift when they are in downdrafts. This close correspondence between actual and predicted aphid densities in the atmosphere suggests that turbulence amplifies rather than dampens the aphids' movements, confirming Kennedy and Fosbrooke (1973). Aphids, unlike spiders or small seeds—which, once airborne, have little or no control over their passage (although spiders may control landing by drawing in their draglines; Dingle 1996)—thus can exert considerable control over their migration and are definitely *not* passive migrants borne willy-nilly on the wind.

Micro- and nanoscale effects

Many small insect species that fly long distances with the aid of synoptic winds control their take-offs under the influence of wind conditions above ground surface at the point of departure. Planthoppers of the winged form, for example, move to the tops of plants and fly upward if winds are calm (Kisimoto and Sogawa 1995). These are the conditions occurring at dusk and dawn during the summer. The dawn take-off is reduced under the cooler conditions of autumn, and the dusk take-off occurs earlier while it is still warm enough to generate some thermal convection. The dusk take-off is also reduced under windy conditions and is completely inhibited when wind speed at 10 m above ground level exceeds ~3 m/s. This inhibition of take-off by wind may have important long-term impact, because aphid experiments demonstrated that the insects increased their tendency to fly after wind inhibition of take-off, with the strength of the behavioral rebound proportional to the strength of the flight-inhibiting wind (Kennedy 1990).

Like small insects, spiders climb to the tops of plants before ballooning, and then display a stereotypic "tiptoe" behavior as they produce their silk threads (Bell et al. 2005). Take-off itself is then determined by the surface wind velocities encountered. The frequency of take-offs was studied in the European Salt Marsh Wolf Spider (*Pardosa purbeckensis*) by Bonte et al. (2007) in coastal France and Belgium as a function of family (clutch), wind velocity, and area of the habitat the spiders inhabited (Figure 5.5). Three results are apparent. First, there is variability between families in the proportion of spiderlings ballooning under a given set of conditions, indicating a genetic component to the likelihood of the behavior. Second, wind velocity influenced the proportion of take-offs. Third, the area of the habitat influenced take-offs in opposite frequencies. In habitats of small area, take-off frequency declined or remained the same as wind velocity increased from 0.3 to 0.8 m/s (Figure 5.5A), whereas the frequency increased in large-area habitats (Figure 5.5B). The habitat difference possibly occurs because, in small areas, departing the habitat (as would more likely occur at higher wind velocities) increases the risk of not finding a suitable place to settle, whereas in extensive habitats settlement could occur within the same area. Suffice to say, interactions with other factors are an important consideration when analyzing the influence of wind and weather on migration.

Migration in the ocean

Like their terrestrial counterparts the creatures of the oceans are subject to the dynamics of the medium in which they live. In none is this more true than in migrants, for in moving from place to place or region to region, whether in estuaries or in the open ocean, these travelers depend to a great extent on currents to assist them in reaching their destinations. The general pattern of the currents in the Atlantic Ocean is shown in Figure 5.6; the basic pattern in the Pacific is similar. There is a clockwise motion of currents in the Northern Hemisphere and a counterclockwise flow in the Southern Hemisphere due to the Coriolis effect, and a decrease in velocity with depth resulting in a downward Ekman spiral. Warm currents flow along the western edge of continents and cold currents flow along the eastern edge as a consequence of the circular nature of the large gyres that move around the ocean basins (see Dingle 1996 for a more complete summary of current patterns).

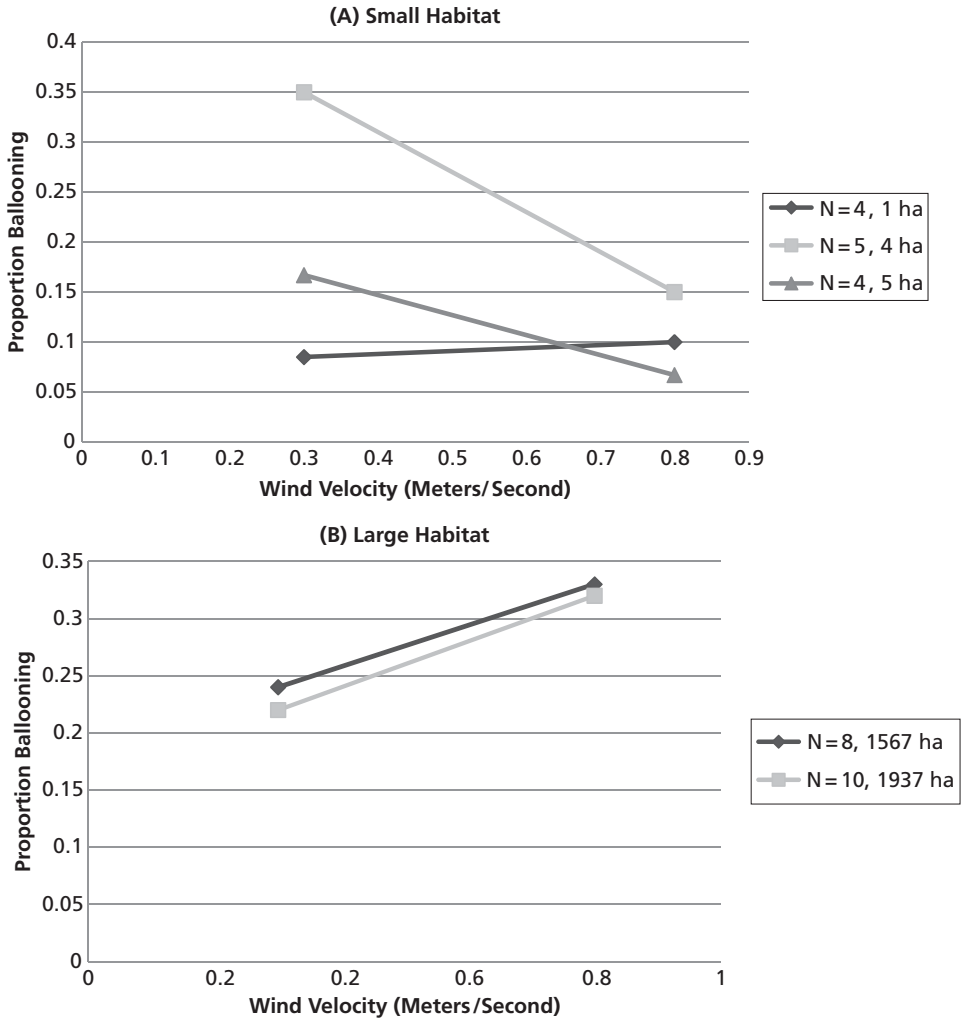


Figure 5.5 The influence of habitat area (hectares) and wind velocity on the take-off frequency in Salt Marsh Wolf Spiders. (A) In small area habitats, take-off frequency declines or is unchanged as wind velocity increases. (B) In large area habitats, take-off frequency increases with increasing wind velocity. From data in Bonte et al. (2007).

Some of the most remarkable of the migratory journeys such as those of Atlantic and Pacific eels, and different species of sharks and sea turtles, have evolved in synchrony with current patterns over large areas of the ocean basins. Many estuary and inshore migrants, on the other hand, make up for what they lack in drama with precise behavioral refinements allowing adaptive migratory patterns that are keys to their survival. As with atmospheric circulation, the movements of ocean waters at all scales influence in profound ways the migrations of the seas' inhabitants.

Planetary-scale currents and pacific eels

There are some 16 species of eel (*Anguilla* and *Arioosoma*) in the world, all but two of which occur in the Indo-Pacific (McDowall 1988; Inoue et al. 2010). In most of the 20th century eels were thought to be completely catadromous, with breeding in the ocean

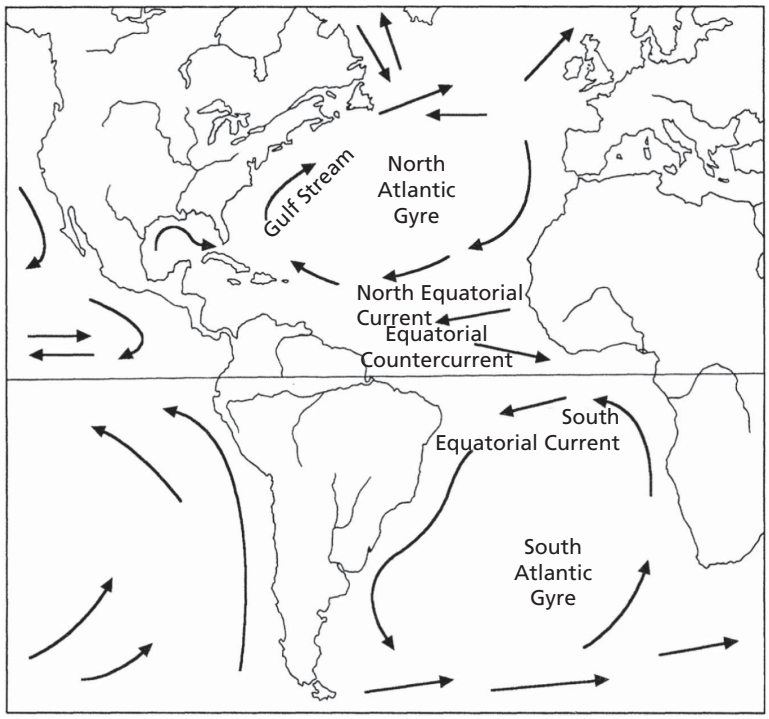


Figure 5.6 The overall pattern of current flow in the Atlantic Ocean. A similar pattern is present in the Pacific (see arrows on the left of the map). Superimposed on this general circulation pattern is considerable local variation (e.g., from tidal currents and upwellings) that is not shown. From Dingle (1996).

basins and a period of maturation in freshwater. Recently, however, it has been determined by analyzing Sr/Ca ratios in the otoliths that this is not the case, and that in both the Atlantic and Pacific species up to 80% of eels mature in coastal ocean waters and in estuaries rather than in fresh water (Tsukamoto et al. 1998; Tsukamoto and Arai 2001). It may also be the case that, among oceanic eels, only the Atlantic species return to the spawning grounds. Again until recently, no breeding sites had been found. Based on analysis of captures of eel larvae and of oceanic currents, it had been assumed that both American and European Atlantic Eels (*Anguilla rostrata* and *Anguilla anguilla*) spawned in the Sargasso Sea (Dingle 1996) and that the Japanese Eels (*Anguilla japonica*) spawned in the Pacific just to the west of the Mariana Islands (Kimura et al. 1994). The Atlantic eels were then transported northward in the Gulf Stream current, with the American eels disembarking in North America and the European species carrying on across the Atlantic to the coasts and rivers of Europe (summarized in Dingle 1996). The Japanese Eel larvae were assumed to enter the North Equatorial Current (NEC) to be carried westward; then east of the Philippines they entered the Kuroshio Current which carried them north to the coasts and rivers of Japan (Figure 5.7). Entry into the Kuroshio Current was thought to be facilitated by vertical commuting upward at night into the Ekman layer, a surface region of more rapidly moving water driven by the easterly trade winds. In this way they would largely avoid southward "dead end" transport by the deeper, slower and southward moving Mindanao Current. The smallest larvae were collected to the south of a salinity front at about 16° N with less salty water to the south caused by greater tropical precipitation. This front was assumed to be a cue for spawning.

This general model of the life cycle of the Japanese Eel has been confirmed by catches made during several oceanographic expeditions at the end of the 20th and beginning of the 21st centuries. Both eggs and pre-leptocephali (see Box 5.3 for eel life-history stages) have been collected along a north–south series of seamounts in the West Mariana Ridge to the west of the Mariana Islands (Ishikawa et al. 2001; Tsukamoto 2006; Tsukamoto et al. 2011) indicating that

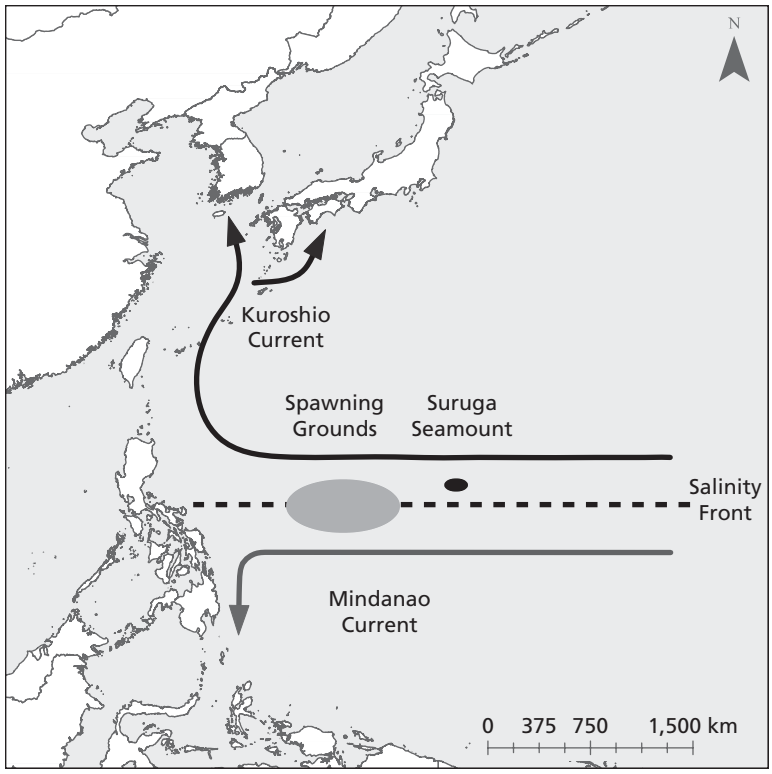


Figure 5.7 The spawning grounds of Pacific eels along the salinity front west of the Suruga Seamount and the Marianas Ridge. The Japanese Eel (*Anguilla japonica*) larvae rise to the depths where they are carried northward by the Kuroshio Current. The tropical eel, *Ariosoma major*, larvae rise only to the level where they are carried southward by the deeper and slower-moving Mindanao Current. Modified from maps in Tsukamoto (2006) and Tsukamoto et al. (2010).

this region of the Pacific is indeed the spawning site (Figure 5.7). These early developmental stages were all collected south of the salinity front which is thus the apparent cue for the eels to locate the spawning grounds. The front moves north to south across years depending on oceanic conditions caused by El Niño, for example, and the exact spawning area varies accordingly (Kimura and Tsukamoto 2006; Tsukamoto et al. 2011). The eels spawn in late May at the time of the new moon, and they apparently spawn more than once before dying. The dark new moon night-spawning probably serves to synchronize spawning aggregations and possibly reduces predation on adults and eggs. Spawning evidently occurs at relatively shallow depths (above 300 m), and the eggs then float to the top of the thermocline at about 150 m where most of the newly hatched pre-leptocephali are collected (Tuskamoto et al. 2011).

As the pre-leptocephali mature to the leptocephalus stage, they enter the NEC. In this current there is a relatively rapid westward flow (20–40 m/s) in the upper Ekman layer (Ishikawa et al. 2001). Two behaviors promote the distribution of leptocephali in this upper layer. First, they commute vertically between depths of 100–200 m during the day and depths of 50–100 m at night so that they spend at least half their time in the more rapidly flowing Ekman layer. Stable isotope analyses suggest that they do most of their feeding in this layer (Miyazaki et al. 2011). Second, the larvae spend increasing time in the upper layers as they age. Interestingly a second eel species, *Ariosoma major*, spawns in the same area, but the leptocephali appear to occur mostly in deeper, slower portions of the NEC which results in their eventually being transported southward in the deeper and slower Mindanao Current (Figure 5.7), whereas *A. japonica* is carried northward in the Kuroshio Current. There is overlap in the feeding areas of the leptocephali of the two species (Miyazaki et al. 2011), so the exact mechanisms promoting carriage of *A. major* in the Mindanao versus Kuroshio Current is not clear.

After a leptocephalus stage of about six months (up to three years in Atlantic eels), the eels metamorphose into the glass eel stage. This is the stage of individuals of that portion of the population that migrates into rivers and estuaries where they become elvers and then transform into yellow eels. Estuarine eels predominate, contributing 57% of individuals in which Sr/Ca ratios were examined. Sea eels contributed 20% with the remaining 23% being freshwater river eels (Tsukamoto and Arai 2001). Some eels also apparently move back and forth between fresh and salt water. Individuals remain in the yellow eel stage for up to 10 years (Tsukamoto et al. 2011) before transforming into the final adult silver eel stage for the migration back to the spawning areas.

Upon completing maturation and transforming to the silver eel stage, Japanese Eels that have been occupying rivers undertake a two-phase migration (Okamura et al. 2002). The first phase involves downstream migration to river mouths and the second a continued seaward migration to the ocean. The first phase occurs from October to January with peaks in November/December, apparently conditioned on lowering water temperatures. Most downstream movement occurs during the days immediately before and after the new moon. Once at river mouths or in adjacent estuaries, the start of seaward migration to the spawning ground is triggered by the passage of an atmospheric "dry depression." The seaward movement may be assisted by tidal stream transport as is known to occur in Atlantic eels (Parker and McCleave 1997). Once in the ocean on the journey to the spawning grounds, a passage that takes five to six months (November/December until late May), the eels do not feed, and the digestive tract degenerates (Box 5.3). They may be assisted by cooler currents moving southward from the North Pacific, and they probably undertake a diel vertical cycle of movement as Atlantic eels do (Aarestrup et al. 2009). Aarestrup and colleagues postulate that this commute is a temperature-regulating behavior. The rise at night to warmer water would allow greater swimming activity with higher metabolisms, whereas descent to cooler water during the day would delay gonadal maturation until the spawning area is reached. The final event of the lifetime migratory cycle is spawning, after which the adult eels die and the new hatched pre-leptocephali begin the cycle again.

Box 5.3 Stages in the life cycles of eels

Eels in both the Atlantic and Pacific undergo a series of transformations from egg to spawning adult as they migrate around the ocean basins, first to maturation areas offshore or in freshwater and then back to the spawning areas. The different stages each bear their own designations.

- *Pre-leptocephalus*. Larvae immediately after hatching. During this stage, eye pigmentation, teeth, and jaws develop.
- *Leptocephalus*. Flattened transparent larva with a small head but complete eyes, jaws, and teeth. The name derives from *Leptocephalus*, a generic name assigned to these larvae before it was realized that they were in fact immature eels.
- *Glass eel*. Young eels after metamorphosis from leptocephali. They are transparent or semitransparent and are the stage that invades freshwater or estuaries.
- *Yellow eel*. The stage that matures over 5–10 years whether in freshwater, estuaries, or coastal oceanic waters.
- *Silver eel*. The adult stage that migrates back to the spawning areas. They are silvery below and black above with well-developed caudal and pectoral fins. The digestive tract, including teeth, degenerates so they apparently do not feed. They die after spawning.

Sources: Dingle (1996); Tsukamoto et al. (2011).

In contrast to the Japanese Eels, several species of tropical eel migrate for only short distances. Molecular phylogenies indicate that catadromous eels, i.e., those that can mature in freshwater, originated in the tropics so that temperate long-distance migrants have evolved from typical ancestors (Aoyama et al. 2001). The larvae of five tropical species, *Anguilla borneensis*, *A. celebesensis*, *A. marmorata*, *A. bicolor*, and *A. interious* have been collected in the Celebes Sea north of the Wallacean

island of Sulewesi (Aoyama et al. 2004). *A. borneensis* is native to rivers on the island of Borneo, and its leptocephali appear to be limited to the Celebes Sea southward into the Makassar Strait between Borneo and Sulewesi. The remaining species occur in the rivers of Sulewesi. Their leptocephali occur in the Celebes Sea, the Makassar Strait, and Tomini Bay which lies between the northern and central peninsulas of Sulewesi. All these species spawn throughout the year, and metamorphosing larvae are recruited into rivers as glass eels at an early age, in keeping with migration from nearby spawning sites. The short synoptic or even mesoscale migrations with year-round spawning of these tropical eels thus contrast with the planetary-scale routes and annually precise spawning of *A. japonica*.

Synoptic-scale currents

Marine turtles characteristically nest on sandy beaches, and their newly hatched offspring then migrate into oceanic current systems where they feed and mature over a period of several years. The Loggerhead Turtle (*Caretta caretta*) nests on beaches on the southeastern and gulf coasts of the USA, and the young migrate offshore into the Gulf Stream System (GSS). Once entering this system they become entrained in the North Atlantic Subtropical Gyre (Witherington 2002) where they grow to adulthood, often temporarily exploiting rich foraging areas such as the waters around the Azores. As adults they home to the same area where they themselves hatched (Lohmann et al. 2008a). Reaching the GSS is critical to the survival of the juveniles because it provides food, shelter in floating patches of sargassum weed, and transport to rich foraging sites. Because active swimming to reach the GSS is very energetically demanding and rapidly consumes residual yolk, and because predation on hatchlings is intense (Whelan and Wyneken 2007), natural selection would be expected to favor turtles selecting nesting beaches that minimized risk to the hatchlings migrating to the offshore current. Putnam et al. (2010) investigated whether beaches closer to the GSS, and therefore minimizing risks associated with travel distance, might be the preferred nesting sites for the Loggerheads.

The GSS consists of two elements (Putnam et al. 2010). The first is a "loop current" that circulates clockwise within the Gulf of Mexico. This current tends to be variable, meandering as much as 125 km back and forth between the Texas and Florida coasts in a manner neither seasonally nor annually predictable. The second element of the GSS is the Gulf Stream itself which flows north along the Florida, Georgia, and Carolina coasts (Figure 5.6). Meanders still occur, but for only about 5–40 km from its mean position not far offshore, especially off the Florida coast. Roughly east of Cape Hatteras, North Carolina, the Gulf Stream veers to the northeast toward Europe and forms the northern portion of the North Atlantic Subtropical Gyre.

Putnam et al. (2010) used three data sets to assess the distribution of Loggerhead nesting relative to distance to the GSS, two on a regional scale extending from Texas to North Carolina, and one on a local scale considering only sites on the coasts of Florida. They also assessed whether latitude correlated with nest density. The data were analyzed using regression and variance partitioning. The latter analysis revealed that on a regional scale distance to the GSS alone accounted for 90–92% of the variation in nest density in the two regional data sets, whereas latitude alone accounted for only 3%. At the local scale of Florida, distance to the GSS alone still accounted for 38% of the variation whereas latitude alone accounted for only 1%. These results are consistent with the hypothesis that nesting distribution is strongly influenced by the distance hatchlings must migrate to reach the GSS. They further demonstrate that not only do currents influence transport of migrants, but also that they act via natural selection to influence the proximity of nesting sites so that the current is more accessible.

On the West Coast of North America the important current influencing migrants is the cold California Current, a part of the large circulating gyre of the Eastern Pacific. This current is the result of westerly winds driving water toward North America at mid-latitudes. When this wind-driven current hits the coast in the vicinity of British Columbia, it is diverted southward as a cold current as far as Baja California. Cold waters are biologically productive due to higher concentrations of dissolved CO_2 supporting rich phytoplankton, and the California

Current is no exception. In addition there is cold water upwelling along with the current, driven by northwesterly winds. These winds cause surface currents along the coast to be driven to the right or to the west offshore (the Northern Hemisphere Coriolis-produced Ekman effect) drawing cooler, deeper water to the surface to replace that moving offshore. This upwelling in turn adds still more nutrient-rich water to that already present from the California Current (see Mann and Lazier 2006 for a summary of the system). Particularly apparent in the California Current system are large assemblages of pelagic marine predators, including sharks, tuna, marine birds, seals, and whales (Block et al. 2011) some of which come from as far away as the Western and South Pacific to exploit its resources.

One of the sharks whose migratory cycle is tied to the California Current is the Eastern Pacific population of the Great White, *Carcharadon carcharias* (Jorgensen et al. 2010; Block et al. 2011; Klimley 2013). These sharks display a highly predictable annual cycle with a peak period offshore between April and July and a peak onshore period between September and November (Jorgensen et al. 2010). The sharks make use of two restricted offshore areas, one the waters around the Hawaiian Islands and one a Panama-sized elliptical region between Baja California and Hawaii known as the shark "Cafe." The Hawaiian waters seem to be used primarily for foraging, and precise diel vertical commuting suggests prey capture in the deep-scattering layer community at around 600 m deep. The "Cafe" area contains similarly sized large males and females overlapping in time, suggesting that it may be used for mating and reproduction. Vertical movements occur here, so it probably also serves as a feeding area. In the late summer the sharks return to the shelf waters of the Pacific Coast of North America and the evidence indicates that they home to very specific locations off both central California and Guadelupe Island 1,000 km south of central California (Domeier and Nasby-Lucas 2008). The sharks resided at key locations for weeks or even months with near-constant local patrolling, presumably to feed. Watchers on the California coast commonly observe dramatic prey capture of pinnipeds by these patrolling Great Whites. This Great White population in the northeastern Pacific in the California Current system is genetically distinct from the population around Australia and New Zealand. It was apparently introduced in the Late Pleistocene with the philopatry involved in migratory destinations resulting in the evolution of a distinct population unit (Jorgensen et al. 2010).

Micro- and mesoscale continental shelf and estuary currents

A number of marine organisms use currents that occur along coasts and in estuaries to facilitate their migrations. A characteristic behavior is selective tidal-stream transport (STST) by which organisms from plankters to fish enter tidal currents that are moving in a direction appropriate to the stage of the migratory cycle (Forward and Tankersley 2001). Entry into the tidal stream is often, although not always, carried out with the assistance of a circatidal rhythm that results in the organism staying on the bottom or in quiet water when the tide is flowing in the "wrong" direction, but rising into the tidal stream via active swimming when the tide is flowing parallel to the desired course. Examples include STST-assisted migration into estuaries by crab megalopae such as *Rhithropanopeus harrisii* on the Atlantic Coast of North America and northward movement in the North Sea off the coast of England by migratory eels and plaice (summarized in Dingle 1996; Forward and Tankersly 2001).

One of the commercially most important creatures engaging coastal and estuarine currents to assist migration is the Blue Crab, *Callinectes sapidus*, resident on the east coast of North America and in the West Indies. Adult crabs live primarily in the brackish water of estuaries. From late spring until early autumn these adults mate in the brackish regions of the estuary; following insemination female crabs migrate seaward, while male crabs remain in brackish waters (Forward et al. 2003). When they reach euryhaline water, which can take weeks or even months, females may continue to the sea, or if it is late in the season they overwinter near estuary mouths prior to spring spawning. At spawning, egg masses are attached to the underside of the abdomen, and after 10–12 days of egg development, females migrate to the mouth of the

estuary and perhaps into nearby coastal waters by swimming upward during nocturnal ebb tides and using the ebb-tide currents for transport. In fact the frequency and swimming direction of the females is related to the magnitude and direction of tidal currents. Furthermore, most crabs seem to float "treading water" in the currents, rather than swimming actively, which probably results in energy saving. After releasing the hatching larvae which hatch within minutes, the females swim vertically to the surface during nocturnal flood times and are transported back to the estuary. Females can produce more than one egg mass, so an individual may undergo multiple spawning migrations in a season. The cycle is summarized in Forward et al. (2003).

The cues used to trigger adult female migratory movements are obscure (Forward et al. 2003; Darnell et al. 2010). The vertical movements to reach ebb-tide currents occur only in ovigerous females, so they are presumably controlled by internal physiological mechanisms. What is interesting is that once larvae are released, the crabs reverse current choice and move upward into the flood-tide currents, the cue for the switch presumably being the quick release of the larvae. Such reversals in STST are common in crustaceans, as are sudden changes in phototactic responses, e.g., in stomatopod larvae (Dingle 1996). Clearly much remains to be learned about how crustacean nervous systems produce such sudden changes in behavior. It is also the case that *C. sapidus* occurs in estuaries with much variation in tides, even including those that are essentially atidal (Darnell et al. 2010). Ovigerous females from estuaries with semidiurnal and diurnal tides had circatidal or circalunidian rhythms with migration coinciding with the time of ebb tides, sometimes switching back and forth between the two rhythms. Egg-laden females from an atidal estuary displayed a circadian rhythm with vertical swimming around the time of sunset. Since this did not concord with any tide, the crabs presumably walk seaward (with perhaps some swimming?) to spawn. Mature females prior to initiating egg production synchronized vertical movements with the period right around high tide, resulting in no net current movement. There is thus an ontogenetic component to the development of rhythms that facilitate STST movements to and from the estuaries to spawn in the ocean.

The second half of the migratory cycle of *C. sapidus* is the return of larvae to the estuaries to metamorphose into adults (Welch et al. 1999; Forward et al. 2007; Ogburn et al. 2009). After hatching, the larvae develop through seven zoeal stages in high-salinity waters along the continental shelf. The final-stage zoea metamorphoses into a postlarval megalopa, and these postlarvae are transported shoreward, primarily by wind-driven Ekman circulation, and then move into estuaries using flood-tide transport. Maximum ingress to estuaries occurs in September and October during periods of winds that favor downwelling (Ogburn et al. 2009). An interesting question concerns how flood-tide transport is cued, because megalopae do not have an internal tidal rhythm. This suggests that selection of flood tides is triggered by environmental cues. These turn out to be salinity and turbulent kinetic energy (TKE) (Welch et al. 1999). The increase in salinity at the beginning of the incoming flood tide triggers the megalopae to ascend into the water column. The continued rise of megalopae into the tidal flow is caused by the increase in TKE with increased flow rate, and above a threshold TKE they are stimulated to swim actively and so remain in the flow. Descent at the end of flood tide is cued by the decrease in TKE during slack water as the tide switches from flood to ebb.

The final step in the migration cycle of *C. sapidus* is the molt of the megalopa to the first stage of the juvenile crab and then settlement on the bottom in estuaries on complex substrates such as seagrass beds. A change in the internally driven circadian rhythm occurs in the pre-molt megalopae which switch phase from a diurnal rise in the water column to a nocturnal rise (Forward et al. 2007). This is an ontogenetic change in the rhythm which survives the dramatic morphological transformation from the free-swimming megalopa to the descending and finally bottom-dwelling juvenile crab. The result is horizontal STST transport at night rather than during the day, which again presumably reduces risk of predation during the tidal current movement into estuaries. Bottom settlement by the juvenile crabs closes down the migratory

cycle until the young crabs mature, and the adult females again move down to the oceanic waters to spawn.

Nanoscale currents

Blanco and Scatena (2006) examined the distribution of migrating snails in Puerto Rico streams with respect to snail size, stream depth, bottom substrate conditions, and stream current characteristics (see also Chapter 3). The assessments were done over a scale of tens of meters along streams and so may be appropriately designated as nanoscale. Densities were highest where stream bottoms consisted of small boulders, cobbles, and gravels, and were lower in finer substrates of pebble and gravel. Densities also increased with stream depth, and, in the case of pools associated with meanders in the streams, this seemed to be a function of increased near-bed current velocities. In straighter stretches of streams, or reaches, the current exerted a significant influence on the distribution of snails.

The influence of current characteristics was assessed via the calculation of two dimensionless numbers. First is the Reynolds number (*Re*) which is a measure of the ratio of inertial to viscous forces and so quantifies the relative importance of the two forces. The second is the Froude number (*Fr*) which is the ratio of a characteristic velocity to gravitational wave velocity (or the ratio of a body's inertia to gravitational forces) and is used to compare the wave-making resistance between bodies of various sizes and shapes in fluids, as applied here to snails (see Box 5.4). *Re* for the occurrence of snails ranged from 10^1 to 10^6, that is, from smooth, almost laminar, flow to highly turbulent flow. *Fr* ranged from 0 to 1.36, that is, from low to a quite high wave making resistance. The relation between snails and currents depended on snail size. Large snails were found in current (habitat) conditions with low *Re* and *Fr*, whereas numbers associated with small snails were higher, indicating that smaller individuals were more likely to be found in more turbulent and erosive currents. In terms of the stream characteristics, snail density—predominantly as a function of the increase in the numbers of smaller snails—was greatest in riffles. Mean snail sizes were smallest in riffles (5.8 mm), intermediate in pools (9.3 and 10.0 mm) and largest in a relatively large marginal pond with less water flow (14.0 mm).

Box 5.4 Reynolds and Froude numbers

Reynolds and Froude numbers are frequently used to characterize the performance of bodies in fluids and have been used to examine the behavior and habitat choice of aquatic organisms. Reynolds number can be defined for different situations where fluid is in motion relative to a surface, and definitions generally include fluid density and viscosity plus a velocity and a length or dimension (e.g., radius).

In general form: $Re = \frac{\rho v h}{\mu}$

where ρ is the density of the fluid (kg/m^3)

ν is the mean velocity of an object relative to the fluid

h is a characteristic linear dimension

μ is the dynamic viscosity of the fluid (e.g., kg/m.s).

Blanco and Scatena (2006) in their study of migratory snails used:

$$Re = UD/\nu$$

where U is the mean near-bed velocity at a sampling point, D is the depth (= 2.5 cm), and ν is the kinematic velocity (= μ/ρ (m^2/s)).

The Froude number is defined as:

$$Fr = \frac{V}{c}$$

where V is a characteristic velocity and c is a characteristic water wave propagation velocity. Blanco and Scatena (2006) used:

$$Fr = U(gD) - 0.5$$

where U and D are as above, and g is the acceleration of gravity (= 9.8 m/s^2).

Source: Wikipedia.

Summing up

The shape of the Earth, its tilt, and its spin around a central axis all interact to generate the major weather and current systems of the atmosphere and oceans. Because the seasons change and because the Coriolis effect and other factors direct winds and currents, many of these atmospheric and oceanic streams are sufficiently predictable to be used

by migrating organisms for assistance in transport. The Bar-tailed Godwits flying south in the autumn from Alaska to Australasia across the Pacific may depend with fair certainty on northerly winds to aid them at departure and favorable or calm winds throughout their journey (Gill et al. 2005, 2009). The larvae of Japanese Eels depend on the North Equatorial and Kuroshio Currents to assist them in their migration from the spawning grounds near the Mariana Islands to their maturation sites in Japan and nearby waters (Tsukamoto et al. 2011). The certainties of the daily tidal cycles both program and assist the estuarine and continental shelf migrations of numerous crustaceans and fish (Forward and Tankersley 2001).

Across a range of temporal and spatial scales the restlessness of the atmosphere and the oceans influences the timing, course, and length of migratory journeys. Proximately, a thermal, a wind stream, or a current may provide a period of assistance to a migrant on its travels; ultimately, the patterns generated by air or water movements may provide the basis in selection for the evolution of specific migratory journeys. Size and degree of locomotor efficiency are not necessarily predictors of wind or current transport. Organisms from large storks and sharks to minute travelers such as aphids, spiderlings, or plankters all take advantage of the atmospheric and oceanic patterns of structure and motion they encounter. It should be stressed, however, that the more robust migrants may sometimes move across or into winds and currents if delays to await assistance are temporally or spatially counterproductive.

Migratory journeys may be only short distances, or they may be very long. In either case the organisms undertaking them are characterized by focused locomotory behavior (see Chapter 2) and a seemingly uncanny ability to select a vehicle traveling in the required direction. Thus the vertical commutes of crab larvae assure their entry into ebb or flood-tidal stream currents, depending on season or larval stage, and moths flying over the UK select winds at altitudes promoting "correct" directional travel and correct for deviations. Similar choices are made by birds and butterflies on all continents. At very small scales, spiderlings launch only when wind velocities are within a favorable range. At intermediate scales birds and butterflies identify and use the lift provided by thermals. The migratory routes of raptors and other large birds migrating between Europe and Africa are largely determined by the availability of thermal kinetic energy which confines them to the two ends of the Mediterranean Basin. The springtime pattern of southerly winds in the Mississippi Valley provides a migratory route for numerous insects in North America. Judicious optimization of routes that provide favorable winds, currents, or thermal and turbulent kinetic energy may significantly reduce the energy required for migration, and in some cases, provide nearly free rides.

Not only do the patterns of winds and currents exert a strong influence on migratory routes, they affect other aspects of an organism's biology. This is especially true of oceanic currents. Thus the nesting beaches of Loggerhead Turtles in the southeastern USA are largely within an easy swimming distance for new hatchlings to reach the Gulf Stream which provides food, shelter, and transport for the maturing turtles. The rich, cold, waters of the California Current provide extensive feeding grounds and the eastern anchoring point for the migratory circuits of numerous large, predatory, vertebrates of the Pacific Ocean, including sharks, seals, whales, and several species of seabird.

The examples in this chapter demonstrate that natural selection has produced a broad array of migratory programs that take advantage of the motions of air and water. These programs depend on the interactions between migrants and their physical environment. As we have seen, migrating organisms, even tiny and seemingly helpless ones, are not simply passively carried by winds and currents. Rather, as pointed out so emphatically by J. S. Kennedy (1985), they are active participants in the process, launching on transporting vehicles when it is advantageous but staying put or moving under their own power when it is not. Sophisticated mechanisms, as yet not fully understood, allow the proper choice of vehicles of the appropriate direction, speed, and energy. Thus, biology is as important as meteorology or oceanography to migrants, and physical and biotic factors are integrated to produce the wonderful array of migration systems we observe.

CHAPTER 6

Physiology of migration

Migration as enhanced locomotory behavior

> The inhibition of responsiveness to stimuli associated with resources has been specifically investigated in surprisingly few species.
>
> A. G. Gatehouse (1997)

There are two major aspects to the physiology of migration. The first is the central nervous system (CNS) control of migratory behavior by means of interactions between migratory and "settling" responses as we saw in Chapter 2 when defining migration. This aspect involves not only the active enhancement of locomotory action, but also the reciprocal inhibition of "vegetative" actions such as feeding and reproduction and of the responses to the stimuli that would ordinarily trigger those actions. There is suggestive evidence from a variety of other animals that such inhibition occurs (e.g., Table 17.1 in Dingle 1996), often accompanied by major changes in gonads or guts, for example. Many songbirds migrate at night when they would otherwise sleep (a vegetative response), and many shorebirds shrink their guts which precludes feeding on at least some types of less easily digestible food items (Piersma and van Gils 2011). It is also commonly observed that suitable habitats are bypassed (e.g., Klaasen et al. 2011b). How these changes in the behavior and/or physiology of the migrants might interact with or within the CNS (aside from neurohormones) has rarely been considered, as noted by Gatehouse (1997) several years ago as quoted.

Important studies have been carried out on other species of aphid and on the Sweet Potato Whitefly (*Bemisia tabaci*) that confirm the basic tenets of migration as outlined by J. S. Kennedy in *Aphis fabae* (summarized in Chapter 2 and Dingle 1996) (Nottingham et al. 1991; Nottingham and Hardie 1993; Blackmer and Byrne 1993; Blackmer et al. 1995). Furthermore in the three species of aphid tested and in the whitefly, host plant odor, as predicted, did not influence the timing of the interactions between excitation and inhibition. This is, however, a distressingly small sample of migrants.

In sharp contrast to the above situation, the second aspect of migratory physiology—the mobilization of hormonal and metabolic pathways to stimulate and regulate migration and support its high energetic demands—is much more extensively studied. The remainder of this chapter deals with these components of migratory activity. This does not imply that this aspect of migratory physiology is by any means completely understood. There is, however, a tradition of studies, especially with some of the better-known migratory birds, fish, and insects, that are now contributing at an increasing rate to our understanding of the physiological adjustments and integrations that creatures make in adapting to, and preparing for, migration. Not surprisingly these studies reveal complex and sophisticated systems of regulation and mobilization. These include responses to external inputs, neurosecretory and hormonal action, the organization of energy reserves, metabolic and morphological shifts, and incorporation of suitable fuels. We begin by examining the ways in which organisms synchronize their migrations to the environmental fluctuations around them.

Environmental stimuli

> As well as daily clocks, living creatures need calendars . . .
>
> Foster and Kreitzman (2009), p. 2

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Organisms must be able to respond to changes in the environment if they are to survive and reproduce. In many, if not most, cases longer-term changes require an alteration of physiologies to respond appropriately, and it is therefore to migrants' advantage if they can *anticipate* changes that will occur (Follett 1982). Thus migration, in particular, has generally evolved to be pre-emptive (Dingle and Drake 2007). At the very least, migration entails mobilization of energy for the journey. It also may require synchronization with other life functions such as reproduction (Ramenofsky 2011), and in some cases—as with flight, polymorphic insects or polymorphic seeds (see also Chapter 13)—it may require reorganization of the developmental program to produce the migratory apparatus. In these latter cases anticipation is a must, or the organism will be caught short without the ability to migrate. The most common and frequent environmental changes are those associated with the seasons, whether cold–hot or wet–dry, and indeed seasonal migrations are the best known of migratory phenomena (Chapter 9).

Across the planet the most reliable predictor of seasonal change is the annual change in day length, occurring with metronomic certainty as the Earth circles the Sun. It is therefore not surprising that a broad array of organisms, including migrants, respond to changes in photoperiod. Photoperiodism is a classic example of a trait that also occurs in non-migrants, but has become modified or amplified by migrants to support extended movement (Ramenofsky and Wingfield 2007). Photoperiodic responses range from diapause in insects to flowering in plants, and studies of phenological responses have spawned an extensive and longstanding literature from the scientific (e.g., Beck 1980) to the semipopular (e.g., Foster and Kreitzman 2009). In migrants day-length changes serve not only to time migration, but also to synchronize the movements with other cycles such as molt in birds or smoltification in salmonid fishes.

In animals, the photoperiod response is mediated by neurosecretory cells in the brain that in species as diverse as birds and aphids may respond directly to light (Hardie and vaz Nunes 2001; Foster and Kreitzman 2009). In at least some mammals, reptiles, and amphibians the pineal is also light sensitive and contributes to photoperiodic responses. Many species respond to remarkably small differences in daylength. Aphids, for example, are sensitive to differences of as little as 15 min or less between day and night length (e.g., Lamb and Pointing 1972). Even tropical species can detect small differences: 17 min in the case of an antbird native to Panama (Hau et al. 1998). Sensitivity to photoperiod has long been established in avian lineages, being present in species as diverse as kiwis, penguins, the Kakapo (*Strigops habroptilus*, the flightless parrot of New Zealand), and a variety of bird migrants in both hemispheres (Cockrem 1995; Dingle 2008). It is no doubt even more ancient in plants and insects.

In many insects, migration is associated with an additional photoperiodic response, adult reproductive diapause (Dingle 1996, 2002). This relation between diapause and migration is an extension of a trade-off between migration and reproduction which has been called the oogenesis–flight syndrome (reviewed in Dingle 1996, 2002). The assumption underlying the concept is that migration and reproduction are alternate physiological states. Reproduction is inhibited during the migratory period and begins after migration is complete, often stimulated to earlier onset by that migration. Adult diapause in temperate zone insects is cued by short days (or more accurately long nights) and results in shutting down the reproductive system with transfer of energy and resources into fat storage. The absence of reproduction allows a longer period of migration. Fat storage can provide fuel for migration, an energy resource to support a long overwintering or aestivating period, or both.

A good example of the relation between photoperiodically cued diapause and migration is provided by the Monarch Butterfly (*Danaus plexippus*). The eastern North American population produces two to three generations during the summer after the initial individuals arrive back from Mexico, beginning in March along the Gulf Coast. Newly emerging summer adults average lipid masses of around 30 mg, and this value varies little as the summer generations feed on nectar, mate, and oviposit. Autumn migrants that return to Mexico enter reproductive diapause and convert sugar obtained from nectaring into large, although highly variable, lipid stores (Brower et al. 2006). Butterflies reaching

Texas and northern Mexico in October had a mean lipid mass of 126 mg. Nectaring can continue in this region during migration so that butterflies reaching the wintering sites in the Transvolcanic Range of Mexico had mean lipid vaues of 142 and 133 mg, respectively, in November 1982 and 1993 (Alonso-Mejia et al. 1997). Once at the wintering sites the butterflies do almost no feeding and consume their lipid reserves up to around 50% of lipid mass. A further 50% of the remainder is consumed during the return northward migration in March. These data indicate that the lipid reserves are required not so much for the southward journey when nectaring can occur, but as an absolute necessity for survival over the winter and on the succeeding spring return flight. The diapause response to the short autumn days leading to reproductive shut down, and re-channeling of energy to produce fat reserves is thus key to successful overwintering and return north in the following breeding season.

In many insects, including the Monarch Butterfly, diapause may be overridden by high temperatures (Dingle 1996). In the case of the Monarch this may result in all or part of a further generation of reproduction. Ectothermic vertebrates such as salmonid fishes also show temperature modifications to photoperiod responses. Salmonids are cold-water fishes with maximum responses to photoperiod around 12°C; higher or lower temperatures inhibit the reactions (Hoar 1988). Birds are endotherms and so are free of temperature-modulated photoperiodic responses. They may, however, delay or advance the timing of migration depending on local ambient conditions, including temperature; in this regard the potential effects of climate change are of concern (Coppack and Pulido 2004 and Chapter 15). Responses to photoperiod may also vary with rainfall in birds and in insects such as the Australian noctuid moth, *Mythimna convecta* (McDonald and Cole 1991). Photoperiodic responses are thus somewhat flexible in response to other environmental cues.

A further issue in birds is that their relatively long lives mean that migration can take place more than once per year and that a migrant's response to cues must be co-ordinated with other life functions such as reproduction and molt (Figure 6.1 and Ramenofsky et al. 2012). In birds

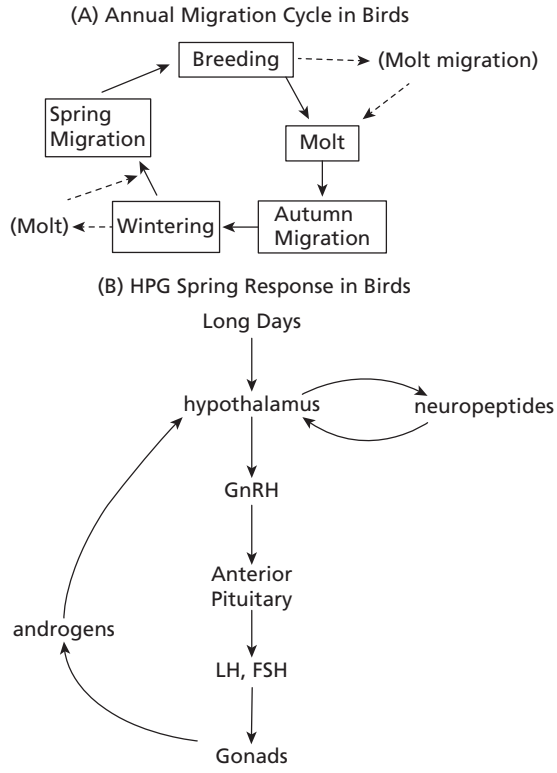


Figure 6.1 (A) The annual cycle of a migrant bird with separate breeding and wintering areas. In addition to spring and autumn migrations, some species undertake molt migrations. In any case, migration is synchronized with the energetically costly molt. (B) The hypothalamus–pituitary–gonad (HPG) axis in birds. In the spring the sequence of migration and breeding is stimulated by long days. GnRH, gonadotropin-releasing hormone; LH, luteinizing hormone; FSH, follicle-stimulating hormone. After Ramenofsky and Wingfield (2007) and Ramenofsky et al. (2012).

the hypothalamic–pituitary–gonad axis (HPG) responds to daylength changes (Figure 6.1), and species or populations differing in the phenology of migration show differences in cue responsiveness. Responses further differ over the course of the annual cycle and involve several physiological processes, including perception and transduction of the cues themselves (Wingfield 2008; Visser et al. 2010; Piersma and van Gils 2011). In a "typical" Northern Hemisphere migrant returning from southern wintering areas, the vernal increase in daylength promotes several life-cycle stages. Often there is a prenuptial molt, then vernal migration and breeding with accompanying physiological changes such as

enlarging of the gonads (Ramenofsky and Wingfield 2006, 2007). As the season progresses, the birds no longer respond to photoperiod, or in other words, they become photorefractive (e.g., see Hahn, T. P., et al. 2009). There appears to be tight coupling (carryover) between spring and autumn events with vernal activation acting as a "remote timer" to terminate breeding and initiate autumnal events such as fattening and in some species a postnuptial molt (Helm and Gwinner 2005; Conklin et al. 2010). Further, there may be renewed photosensitivity with acceleration of physiological changes by shortening days (Helm et al. 2009). Photoperiod and other cues are thus interpreted according to stage in the annual cycle and are fine-tuned by natural selection to precisely time events for a given species or population (Helm et al. 2009; Visser et al. 2010; Ramenofsky et al. 2012).

Endogenous factors

In addition to exogenous factors like photoperiod, endogenous timing mechanisms play an important role in migration and the co-ordination of migration with other associated life-history events such as molt and fattening (Dingle 1996; Gwinner and Helm 2003; Ramenofsky et al. 2012; Helm et al. 2013). Chief among these endogenous factors are rhythmic cycles. In terrestrial organisms the two most important are daily (circadian) and annual (circannual) rhythms. As we have seen in Chapter 5, tidal rhythms can be equally important in the migrations of marine organisms in assuring appropriate current transport. When organisms are kept under constant conditions, their daily and annual rhythms will "free run" independently of external inputs, although with periods that only approximate a day or a year, thus demonstrating that they are endogenously driven. Rhythms are precise in natural populations because they are synchronized by external *zeitgebers* or "time givers" in most cases by photoperiod, especially the changes in light levels of dawn or dusk. This is true for both circadian and circannual rhythms.

In the short lifespans of insects circadian rhythms can synchronize migration with activities such as feeding, mating, and reproduction. As we shall see in Chapter 8, they can also be involved with orientation (Merlin et al. 2009). A good example is the milkweed bug, *Oncopeltus fasciatus* (Caldwell and Rankin 1974; Dingle 1996). There is a daily pattern of activity in young adults, with mating and feeding peaking at the end of the daily light cycle and migratory flight peaking in the middle, 6–8 h after light onset. Thus migration is separated from these other activities. Once oviposition begins, it too occurs around midday, but is separated from migration by ontogeny (the oogenesis–flight syndrome—see next section) because migratory flight has now largely ceased. Under long days the period of migratory flight lasts only a few days, but under short days, the bugs undergo a reproductive diapause, like the Monarch Butterfly, and the autumn migration period is extended, allowing escape from temperate zone winters. These relationships among flight, reproduction, and feeding are consistent with J. S. Kennedy's (1985, Chapter 2) model in which migration suppresses non-migratory station-keeping activity and vice versa, albeit on a longer timescale than the reciprocal interactions occurring during aphid flight.

Migratory birds are much longer-lived than insects and can make several migratory journeys over the course of a lifetime. Species covering often great distances between a high-latitude breeding ground and a lower-latitude wintering area will experience different latitude-specific photoperiodic cycles, so that simply relying on ambient photoperiod cues to synchronize life-cycle events will not be a workable strategy. In these cases evidence shows that circannual rhythms come into play, and are reset each year by a photoperiodic trigger (e.g., Gwinner and Helm 2003). Experiments in which birds are kept under unvarying photoperiods indicate that circannual rhythms are present and free-run. Comparative studies reveal how these rhythms are adapted to synchronize life-cycle events such as migration, reproduction, and molt to the particular environmental circumstances faced by different species and populations. These rhythms are particularly important for the migration timing of trans-equatorial migrants because the annual photoperiod cycle is disrupted by the Equator crossing (Dingle 1996 for summary).

A comparative study of Stonechats (*Saxicola torquata*) reveals the sorts of adjustments made

(Helm et al. 2009). Central European Stonechats are short-distance migrants to North Africa and the Middle East that spend more than six months on the breeding grounds (March to October) where they may produce several broods and display a relatively protracted molt. Siberian Stonechats from Kazakhstan are long-distance migrants to peninsular India. In the short-season continental climate of Kazakhstan they raise but a single brood followed by a rapid molt prior to return southward migration. The two subspecies experience similar photoperiods on their breeding grounds but quite different daylengths in their wintering areas. The Siberian birds experience longer days in the winter quarters, but shorter days after the spring equinox until both populations are again on the breeding grounds.

The reproductive and molt cycles of birds kept in the laboratory under the same annual photoperiod regimes they should have experienced in nature reflect the natural migration and reproductive patterns (Figure 6.2A). For example, in European birds the testes enlarge early and stay large for about four months, whereas in Siberian birds they enlarge later and remain large for only about two months. Similarly there is a long-duration molt in European Stonechats, and a shorter molt period in the Siberian subspecies. Both subspecies displayed a circannual rhythm of testis size when maintained for two years under a constant 12.25 h light period (Figure 6.2B), but the patterns for the two groups differed considerably. In another experiment birds were maintained under reciprocal annual photoperiodic regimes, i.e., European birds under the Siberian regime and vice versa. Although timing responses did not differ, peak plasma testosterone levels were highest in each taxon under native rather than reciprocal conditions. These and other data led to the conclusion that the circannual rhythms of the two populations reflect geographically different periodic changes in seasonal patterns and cue–response mechanisms. It is likely that under natural conditions the phase relationship of the circannual rhythm to the photoperiods experienced annually determines how the birds respond to daylength.

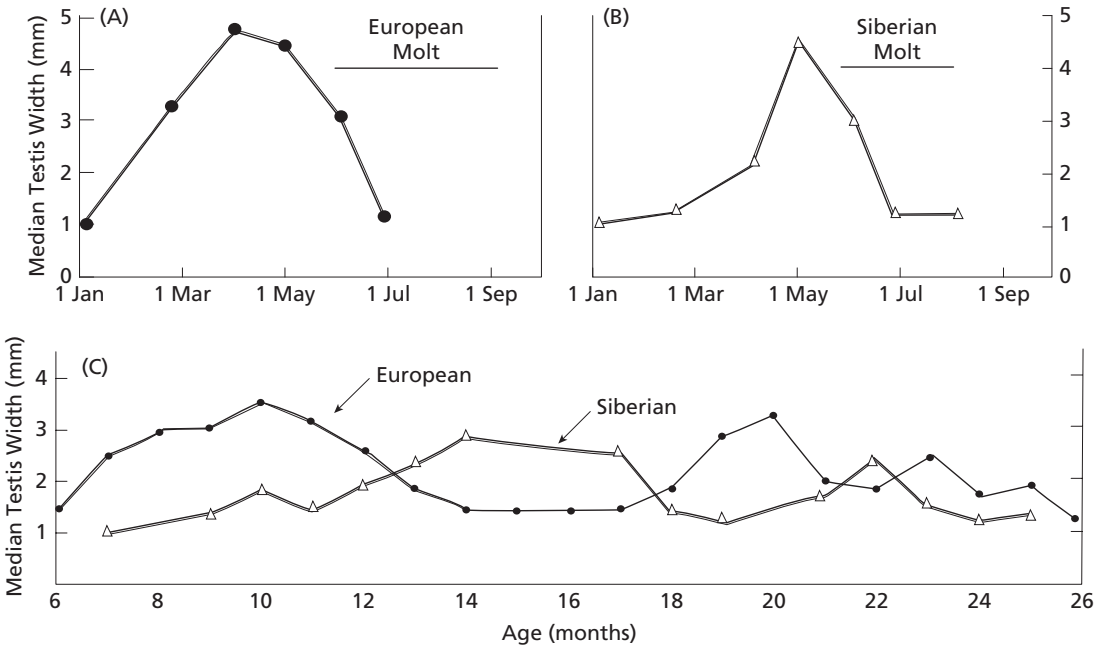


Figure 6.2 (A) Testis and molt cycles of European and Siberian Stonechats kept under the same conditions in the laboratory. European birds maintain large testes for longer and molt over a longer period. (B) Both populations maintain circannual rhythms over two years of constant photoperiod in the laboratory, but the patterns differ. Data from Helm et al. (2009).

Circannual rhythms also occur in other avian species with varied geographical distributions. In a Southern Hemisphere case, Australian Silvereye (*Zosterops lateralis*) populations may be partially migratory or sedentary. Munro et al. (2006) captured Silvereyes from Tasmania (partially migratory) and New South Wales (sedentary), reared each group in the photoperiodic regime appropriate to their geographic location, and assessed molting patterns. On average the Tasmanian birds began their post-breeding basic molt earlier than the non-migratory mainland birds. Furthermore in the Tasmanian birds there was a statistically significant relationship between the duration and date of commencement of the molt; the later the molt began, the more rapidly it was completed (r^2 of the regression = 70.7% of the variance explained). In the mainland birds there was a similar relationship, but it was much more variable (r^2 = 29.1%). The period during which Tasmanian birds can molt is much more confined, as was also the case with Siberian Stonechats, with presumably more selective pressure to complete it within the favorable period.

Circannual rhythms may be present in tropical species experiencing little change in the photoperiod. A migratory Panamanian population of the Yellow-green Vireo (*Vireo flavoviridis*) displayed apparent circannual control of juvenile molt and onset of migratory restlessness (Styrsky et al. 2004). Nestlings aged six to eight days were brought to the laboratory and hand-reared under a 12.5 h daily light regime, corresponding to that in central Panama at the summer solstice which is within the breeding season. The date at which these nestlings had hatched was compared to the date of onset of the two life-history variables occurring once the birds matured, with migratory restlessness measured as nocturnal hopping between perches located one at each end of the cage. Even though the hatching dates were spread over about 75 days, the spread of fat and restlessness onsets were much less, on the order of 40 days and even less for each variable singly. The circannual rhythm controlling this synchrony of restlessness and fat deposition must be synchronized by a photoperiod that varies by only 33 min between earliest and latest hatch dates, once again demonstrating that tropical species are sensitive to even small changes in daylength (see also Hau et al. 1998). Presumably these vireos are sensitive to photoperiod as early hatchlings and even in the embryo, as has been noted for starlings (Gwinner et al. 1997).

Endocrine influences on migration: arthropods

Arthropods and insects in particular have, like vertebrates, two basic types of endocrine organs that produce hormones influencing an array of physiological and life-history functions, including migration (Nijhout 1994; Dingle 2002). The first type consists of glandular tissue, and the two principal organs of this type in insects are the prothoracic glands and the corpora allata (Table 6.1; Figure 6.3). The prothoracic glands produce ecdysteroids, for example ecdysone, which are primarily involved

Table 6.1 Insect central nervous system and some insect hormones important in life histories including migration.

Hormone	Source	Action
Allatotropin	Brain neurosecretory cells	Stimulates corpora allata to produce juvenile hormone
Allatostatin	Brain neurosecretory cells	Inhibits juvenile hormone production by corpora allata
Prothoracicotropic hormone	Brain neurosecretory cells (released by corpora cardiaca)	Stimulates prothoracic gland to produce ecdysteroids
Adipokinetic hormone	Corpora cardiaca	Induces fat body to release stored lipids (important in migration)
Ecdysteroids	Prothoracic glands	Molting; implicated in wing polymorphisms
Juvenile hormone	Corpora allata	Delays metamorphosis; also influences egg development, diapause and migration

Sources: Nijhout (1994, 1999); Dingle (2002).

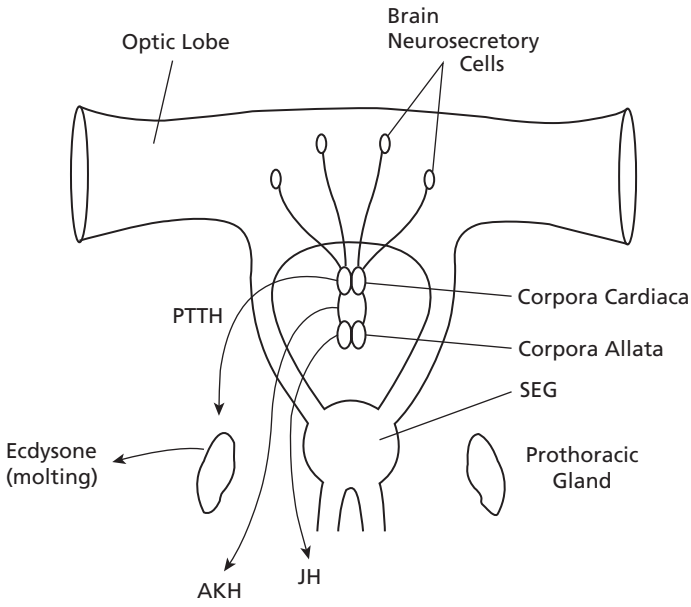


Figure 6.3 The insect brain and endocrine system showing sources of hormones influencing migration. AKH, adipokinetic hormone; JH, juvenile hormone; PTTH, prothoracicotrophic hormone; SEG, subesophageal ganglion. From Dingle (1996), drawn by Mitchell Baker.

in molt and metamorphosis and seem also to have an action in wing polymorphisms. These prothoracic glands degenerate in adult insects through a process of programmed cell death. The corpora allata produce the juvenile hormones (JHs). These hormones are perhaps the most versatile of animal hormones because they play a role in almost every aspect of insect development and activity including metamorphosis, reproduction, diapause, polymorphisms and polyphenisms, and as we shall note here, migration. The second type of endocrine organ in insects (and crustaceans) consists of specialized neurosecretory cells in the central nervous system (CNS). Most arthropod hormones are neurosecretory products that act either directly or indirectly via trophic or inhibitory actions on other glandular tissues. Neurosecretory cells occur in all ganglia of the insect CNS, but the greatest number and diversity occur in the brain. Among other functions, they produce hormones that regulate JH production by the corpora allata and, via the corpna cardiaca, stimulate ecdysteriod production in the prothoracic glands. A brief overview of insect hormones as related to migration is given in Table 6.1.

As indicated in the discussion of diapause and migration in the Monarch Butterfly, there is in many insects an ontogenetic separation of migratory behavior from reproduction, the oogenesis–flight syndrome. In the Monarch, JH (apparently in both its forms, JH I and JH II) is responsible for the post-eclosion growth of the reproductive tracts of both sexes under long-day summer conditions. In butterflies entering adult diapause late in the summer prior to migration, the reproductive tracts are reduced, a reduction accompanied by a two orders of magnitude decline in JH activity (Herman 1985). JH thus plays an important role in integrating migration into the Monarch Butterfly life cycle (Dingle 2002).

In the migratory Armyworm Moth, *Pseudaletia punctata*, there is a syndrome of linked reproductive traits that includes oocyte maturation, female sex pheromone synthesis, and female calling (behavior associated with pheromone emission). All of these processes are JH dependent (Cusson and McNeil 1989a,b). Under the cool conditions of autumn, JH production is reduced, as is the production of JH acid which influences male responsiveness. Both field and laboratory data suggest that autumn migration is undertaken by sexually immature adults with low levels of JH production (McNeil et al. 1995). A complication is that these moths (and other Lepidoptera) produce three forms of JH (JH I, II,

and III) whose rates of biosynthesis change with age and temperature. It is possible that effects on reproduction may depend either on a subset of the homologues or the ratios among them (Cusson et al. 1993; McNeil et al. 1995).

Further intra- and interspecific studies of moths and butterflies indicate trade-offs between reproduction and migration. In the seasonally polyphenic butterfly, *Pieris napi*, the spring generation of females produced more eggs, whereas in the summer generation egg production was less, but flight capacity was greater (Karlsson and Johansson 2008). Populations of *P. punctata* from the Azores do not migrate, and females mature sexually earlier than their North American counterparts (McNeill et al. 1996, 2000). In these island populations lower JH titers initiate calling, and the titers rise more rapidly following adult eclosion (McNeill et al. 2000). These interpopulation differences in JH dynamics are consistent with differences in behavior, i.e., no migration and earlier reproduction in the Azores. Another moth, the Black Army Cutworm, *Actebia fennica*, is a migrant associated with recently burned grasslands. Migrants orient upwind in the presence of smoke volatiles to locate suitable habitats. The volatiles also stimulate JH synthesis in virgin females, resulting in rapid oocyte maturation and onset of calling when the habitat is reached (Everaerts et al. 2000).

In addition to its influence on reproduction, JH can exert a direct effect on migratory flight in several species of insect including well-known migrants such as the Monarch Butterfly (summarized in Rankin 1991 and Dingle 1996, 2002). The effect has been demonstrated both with direct topical applications of JH or its analogues and by removal of the corpora allata or inhibition of JH release chemically by application of precocene. Because JH also stimulates reproductive development which in turn inhibits migration, a critical question was how the trade-off between the two activities was regulated. Rankin (1978), working with the milkweed bug *Oncopeltus fasciatus*, demonstrated by selecting for delayed reproduction that it was intermediate titers of JH that promoted migration which was then terminated by the stimulation of oogenesis by higher JH titers. This result is consistent with the fact that migratory flight itself may accelerate egg maturation and oviposition, as has been shown for aphids (Kennedy and Booth 1963b), milkweed bugs (Slansky 1980), and the grasshopper, *Melanoplus sanguinipes* (McAnelly and Rankin 1986) among others. Further, in *M. sanguinipes* male flight promotes oviposition by their mates (Rankin and Burchsted 1992). This priming of reproduction by flight is apparently the result of stimulation of increased outputs of JH. In *M. sanguinipes* treatment with JH III mimicked the effect of long-duration flight in stimulating reproduction (Min et al. 2004a and Figure 6.4). Min and colleagues also examined grasshoppers after long flights to "exhaustion" and found that such flights themselves stimulated JH production. Thus the increase JH titer induced by long migratory flights is at least one component of flight-enhanced reproduction and the oogenesis–flight syndrome is a complex interaction between migratory and reproductive components.

Flight, and especially long distance flight in insects, requires fuel mobilization to sustain it, and hormones are involved in this mobilization (Kent et al. 1997; Goldsworthy and Joyce 2001). In locusts and grasshoppers flight initially is fueled by carbohydrates and then, as it proceeds, by diaglycerols mobilized from stores of triaglycerol in the fat body. In the first phase octopamine (a catecholamine similar to vertebrate noradrenalin) promotes glycolosis. In the second phase adipokinetic hormones (AKHs) cause greater mobilization of fat body triaglycerol; with no octopamine fatty acid oxidation in the flight muscles inhibits glycolysis, so a function of octopamine may be regulating the transition from carbohydrates to fatty acids in the support of longer and migratory flight (Goldsworthy and Joyce 2001). Flight stimulates both the release of AKHs from the corpora cardiaca and the synthesis of these hormones. In the Monarch Butterfly AKHs may also have a direct role in stimulating migration similar to that of JH (Rankin et al. 1986).

Min et al. (2004b) examined the role of AKHs I and II in migratory propensity in the grasshopper, *M. sanguinipes* (Figure 6.5A,B). The tests performed were on animals that did not fly for long periods (non-migrants) and on those that flew in tethered flight for 1 h or to "exhaustion" (voluntary cessation of flight). No significant differences in AKH levels were detected between resting migrants and

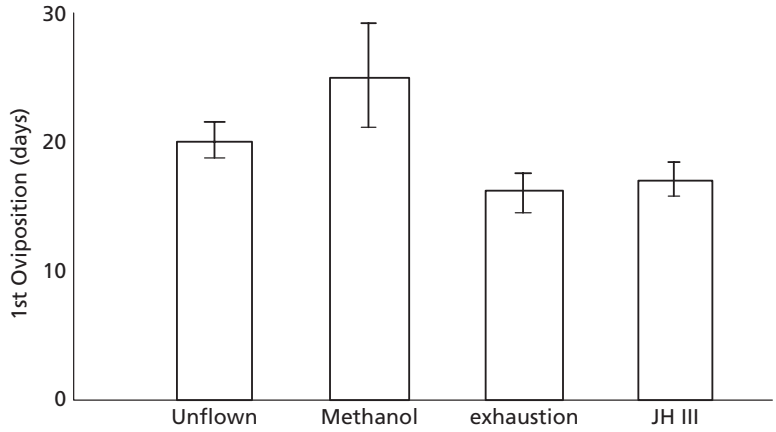


Figure 6.4 Stimulation of reproduction in the North American grasshopper *Melanoplus sanguinipes*. Both juvenile hormone (JH) and long flights to "exhaustion" stimulated grasshoppers to begin reproducing. Data from Min et al. (2004a).

non-migrants. When lipid increase in response to AKH I and II (the adipokinetic response) was compared between migrants and non-migrants, the response was approximately twice as great in the migrants. During long flights mean AKH titer increased rapidly for about 30 min and decreased gradually thereafter, leveling off after 3 h of flight. The adipokinetic hormones thus play an important role in long (migratory) flights of this species and produce greater lipid mobilization responses in individuals predisposed to undertake these migratory flights.

In addition to displaying behavioral variation in migration, many insects are wing polymorphic with populations varying in the proportions of wing forms from long (macroptery), to intermediate, to short (brachyptery), to wingless (aptery) (see Chapter 13). Generally the long-winged morphs are migrants, whereas brachypterous or apterous individuals display higher reproductive capacity (Roff 1990; Dingle 1996). In several species of insect, flight muscles histolyze at the termination of migration with the protein from the histolyzed muscles used to support oocyte development. Such histolysis

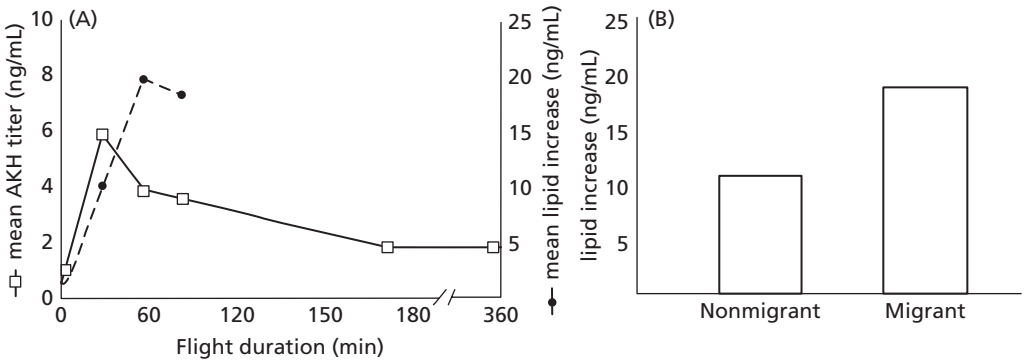


Figure 6.5 Adipokinetic hormones (AKH) and lipids in migrant and non-migrant grasshoppers (*Melanoplus sanguinipes*). (A) The increase in lipids and the time course of AKH after tethered flights of increasing duration. (B) The difference in the amount of lipid increase in migrants and non-migrants treated with AKH I and II. Data from Min et al. (2004b).

can occur in species wholly macropterous and is a further aspect of the oogenesis–flight syndrome. In species such as the Soapberry Bug, *Jadera haematoloma*, in populations that differ in the frequency of the different wing morphs, the flight muscles of the macropters differ in the activity levels of oxidative enzymes such as citrate synthase. In this true bug an ancestral population in the Florida Keys feeding on a sparsely fruiting native host plant with a scattered distribution displays greater migratory capacity and a higher frequency of macropters than a population derived from it that feeds on a concentrated and explosively fruiting exotic host tree (Chapter 13). Individuals from these ancestral populations with a higher frequency of migrating individuals displayed higher concentrations of these oxidative enzymes in the wing muscles of the flying macropters (Winchell et al. 2000 and Figure 6.6). Similar observations have been made on crickets (Zera et al. 1999).

In the cricket, *Gryllus firmus*, the flight-capable morph, which delays reproduction, oxidized a higher proportion of glycine and converted more into somatic lipid, mostly triglyceride (a flight fuel), than flightless morphs. The latter converted more glycine into ovarian protein (Zera and Zhao 2006).

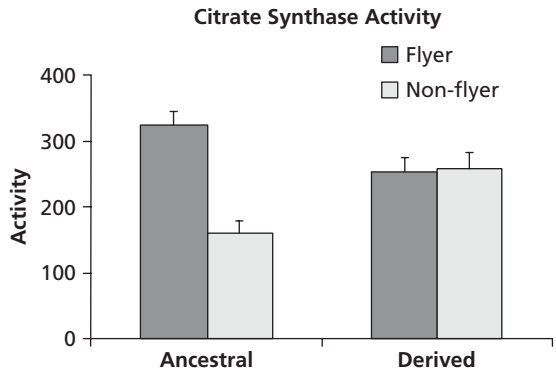


Figure 6.6 Activity (nmol/min/mg thoracic tissue protein) of the oxidative enzyme citrate synthase in flight muscles of *Jadera haematoloma*. Ancestral bugs from the Florida Keys (migratory) show a higher level of citrate synthase activity in flight muscle in individuals that fly in laboratory tests than in individuals that do not fly. They also show more activity in these muscles than derived non-migrant bugs that flew. The non-migrants did not differ in activity between flyers and non-flyers. From Winchell et al. (2000); used with permission of Elsevier.

Apparently increased oxidation of amino acids in the flight morph spares fatty acid for greater conversion to triglyceride fuel, whereas fatty acid oxidation by flightless individuals allows more amino acid for biosynthesis of ovarian protein. In lines of *G. firmus* selected for long and short wings, the short-winged line displayed 100–400% increase in ovarian growth and 30–40% reduction in triglycerides relative to the long-winged line, a difference not due to variation in nutrient acquisition but due to differences in internal allocation (Zera and Harshman 2001; Harshman and Zera 2007).

Although the trade-off between wing muscles and reproduction is most apparent in females, it can involve males in some species (see also Chapter 13). *Gryllus firmus* short-winged males call (by wing stridulation) for significantly longer periods than long-winged males and attract more females for mating (Crnokrak and Roff 1998). In some hemipterans there also seems to be a mating advantage in short-winged females (Fujisaki 1992; Kaitala and Dingle 1993; Fairbairn and Preziosi 1996). In these species, at least, there is an apparent male fitness cost to long wings. In the Japanese cricket, *Modicogryllus confirmatus*, morphs do not differ in testis size at eclosion, but after 5–10 days those of the short-winged form are heavier, as are the male accessory glands (Tanaka 1999). Testis development is stimulated by the JH analogue methoprene, suggesting that JH is a hormone involved in the flight–reproductive trade-off.

A large body of evidence from crickets suggests that JH, and its interaction with the enzyme that breaks it down, juvenile hormone esterase (JHE), is a hormone intimately involved in wing polymorphisms (Zera 2004, 2006 and Roff and Fairbairn 2007 for summaries). The possible interaction between JH and JHE was noted by Zera and Trebel (1989) on *G. rubens*; they showed that JH application either in the penultimate or early last nymphal instar induced brachypterous adults. This result occurred both in lines artificially selected for long wings or in long-winged lines produced by crowding. Thus JH produced short wings regardless of whether the presumptive long-winged crickets resulted from genetic (polymorphism) or environmental (polyphenism) control. If JH titers were measured in nymphs destined to be long- versus short-winged,

no differences were found. Further analysis showed that in the last-instar nymphs of macropters, JHE is considerably higher at mid-instar five to six days before adult eclosion than in nymphs destined for brachyptery, suggesting that a key factor is the degradation of JH and lowering of its titer by JHE, permitting molt to a macropter.

Further experiments using artificial selection to produce long- and short-winged lines in other cricket species have further confirmed a role for JHE and its genetic basis (Fairbairn and Yadlowski 1997; Roff et al. 1997; Fairbairn and Roff 1999; Zera and Huang 1999). In these experiments crickets were subjected to bidirectional selection in the laboratory for an increase or decrease in the frequency of macroptery (see also Chapter 14). In all three *Gryllus* species examined by such selection, the hemolymph JHE activity was higher in nascent maropters than in nascent brachypters, as measured midway through the final nymphal instar. Thus the results from all three species indicate that wing form and JHE are genetically correlated, indicating a functional relationship between JHE and wing form (Fairbairn and Roff 1999). A genetically correlated response also occurs in fecundity, with higher fecundity in brachypters indicating a functional relationship here as well (Roff et al. 1997; Roff and Fairbairn 2007). The genetic correlations are not unity, however, so factors other than JHE must also be involved.

One of these other factors may be ecdysteroid, although its precise role is not entirely clear (Zera 2004). In *G. rubens* titers of this hormone varied more than those of JH. In the penultimate stadium, the ecdysteroid titer rose later and remained high for a shorter duration in the short compared with long-winged morphs, although there was no difference in the absolute height of the peak. In the last stadium no difference between morphs was observed in timing, but the height of the ecdysteroid peak was much lower in brachypterous morphs. These results are consistent with some role for ecdysteroid in morph determination with such determination regulated by combined differences in the titers of more than one hormone (Zera 2004; Zera et al. 2007). It is also possible that there are differences between morphs in the characteristics of hormone receptors (Roff and Fairbairn 2007).

A circadian rhythm of JH titer seems to be involved in the co-ordination of flight and reproduction in *G. firmus* (Zera and Cisper 2001; Zhao and Zera 2004; Zera and Zhao 2009). External application of JH to long-winged adults a few days after eclosion leads to premature histolysis of the flight muscles and onset of ovarian growth. It is also known that JH promotes migratory flight which is obviously terminated when muscles histolyze and/or oviposition begins. Premature termination of flight may be prevented in *G. firmus* by the JH diel cycle. Beginning almost five days after adult eclosion in the long-winged morph, there is a surge in JH hemolymph titer near the end of the photophase which is a >15–20-fold increase and is up to a >100-fold increase in some individuals (Figure 6.7). No such surge occurred in brachypters. This is consistent with the notion that the JH rise promotes flight in these night-flying insects since it occurs shortly before dark. The pulse in JH titer may serve to promote flight without causing premature and maladaptive histolysis of flight muscle and ovarian growth (Zera and Cisper 2001). The results also indicate the importance of considering possible hormonal circadian rhythms, because failure to identify such hormonal cycles can lead to errors of interpretation of the role of hormones in behavior and other functions (Zera et al. 2007).

Other wing polymorphic insects also display a relationship with JH. Ayoade et al. (1999) applied the JH analogue methoprene, JH II, and JH III to nascent macropterous Brown Planthoppers, *Nilaparvata lugens*, and produced brachypterization and enhanced ovarian growth. There was variation in response depending on when hormones were applied, reinforcing Zera's warning about the timing of hormone titers. Dingle and Winchell (1997) used methoprene to induce brachypters in the Soapberry Bug *J. haematoloma* and found considerable genetic variation within and between populations in response to this JH analogue (see Chapter 14). All the observations and experiments indicate a role for JH (and JHE) in the development of the various morphs in flight polymorphic and polyphenic insects, but it is apparent there is still much to learn (Zera 2004; Roff and Fairbairn 2007). It is also apparent that there are common patterns, but a rich diversity of detail among species and populations.

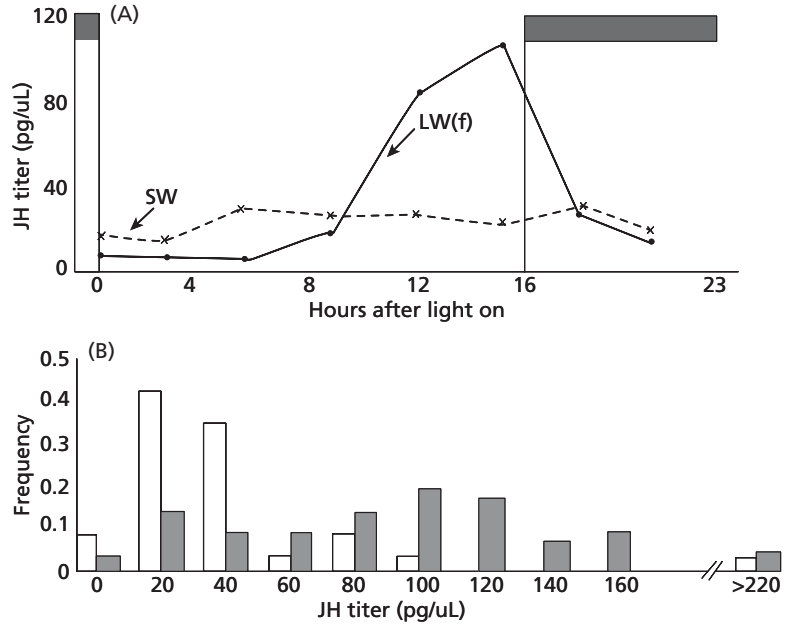


Figure 6.7 (A) The surge of juvenile hormone (JH) that occurs late in the daily light period of young adults of flying long-winged (LWf) Sand Crickets. There is no surge in the short-winged (SW) crickets. Upper bars indicate the dark period. (B) The frequency (number) of Sand Crickets that display JH titers of the indicated levels on the abscissa. Shaded bars are long-winged flyers, and unshaded bars are short-winged non-flyers. The circadian rhythm of JH results in higher titers in the crickets that fly. From Zera and Cisper (2001); Zhao and Zera (2004); Zera and Zhao (2009).

A summary of differences in physiology and development between flight morphs in wing polymorphic insects is given in Table 6.2.

In contrast to the situation in insects, studies of crustacean hormones and migration are in their infancy. The influence of crustacean hyperglycemic hormone (CHH) has been examined in the Christmas Island Red Crab (*Gecarcoidea natalis*) by Morris et al. (2010). This hormone is a product of eyestalk sinus glands (in Crustacea) and is widespread among crustaceans and other arthropods (Montagué et al. 2010). It is a neuropeptide whose primary function is the maintenance and control of blood glucose levels, although it also seems to have roles in ionic regulation, molting, and reproduction (Keller 1992; Webster 1996). The spectacular wet

Table 6.2 Summary of differences between migrant or flying (long-winged) and non-migrant or flightless (short- or absent-winged) morphs in insects (most data from crickets).

Flying or migrant	Flightless or non-migrant
Slower development and growth	Faster development and growth
Reduced reproduction (lower fecundity and/or later oviposition)	Higher reproduction (higher fecundity and/or earlier oviposition)
Wing muscles present and large (may be histolyzed when reproduction begins)	Wing muscles absent or small
Higher concentrations of flight muscle oxidative enzymes	Lower concentrations of oxidative enzymes even if flight muscle present
Metabolism promotes triglycerides for flight fuel	Metabolism promotes amino acids for biosynthesis of ovarian protein
JHE higher in last instar nymphs—reduces JH	JH in higher concentration in last instar nymphs—less JHE

Sources: Dingle (2002); Zera (2004); Roff and Fairbairn (2007).

season migration of the Red Crab (see Chapter 3), with its dramatic change in metabolism, led Morris and colleagues to postulate a role for CHH, because its release from the sinus gland results in hyperglycemia. During forced extreme exercise in the crabs, there was a rapid pulsatile release of CHH. During the wet season migration phase, glucose levels were significantly elevated, and daytime CHH levels, when most locomotion occurs, increased. These migrations require extensive locomotor activity; crabs have limited aerobic capacity, so they become rapidly anaerobic with accompanying rapid increases in hemolymph lactate under intense activity. Evidence suggests that lactate increases CHH release which in turn causes a significant increase in tissue hyperglycemia. Thus in intense locomotion beyond aerobic capacity, CHH would be of clear adaptive significance in supporting metabolism associated with the intense (anaerobic) locomotion of migration (Morris et al. 2010). Crabs do, however, display behavioral adjustments during migration by walking slowly or intermittently for extended periods, presumably to avoid lactate build-up (Adamczewska and Morris 1994).

Endocrine influences on migration: vertebrates

There are many parallels between endocrine influences on migration in arthropods and vertebrates. Chief among these is the "capture" of hormones evolved for other functions to modulate migratory physiology and behavior. A summary of the multiple functions of vertebrate hormones, including their influence on aspects of migration, is given in Figure 6.8. It is apparent that vertebrate hormones

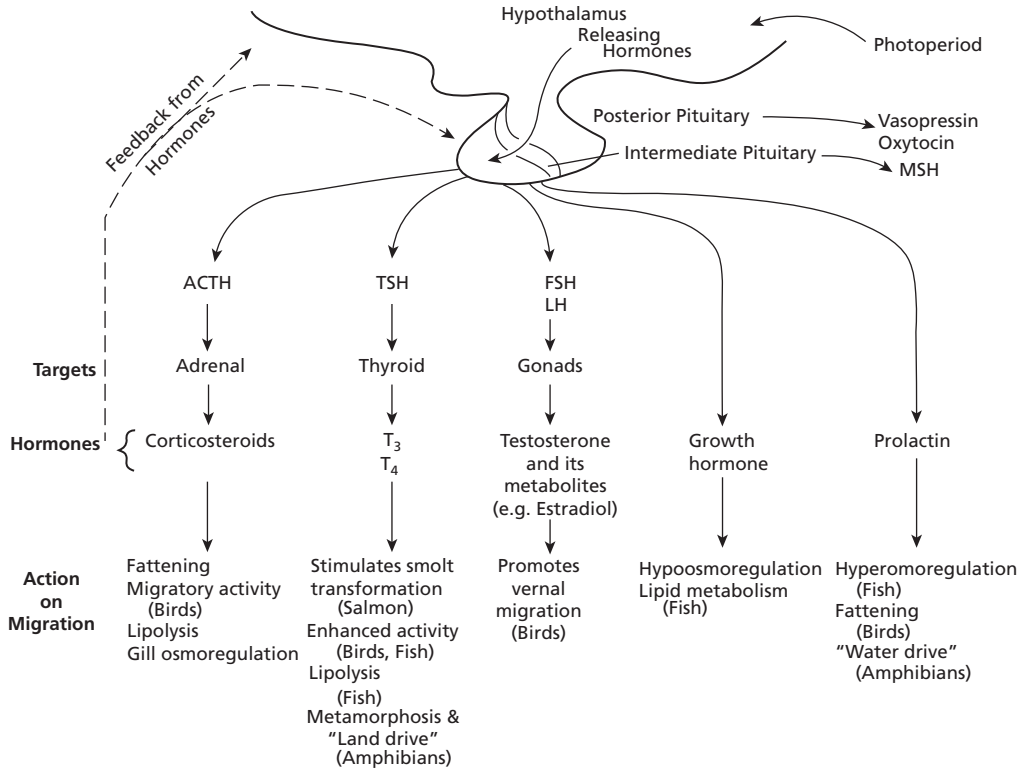


Figure 6.8 Summary of the action of various vertebrate hormones on the physiology of migrants. ACTH, adrenocorticotrophic hormone; FSH, follicle-stimulating hormone; LH, luteinizing hormone; MSH, melanocyte-stimulating hormone TSH, thyroid stimulating hormone; T3, tri-iodothyronine; T4, tetra-iodo-thyronine. From Dingle (1996) after a drawing provided by Eugene Spaziani.

are involved in functions ranging from energy mobilization to reproduction, and that these also play a role in migration. Such cross-functioning hormones are evident, first in the migratory life cycles of fishes.

Although a large majority of migratory fishes migrate within the oceans or within fresh water, most studies of fish migratory physiology involve commercially important species that migrate between fresh and salt water habitats (Dingle 1996). Two prime examples are eels (*Anguilla* spp.) that breed in the oceans and mature in fresh water and salmonids (*Salmo* and *Oncorhynchus* spp.) that do the reverse. Salmon in particular have been studied extensively. The early post-hatching stages of salmon in fresh water (egg, alevin, fry) culminate in a juvenile stage or parr (Cooke et al. 2011). Under the influence of increasing spring photoperiod, the parr undergo a transformation to the smolt (smoltification), the stage that migrates to the ocean (McCormick et al. 2000). The effect of photoperiod is dependent on temperature; accelerated smoltification occurred in Atlantic salmon (*S. salar*), for example, when water temperature was raised from ambient 2°C to 10°C.

Smoltification is a prerequisite for downstream migration to the ocean, and it is accompanied by morphological and behavioral changes that promote migration (Cooke et al. 2011). As the process proceeds, the fish become silvery and streamlined (McCormick et al. 1998), and their muscle physiology is altered. In smolts of Coho Salmon (*O. kisutch*) mean values of maximum aerobic swimming speed (U_{crit}) decrease, but prolonged muscle contraction, and twitch rates of muscle relaxation, contraction, and maximum force were increased (Katzman and Cech 2001). This change in muscle function is presumably an adaptation to allow more effective bursts of swimming during migration in fluctuating downstream-flowing currents. These changes in muscle are induced by the thyroid hormone T_3 (tri-iodo-thyronine). These changes in muscle physiology are accompanied by a loss of positive rheotaxis and replacement of territoriality by schooling behavior, both of which mean the fish lose their tendency to stay in place and instead move with the current downstream. At this time they show an increased preference for higher current velocities (Katzman et al. 2010). A natural surge of thyronine T_4 (tetra-iodo-thyronine, a derivative of T_3) may be a trigger for this downstream migration (McCormick et al. 1998; Cooke et al. 2011). Thyroid hormones also enhance lipid mobilization and a more active metabolism during migration (Hoar 1988; McCormick et al. 1998).

A major physiological requirement of migration from fresh to salt water is the ability to switch from acquiring ions from the medium to extruding them to maintain osmotic balance. In fishes this balance is maintained by so-called chloride cells in the gills. The gills excrete salts in the hyperosmotic marine environment to keep plasma electrolytes about one-third of seawater concentration. Changes in the gill are accompanied by reduced glomerular filtration in the kidney and by transport of non-valent ions across the hindgut wall. Water follows these ions into the tissues with the excess ions then excreted by the gills. As with the metabolic and muscle activity changes, these modifications of osmoregulation involve the action of hormones, in particular growth hormone (GH), insulin-like growth factor I (IGF-I), and cortisol. These hormones stimulate and regulate increased gill Na^+-K^+-ATPase activity to enhance excretion of excess ions, and GH stimulates the differentiation of freshwater chloride cells toward a seawater type (Prunet et al. 1994; McCormick et al. 2003; Sakamoto and McCormick 2006). The neuroendocrine hormone arginine vasotocin (AVT) is an additional hormone promoting gill NaCl excretion and renal water conservation, and provides integration across other physiological activities including stress responses, metabolism, and reproduction (Balment et al. 2006). In the return migration to fresh water, osmoregulatory gill activity is reversed, with uptake of ions rather than their excretion. In this case prolactin (in the same hormone family as GH), in company again with cortisol, regulates the gill chloride cells to promote uptake of ions in the now hypo-osmotic medium (Sakamoto and McCormick 2006). A summary of the complex smoltification process is illustrated in Figure 6.9.

Another species that migrates from breeding grounds to the sea and back is the Green Sturgeon (*Acipenser medirostris*). In this species juveniles tested in summer and early autumn that had not yet reached seawater tolerance (mean age of 98 days) had a positive relation between U_{crit} and total

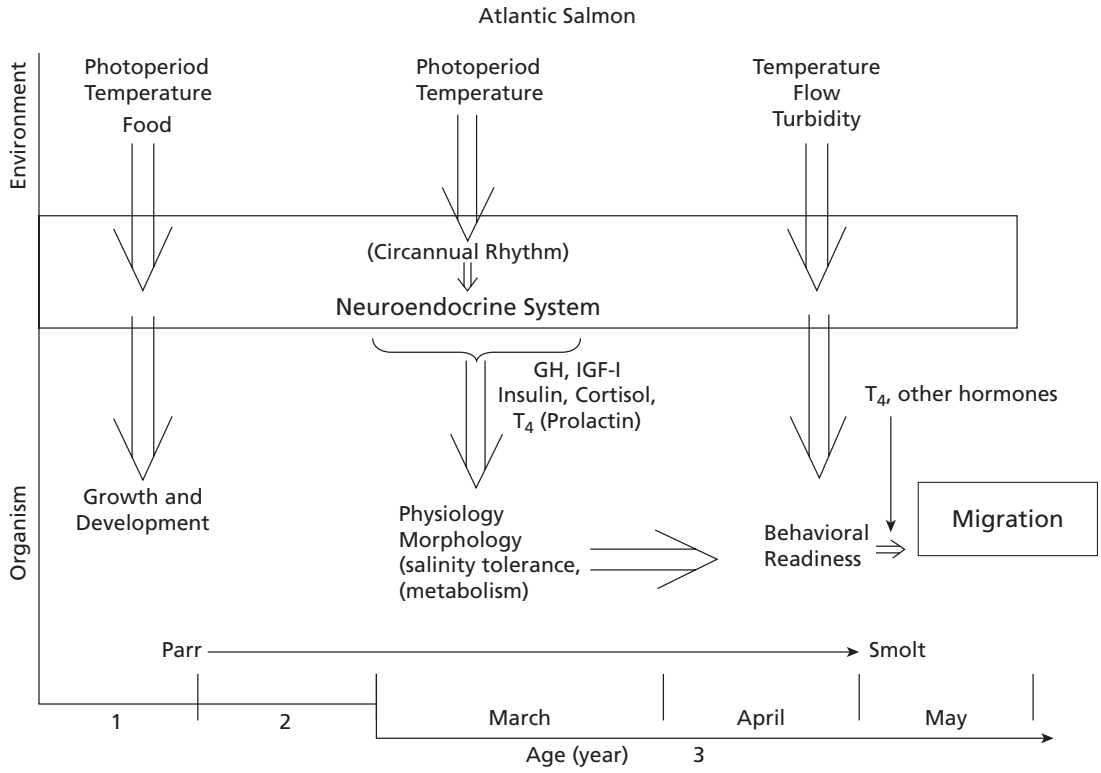


Figure 6.9 Interactions between the environment and the physiology of the fish that influence the transformation from parr to smolt to seaward migration in Atlantic Salmon. Note that both growth and physiological changes such as increased salinity tolerance contribute to developmental and behavioral changes. Based on a diagram and data discussed in McCormick et al. (1998).

length (Allen et al. 2006). Once they became seawater tolerant at 150 days mean age, they displayed a negative relation between U_{crit} and length. This latter effect may have been seasonal, however, as 288-day fish tested later again showed a positive relation between size and swimming speed. The smaller, younger fish had a larger relative pectoral fin surface area and a behavioral tendency to wedge the rostrum in the substrate (or in the wire mesh of a laboratory swim chamber; Allen et al. 2006) to avoid active swimming against the current. When they became older and seawater tolerant, they changed to a preference for downstream movement (Kynard et al. 2005). Osmoregulatory ability apparently increases with age and size. Juveniles occur in both fresh and brackish water, and osmoregulatory costs, as measured by oxygen consumption rates, are not prohibitively high. Only larger, older fish (1.5 years, 75 cm, 1.5 kg), however, seem to have the ability to enter sea water (Allen and Cech 2007). These various changes in sturgeon performance are apparently the result of thyroid hormones as suggested by data from salmonids (Coughlin et al. 2001), but clearly much more research is needed on hormone relationships (Allen et al. 2006).

Whereas salmonids and sturgeon breed in freshwater and migrate to the sea, the various species of *Anguilla* eels do the opposite. They must still, however, deal with the physiological changes necessary to effect the transition between the two salinities. The transition has been studied in the transition from freshwater yellow eels to the silver eel phase that migrates back to the breeding grounds. One change that takes place is a shift to higher mass-specific power output in the slow muscle of silver eels, presumably an adaptation to the sustained

swimming of this part of the migratory cycle (Ellerby et al. 2001). In addition there is morphological alteration of two types of gill chloride cells (Sasai et al. 1998). Lamellar cells are common in the gills of yellow eels, but decrease in number or even disappear in silver eels. At the same time filament cells are activated and presumably are responsible for the excretion of excess salt in hyperosmotic seawater. Accompanying the change in chloride cells is an increase in Na^+-K^+-ATPase activity. Two hormones seem to be involved in the process: somatotropin, a hormone stimulating growth and cell production, and cortisol, a corticosteroid that stimulates energy mobilization and is thought to stimulate increased Na^+-K^+-ATPase activity (Righton and Metcalfe 2011). Thus the changes occurring in the transition from yellow to silver eels pre-adapt the latter to marine life.

There are parallels between hormonal involvement in migratory diadromous fish and the migrations of urodele amphibians between terrestrial and aquatic habitats (Rankin 1991). In urodeles the two primary hormonal influences come from thyroxin (T_4) and prolactin (PRL). Thyroxin promotes metamorphosis and movement away from water, requiring responses such as water conservation as in fish entering the sea. Water conservation is aided further by roughening of the skin and reduced skin gland secretion (Iwata et al. 2000). The role of T_4 is not entirely clear because it is antagonized by PRL. That being the case, it is possible that metamorphosis and movement to land may be as much due to the absence of PRL as the presence of T_4 (Rankin 1991).

Studies of two Japanese newts, *Cynops pyrrhogaster* and *C. ensicauda*, reveal the role of PRL in the migration from land to water and subsequent reproductive activities (Iwata et al. 2000; Haraguchi et al. 2010). PRL induces increased locomotor activity and migration to water where reproduction takes place. Accompanying this movement are skin changes from rough on land to smooth with mucous secretions in water. PRL further increased male tail height, which results in increased power and efficiency of swimming, and, in concert with androgens, increased the number of Mauthner cells and their synapses in the brain. These cells are primarily involved with tail movement. A further PRL–androgen synergy enhanced the production of female-attracting pheromone and courtship movements on the part of males. These movements are also augmented by arginine vasotocin, another endocrine factor. The combination of PRL and estrogens resulted in development of the oviducts and secretion of the jelly in which the eggs are embedded at oviposition. An additional function of PRL is the stimulation of 7α-hydroxypregnenolone synthesis in the brain (Haraguchi et al. 2010). This neurosteroid is another factor stimulating male newt locomotion during the breeding period, contributing to migration to aquatic breeding habitats and subsequent courtship and mating. The transition from terrestrial resident, to migrant, to aquatic courtship and mating is thus facilitated in these urodeles by a sequence of synergistically acting hormones.

The most extensive studies of the action of vertebrate hormones on migration have been in birds, although the number of species assessed is still limited. As noted for other taxa, migration in birds involves several physiological functions with many regulated by hormones (Wingfield et al. 1990; Piersma and van Gils 2011). These functions include (1) fat deposition, (2) enzyme integration for energy storage and locomotion, (3) increased hematocrit for enhanced oxygen transport, (4) hypertrophy of flight muscles, (5) reduction in gut mass, and (6) development and synchronization of migratory behavior including organization of diel patterns. All of these must be integrated into the migratory life history cycle (Figure 6.1a and Bowlin et al. 2010). Not surprisingly hormonal regulation of these processes is complex and often not clear as a consequence. This regulation must also be integrated with other avian life-history functions such as breeding and molt. In spite of the complexities, the knowledge we do have suggests that hormones evolved for a number of different actions have been incorporated in support of physiological mobilization for migration, consistent with observations from other taxa.

The majority of studies on the role of hormones in bird migration have been on North Temperate birds with a pronounced seasonal cycle of spring and autumn long-distance migration (Figure 6.1a). Perhaps the best-studied species is the North American White-crowned Sparrow (*Zonotrichia leucophrys*)

with both migratory and non-migratory subspecies (summarized by Ramenofsky 2011). For convenience we can begin a summary of hormones and the annual migratory cycle in such a bird with the initiation of migration in the spring. Increasing daylength stimulates neuroendocrine pathways in the brain in birds in general (Hahn and MacDougall-Shackleton 2008 and Figure 6.1b). These pathways produce gonadotropin-releasing and -inhibiting hormones which are transmitted to the median eminence of the hypothalamus and the pituitary (Figure 6.8). Both types of hormone influence and regulate the secretion of the gonadotropins luteinizing hormone (LH) and follicle-stimulating hormone (FSH). In males LH induces testosterone production whereas FSH induces the steps to spermatogenesis. In females these gonadotropins enhance follicle development and estradiol and progesterone production. Feedback from progesterone and gonadotropin-releasing hormone induces a surge in LH that results in ovulation and egg-laying at the terminus of vernal migration on the breeding grounds. In both sexes, sex steroids feedback to the HPG axis to regulate the gonadotrophic hormones. The priming of this hormonal cascade means that birds arrive at the breeding grounds in condition to begin reproductive activities and nesting shortly after arrival (e.g., Bauchinger et al. 2007).

In addition to the changes in the reproductive systems that accompany spring migration, birds also display hyperphagia, fattening, and migratory restlessness prior to departure. The role of hormones in generating these responses is still not very clear. The neuroendocrine pathways controlling fattening versus restlessness and gonadal activity are apparently separate, as revealed by electrolytic lesions in specific sites in the hypothalamus (Ramenofsky 2011). Furthermore, destruction of the anterior portion of the median eminence did not affect fattening, gonadal development, or restlessness, whereas destroying the posterior portion eliminated all three. The posterior median eminence (and the brain infundibular nucleus) thus seems to produce neurosecretory products that regulate photoperiodic induction of both migration and breeding. It has also been speculated that androgens organize feeding centers to promote fattening and have organizing effects on subsequent stages of migration. How this organization works and how it may carry over to migration in the autumn remains frustratingly obscure. It is the case, however, that gonadal hormones do stimulate fattening prior to spring migration, as demonstrated by gonadectomy and replacement therapy, although the effect of replacement is delayed.

Other hormones may also be involved in bird migration. Prolactin has been assumed to stimulate appetite and fattening, but experimental results are unclear. Peak prolactin production is not coincident with the onset of fattening in either White-crowned Sparrows or Dark-eyed Juncos (*Junco hyemalis*) (Holberton et al. 2008; Ramenofsky 2011). There is, however, increasing evidence that corticosterone (CORT) plays an important role in behavioral and metabolic processes during migration itself; this is true in several species (Landys-Cianelli et al. 2002; Landys et al. 2006; Holberton et al. 2008). For example, in Bar-tailed Godwits, baseline plasma levels of CORT declined during the period of refueling on the wintering grounds, but rose sharply as birds reached peak mass in preparation for departure back to the breeding grounds. Baseline levels of CORT were high in Red Knots (*Calidris canutus*) arriving at the breeding grounds in spring, but dropped rapidly thereafter (Reneerkens et al. 2002). CORT is also a stress hormone that promotes fat metabolism and provides glucose to target tissues. As a consequence it may play at least two roles during migratory flight: (1) to mobilize stored fuels needed for flight, especially if unpredictable (metabolically stressful) conditions are encountered; and (2) to sustain the availability of fuel for target tissues including flight muscles, heart, and brain. Additional mobilization of activity may involve thyroid hormones such as T_3 and T_4. Great gaps in our understanding of hormone involvement in bird migration occur with respect to the cessation of migratory flight on both breeding and wintering grounds and in the transition to autumn migration when gonads are regressing. The reviews by Ramenofsky (2011) and Ramenofsky et al. (2012) give full attention to the issues.

The transition from migration to breeding is an important one for birds, but the physiological mechanisms mediating the change-over are not well known. Of particular interest are "carryover

effects" whereby events or activities at one season or life-history stage influence events at a subsequent stage (Harrison et al. 2007). These influences were studied in Black-browed Albatrosses (*Thalassarche melanophris*) by Crossin et al. (2012) in a South Georgia breeding colony. These seabirds spend the non-breeding season in foraging areas distant from the colony from which they migrate back to South Georgia to breed. Females experience three outcomes on the breeding grounds: (1) deferred breeding or breeding that can either (2) succeed or (3) fail. Crossin et al. examined the role of carryover effects on these outcomes, including measurements of body condition and hormone titers.

Carryover effects differed between breeding deferral and breeding success. Body condition measures such as low mass and low hematocrit and hemoglobin levels led to deferred breeding, not unexpectedly. Similarly low levels of progesterone, testosterone, and vitellogenin (an estradiol-dependent yolk precursor) were prevalent in deferring females. With respect to breeding, however, there were no detectable differences in body condition between failed and successful breeders. In contrast there were hormonal differences. Successful breeders displayed high levels of progesterone, low testosterone, and high vitellogenin, whereas the unsuccessful females displayed high testosterone and low vitellogenin. Thus it seems that the acquisition of resources that impact body condition can influence the decision on whether or not to breed or defer to a future date, a carryover effect. In terms of success once breeding is initiated, however, a more complex set of interactions involving hormones and presumably other physiological regulating mechanisms seem to be involved. This seems also to be true in other species (Harrison et al. 2011).

Fueling migration

> The metaphor of marathon running is inadequate to fully capture the magnitude of long-distance migratory flight of birds . . . a journey to the moon seems more appropriate.
>
> Guglielmo (2010), p. 336

If a journey to the Moon is an appropriate metaphor, how does one fuel such a journey? Marathon runners and other mammals fuel primarily with glycogen stored in muscle cells; migrant birds, however, store fat, and fuel their long-distance flights primarily though fatty acid metabolism (McWilliams et al. 2004; Pierce et al. 2005). The overwhelming majority of migrants use fat to fuel their journeys, because, relative to other fuel sources, it has great advantages (Dingle 1996; Piersma and van Gils 2011). When oxidized, 1 g of fat yields 38 J of energy compared with 5 J for wet protein and 4 J for wet carbohydrate. This is largely because fat does not require water for storage; each gram of carbohydrate (as glycogen), in contrast, requires an additional 3 g of water. Even without water, fat is more than twice as energy rich as "dry" carbohydrate or protein (Jenni and Jenni-Eiermann 1998; Piersma and van Gils 2010). Because maintenance costs for adipose tissue are also roughly 10 times less than for other tissues, it is hardly any wonder that fat predominates as the fuel for migration.

Before setting off on their journeys, migrants can store enormous amounts of fat. Monarch Butterflies, for example, can store up to 125% of their lean dry weight as fat, and even tiny insects such as aphids may store fat up to 30% of body weight (Brower 1995; Dingle 1996). Migrating seeds that are wind- or animal-transported average about 25% of their dry weight in fat (Lokesha et al. 1992). In silver eels 25–30% of body mass is in fat at the start of their oceanic journey to the breeding grounds. They do not feed at this time, and the reduced gut serves only to assist osmoregulation (Righton and Metcalfe 2011). White Sharks (*Carcharodon carcharias*) also store fat for migration, and this increases buoyancy. Measurements of buoyancy reduction during long-distance migration (4,000 km) in these large elasmobranchs demonstrate the use of lipid reserves to fuel the effort (Del Raye et al. 2013). Many migratory songbirds virtually double their body weight by depositing pre-migratory fat; Red Knots weighing roughly 130–160 g carry about 80 g of added fat on flights from stopover in Iceland to breeding grounds in Greenland and eastern Canada and consume about 50 g of this fat in flight (Piersma et al. 1999; Morrison et al. 2005). Like eels, Red Knots reduce their guts prior to departure.

There are trade-offs involved in carrying so much fat. A bird with 50% body fat consumes about 40% more energy than a bird covering the same distance

with only a 10% fat load, even though a 50% load allows a small bird to fly for three to four days up to about 4,000 km (Alerstam 1990). In the case of breeding migrations, the migrants also need some fat at the end of the journey to contribute to offspring production. There are some additional problems with fat itself. The insolubility of the component fatty acids means that they are difficult to transport to working muscles at a rate fast enough to support the aerobic demands of flight (Guglielmo 2010). Birds compensate for this by expressing large amounts of fatty acid transport proteins on muscle membranes and in the cytosol. Just how important fatty acid composition is to migration success or whether particular types (e.g., ω-3 or ω-6) serve better is at present unclear. Protein may be important in other ways as well. The central nervous system cannot oxidize fatty acids and therefore needs amino acid-derived glucose (Jenni and Jenni-Eiermann 1998). Furthermore, burning protein yields much more metabolic water than fat and so may prevent dehydration; indeed more protein may be burned on migrations over large deserts (Piersma and van Gils 2010). All these attributes and complexities of fuel utilization suggest that migration is more a "Moon shot" than a simple marathon (Guglielmo 2010).

Bats are additional warm-blooded vertebrates that undertake long-distance migrations, in some species for distances of ≥1,000 km. There is some speculation, but at this juncture little data, on the energetics of bat migration (McGuire and Guglielmo 2009; Guglielmo 2010). Bats likely have evolved similar physiological mechanisms to birds but with some interesting differences. Activity levels of oxidative enzymes in bat pectoralis muscle are among the highest in any vertebrate muscle, and the relative capacities of lipid- and carbohydrate-specific enzymes suggest that lipids are the chief flight fuel, especially in insectivorous, as opposed to frugiverous, species; the latter use more glucose. In birds migration and reproduction are separated, but in some migratory bats mating may occur in autumn, with females storing sperm over the winter and becoming pregnant during spring migration. Males conserve energy by entering overnight torpor when it is cold. In contrast females must remain active under the same conditions and so incur higher energetic costs than males. How these conflict situations are resolved is a subject for future research. Interesting opportunities for comparative studies are provided by partial migrants like the Free-tailed Bat, *Tadarida braziliensis* (Fleming and Eby 2003).

In insects with their open circulatory systems fuel is more slowly transported to active muscles than with the closed system of vertebrates. One result is that at the beginning of long flights, at least in locusts, the flight muscles oxidize carbohydrate to "kick start" flight (Goldsworth and Joyce 2001). After about 10 min of flight, octopamine increases in the hemolymph and stimulates fructose synthesis (as fructose 2,6-biphosphate), increasing glycolysis and modulating the power of muscle contraction that insures a smooth transition from carbohydrate fuel to fat. This hormone comes from cells in the metathoracic ganglia. After some 15 min of flight, locust flight muscles switch over to using fat and adipokinetic hormones (AKSs—see 'Endrocrine influences on migration'); the latter mobilize diacylglycerols from stores of triacylglycerol in the fat body. After about 30 min diaglycerol in the hemolymph reaches a steady state and fatty acids become the major fuel supporting long-duration flight and migration. The diacylglycerols are not water soluble and require lipoproteins for transport. These lipoproteins are interesting because they operate as a continuous shuttle system carrying diacylglycerol from fat body to flight muscle as low-density lipoprotein and return to the fat body as high-density lipoprotein to pick up more diacylglycerol. This is in contrast to the transport system in vertebrates where the lipoprotein complexes are not reusable (Goldsworthy and Joyce 2001). The energetics of locust flight fuel transport is summarized in Figure 6.10.

In addition to carbohydrates and fat, proline is used as a flight fuel in several insect species especially, apparently, in beetles (Goldsworthy and Joyce 2001). Scarab beetles may use proline as a flight substrate almost exclusively (Gäde 1997a,b), and other beetle species use a combination of carbohydrate and proline. The Tse-tse Fly (*Glossina morsitans*) also uses proline almost exclusively (Bursell 1981). It is not clear, however, whether proline is actually used in prolonged migratory flight.

The accumulation of the energy reserves for migration occurs by means of diet shifts and the

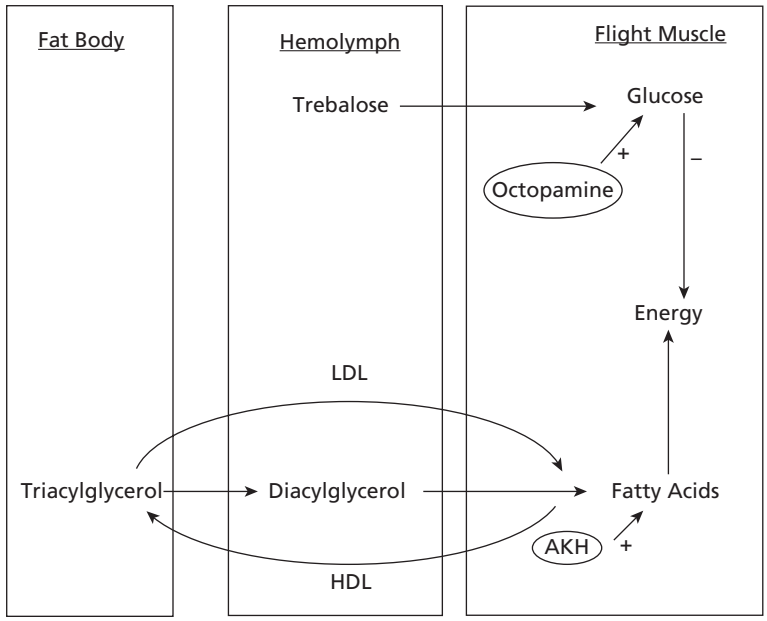


Figure 6.10 The mobilization of resources in fat body and hemolymph to support activity in locust flight muscle. Transport and recycling is provided by low- and high-density lipoproteins (LDL and HDL) and the glucose and fatty acid products are metabolized via the hormones octopamine and adipokinetic hormone (AKH). From data in Goldsworthy and Joyce (2001).

modification of metabolic pathways. These changes in birds are of three sorts (Dingle 1996; Bairlein 2003). First, pre-migrants greatly increase their appetites. This hyperphagia involves more rapid rates of feeding rather than increases in meal size. Second, accompanying enhanced appetite are increases in lipid synthesis and rapid deposition of fat in subcutaneous and visceral "depots." These fat deposits are visible through the skin if the feathers are spread, notably on either side of the sternum, allowing a rapid visual assessment of the condition of the bird. This hyperlipogenesis depends not only on increased dietary intake, but also on increased rates of fatty acid synthesis in the liver, so that metabolic adjustments occur as well as those involved in feeding. These adjustments may alter fatty acid composition of fat stores and even muscle membranes to enhance endurance, since birds fuel high-intensity endurance flights such as migration primarily with fatty acid oxidation (McWilliams et al. 2004; Guglielmo 2010).

The third contributing factor to increase fat accumulation is diet shift. For example, observations on a number of species in both the Old and New Worlds have noted that autumn migrants feed heavily on fruits (Bairlein 1990, 2003; Dingle 1996). This appears to be a significant adaptation because fruits are often locally abundant and easily procured, and they provide a rich carbohydrate source to support fat deposition. Some species may make deliberate choices toward diets higher in protein and fats. Garden Warblers (*Sylvia borin*), when offered a choice among experimental diets varying in fats or proteins independent of caloric levels, consistently take foods higher in these two nutrients (Bairlein 1990). Choices may vary as migration approaches, as is the case with American Robins (*Turdus migratorius*) (Lepczyk et al. 2000). These birds were offered a choice between synthetic sugar-rich and lipid-rich fruits of equal caloric value. In both summer and autumn, robins preferred the sugar-rich fruits. However, assimilation efficiency for lipids increased in autumn, and the overall intake of the lipid-rich fruits increased at that time even through the birds still preferred the sugar-rich diet. The result was a nearly equal rate of energy gain from these lipid-rich fruits.

The composition of fatty acid in foods can also apparently influence migratory performance (Pierce and McWilliams 2005; Pierce et al. 2005). For example, Red-eyed Vireos (*Vireo olivaceous*) fed for four months on diets of either 82% or 58% unsaturated

fats developed into birds with fat stores of 77% versus less than 66% unsaturated fatty acids. Mass-specific resting metabolic rates were similar, but the mass-specific peak metabolic rates were 25% higher in the birds fed and storing the lower levels of unsaturated fats. Thus the fatty acid composition of stored fats was mainly a function of diet composition, with potentially important consequences for fueling prior to migration and at stopovers to replenish fat stores during migration. There is still, however, much work needed before we can fully understand the relation between fatty acid composition and exercise performance during migration (Pierce and McWilliams 2005; Pierce and Guglielmo 2009).

Summing up

Specialized migratory behavior is accomplished by a syndrome of physiological activity and morphological changes that function at several levels. They incorporate the action of hormones, programmed variation in metabolic pathways, and actions of the central nervous system. All of these functions must be integrated not only with each other but also with the environmental factors and events that determine the migration program and its long-term fitness (Piersma and van Gils 2010). The syndrome is synchronized with the external world by both circadian and circannual rhythms that allow precision cue responses of great complexity that are often exquisitely sensitive to daily changes and seasonal calendars. Birds and insects can both respond to daylength changes of as little as 15 min, allowing pre-emptive migration in pursuit of optimal habitats. Birds can adjust to asymmetric changes in external time-givers when they cross the Equator and so assure that their migratory life cycles are appropriate to their breeding grounds. Insects use daily rhythms to separate migration from other activities and daylength to incorporate diapause into migratory cycles or to trigger developmental events to produce or eliminate wings. Marine fishes and crustaceans can time their migrations to correspond with the flows of the tides.

The physiological functions of migrants and their co-ordination with other life-cycle events such as reproduction are mediated by systems of hormone action. The oogenesis–flight syndrome in insects is a function of juvenile hormone. Migration is stimulated by low titers, whereas at higher levels reproduction is triggered. There may be feedback from long flights to accelerate the rise in JH toward promoting mating and egg production. In certain moths, JH contributes to the sequencing of first migration and then the production of mating pheromones. The alternation of forms in insect flight polymorphisms and polyphenisms is controlled by JH whose levels are then regulated by its esterase, JHE. The hormone translates genetic and environmental information into the adaptive behavioral and life-history outcomes. The multi-functioning of hormones is seen again in vertebrates where it is also the case across the vertebrate classes. As in insects, hormones evolved for a variety of different functions are "captured" for use in migratory syndromes. Thyroid hormones enhance metabolic activities in service of a number of adaptive functions. In the service of migration they are involved with smoltification in salmon, exodus from water after breeding in urodeles, and mobilization of fuels in fish and birds. Prolactin is interesting because in urodeles it stimulates movement to water prior to breeding and subsequent mating activities. It may have a role in birds, but this is not clear. Its other functions include mammalian lactation. In addition to its functions in growth and development across vertebrates, growth hormone regulates the gill osmoregulation that must accompany migration in diadromous fishes.

In spite of the variety of regulation, however, migration syndromes display commonalities across taxa from hormone capture to fueling with fat, to synchronization with other life-history functions, especially reproduction. The evolution of migratory behavior in all its spectacular variety has been accompanied by the incorporation of basic physiological mechanisms that have diverged relatively little. The similarities occur in spite of variation in phylogeny, environment, and mode of life, although all three profoundly influence the details of migratory tactics that meet the demands of a grand strategy of assuring successful breeding when conditions are favorable, successful escape when they are not, and successful preparation prior to breeding events.

CHAPTER 7

Biomechanical and bioenergetic constraints on migration

To undertake movement an organism must have the apparatus necessary for the undertaking and the energy to drive the apparatus. Moreover, different movements require different types of structures for optimal performance. In birds, long pointed wings are most efficient for soaring, and these we see in dynamically soaring seabirds such as albatrosses. Maneuverability in a forest understory, on the other hand, is much more efficient with short rounded wings like those seen in thrushes. Because both albatrosses and thrushes migrate, they must compromise in some way to serve both foraging and migration. Such compromises require trade-offs brought on by selection imposed by the constraints of the two basic life-history requirements. Furthermore, as we have seen in Chapter 6, migration usually requires large stores of energy in the form of fat. The accumulation of fat stores can change the shape and mass of a migrant substantially with consequences for wing loading (Table 7.1) and flight performance. In this chapter, I consider biomechanical and bioenergetics costs and trade-offs that constrain locomotion as it relates to migration. Trade-offs involving energetic, genetic, and life-history constraints also enter into the migration equation and are considered in Chapters 6 and 14. I use the term constraint in the sense that "evolutionary constraints are restrictions or limitations on the course or outcome of evolution" (Arnold 1992).

Not all forms of locomotion are equally efficient. Flight is a far more effective means of transport than either swimming or any form of terrestrial locomotion (Schmidt-Nielsen 1975). Expressed as energy required per unit of body mass, it takes much less energy to fly than to swim or walk; swimming takes less energy than walking or running. With flight or swimming, efficiency can be greatly increased by engaging winds or currents to aid transport (Chapter 5). All else being equal, we would expect more migration, or at least more long-distance migration, among flyers or swimmers than among groups of organisms constrained to move by walking, running, or slithering over the land surface. Generally, this is the case, although some large land animals such as the wildebeest in Africa or caribou in the Arctic move impressive distances. Within flying and swimming taxa, nevertheless, there is still great variation in performance, including energetic and mechanical performance accompanying migration. A further aim of this chapter is, then, to explore migration-related constraints in those groups. Before doing so, however, I shall consider some rather special cases of migration, first that incorporate devices, in one set of cases the silken threads used by spiders and some larvae of Lepidoptera, and second, the seeds evolved for transport in vertebrate guts. In both instances, mechanical constraints are an integral part of the migration process.

The constraints of silken threads

Spiders and the lepidopteran larvae that use silk threads for aerial transport use silk for other purposes as well, spiders for webs and the larvae for webs or cocoons. The use of silk in travel may therefore be a consequence of "capture" for an additional and temporary use. In the Lepidoptera adults possess wings, so larval transport seems to be a secondary

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Table 7.1 Definitions of some terms used in the biomechanics of performance.

Term	Definition
Induced power	Kinetic energy per unit time imparted to the medium to produce momentum
Parasite power	Power required to overcome drag forces on the body
Profile power	Power required to overcome drag forces on propelling structures (wings, fish tail, etc.)
Wing (fin) chord	Width measured along direction of flight or swimming (variable along span)
Span	Tip-to-tip distance when wings (tail) fully spread
Aspect ratio	Ratio between span and average chord
Wing loading	Weight (not mass) per unit wing area (weight = mass + gravity)

Source: Dingle (1996) after various sources.

mode of travel, probably best considered as ranging with dispersal away from siblings to optimize foraging opportunities by reducing competition. In some cases, however, especially in those species where adult females are wingless, the greater travel distance afforded by ballooning may afford some colonization potential. These latter, especially, are likely to be denizens of forests where the presence of trees will be an impediment to movement on parachutes. Modeling studies suggest that, given wind and structural conditions in forests, less than 2% of airborne larvae would move more than a few tens or hundreds of meters (summarized in Dingle 1996). However, this is potentially an important means of transport, either to optimize foraging or colonize, if the alternative is no or little movement due to the size limits of tiny larvae. The question of the adaptive vale of ballooning by lepidopteran larvae is very much in need of further investigation in the context of a foraging/ranging/colonizing perspective.

In spiders, as well as lepidopterans, the effectiveness of ballooning is strongly influenced by the effectiveness of take-off behavior. We have seen in Chapter 2 that spiders climb to the tops of vegetation to assure movement in the airflow free of intervening obstacles. As soon as some vertical acceleration is assured, the aeronaut should deploy silk thread rapidly. Furthermore, deployment rate should increase with spider mass and latency should decrease; to put it another way, a 0.2 mg spiderling has more flexibility in choice of take-off conditions than a 0.4 mg spiderling (Suter 1999). In any case the fact that the atmosphere is turbulent produces the constraint that the whole process is probabilistic.

This constraint is further emphasized by Reynolds et al. (2006, 2010). In contrast to earlier models by Humphrey (1987; summarized in Dingle 1996) which assumed rigid silk threads, these authors modeled draglines as being extendable and flexible. They concluded that movement in the naturally occurring turbulent flows that the spiders will experience does not depend very much on the length of the draglines. As one consequence, dragline length has little predictive value in determining distances traveled. Ballooners with flexible, extendable draglines will rise in the air when those with rigid silk would not, and so can travel considerable distances. Ballooning is likely to be most effective when the stability of the atmosphere is "non-ideally convective," a condition present in warm temperatures and a light breeze. Observations of spider take-offs indicate that the ballooners are in fact constrained to non-ideally convective conditions of the atmosphere. They avoid the hazardous conditions for ballooning that occur with high winds.

The properties of silk and the limits on its length imposed by the possibility of entanglement limit the size range of ballooning spiders (Roff 1991; Dingle 1996). Mean frequency distributions of spiders ballooning over Missouri, USA, and New South Wales, Australia, confirm that ballooners are generally small. The great majority was <2 mg, and only a negligible fraction exceeded 4 mg (Greenstone et al. 1987; Figure 7.3 in Dingle 1996). At least one spider species has, however, found a way around the size constraint. This is the social spider, *Stegodyphus dumicola*, of the semi-desert regions of Namibia (Schneider et al. 2001). Adult females of this species are 7–14 mm in body length, very large by the standards of ballooning spiders. Nevertheless, they were observed to undertake ballooning by tiptoeing at the tops of objects and rising in the light breezes to a height of about 30 m before they were lost to sight. They performed this rather remarkable

feat by spinning out a number of silk threads which then fanned out from the spider's body in a triangular sheet of about a meter in length and a meter width at its distal end, forming a large and effective parachute. In the largely open habitats of Namibia such a sheet is probably not much subject to entanglement. Other species in the genus occur over southern Africa and are also known to balloon. Only females mated but not yet with developing eggs were observed to balloon, suggesting that ballooning is a major colonization migration in the life cycles of these colonial spiders. Both the mechanical and ecological aspects of the migration, however, remain to be fully worked out.

Vertebrate transport of fruits and seeds

Insects and spiders are not the only organisms that migrate with the aid of special devices that involve constraints. There are several examples from plants. Many species such as the familiar milkweeds and dandelions rely on a parachute-like pappus. As with ballooning spiders, seeds that rely on wind transport by means of a pappus will be size-limited. A second example of devices used for seed transport is the sticky, spined, or hooked seed coats which function effectively for transport in mammalian fur coats, as any dog owner who has tried to remove "burrs" from a family pet can readily testify. Here the most effective form of transport will be designed by natural selection to match the thickness and other properties of the fur of the local mammal fauna, but in any case there is likely an upper size limit to the seeds. Finally many plant species, especially tropical trees, are transported in both avian and mammalian guts. Many of these seeds possess a seed coat or fruit pulp that must be scarified or partially digested before they can germinate (Samuels and Levey 2005; Robertson et al. 2006). The seed coat is thus analogous to the temporary inhibition of "vegetative" (growth and reproduction) responses of animal migrants. The evidence for this is preliminary and in need of further confirmation, however.

One of the plant groups that relies on avian seed transport is the sandalwoods (*Santalum* spp.), tropical trees highly valued for the aromatic oils of the heartwood and in danger of overexploitation. The fruit of an Indian species, *S. album*, is consumed and the seeds transported by at least 10 species of bird (Balasubramanian et al. 2011). The most important of these are the Asian Koel (*Eudynamys scolopaceae*), a jay-sized member of the cuckoo family, and the Common Myna, *Acridotheres tristis*, similar in size to the koel. Studies using the koel demonstrated that size variability of the seeds imposed a trade-off (Hegde et al. 1991). Larger seeds were more successful at germinating, but the birds prefer smaller fruits and distribute them farther; when they do swallow large fruits, the seeds are usually deposited very near the parent tree. In the sandalwood of New Caledonia (*S. austrocaledonicum*) seed transport is primarily by the Cloven-feathered Dove, *Dreptanoptila holoserica*. Passage through the gut of this pigeon increased the rate of germination and shortened seed dormancy (Tassin et al. 2008). The former result is a clear fitness advantage; the latter may be so, but it depends on environmental conditions. In general, however, gut passage improves fitness, fulfilling the requirements for being a migrant.

A survey of Southern Hemisphere plant species with vertebrate-disseminated fruits further confirms the influence of the transporting agents on the size and shape of fruits and seeds (Lord 2004). Some 75% of New Zealand plant genera share some species with Australia, but Australian species have evolved in the presence of large mammals whereas New Zealand species have not. Furthermore, New Zealand bird species that consume fruits and transport seeds are on average smaller than Australian birds that do so. Comparisons within genera reveal that New Zealand plants had significantly smaller fruits, and these fruits were more ellipsoid in shape, as would be predicted for easier swallowing by smaller birds. The same result is observed in overlapping genera between New Zealand and South America. In contrast, no size or shape differences occurred between New Zealand and New Calendonia, where plants also evolved in the absence of mammals or large frugivorous birds. In the recent past, species of moa were frugivores, but these large birds appear to have been neither specialist nor selective frugivores and ate all sizes of fruits. The result was that the moas seemed to have exerted little selective pressure on fruit or seed size (Lord 2004).

Constraints in swimming

Swimming requires sustained motion through a relatively dense and slightly viscous fluid, a fluid that is denser than air. The generation of movement thus places relatively high energy demands (relative to flight) on the swimming organism which must produce thrust to create the required motion. This is partly compensated for by flotation which means that, unlike airborne organisms, little energy is required to stay above the substrate. In fishes thrust is generated by oscillations of the entire body in the case of "anguilliform" or eel-shaped fishes or of the caudal fin in the case of "carangiform" fishes, those with a distinct tail fin. In general, swimming efficiency is increased with a fusiform or torpedo-shaped body, which reduces drag due to turbulence on the body and reduces parasite power (Table 7.1) and the energy needed to overcome drag. The degree of "streamlining" is often expressed as the fineness ratio which indicates the relationship between length and height/width in fish (e.g., Assumpção et al. 2012). Migratory fishes that travel long distances or against currents such as herring, tuna, or salmon or various species in tropical rivers (Assumpção et al. 2012) are fusiform in shape, whereas non-migrants such as bass, sunfish, and many reef fishes assume other shapes, especially lateral flattening which has advantages for moving through narrow spaces, for example weed beds or between coral heads. These generalizations, however, mask a great deal of variation and numerous exceptions brought on by ecological demands other than migration.

Carangiform fishes experience less drag on the body than anguilliforms, but a much smaller part of the body, most notably the tail, is used to generate thrust. This requires an efficient propulsor, for instance the "lunate" or crescent moon-shaped tail. This form of caudal fin has a large aspect ratio (Table 7.1), which increases the lift:drag ratio up to a maximum value of ~5–10, creating a very effective mechanism for propulsion. Its effectiveness is further increased by stiffening the fin so that it does not bend as it oscillates back and forth. Again many migrant fishes have evolved lunate tails, notably powerfully swimming species such as salmon and tuna. These species also possess muscles of high metabolic rates as drivers of propulsive forces (note the high values of ω-3, so valuable in human diets!).

The relatively greater drag on anguilliform bodies had led earlier workers to view eels as relatively inefficient swimmers, with selection favoring the shape for reasons other than swimming efficiency (Dingle 1996). There was also considerable debate as to whether Atlantic eels, for example, stored sufficient energy reserves for their long return migrations to the breeding grounds, in view of the great reduction in the gut and absence of feeding en route. It turns out, however, that migratory eels are remarkably efficient swimmers (van Ginneken et al. 2005). Atlantic eels, first, increase the mass-specific power output and operating efficiency of slow muscle as they transition from the yellow phase to the oceanic migratory silver eel phase (Ellerby et al. 2001). The increase in power was three-fold from 0.24 W/kg in the yellow phase to 0.74 W/kg in the silver phase, and power peaked at higher contraction cycle frequencies (0.5–0.8 Hz in silver eel muscle versus 0.3–0.5 Hz in yellow eel muscle). These changes would be an advantage at the sustained swimming speeds of migration. It is also the case that eel muscles deliver peak power at much lower contraction frequencies than do the muscles of the carangiform trout in which peak power is around 2–3 Hz (at 11°C; Hammond et al. 1998).

Further comparisons between eels and trout swimming revealed just how efficient eels are (van Ginneken et al. 2005). One measure of efficiency is the cost of transportation (COT) which is the mean gross energy cost of travel (Schmidt-Nielsen 1972). This was calculated from measurements on eels swimming in a flow tank for 5,533 ± 334 km over a period of 173 days. A second experiment compared eels and trout at the optimal swimming speeds for each species. Measurements included rate of oxygen consumption and energy loss from bomb-calorimetry. From the data obtained the COT values for eels and trout were 0.68 and 2.783 kJ/kg/km, respectively; in other words, eels were by a considerable margin the more efficient swimmers (efficiency = rate of useful energy expenditure divided by the total rate of energy consumption). In general, anguilliform swimmers are more efficient at low speeds whereas carangiform ones are more efficient at higher speeds (Tytell et al. 2010). Routine

metabolic rates of eels are similar to other equal-sized fish and other animals, so special adaptations in metabolic rate cannot explain the eel's higher efficiency. Nor apparently can various adjustments in muscle recruitment. Eels, however, migrate in the deep sea, and it is known that increased pressures increase the efficiency of oxidative phosphorylation (Theron et al. 2000). The lower temperatures of the deep sea may also influence efficiency, and, as we saw in Chapter 5, eels take advantage of favorable currents. Their efficiency may also be enhanced by slower swimming (Tytell et al. 2010). Although we still lack a full understanding of the phenomenon, the fact remains that eels swim four to six times more efficiently than other fish, even across swimming styles. Thus fasting European eels should have no problem swimming the ~5,500 km from the coasts of Europe to the presumptive spawning grounds in the Sargasso Sea. They are quite able to overcome the constraints of a drastically reduced gut.

A general way to maximize efficiency for migrating fishes is to swim at optimal speed, or the speed at which energy expenditure is least per unit of distance traveled. This value scales to size roughly according to the formula $S_O = kL^{0.43}$ (Weihs 1984), where S_O is the optimal swimming speed, k is a constant that has a value of ~0.5 if speed is measured in meters per second, and L is the "fork length" or the distance from the nose to the point at which the tail forks. The relationship indicates that the optimal speed will be greater for larger fishes and so migration should be favored in larger fishes. The situation is more complicated if fecundity trade-offs are factored in. A migration distance corresponding to the energy equivalent of the gonads can be defined as the "fecundity equivalent distance" (Roff 1991). For an average fish FED [km] = 52 $GL^{1.03}$ where G is the ratio of gonad to somatic weight and L is fork length. Like optimal speed, FED scales to size, favoring a smaller trade-off between fecundity and migration distance in larger fishes. Empirical data suggest that this is true across taxonomic levels. Within species, for example, migrant stickleback (*Gasterosteus aeuleatus*) populations are larger in mean size than non-migrant (Snyder and Dingle 1989) and among the Gadiformes migrant species are larger than more sedentary forms (Roff 1991). A number of behavioral mechanisms including schooling, selective tidal-stream transport, and selection of currents may further increase efficiency of transport during migration (Chapter 5 and Dingle 1996).

Constraints on flight

Migration in birds, bats, and insects depends on flight, and flight performance is subject to constraints (Dingle 1996 and references therein; Åkesson and Hedenström 2007). We can start our consideration of flight constraints and the constraints of migration by examining what it takes to become and remain airborne. The force required to raise a body in a fluid and overcome gravity is known as *lift* and a body of suitable design will be influenced by a lifting force if placed in a current or wind stream. A design that accomplishes this is an airfoil or wing constructed so that the fluid passes more rapidly over the upper surface than over the lower, at the same time directing the current slightly downward. Bernoulli's law states that the sum of kinetic pressure and static pressure around a body is a constant. This means that when the velocity of a current—and thus its kinetic pressure—increases, the static pressure falls and vice versa. Because of a wing's shape, air moves more rapidly over the upper surface and decreases the static air pressure above relative to that below the airfoil, generating lift. The lower pressure above the wing contributes about twice the lift of the higher pressure below, so that, somewhat counterintuitively, an airplane or a bird is actually suspended in the air rather than resting upon it. Note that lift does not have to be directed upward, but occurs at right angles to the direction of flow (cf. fish tails). One can also describe lift by the movement of vortices around the airfoil (the "bound vortex"). Behind the wing is a wake of trailing vortices with the same circulation as the bound vortex; the vapor trails of high-flying aircraft are caused by these trailing vortices under the right atmospheric conditions.

In order to move through the medium, an organism must generate power (= the energy consumption per unit time). A flying bird must produce power to accelerate the air downward. This is *induced power* (see Table 7.1 for definitions), and it increases with weight (it takes more power to move heavier bodies), but it decreases with flight speed,



Figure 7.1 A Western Sandpiper (*Calidris mauri*) flying in the University of Western Ontario wind tunnel. By passing a fine spray of oil droplets over the flying bird, factors such as the patterns of drag and lift forces can be observed. Photo by Brock Fenton courtesy of Chris Guglielmo.

wing span, and air density. Countering this decrease is the fact that movement generates friction on the bird and turbulence around it, both of which cause drag that increases with speed. Birds can be flown in wind tunnels such as that at the University of Western Ontario (Figure 7.1), and the pattern of air currents over the flying bird can be seen with a fine spray of oil droplets that passes over its body while in flight. The power used to overcome drag on the body is called *parasite power* (because the body is only being carried along and does not itself produce power); the power used to overcome drag on the wings is the *profile power*. The algebraic sum of the three power outputs is the total power needed to propel the bird through the air, P_{fl} or flight power, a value which varies with weight, speed, and air density.

The relationships of P_{fl} to weight and speed are illustrated in Figure 7.2 (and see Dingle 1996; Alerstam and Hedenström 1998; Rayner and Mayberry 2003; Åkesson and Hedenström 2007). The values of P_{fl} form approximately U-shaped curves, shown here for birds of two weights, but the same wing span and shape. For complex reasons the curves tend to become slightly concave at slower speeds. Birds put on weight (fat) prior to migration so a curve for a heavier bird with the same wing form is realistic. The lowest point on the curve, at which flight speed requires power, is designated V_p or speed at minimum power; note that this is a bit higher (V_p) for the large bird (which still must use more power). The minimum cost of transport (V_c) is given by the tangent to the curve of a line drawn from the origin or zero power. The minimum time for migration, V_t, depends on the rate of energy accumulation, P_e, indicated on the negative ordinate,

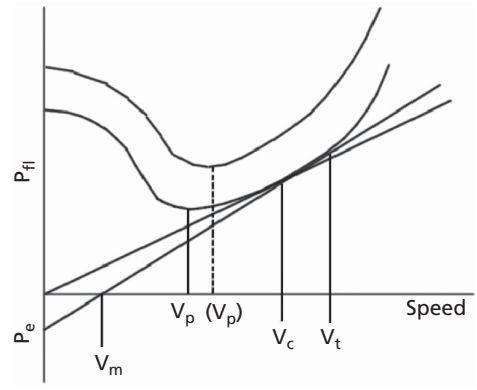


Figure 7.2 The relation between the power required to fly (P_{fl}) for a bird and its air speed. The flight speeds associated with minimum use of power (V_p), minimum transport costs (V_c), and minimum time of migration (V_t) are shown by vertical lines from the curves to the abscissa. V_c is determined by a line drawn from the origin tangent to the power curve. V_t depends on the rate of energy accumulation, indicated by P_e on the ordinate as below the origin; the tangent of a line drawn from P_e past the power curve gives V_t. The point at which the line drawn from P_e crosses the abscissa gives V_m or the overall migration speed.

Sources: Rayner (1988); Dingle (1996); Åkesson and Hedenström (2007).

and a line from a point representing this rate, drawn tangential to the power curve, gives V_t. The point at which this tangent crosses the abscissa, V_m, is the overall migration speed. This overall speed is a function of cost, time (including any necessary stopovers), and rate of energy accumulation before and during migratory passage. If birds have plenty of time for migration, more likely in the autumn when not pressed to start breeding, they may favor a slow speed with the low cost of minimum power and fueling (see also Chapter 12). The demand for early arrival to establish territories in the spring may select for V_t, but this will require more energy.

Scaling relationships influence the generation of power in birds (Rayner 1988; Ellington 1991). Power requirements increase with mass as $M^{7/6}$, a more rapid increase than resting metabolism, which scales at $M^{3/4}$, with the consequence that large birds face tight constraints on the amount of energy they can devote to flight. It is worth noting here that most migrants are smaller birds. Large birds may even lose the power of flight as seen in ratites, island rails, and some South American Streamer Ducks. One way in which large birds can "defeat" the constraints imposed by size and power is by gliding and soaring. The best wing design for this is one that combines high aspect ratio with low wing loading. The best properties are associated with long, narrow wings as seen in albatrosses, the quintessential soaring, gliding sea birds capable of spending hours on the wing with little energy expenditure (Figure 7.3). Long pointed wings not only provide efficient lift, but they also shed tip vortices that create drag (Kerlinger 1989). The glide ratio, the ratio of gliding speed to rate of descent, for albatrosses is around 24:1, the highest known for any animal.

Small birds spend almost no time gliding and glide not at all during migration. The reason is shown elegantly in Pennycuick's (1989) calculations comparing flapping and gliding performance of a 5.5 kg crane (*Grus* sp.) with a 17 g Ovenbird (*Seiurus atricapillus*). In a rising thermal of 3 m/s an Ovenbird's cross-country speed while soaring and gliding would be about 0.6 V_t, about the same percentage of V_t as a crane but at less than half the crane's speed. The problem for the Ovenbird is that it requires 63% as much energy per kilometer when soaring as when in flapping flight at V_t; in contrast the crane requires only 9% as much. If air in the thermal rises at 1 m/s the Ovenbird actually requires 6% more energy than for flapping, because in a small bird basal metabolism is a much higher fraction of total energy requirements. The reduced speed of a soaring, gliding Ovenbird means that it spends up to three times as long traversing each kilometer, and the extra time uses too much fuel just in maintaining the basal metabolic rate. Any fuel saved by soaring and gliding is negated.

An interesting adaptation to migration occurs in small birds that accumulate large fat deposits to migrate, sometimes doubling lean mass. These small migrants insert pauses between bouts of flapping



Figure 7.3 Two species of albatross in flight over the ocean. Left: a Black-footed Albatross at the Cordell Bank off Bodega Bay, California. Right: a Laysan Albatross off Half-moon Bay, California. Note the long wings of high aspect ratio typical of soaring, pelagic seabirds. Photographs by Marcel Holyoak. (See also Plate 2.)

so that the mean power output between flapping and pausing is at the required level (Rayner 1988). The birds travel with a characteristic undulating or "bounding" flight. For reasons of scaling the behavior is confined to smaller birds with wings of low aspect ratio. It is the typical flight pattern, for example, in relatively small passerines, hummingbirds, and smaller owls, kingfishers, and woodpeckers. In apparent convergent evolution undulatory gait patterns are used by migrating marine species as well as birds. Gleiss et al. (2011) attached accelerometers to free-swimming sharks and pinnipeds and found that both groups swam during migration with intermittent gliding interspersed with powered swimming, producing a regular undulating pattern of locomotion. The convergent use of these gait patterns by diverse animal groups suggests that some universal physical and physiological principles may be at work.

In addition to defeating constraints with bounding behavior, many migratory passerines and other birds, for example eels, reduce the length and weight of the gut (McWilliams and Karasov 2005; Piersma and van Gils 2011) which compensates in part for the fat added prior to migration. This adds the constraint of a more limited diet. A classic example is the Red Knot (*Calidris canutus*) migrating from South America to the Nearctic. They have a reduced gut that imposes a requirement of soft food (rather than the usual small molluscs) in order to refuel en route. Refueling is accomplished by feeding on the immensely numerous Horseshoe Crab (*Limulus polyphemus*) eggs in the mudflats of Delaware Bay on the east coast of North America. A significant conservation issue is the preservation of the horseshoe crab population so as not to put the Red Knots at risk of starvation through lack of soft food.

A further behavioral response that can increase energy savings during flight is flocking. Because air is driven downward by the wings during flight, there is compensatory movement of air upward off the end of a bird's wing. This will be strongest in the vortices that form just off the wingtips (Alerstam 1990), and it means that birds flying close to each other, as in a V-formation, can in effect gain some free lift up to about 40%. This would imply that there would be strong selection pressure to travel in groups, especially in long-distance migrants (and see also orientation in Chapter 8). This hypothesis was tested by Beauchamp (2011) who examined evolutionary transitions in migration distance and predicted that traveling flock sizes would be larger in long-distance migrating species; larger flock sizes during migration were clearly associated with the long-distance routes. There were no other significant differences among traits such as body mass or group size during the non-breeding season. It is not clear, however, whether larger flocks facilitated the evolution of long-distance migration or whether long migration distance favored large flock size. Selection favoring flock size could also be a function of navigation accuracy (Chapter 8).

Turning to insects, there is much less information on the power required for flight relative to that available for birds, partly because of the difficulties of measurement in small organisms. The mechanical power curve for the migrating diurnal tropical moth, *Urania fulgens*, has been examined during migrations in Panama by Dudley and DeVries (1990) and Dudley (1995). Bumblebees display a rather flat power curve associated with their high wingbeat frequencies (Figure 7.4). For the moth, however, the power curve rises steeply with airspeed. This is because, with much lower wingbeat frequencies associated with synchronous flight muscle (one muscle contraction per nerve impulse), an increase in airspeed increases significantly the relative air velocities over the different wing sections. This means that, in particular, profile power (Table 7.1) will increase sharply because it is proportional to the cube of the relative velocity and will be major contributor to total power requirements for forward flight (Figure 7.4). Because reliable airspeed data are not available for any migrating insect with asynchronous muscle (several self-stimulating muscle contractions per nerve impulse) such as hover flies or bumblebees, little can be said about power requirements. It does seem logical, however, that for insects with high wingbeat frequencies, as with the bumblebee curve in Figure 7.4, choice of airspeed will be less critical for minimizing energy use during flight (Dudley 1995).

DeVries and Dudley (1990; Dudley and DeVries 1990) further analyzed the annual migrations of *Urania fulgens* by following (with a boat) the migratory

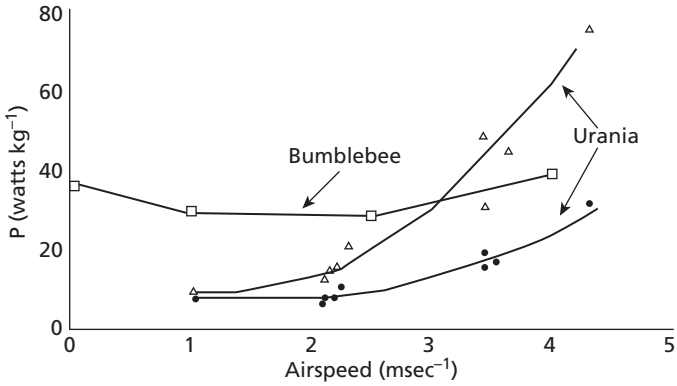


Figure 7.4 Power curves for insect flight. The bumblebee flies with high frequency wingbeats resulting from asynchronous muscle. The migratory *Urania* moth has large wings that are powered by synchronous muscle and beat relatively slowly. The two *Urania* curves are for profile drag coefficients of 0.3 (upper curve) and 0.1 (lower curve). Data from Dudley (1995).

flights across Lake Gatun in Panama. Airspeeds, wing kinematics, morphology, and lipid reserves were assessed for several individual moths, and the biomechanical and morphological data were used to analyze aerodynamics and power requirements. By comparing lipid reserves with estimated flight metabolic rates, they concluded that moths could probably fly for 110 km or less using stored energy. The moths are known to migrate several thousand kilometers, so they must restore energy balance by nectaring en route (Dudley 1995) (and see the discussion of Monarch Butterfly migration in Chapter 6).

The relation between body size and migration in insects has been examined by Roff (1991). The distance an insect can fly on a given fuel load (assuming still air) is given by the equation:

$$\text{Distance} = \frac{\text{flight speed} \times \text{stored calories}}{\text{metabolic rate during flight}}$$

Flight speed increases with body mass raised to the power 0.38, whereas metabolic rate increases as mass to the power 0.84 on average. For reasons of geometry the stored calories can be assumed proportional to body mass. Combining these relationships gives

$$\text{Distance} \propto (\text{body weight})^{0.54}$$

Thus all else being equal, the distance an insect can fly increases with body size. As we have seen in Chapter 5, insects are masters at taking advantage of wind to defeat these constraints and facilitate migration. Still, it does seem to be the case, although with many exceptions, that both within and between taxa, migrants tend to be larger (Dingle 1996). Much, however, remains to be resolved concerning size–migration relationships.

Ecology and wing morphology

A further aspect of the notion that migration is but one of many factors influencing morphological adaptations is that all aspects of morphology and behavior cannot be favored simultaneously. This is particularly evident with respect to wing shape and flight performance (Rayner 1988, 2003), and compromises among various aspects of wing shape and body size will be the inevitable result, although general trends may still be apparent. There are some general principles. Low transport costs, for example, are associated with high aspect ratio, especially if combined with low wing loading to reduce required power. However, although reducing aspect ratio and increasing wing loading increase power requirements, flight speed is increased, as in ducks and some other water birds. Speed can also be increased by flexing wings as seen in the "power glides" of hunting or displaying hawks and falcons. Maneuverability is enhanced by short rounded wings and a long broad tail that can be fanned to give added lift or ruddering. The latter traits are common in small birds living in dense marsh vegetation or thick scrub.

These general principles and the trade-offs they engender largely determine the shapes of birds and other flying animals (Dingle 1996). Marine birds such as terns, petrels, and albatrosses are characterized by long pointed wings of high aspect ratio. These are undoubtedly adaptations for nearly continuous soaring, taking advantage of the winds over the unbroken surface of the ocean. Albatrosses, for example, during intervals between breeding

events can soar continuously for weeks and can obtain food more or less anytime during often circumglobal migrations. Terns, petrels, shearwaters, and albatrosses all make long-distance migrations, taking advantage of prevailing winds, experiencing little in the way of environmental constraints on wing shape. Maneuverability is of little concern.

Land birds do face constraints imposed by the need to maneuver. Thrushes, for example, spend much of their time near the ground, often in or near vegetation cover. Selection in this case will favor the ability to change course quickly and in tight spaces. Short rounded wings and relatively large tails are the shapes that should be optimized, as indeed is the case. Migrant thrushes are small birds, and so, for the reasons previously discussed (Pennycuick 1989), there will not be selection for soaring efficiency and accompanying long wings of high aspect ratio. At the extreme of birds living in dense cover are the ground-feeding ant pittas which have short rounded wings and are actually tailless, presumably because the ground-feeding mode minimizes the need for ruddering with long tails. Large terrestrial birds such as storks, hawks and eagles, and pelicans have broad wings with squarish tips and separated, or "slotted," primary feathers. Raptors have large tails which provide maneuverability, presumably an advantage in prey capture or maneuvering in the vicinity of hills and cliffs. Storks—which are ground feeders and not pursuit hunters—have short tails. Slotted wing tips aid in shedding vortices and thus enhance aerodynamic performance, but there is still uncertainty about the selection favoring them. In any cases it is apparent that terrestrial life imposes different constrains on form and function in birds than does marine life.

Migration further influences size and shape of wings and body between populations within species. There is a history of studies that show a general tendency for migrants to have longer wings than resident populations of the same species. This is true for both birds and insects (Dingle 1996). Recent studies have shown this tendency for migratory versus resident populations of the Monarch Butterfly (Dockx 2007; Althiser and Davis 2010). As indicated in Table 7.2, migratory Monarchs that reach Cuba have longer wings than butterflies that do not leave the island (Dockx 2007). Dockx was

Table 7.2 Forewing lengths of migrant and resident Monarch Butterflies.

	Females	Males
Migrant		
Cuba	47.4 (3.1)	48.8 (2.8)
Eastern US Wild	51.2 (0.19)	51.4 (0.19)
Western US Wild	49.1 (0.26)	50.6 (0.17)
Eastern US Lab	50.7 (0.014)	51.1 (0.13)
Western US Lab	50.6 (0.19)	50.8 (0.19)
Resident		
Cuba	45.8 (3.6)	46.1 (3.6)
S. Florida Wild	48.6 (0.53)	48.8 (0.46)
Hawaii Wild	48.5 (0.29)	49.3 (0.21)
Costa Rica Wild	44.8 (1.56)	47.9 (0.73)
Puerto Rico Wild	44.8 (0.41)	45.5 (0.41)
S. Florida Lab	47.4 (0.32)	48.3 (0.30)

Lengths are in millimeters. Variation is ± SD for Cuba and ± SE for all others. Sources: Dockx (2007) for Cuba; Altizer and Davis (2010) for all others.

able to distinguish migrants from residents by the use of independent techniques of thin layer chromatography and stable hydrogen and carbon isotope measurements (Chapter 4). Althiser and Davis (2010) compared migrant butterflies from both eastern and western North America with resident tropical butterflies from both island and mainland sources. Statistical tests indicated that the wings of both male and female migrants were significantly longer than those of the residents of both sexes. Laboratory common garden experiments and the presence of family-level effects demonstrated that these differences in wing morphology were the result of between-population gene differences.

Migration also affected the shape of the wings. Dockx (2007) found that for her Cuban butterflies the roundedness of the wings differed between migrants and residents. She computed the angle between a tangent to a circular section of the forewing tip and a line drawn parallel to the outer wing edge. Differences in this angle indicated that migrants had longer and narrower forewing tips than residents, a shape that would reduce drag and enhance long-distance flight (a parallel to seabirds). Altizer and Davis (2010) used principle components analysis to

assess composite measurements of size and shape in the wings of migrant and resident monarchs. Size was greater in the longer-migrating eastern migrants than for western ones, and both sets of migrants had larger wings than residents. Shape also differed. Eastern migrants displayed longer, larger wings whereas those from the west had shorter and more rounded wings, especially evident in butterflies reared in a common environment. Reasons for this difference are not clear, although it should be noted that the western sample was dominated by the shorter-distance California migrants (cf. Dingle et al. 2004). What is clear is that natural selection has produced distinctive differences in wing morphology between migrants and residents and between migrants from different parts of the Monarch's range.

Monarchs are not the only insects in which wing shape is influenced by migration. Johansson et al. (2009) used a phylogeny-based comparative method to analyze the effects of migration and mate guarding on wing morphometrics across anisopteran dragonfly species. Both front and hind wings were influenced by migration. For the forewing, migrants tended to have a lobe situated about one-quarter of the wing out from the base, and the wings tended to be narrower over the outer half. There was an even greater difference between migrant and non-migrant hindwings, with the migrants displaying a lobe at the wing base and a more inward-pointing frontal tip. Dragonflies can beat their fore- and hindwings out of phase, and because the gap between them is small, shape changes in the forewing could interfere with hindwing action. The greater difference with respect to migration in the hindwings may also indicate that these are of greater importance in long-distance flight, possibly because the conspicuous basal lobe serves to reduce drag. This lobe was even more conspicuous in dragonflies with tandem mate-guarding, suggesting a possible synergistic effect of the two behaviors. Interestingly neither behavior influenced aspect ratio.

The influence of mate guarding on dragonfly wing shape is but one illustration of the fact that migration acts in combination with other behaviors to influence morphology. Combined influences have been most intensively studied in birds, especially by Bernd Leisler and Hans Winkler (Leisler and Winkler 2003; Winkler et al. 2004; Winkler and Leisler 2005). Bird morphology is influenced both by the type of habitat in which a species lives and the type of hunting method by which it captures prey or otherwise feeds (e.g., pursuit or sit and wait). Leisler and Winkler (2003) used multiple regression methods to examine the relation between body and limb measurements and migration distance in Old and New World Warblers (*Sylvia*, *Acrocephalus*, *Hippolais*, Parulidae), residents primarily of highly vegetated habitats such as woodland or marsh, and in pipits (*Anthus*), residents primarily of open country. Results for the New World warbler genus *Dendroica* and for pipits are illustrated in Figure 7.5.

In the case of *Dendroica* the variable "morphology" was a combination of femur and ulna lengths and the height of the skull. This measure was regressed against migration distance in kilometers and explained 91.1% of the variance in migration distance (90.8% with a phylogenetic correction included). Femur length and ulna were positively correlated with distance (longer legs and wings) and skull height was negatively correlated (smaller brains). In the pipits only variables associated

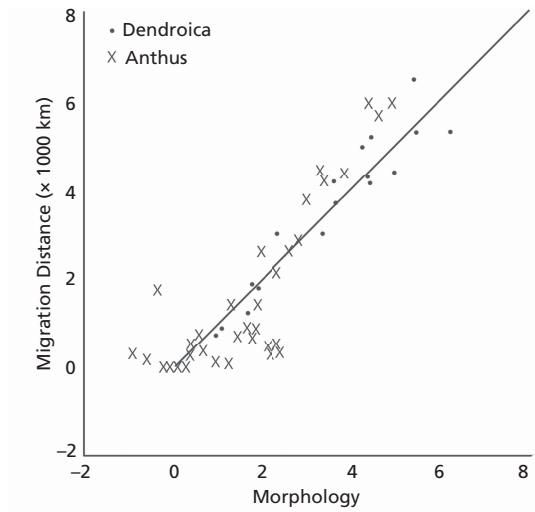


Figure 7.5 The relation between multivariate measures of wing and body shape and migration in New World Warblers of the genus *Dendroica* and in pipits (*Anthus*). Morphology in *Dendroica* includes femur, metacarpal bone, and skull height; in *Anthus* it includes primary feather projection, notch extent in the primaries, and tail graduation. Note that in the open-country pipits, it is only morphology associated with flight that is involved. Data from Leisler and Winkler (2003).

with the flight apparatus were involved, as might be expected of open-country birds all foraging in more or less the same way. In this case morphology was a combination of primary feather projection (Kipp's distance), length of wing notch, and degree of graduation in the tail, and it explained 64.3% of the variance in migration distance (63.7% with phylogenetic correction) with the latter two variables entering negatively. In Wheatears (*Oenanthe*), also largely open-country birds, more sedentary species have more rounded and slotted wings except in desert areas where wings are pointed like migrants, probably because in dry areas more extended foraging flights are necessary (Kaboli et al. 2007). Comparing the results across groups of birds, it is clear that migration shapes the whole avian body with the degree of influence on various parts dependent on various aspects of the lifestyle.

The smaller brains of long-distance migrants are interesting. Skull height is a clear predictor of brain size (Winkler et al. 2004), so one hypothesis to account for the relation to migration distance could be that a smaller, lighter skull would be advantageous. However, differences in brain size are mainly due to differences in the size of the forebrain. The smaller forebrains of migrants versus residents seem counterintuitive, as migration would seem to involve an integrated system of several complex traits (Rappole et al. 2003). The selective agent may be a function of energy. The brain is an energy-demanding organ, and migration is an energy-demanding behavior (Alerstam and Hedenström 1998), so that any energy savings with respect to other functions could be advantageous. A large forebrain may also be less necessary for migrants if they are pre-adapted to niches common to many habitats that do not require skilled or innovative foraging. Obviously such hypotheses need further testing (Winkler et al. 2004). Migratory bats also possess smaller brains than their sedentary counterparts. A phylogenetically controlled analysis found that migratory bats had smaller brains largely due to a smaller neocortex; the hippocampus did not differ in size (McGuire and Ratcliffe 2011). Because bats do not show the same flexibility in diet selection as birds, McGuire and Ratcliffe favor energy trade-offs as the most likely selective factor favoring the smaller brains of migratory bats.

As a final word on migration and morphology in migratory birds: in at least one species, the Blackcap, *Sylvia atricapilla*, there is a developmental influence (Pérez-Tris and Telleria 2001). These authors compared Spanish populations of migratory and sedentary Blackcaps with respect to wing shape in juveniles and adults. The migratory population had longer and more pointed wings than the sedentary one consistent with data from several other species. In the sedentary birds the wing shape of juvenile and adult birds did not differ. In the migratory population juveniles had shorter wings and in females the wings were more pointed in the adults. Because shorter and more rounded wings confer greater maneuverability, Pérez-Tris and Telleria speculate that escape from predation in juveniles would compensate for the somewhat greater migration costs of less efficient wings. The greater difference across age in females likely reflects increased migration in females in what is a partially migratory population. Because there are no migration costs in sedentary birds, maneuverability would be favored in adults and juveniles alike.

Morphological adaptations for migration must compete with other life-history demands. Evolutionary compromises, i.e., trade-offs, will clearly occur, and in many cases feeding mode or other aspects of ecology may supersede adaptation for migration. Migration does not seem to impose the extreme selection pressure it was once thought to do. At least in the case of flight, migration seems well within performance capability, with further morphologic modification simply enhancing this capability relative to other demands on flight.

Migration distance

The issue of how far migrants travel has been addressed by Hein et al. (2012) with a model that examines the various mechanical and metabolic constraints across migrants of all sizes and means of locomotion. They included walking, swimming, and flying animals in their model, and they incorporated body mass-dependent costs of locomotion, changes in migrant body mass as they consumed stored fuel in transit, and scaling of morphological characteristics and maintenance metabolism among migrants of different body masses. Data to evaluate the body mass model were taken from published

measurements of migration distances of terrestrial and marine mammals, fish, and flying insects and birds that had been tracked by mark–recapture, telemetry, or other means that gave reliable estimates of the distances traveled. The equations derived from the model predicted how the number of body lengths traveled (used as a measure of relative distance) varied with body mass. These relative distances could then be converted to actual distances in kilometers.

A prediction of the model was that the number of body lengths traveled by walking and swimming animals would be independent of body mass. This turned out to be the case, although the more efficient swimmers moved more body lengths than the walkers. In flying migrants the number of body lengths traversed declines with increasing mass, as predicted by the model, because the cost of flight increases more rapidly with increasing body mass than does the cost of walking or swimming. The energetic cost of flight increases rapidly with increasing mass such that the increased fuel required provides diminishing returns with respect to increases in migration distance. This works out to small flying migrants such as moths, dragonflies, and hummingbirds covering roughly 25 times in body lengths the distances covered by large ducks or geese. Among swimmers the distance traveled in body lengths is up to four times greater in fish than in mammals, a difference which may be driven by differences in the maintenance metabolism of cold-blooded fish as opposed to warm-blooded mammals, for example cetaceans.

When converted to actual distances traveled and plotted against predictions of the model on a log-log plot, the points from walkers, swimmers, and flyers cluster around a 1:1 line as shown by the three examples plotted in Figure 7.6. The body size model thus predicts quite well the distances traveled by migrants as different as walking mammals, swimming fish, and flying insects, animals that vary in size by more than 11 orders of magnitude. There is, however, still a substantial amount of variation that remains to be explained. This variation may be due to time minimization by at least some migrants (not included in the model) or it could be due to the fact that many migrants interact with winds and currents as outlined in Chapter 5. Nevertheless the model provides a useful framework for analyzing the influences of energetic and biomechanical constraints on migration distances.

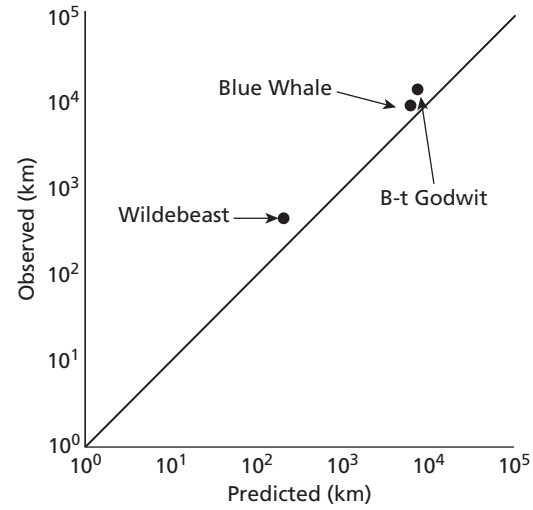


Figure 7.6 Double-log plot of observed versus predicted migration distances from the body size model. The line indicates perfect match and most migrants fell on or very close to this line, as illustrated for the mean distances of three migrants discussed in this book, the Wildebeest, Blue Whale, and Bar-tailed Godwit. Data from Hein et al. (2012).

Special problems faced by migrants

Many migration routes can potentially place particularly high demands on those traversing them, and it is legitimate to ask how migrants cope with these. Many European bird migrants to Africa, for example, must cross the Alps, the Mediterranean, or the Sahara with different routes crossing one, two, or all three of these barriers. Arctic migrants may need to cross wide expanses of ocean, mountain ranges, glaciers, and cold deserts in journeying to and from their breeding and wintering destinations (Henningsson and Alerstam 2005). Favorable winds may assist with barrier crossings (Chapter 5), but considerable energy resources are still required to complete them successfully. Insects migrating to diapause sites must face long periods without feeding and, in high latitudes, often extreme cold. If they emerge prematurely in a warm early spring, they run the risk of death by freezing if there is a subsequent cold snap. Indeed diapause in such

species is often resistant to such early emergence (Danks 1987 for a review). Thus the diapause phase of a migration/diapause cycle can also act as a "barrier" in a migration system. In both barrier crossings and diapause periods (and other special problems) we need to ask what sorts of adjustments migrants make to the potential stresses that might be induced by the barrier crossings.

If migrants do not carry enough fat to provide the fuel for a barrier crossing, they must replenish fuel if they are to make the transit. The result is that migrants may interrupt their journeys to refuel at stopover sites. Stopovers have been extensively studied by Frank Moore and colleagues in North American migrants crossing the Gulf of Mexico that take off from, or make landings on, the Gulf Coasts of Alabama, Louisiana, and Mississippi (Woodrey and Moore 1997; Moore et al. 2003, 2005a,b; Cimprich et al. 2005). There are several issues faced by the migrants in selecting stopover sites that will provide adequate opportunities to refuel. Several lines of evidence indicate that migrants are indeed "choosy" about stopovers and selectively use habitats out of proportion to their availability and that the choice is positively correlated with food availability but can be modified by the energetic condition of the migrants (Moore et al. 2005a). For example, at six sites within 85 km of the coast of Mississippi, migrants were more abundant in hardwood forest as opposed to pine forest with or without understory; hardwood forests provide more and/or richer food than pine forests (Buler et al. 2007). Migrants arriving in the vicinity of potential stopover sites appear to assess habitats during an exploratory phase whose duration is determined by the bird's condition, as well as factors such as wind, weather, and distance from the arrival point if completing a crossing of the Gulf of Mexico.

The condition of a migrant further determines its behavior at the stopover site. Cage orientation experiments with Red-eyed Vireos (*Vireo olivaceus*) stopping in the autumn revealed that birds with enough fat to cross the Gulf of Mexico oriented cage activity toward the south, appropriate to fall migration, whereas lean birds oriented in a westerly direction parallel to the coast. Reduced fat load in three European passerines reduced the amount of migratory restlessness they displayed during cage experiments (Fusani et al. 2009). Length of stay is also correlated with arrival fat load. Social dominance can influence access to food and hence fat score both for the initial migration flight and for access to food, and hence rate of fat deposition during the stopover. Because age is a major factor in dominance, mature birds can be at considerable advantage. Age-related dominance can vary with species. Both age classes of Magnolia Warblers (*Dendroica magnolia*), for example, generally arrive in autumn on the Gulf Coast with sufficient stores for a trans-Gulf flight. Young Swainson's Thrushes (*Catharus restulatus*), White-eyed Vireos (*V. griseus*), and American Redstars (*Setophaga ruticilla*), on the other hand, did not carry sufficient fat stores to make the flight and would need to accept the risk of stopover to refuel (Woodrey and Moore 1997).

One of the risks of stopovers is predation; the longer the time spent at a stopover site, the greater risk of becoming a meal for a hawk or other predator before reaching one's final destination. Migrants do display predator-avoidance behaviors, but time spent avoiding predators also means less time foraging and as a result longer refueling time (Cimprich et al. 2005). For example, American Redstarts and Blue-grey Gnatcatchers (*Polioptila caerulea*) move farther into oak shrubs as the frequency of Sharp-shinned Hawks (*Accipiter striatus*) increases at stopover sites. This hawk is a noted predator of small birds. The dense habitat of the oak shrubs necessarily restricts movement and likely restricts foraging efficiency as a consequence. Direct measurements of movement revealed an overall lower rate in Gnatcatchers, but no significant change for the Redstarts. The restriction of foraging via either the necessity to seek shelter or to reduce conspicuousness by moving more slowly is a constraint imposed upon migrants who must seek stopover sites to refuel. The need to deposit fat could also force a trade-off between precise risk assessment and foraging effort (Cimprich et al. 2005).

To all appearances the combination of the Mediterranean Sea and the Sahara Desert may present an even more formidable barrier to migrating birds than the Gulf of Mexico. There has been debate, dating back to the work of Moreau (1961, 1972), about whether the wide expense of the Sahara, with its intense heat and lack of food resources for refueling,

would require a non-stop flight or could be crossed in stages with intermittent flights (summarized in Dingle 1996, pp. 192–195). Moreau favored non-stop flights, but more recent evidence suggests that migrants are making the crossing in stages. Trapping stations, for example, were established in the Sahara both at oases, where birds could refuel, and in the open desert where they could not. Lean birds were the majority trapped at oases, which makes ecological sense, but the surprising result was that many birds were trapped in the desert sites with no food or water. These grounded migrants were generally fat, were not exhausted, and, based on re-traps, rapidly resumed migration. Observations in the field revealed that the birds were most likely simply resting in the shade during the day to avoid heat stress and water loss. Migrants fly at a lower altitude at night (night median 391 m; day median 573 m for the Negev in Israel; Klaasen and Biebach 2000), and modeling studies based on energy requirements and rates of water loss predict fairly accurately altitudes at which migrants cross the desert, based on radar observations (Klaasen and Biebach 2000), implying that the birds take water loss into account. Water loss will, of course, be less at night when temperatures can be several degrees cooler than during the day.

Indications that the majority of flights across the Sahara are intermittent come from further studies in Egypt (Biebach et al. 2000) and Mauritania (Schmaljohann et al. 2007). In the Western Desert of Egypt five radar stations were established along a transect from the Mediterranean coast to 600 km inland across the Sahara. During autumn migration the number of passerine birds passing over each site was recorded on a per-hour basis over the 24 h of the day. This meant that, for example, birds taking off from the coast and flying continuously inland over the desert would overfly each radar at a later and later time as the flight progressed from north to south (Figure 7.7). From the site passage data three distinct groups of migrants could be discerned: (1) a day group that flew non-stop across the Mediterranean and at least the northern part of the desert; (2) a night group that performed intermittent flights with a stopover on the Mediterranean coast of Egypt and a continuation of migration the next evening; and (3) an evening group that was

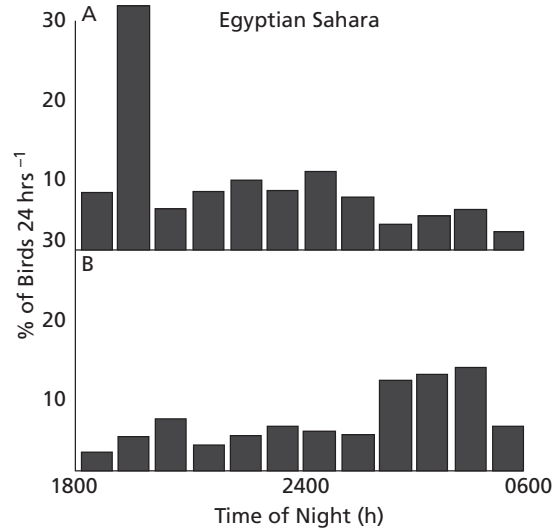


Figure 7.7 The passage of autumn migrant birds across two radar sites in the Egyptian Sahara (Western Desert). The percentage of the total number of birds seen in 24 h is plotted for the duration of the night. Site A is near the Mediterranean coast and large numbers of birds take off around evening dusk. Site B is some 600 km inland, and birds presumably arriving from the coast fly over mostly during the hours just preceding dawn. Data from Biebach et al. (2000).

also intermittent but that stopped in the desert after flying continuously across the sea and part of the desert. About 20% of the birds were non-stop migrants. Of the 80% that were intermittent migrants about 70% stopped near the coast with the remainder stopping in the desert. Biebach and colleagues suggest that any small passerine could adopt any of these patterns, presumably based on factors such as temperature and tailwind.

In Mauritania there were three radar sites, one at an oasis and two at locations surrounded by at least 300 km of nearly vegetationless desert (Schmaljohann et al. 2007). Here in the Western Sahara during both autumn and spring migration there was a clear prevalence of intermittent migration by passerine birds. This was indicated by the fact that at all three radar sites there were massive departures of songbirds in the early evening independent of season, strongly suggesting that birds had spent the day on or near the ground in the desert. In the autumn migration occurred when temperatures were high and was largely confined to night-time. In the spring some passerines extended migratory flight

into the day, but with high variance. Continuation of flights into daytime hours was more likely when there were good tailwinds. In the spring, therefore, there may be some opportunistic non-stop migration, but intermittent flights predominate and are exclusive in the autumn. Daytime transects through the desert around the radar sites and intensive searches of the few small bushes present recorded migrant songbirds, confirming daytime cessation of flight activity. Such resting in terrestrial areas during the day would conserve water and energy and favor intermittent nocturnal flights over continuous flight that would include hot daytime hours (Schmaljohann et al. 2007).

The hazards of the Sahara Desert crossing for raptors were investigated in a satellite tracking study by Strandberg et al. (2010). They analyzed some 90 desert crossings made by Ospreys (*Pandion haliaetus*), Honey Buzzards (*Pernis apivorous*), Marsh Harriers (*Circus aeruginosus*), and Eurasian Hobbies (*Falco subbuteo*). The hazards were, not surprisingly, greater for juvenile birds making their first crossings than for experienced adults; four out of 13 juveniles died on the crossing whereas only two adults died during a total of 82 crossings, a statistically significant difference even with the small sample of juveniles. Furthermore birds which showed "aberrant behavior," such as distinct course changes or interruptions of migration, experienced much lower breeding success (one success out of 10) after spring migration compared with birds migrating without aberrations (nine out of 17). Part of the depressed rate was probably due to late arrival on the breeding grounds, indicating that the hazards of desert crossing may impact breeding success as well as cause death. It seems likely that the desertification of the Sahara over the last 5,000 years has increased the hazards of migrating to Europe for these raptors and has had an effect on the evolution of routes and strategies (Strandberg et al. 2010).

For insects migrating to diapause sites, the basic problem is the same as that for birds migrating across barriers, namely, to transit a stressful period on a limited fuel supply. The problem for diapausing insects is to burn enough fuel (and/or provide enough antifreeze) to keep from freezing to death but not so much as to run out of reserves. The antifreeze option is used almost exclusively by non-migrant insects, which produce substances such as glycol to prevent freezing (see Danks 1987 for an excellent review). Migrants usually move to and from diapause sites in sheltered places. Insects from several orders do this at sites that include old buildings, caves, wood- and rockpiles, old logs, and leaf litter. Diapausing insects also possess mechanisms to prevent emergence and reproduction in late-winter warm spells, although the exact nature of these is not well understood (Tauber et al. 1986; Dingle 2002).

The outstanding example of diapause tactics designed to survive overwintering is the Monarch Butterfly of which the largest portion of migrants overwinters in the Oyamel Fir (*Abies religiosa*) forests of the Transvolcanic Range in central Mexico (Brower 1995 and Chapter 3). Large colonies (up to 15 million individuals) occur on southwestern-facing sunny slopes in high altitude (3,000 m) mesic habitats with the butterflies forming large clusters on the branches of the fir trees. The combination of high altitude and tropical latitude provides a generally stable daily and seasonal thermal regime during the winter with daily shade temperatures below flight threshold for the butterflies. The clusters themselves provide microclimatic advantages supplementing the overall climate conditions (Brower et al. 2008). Miniature digital hygrothermographs were inserted into clusters so that both temperature and humidity could be recorded and compared between inside and outside clusters. Although small, differences in temperature between inside and outside were statistically significant (inside ~0.2°C warmer at night and ~ 0.3°C cooler during the day). By lowering the warmest temperature, the small daytime difference can reduce the metabolic rate by around 6%, a considerable potential saving in fuel reserves if extended over the entire overwintering period. The inside of the clusters was also greater than the outside, adding some additional protection from desiccation. The configuration of branches and fir needles also confers some benefits, adding to the matrix of site and cluster characteristics that confer protection and fuel saving.

In addition to clustering, other behaviors of the butterflies promote survival on the available fat reserves (Masters et al. 1988). Tens of thousands of butterflies bask in the sunshine on clear or partly cloudy days, many fly up to 1 km to drink, there is

much shivering and crawling or flying up off the ground, there are hovering flights above the trees when basking butterflies are shaded, and flights above the colony are common on clear cold days. Given that the costs to shiver or fly at the flight threshold of 15.5°C are 25–28 times as energetically expensive as resting, why is there so much activity within the colony? Answers differ for different behavior. Basking raises the thoracic temperature quickly without the butterfly using energy. Once above flight threshold temperature, individuals take off and can either fly to a more shaded area or use flight and especially gliding to cool. A body temperature rise in direct sunlight raises metabolic rate and causes too much consumption of lipid reserves. Butterflies are thus "sun minimizers," with choice of colony site and the relation between basking and flying serving as means toward that end.

The clouds of flying butterflies on clear days reflect behavioral thermoregulation. The flight response to sudden shading apparently serves to avoid being thermally trapped where they might be exposed to freezing or predation. Body temperature below –2°C begins killing Monarchs so they must avoid situations, especially at ground level, where freezing might occur. Shaded individuals in the colony fly and hover for about 3 min before re-aggregating, while those that are drinking away from the colony instantly fly back if shaded. Flights to drinking sites must be only 1–2 km; on longer flights butterflies would risk becoming too cold to fly. Shivering allows Monarchs to raise body temperature enough to fly or crawl off the ground to vertical surfaces and so avoid freezing or mouse predation. Huge numbers may gather on tree trunks after being knocked to the ground in a storm. The choice of cool sites and the low body temperature resulting from thermoregulatory behavior also maintain reproductive diapause, but the conservation of lipid reserves is both a major function and a key element in the maintenance of the Monarch migratory cycle. Successfully adjusting the trade-off between freezing and overwarming is the major adaptation that permits winter survival.

Summing up

Perhaps the most immediate conclusion to come from the survey in this chapter is that with respect to migration constraints do matter. They can shape not only migration strategies but also the bodies of the migrants. Adult tarantula spiders do not migrate by ballooning on silk threads; the length and strength of a thread necessary to support a tarantula are apparently simply too great for natural selection to favor ballooning as a viable means of transport. Thrushes and other small forest birds do migrate and often for very long distances. They do not, however, do so by soaring because any energy gains are negated by the metabolic costs of being small accumulating over the extra time taken by soaring. In contrast, albatrosses, large animals that are little-constrained by requirements for maneuverability in the open ocean, possess long pointed wings that allow them to soar for hours and even days at a time. Size in vertebrate-transported seeds is apt to be a compromise between increasing the likelihood of long-distance transport away from the influence of the parent (small seeds) and increasing the likelihood of successful germination and establishment (large seeds).

At the same time that migrants have been influenced by constraints, they have been superb innovators at working around those constraints. The large Namibian desert spider *Stegodyphus* spins sheets of threads so that in the open desert environment it can indeed balloon. Eels (and many birds) shrink their guts to embark on their long journeys, limiting their ability to refuel en route. Eels conserve energy, however, by remarkably efficient swimming enhanced both by muscular adjustments and swimming at depths that allow them to gain advantage from the metabolic gains afforded by cooler temperatures and higher pressures. Other behavioral adjustments by fish (and marine larvae) include masterful use of tidal streams and oceanic currents (Chapter 5) to reach their destinations. Songbirds facing the extremes of daytime temperatures, plus the absence of refueling opportunities when migrating across the Sahara, land and rest in the shade before continuing their journeys. When conditions are right, however, they are flexible enough to make the crossing in one go. Monarch Butterflies seek out and congregate in cool locations on the right trees at the right altitude where they behaviorally thermoregulate by clustering; these tactics allow them to conserve the energy necessary to see them over the winter diapause portion

of their annual migratory cycles. Modulation of behavior thus allows migrants to deal both with their own limitations and the environmental exigencies imposed upon them.

Considering the entire life history of organisms, migration is one of many factors that influence body plans. Long narrow wings and fusiform bodies with lunate tails are optimal designs for extensive travel in flying and swimming animals, respectively, but other considerations also enter in. Migrant birds that live in forests or thickets need to maneuver effectively; for this purpose short rounded wings and long broad tails are the best design. Fishes living in reed beds or on coral reefs need laterally compressed bodies for optimal swimming performance in restricted spaces between reed blades or coral heads. The design of an organism is perforce a compromise between often conflicting demands, in fish and birds between lift and drag. By understanding the nature of these compromises and the way natural selection organizes them, the effects that arise from migration become apparent. Within a group of small short-winged birds of brushy or wood habitats (for instance both Old and New World warblers), migrants tend to have longer wings and less developed legs and feet than their sedentary counterparts. Even brains are affected as skull shape (and hence brain size) influences drag and so migration efficiency. The involvement of legs and feet emphasizes the multivariate nature of the whole organism that migration—or any other imposed selection—influences. In open-country birds, for example wagtails and pipits, selection influences differences in legs and feet less, because of fewer demands for grasping and maneuvering placed on these structures; instead selection is "free" to act on the flight apparatus. Even sexual selection can enter in. Some dragonflies face conflicting demands between migratory flight and the maneuverability required in mate guarding, with subtle differences in wing shape the result. In a sense it is because organisms, migrant or otherwise, cannot optimize everything at once that they have become the behavioral innovators they are. Migration is one of the innovations; behavior, physiological, and morphological compromises help to contribute to its success as a strategy.

CHAPTER 8

Orientation and navigation

The ability to orient to the surroundings is a fundamental property of life, and all organisms must orient at some point during their life cycles. At even the simplest organizational levels, there exists the ability to process information, and that information is frequently used to orient in space. Migrants travel over a great deal of space, so the ability to know and control one's position on the surface of the Earth becomes very important indeed. The degree of importance, however, and the degree of sophistication required to orient are very much functions of behavioral capability or the necessities imposed by the lifestyle. Bacteria, for example, may require only the ability to detect differences in chemical concentrations to arrive in a suitable environment (Table 1.1). It is even possible to imagine a migratory episode in which no orientation is necessary, as would be the case if all habitats to which migration may occur are ecologically equivalent; although such a situation is highly unlikely (see Dingle 1996, p. 199ff., for fuller development of this notion). Minimum orientation may suffice if winds or currents are sufficiently predictable to guarantee that enough migrants reach suitable habitat that selection continues to favor the behavior. The demands for orientation may differ with respect to type and sophistication both on the route and at the destination where food, a breeding site, and often a home range or territory must be found.

Most migrants home to precise locations to breed or to precise habitats that meet the demands of breeding or wintering. Monarch Butterflies winter in the same Mexican sites year after year; sea turtles return to nesting beaches; and many songbirds annually return to the same territory. In view of the necessity to find breeding or wintering sites following migration, it is a requirement that environmental cues used to orient or navigate (Box 8.1) are both reliable and available. If migration covers long distances, the reliability and availability must hold true on a global scale. Cues may be available for only part of the time or over only part of the route, so it will be necessary to rely on more than one such cue. Clouds may cover the Sun, for example, or landmarks may be obscured by darkness or fog. The migrant must therefore be imbued with sufficient flexibility to allow use of multiple cues and adjustment to changing conditions.

Migrants further face a variety of orientational and navigational problems that depend on their sensory and cognitive abilities, the distances traveled, and the specificity of the goals. There seem to be only a limited number of ways these problems can be solved, as indicated by common themes that apply across the migration systems and taxa so far analyzed (Able 1991). The ultimate causal basis for the similarities is still not entirely clear, although the necessity for reliability is a common theme. The presence of similar mechanisms and uses of cues in phylogenetically distinct groups may represent convergence, but we lack adequate data against which the convergence hypothesis can be tested because our sample of organisms still contains too few species. The same can be said for the notion that common themes may exist because they represent characters that are phylogenetically ancient, being long conserved and honed during the course of evolution. Whatever their basis, they are clearly present. Nevertheless we are gaining an understanding of the often intriguing nature of mechanisms that are outside the capabilities of human senses and allow migrants to follow routes with precision and arrive at destinations with astonishing accuracy.

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Box 8.1 Four categories of orientation behavior and guidance systems used by migrants

Piloting—The ability to use fixed, known reference points (landmarks) to orient or navigate. These may be either points on the landscape such as a hill or "leading lines" such as a row of hills, a shoreline, or a river that may guide movement over considerable distances.

Compass orientation—Orientation in a given direction without reference to landmarks and without reference to origin or destination. The organism does not necessarily know where it is, but only in which direction it is facing or moving. The duration of movement may be timed by an internal clock ("clock-and-compass orientation").

True navigation—The ability to move toward a particular goal while in unfamiliar territory in the absence of any sensory contact with that goal. The ability to so navigate implies that the organism possesses a "map" ("cognitive map") that is an internal representation of geometric relations among points in the environment. These points can be a considerable distance apart.

Guiding—The ability to complete migration by following other migrants that know the way. This could be a strategy used by flock migrating birds and is most likely for young or otherwise inexperienced individuals.

The categories do not necessarily reflect increasing complexity nor the order in which the capabilities evolved.

Sources: Dingle (1996) and Mouritsen (2003) after various authors.

Seasonally directional travel

Large annual shifts in population distributions and ranges are a common phenomenon, and the primary means through which these shifts occur is migration (Chapter 3). Because this is the case, there should be strong selection on individuals favoring the direction of migration appropriate to season. In migrants moving between tropical and subtropical areas and temperate breeding habitats, birds being the best-known example, movements are generally along a north–south axis; in the southern hemisphere southward in the spring and northward in the autumn, and vice versa in the northern hemisphere. There are, however, exceptions depending on the exact nature of seasonal gradients. In Australia, for example, the drier interior poses a more variable and extreme environment compared to the wetter coastal areas, so one might expect some migrations to display an east–west component as well as a north–south axis. Examination of seasonal migratory patterns in Australian migratory butterflies reveals that, at least for some species, there does seem to be an east–west component (Dingle et al. 1999).

In the Australian natural history literature there are frequent observations of mass migrations of butterflies, and often these movements are noted as to direction. The movements are frequently characterized as "purposeful" and undistracted, as would be expected for true migration. By compiling these observations, it was possible to obtain a large enough sample of mass movements in several species to assess in which direction migrants were traveling in the different seasons, and mean bearings could be computed. Because samples were small for most species, spring and summer were lumped into a single "season," as were autumn and winter. It should further be noted that all data are for populations east of the Great Dividing Range, so there are no data for inland Australia. In spite of the fact that many observations were not exact and seasons were lumped, it was still possible to determine season-specific directions of migration for several species (Table 8.1).

For five species of Australian butterflies, both *Vanessa* spp., both *Danaus* spp., and *B. exclamationis*, there is evidence that migratory flights are primarily southward in spring and summer, and northward in autumn and winter. All else being equal, these would be the "expected" seasonal directions of migration. In the two *Vanessa* spp. and *D. chrysippus*, there is also a westerly component to spring movement which, for these coastal and subcoastal populations, would take the migrants inland to increasingly suitable habitats. For two species, *J. villida* and *E. smilax*, the predominant directions of movement seem less obviously adaptive. In the former, spring movement is westerly (WNW), and the autumn transit is northerly, but the difference, although statistically significant ($P < 0.05$), is slight. In the case of *E. smilax*, movement is southerly in both seasons, but again the seasonal difference is slight although significant. Relatively small samples and imprecise observations may contribute to these results, and only further and more precise

Table 8.1 Mean bearings by season (S/S spring/summer, A/W autumn/winter) for flights of Australian migratory butterflies.

Species	Season	Mean bearing
Vanessa kershawi	S/S	213° (SW)
	A/W	349° (N)
Vanessa itea	S/S	226° (SW)
	A/W	337° (NNW)
Danaus chrysippus	S/S	255° (W×S)
	A/W	348° (N×W)
Danaus plexippus	S/S	163° (S×E)
	A/W	44° (NE)
Junonia villida	S/S	293° (WNW)
	A/W	280° (W×N)
Badamia exclamationis	S/S	142° (SE)
	A/W	321° (NW)
Eurema smilax	S/S	183° (S)
	A/W	213° (SW×S)

All seasonal differences are statistically significant.
Source: Dingle et al. (1999).

observations can reveal whether the results for these two species are anomalous or reflect real ecological adaptations. What is apparent from all the species in Table 8.1, however, is that these butterflies change the direction of migration with the seasons.

Not only Australian butterflies, but also many other insect migrants, are known to change their direction of travel with the seasons. This ability is of obvious selective advantage for colonizing breeding habitats in the spring or in a wet season and for escaping to non-breeding habitats until breeding again becomes possible. An important question is what cue do migrants use to determine direction? The existence of a compass sense determining that a Northern Hemisphere nocturnal migrant moth, *Autographa gamma*, will select winds taking it north in the spring and south in the autumn has been demonstrated by Chapman et al. (2008b). Photoperiod seems the most likely cue triggering the change in direction. In a British pierine butterfly, long-distance northward oviposition flights abruptly switch to southward orientation as the decreasing daylengths of August pass a threshold in the middle of the month (Baker 1968). Migrants can be highly sensitive to daylength differences, so abrupt switches in direction of migration are quite possible. As an example of this possibility, I observed a mass migration of the Blue Tiger butterfly (*Tiramala hamata*) through the University of Queensland campus in Brisbane, Australia in March, 2006. On the 14th and 15th there was a steady stream of migrants flying south through the campus, including flying up and over three- or four-story buildings. This was followed by two days of butterflies milling about with no obvious direction of flight. On the 18th there was again a steady stream of "purposeful" migrants flying at 2–4 m above the ground and up over buildings, but this time they were flying north as would be expected if the migrants were seeking wintering sites. These observations are anecdotal, but they occurred around the autumnal equinox and certainly hint at a photoperiodic switch in orientational direction. Clearly, however, the cliché of "more research is needed" applies!

A major event in insect life histories that is most frequently cued by daylength (or nightlength) is diapause. Characteristically short days/long nights are the relevant cue for entering diapause; this is the case for European populations of the migratory butterfly, *Pieris brassicae* (Spieth et al. 1998). Spieth and colleagues used an outdoor flight cage to test for flight direction in butterflies from northern Germany. Butterflies that had been in diapause as pupae—the diapause stage that overwinters—oriented toward the north as the wild population would do in the spring, whereas those that had not been in diapause and emerged in middle to late summer flew to the south, again as expected for this generation. The mean direction of migratory flight was influenced by the location of the population. Butterflies from northern Germany flew SSE (162° where south is 180°) in the autumn whereas those from the south of France flew approximately WSW (248.5°), a course that paralleled the Mediterranean Coast and would take them into Spain (Spieth and Kaschuba-Holtgrave 1996). It is possible that directions in the Australian butterflies discussed also reflected piloting by topographical features, leading to apparent anomalies in flight direction (Dingle et al. 1999). In neither case is it clear whether piloting (Box 8.1) modifies an innate course or whether the course itself is genetically programmed.

The ability to orient and navigate

The environment abounds with cues that organisms could potentially use to determine their location in space and to orient or navigate. The cues can also inform on the condition of a host of biotic and abiotic factors of potential importance. These cues arise from an array of chemical and physical inputs which organisms can detect. We are familiar with the inputs from our own five senses, but there are other reliable sources of information that we are (apparently) unable to detect, at least consciously, such as the Earth's magnetic field or polarized light. Numerous studies have shown that many other organisms can use these sources and rely on them to supply useful and necessary information. Our own sensory capabilities are not necessarily a reliable guide to the sensory world of migrants. In the following sections I briefly explore the cues that migrants can use both to find their way on migratory journeys and to locate specific breeding and nonbreeding sites necessary for survival.

Chemical cues

Anybody who has ever walked a dog that insists on sniffing every tree or signpost is aware that dogs live in a very different chemical world from our own. So too is this the case with many migrants (and other animals) that may be extraordinarily sensitive to the odor worlds that surround them. The enormous arrays of volatile chemicals that can be emitted into air or water provide highly specific information about their sources to those organisms with the ability to detect them. Organic molecules in particular, because they can be formed by increasing chain lengths or changing configurations of carbon atoms, provide an almost unlimited number of chemical signatures. These can be increased even further when combined with other organic or even some inorganic molecules as elaborated by Wilson and Bossert (1963). The species and sometimes even individual-specific (as in the case of our dogs) pheromones that numerous taxa use to communicate are useful examples of the adaptability of chemical information. Chemical cues are extensively used by migrants, especially to locate a particular "home" or site.

One of the best known and extensively studied uses of chemical cues by migrants is the homing to stream odors by salmon, studied for many years by Arthur Hasler and his students at the University of Wisconsin (summaries in Hasler and Scholz 1983; Dingle 1996; and Barinaga 1999). Hasler and colleagues developed the hypothesis of homestream homing by following odor cues based on three primary assumptions: (1) each breeding stream had its own odor based on soil and substrate chemicals in the stream basin; (2) juvenile salmon became chemically imprinted on the home stream; (3) adult salmon used the imprinted odor to locate the home stream when they returned after maturation in lakes or the sea. Imprinting is the special form of learning that does not involve conditioning and is confined to a "sensitive period" during maturation. Experiments demonstrated that salmon hatched and reared through smolting in stream water that was not from their home stream returned to the stream in whose water they were reared. Furthermore salmon could be conditioned to an artificial chemical, morphaline or phenethyl alcohol (PEA), and would then return to a stream into which that chemical was introduced. As a practical matter this was very useful in building up populations of coho salmon (*Oncorhynchus kisutch*) introduced into the Great Lakes of North America.

In the coho, fish were most susceptible to imprinting on stream odor at the transition from the parr to the smolt stage at which they migrate out of the streams in which they hatch. At this time there is a surge of thyroid hormone (T_4) which is then converted outside the thyroid into T_3 (Chapter 6), and T_3 is critical for imprinting on stream odor (Nevitt and Dittman 1998). If T_4 release is stimulated in younger fish, they, too, imprint on stream odor even though they should not otherwise have done so. Especially interesting is the case of the Sockeye Salmon (*O. nerka*). This species does not migrate directly to the sea, but first proceeds to lakes, where smoltification occurs, and it matures for two to four years before migrating onward to the ocean. In Sockeye there is a surge of thyroid hormone in the young fish shortly after hatching so that imprinting on stream odor occurs at that stage. Thus Sockeye home not only on the lakes where they spend intermediate years, but also on the tributary stream in which they hatched.

Further studies revealed that the electroencephalogram (EEG) of the olfactory bulb increased when the olfactory epithelium was bathed in homestream water, leading to a natural conclusion that the imprinting to odor occurred in the brain.

Further studies, however, indicated that the imprinting occurs in the peripheral olfactory epithelium (Nevitt and Dittman 1998). These authors exposed laboratory-reared salmon at smolting to PEA and then measured PEA responses the following autumn in isolated olfactory receptor cells with electrical recording techniques. The cells of fish previously exposed (imprinted) were about twice as likely to respond to PEA as were those of fish that had not been exposed to the chemical. The isolated cells of 77% of the exposed fish responded to the applications of water containing PEA whereas those of only 43% of the control fish did so. At least part of the homestream-imprinted "memory" thus resides in the peripheral nervous system in the olfactory epithelium. Other odorants failed to elicit responses from olfactory cells of either group of fish. Further experiments revealed that guanylyl cyclase activity was stimulated by PEA in previously exposed fish compared with PEA-naive fish, but only at the time of the homing migration some two years after PEA exposure. The early exposure to a homestream chemical may thus sensitize olfactory guanylyl cyclase, and so cyclic GMP may play an important role in olfactory imprinting and hence return to the home stream. Studies of other salmonids indicate that olfactory imprinting is widespread. Olfactory imprinting is not necessarily confined to the parr–smolt transition but may occur whenever there is a surge in thyroid hormone (Nevitt and Dittman 1998). This becomes particularly important in fish such as the Sockeye which may imprint both on the home stream and on the lake in which intermediate maturation lakes place. Thyroid hormone also may induce olfactory cell proliferation, further increasing the efficacy of imprinting to home stream or lake (Lema and Nevitt 2004).

As we saw in Chapter 1 the detection and location of chemical signals requires the specific behaviors of zigzagging and casting in an upcurrent direction to maintain contact with the signal and eventually locate its source. This is the case with salmon locating homestream odor when moving to freshwater from the ocean as indicated in Figure 8.1. The odor profile of a large diffuse source such as a river entering the sea will consist of water with odor at different concentrations. The vertical distribution of the odor will be related to variables such as differential velocities in different layers, temperatures, and salinities leading to considerable vertical fine structure and a horizontal quasi-mosaic odor pattern. Moving up the odor gradient would require both vertical and horizontal zigzagging and casting against the current shear in the gradient layers. The mean direction of shear would be in the direction of the river mouth, so that the mean path of the fish would be in the correct direction. Atlantic salmon (*Salmo salar*) tracked by transmitter on their homing migration through a Norwegian fjord did indeed display such movements (Døving et al. 1985 and Figure 8.1) as well as a preference for a particular water layer.

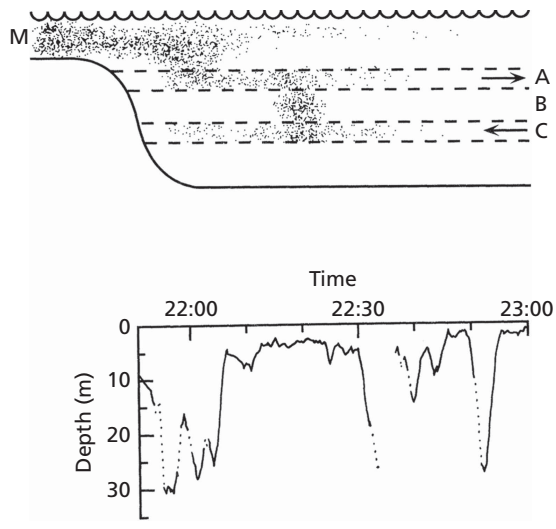


Figure 8.1 (Upper panel) Odor layer formation in near-shore areas. Odor enters the ocean from a river mouth, M, and spreads at the surface. At a region of higher concentration some odor "leaks" into a current (A), which causes more rapid spread. In turn there is leakage into slower-moving water (B), and again into a current (C). The result is a pattern of odor concentration varying horizontally and vertically. The horizontal scale is compressed. (Lower panel) Swimming record of a salmon during 1 h, showing pattern of vertical movements. Dotted lines indicate loss of data due to high signal:noise ratio and other factors. From Dingle (1996) after Johnsen (1987) and Døving et al. (1985).

Another species that homes to a specific breeding site is the marine Green Turtle (*Chelonia mydas*). One population of this turtle makes a lengthy round-trip migration between feeding zones on the coast of Brazil to egg-laying beaches on Ascension Island some 2,200 km away in the tropical Atlantic. Ascension is a tiny island in the midst of a literally vast ocean, so the question of how they find it naturally arises. The final step of finding the island after travel from Brazil seems to be a response to odor emanating from Ascension itself. This was suggested by a study in which 18 females from Ascension were displaced to 60–450 km from the island and tracked by satellite (Luschi et al. 2001; Åkesson et al. 2003). Four turtles headed to Brazil after release, four wandered before heading for Brazil, and ten came back to the island. The tracks of these ten tended to wander for a period and then make a sharp turn followed by a straight track back to Ascension (Figure 8.2A). These straight tracks were all upwind, as would be expected if the turtles were orienting to odor (Figure 8.2B). In a later experiment three turtles were displaced 50 km downwind to the northwest and three more were released 50 km upwind to the southeast (Hays et al. 2003). The turtles released downwind returned to Ascension in one, two, and four days, respectively. Those released upwind had great difficulty returning; two returned after 10 and 27 days, but only after crossing into the downwind region, and one apparently gave up and was heading toward Brazil when satellite transmission ended. In spite of alternate diving and surfacing—a pattern which might facilitate odor detection (Figure 8.1)—evidence does not support the use of water-borne odor to locate the island (Åkesson et al. 2003).

Like marine turtles, albatrosses and petrels forage and migrate over wide areas of ocean and nest on small islands. Recent evidence has shown that these birds are very sensitive to odor. They use olfactory cues at large spatial scales of hundreds to thousands of square kilometers and at small scales of a hundred square kilometers or less (DeBose and Nevitt 2008; Nevitt 2008). At the large scales odor is used to locate foraging areas, and at small scales it is used, in combination with other cues, to track prey directly. Odors thus provide a foraging "map" of the ocean for these birds, but apparently not a migration map. Odor, however, could be used to home to nesting islands as happens in marine turtles. Many petrels return to their nests in total darkness after foraging at sea and locate their home burrows by smell (Bonadonna and Bretagnolle 2002). There is thus the possibility that odor could be a cue allowing birds to locate nesting islands on the last leg of a return migration from non-breeding forays at sea. This possibility, however, remains to be tested.

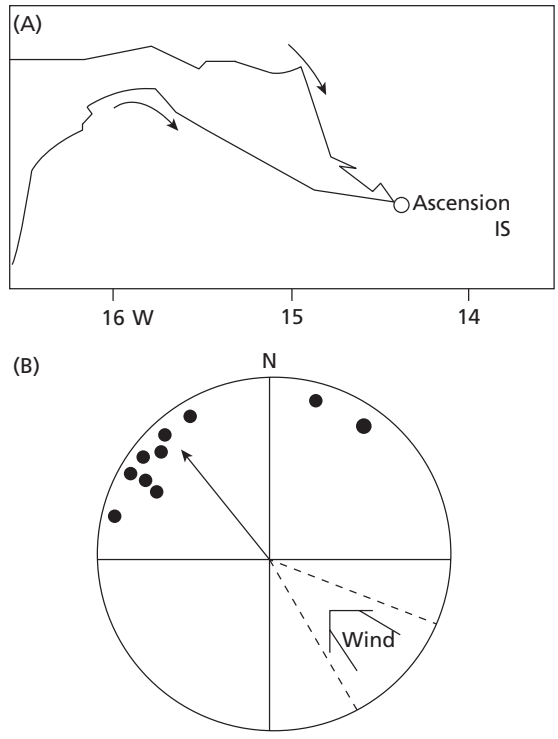


Figure 8.2 Return of displaced Green Turtles to Ascension Island. (A) Two sample routes of returning turtles indicating a sharp turn (arrows) toward the island after a period of wandering. (B) Circular distribution of the first fixes (point of sharp turn) of the final legs of the routes of 10 turtles returning to Ascension. These are downwind of the island so that the subsequent, nearly straight, paths (as seen in A) were upwind as indicated by the wind arrow showing range of wind directions in the month previous to the returns. Modified from data and illustrations in Luschi et al. (2001).

Visual cues

Migrants travel both by day and by night, and the sky provides potential sources of orientation and

navigation information at both times and at the dawn and dusk transitions. During the day the Sun is a prominent cue used by migrants to determine and maintain routes. The position of the Sun in the sky, differential brightness patterns, polarization patterns, and the points of rise or set are all potential sources of information to guide migrants, and all are used to one or another degree by various species. At night the stars and Moon are available, although the latter presents special problems because, for part of its monthly cycle, it is not visible for the whole night, and its phase is shifted by 50 min a day. The stars provide an overall pattern but rotate during the course of the night (around the North or Pole Star in the Northern Hemisphere), and this turns out to be an important consideration in the use of stellar sources of information (Deutschlander and Muheim 2010). In the discussion of visual cues, I begin with simple pattern discrimination.

Newly hatched sea turtles face the problem of moving from the upper beach, where they hatch, to the ocean to begin their movement out to sea. On Atlantic beaches of Florida, Loggerhead Turtles (*Caretta caretta*) emerge at night, probably under selection to avoid predation by gulls. Seafinding orientation is apparently facilitated by background illumination from the Moon since appropriate orientation is strongest when the Moon is full and experiments show there is no attraction to the Moon itself (Salmon and Witherington 1995). The major cues in seafinding are taller, spatially uneven objects such as dunes, bushes, and trees behind the beach (and even buildings). The hatchlings move away from such objects and toward the lower spatially uniform view over the ocean. Brightness can also be a cue, but "cue-conflict" experiments, where the hatchlings must choose between conflicting information as to direction, demonstrate that the turtles ignore intensity differences and prefer object avoidance/uniform view orientation (Salmon and Wyneken 1994). Once they reach the sea, the hatchlings ignore visual stimuli and orient to the orbital motion of surface waves, and, after a further brief period, switch to a magnetic compass (Lohmann and Lohmann 1996; Wang et al. 1998).

Orientation in response to brightness or large objects is the simplest use of visual cues. At a more complex level is the use of the Sun itself, which can be done in two ways. First and simplest, the organism can move toward or away from the Sun without correcting for its movement during the day. Under these circumstances orientation cannot be precise because, as the Sun moves across the sky during the course of the day, the direction of movement will also change. One possible advantage, however, is that the resulting route will approximate an orthodrome (Box 8.2). The second way to use the Sun—which vastly improves accuracy—is to compensate for the Sun's movement and change the angle of orientation with respect to the Sun, so that a constant direction is maintained. Such a bi-coordinate system with two reference points, the Sun and the time of day, requires some sort of internal biological "clock." The actual demonstration of a Sun compass dates to Felix Santschi (1911), who studied the homing of desert ants in Tunisia. By shifting the apparent position of the Sun with mirrors, he could shift the orientation direction of the ants. Santschi (1913) suggested that animals might possess an internal representation of time.

A further aspect of the Sun is that theoretically animals could use it to determine latitude, because the path of the Sun through the sky (its arc, Figure 8.3) depends on latitude. The arc passes directly overhead at the Equator, but is progressively reduced poleward. It also changes seasonally, being highest at the summer solstice and lowest at the winter solstice. Animals, however, do not seem to use this information. Rather they use the Sun azimuth (Figure 8.3), an imaginary line traversed by the projection of the Sun on the horizon.

The standard test for whether an organism uses a Sun compass with time compensation is the "clock shift" experiment. The organism is reared under a daily light–dark cycle that is out of phase with the natural photoperiod. If the rearing cycle is, say, 6 h out of phase, when tested under natural conditions with the Sun visible, the organism should displace its orientation by 90°, or one-fourth of the 360° horizon. The Sun moves 15° along the azimuth in 1 h on average, so if x is the number of hours of clock shift, $15x$ gives the predicted displacement. Time-compensated Sun-compass orientation has been found in a wide array of animal groups. It occurs in crustaceans (decapods, amphipods), several insects, fish, amphibians, reptiles, mammals, and birds. The

Box 8.2 Possible migration routes over the surface of the globe

Because the Earth is a spheroid, there is variation in the "direct" distance between two points depending on the nature of the route followed. The following types of route could be used by migrants either alone or in combination.

Orthodromes (great circles)—The shortest routes between any two locations on the surface of a spheroid such as the Earth. Airlines use great circle routes to save fuel, and migrants could do likewise. Planes flying from London to San Francisco do so via Greenland and Baffin Island, a route ~20% shorter than a flight over Boston and Chicago (loxodrome). An orthodrome would be complicated for, say, a bird which would need to shift compass course constantly, except that simply following the Sun's daily movement across the sky (with no adjustment of internal clock) means that the bird would approximately follow a great circle.

Loxodromes (rhumb-lines)—Routes following a constant geographic course such as the roughly WSW route from London to San Francisco via Boston and Chicago. All else being equal, loxodromes are ~20% longer than orthodromes and so energetically more costly.

Magnetoclinic routes—Routes on which an organism maintains a constant magnetic angle of inclination relative to its heading. Many animals can detect magnetism and so are theoretically capable of such routes, which would be curved and so approximate some routes followed on natural migration.

Magnetic loxodromes—Routes with a constant angle between heading and the horizontal component of the geomagnetic field. A problem is that in polar areas these routes would spiral in toward the geomagnetic North Pole which probably prevents their use by migrants.

Topographic routes—Routes that follow coastlines, rivers, mountain chains or other topographic features. Large-scale topographic features are known to cause major course shifts by migrants (see *Piloting*, Box 8.1).

Source: Åkesson and Hedenström (2007).

Sun compass is used for a number of functions from beach slope orientation in amphipods, to food caching in birds, to migration in birds and insects (Dingle 1996 and references therein). The presence of a Sun compass in so many animals and its functioning under a variety of circumstances imply that it did not evolve specifically for migration but rather could be

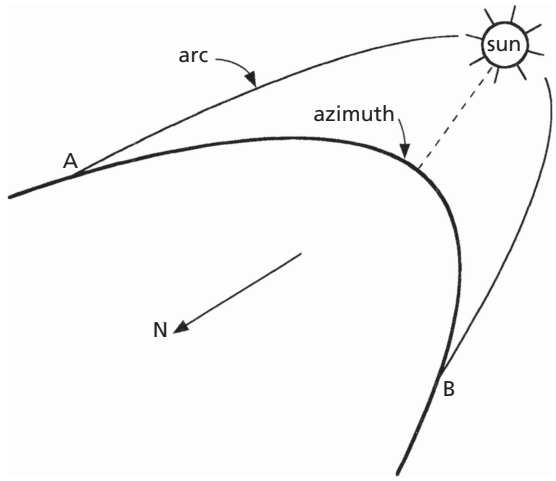


Figure 8.3 The Sun arc, or path of the Sun through the sky, and the Sun azimuth, or path of the Sun projected on the horizon, diagrammed here for the Northern Hemisphere. The Sun rises at A and sets at B. From Dingle (1996).

rapidly incorporated as necessary as part of migratory syndromes.

The use of a Sun compass with respect to Sun azimuth has been assessed in two butterflies, *Aphrissa statira* and *Phoebis argante*, migrating in tropical Panama (Oliveira et al. 1998; Srygley and Oliveira 2001). These two species regularly migrate across Lake Gatun in the Panama Canal where they can be followed by boat and their headings noted; they migrate in a southerly direction during the day. The Sun's azimuthal course is not constant, but is slower in the morning and evening and sweeps more rapidly in the middle of the day at a rate depending on latitude and time of year (Figure 8.4). If the butterflies use a Sun compass, they would need to adjust for this in some manner. Three alternatives are possible: (1) full compensation for the changes in daily motion; (2) averaging of the Sun's position over the course of the day (15°/h as described previously); or (3) a step function that approximates the Sun east in the morning and west in the afternoon. Plots of the orientation of the butterflies during the course of the day under natural conditions support the notion of full compensation (Figure 8.4). A clock shift of a 4 h advance, however, produces an ambiguous result. Full compensation would mean a 120° shift in heading, whereas time-averaging would result in

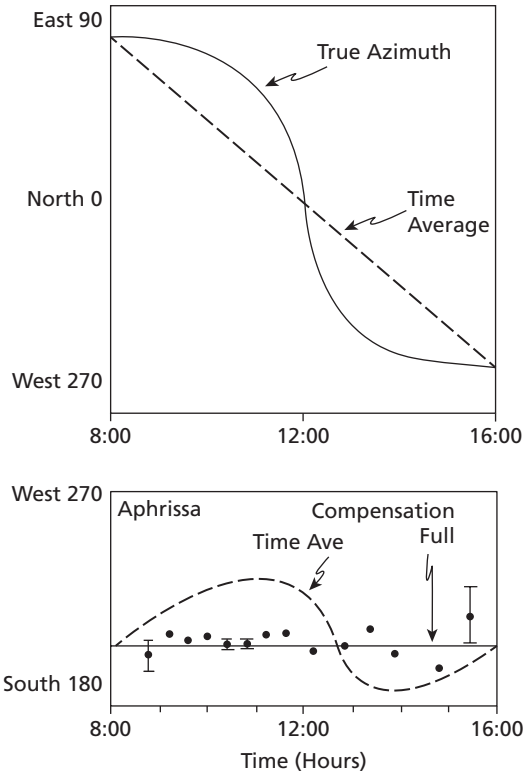


Figure 8.4 (Upper panel) Variation in the actual course of the Sun azimuth over the day (solid line) and the time-averaged course (dashed line) for the Sun in Panama. (Lower panel) The flight direction of the Panamanian butterfly *Aphrissa statira* (solid circles) and the predicted flight directions for full and time-averaged compensation for the passage of the azimuth. Mean flight directions of butterflies migrating across the Panama Canal support full compensation. A clock-shift experiment, however, gave ambiguous results. Modified from Oliveira et al. (1998) and Srygley and Oliveira (2001).

a 60° shift (4 × 15°/h). *A. statira* shifted 91° with a 56–126° confidence interval, and *P. argante* shifted 83° (5°, 161°). The data, therefore, eliminate the step function hypothesis, but do not eliminate full compensation or time-averaging. Hence these butterflies use a Sun compass, but the mechanism used to compensate for the Sun's movement along the azimuth is as yet not known.

Another lepidopteran that migrates with consistent headings across Lake Gatun is the large moth *Urania fulgens* (Sane et al. 2010). If the antennal flagella are removed, 59% of the moths thus treated were apparently no longer able to fly, crashing into the lake following take-off. The remaining 41% were still able to fly and flew at the same airspeeds at which they were traveling before antennal removal. What was particularly interesting, however, was that these antenna-less moths could no longer maintain proper orientation, implying that the antennae are necessary for long-distance navigation.

A fascinating role for the antennae in navigation during migration has been revealed in the Monarch Butterfly. Tethered flight tests on migrating monarchs revealed that, like the tropical butterflies studied in Panama, Monarchs orient by using a Sun compass (Mauritsen and Frost 2002). The butterflies were placed in a small chamber and attached to a tether that allowed determination of the preferred direction of flight over several hours. The tested butterflies were autumn migrants that flew in a southwestern direction. Butterflies kept under photoperiod conditions that time-advanced them by 6 h oriented toward the southeast, whereas those time-delayed by 6 h flew toward the northwest. In both cases the shift in orientation was about 90° as predicted from the amount of clock shift. Thus both the direction and magnitude of the mean shift induced indicated that the Monarchs were indeed using a Sun compass. The antennae, it turns out, are involved with the integration of skylight cues from the Sun with timing information.

This integration has been demonstrated in an extensive analysis of the role of the antennae in Monarch orientation carried out by Steven Reppert and colleagues (Reppert 2007; Merlin et al. 2009, 2011; Guerra et al. 2012). Circadian clocks in the antennae coordinate Monarch Sun-compass orientation. The clock mechanism of the Monarch is based in a transcriptional feedback loop with two transcription factors, CLOCK and CYCLE, which drive the expression of two genes *period* (*per*) and *timeless* (*tim*) and a vertebrate-like *cryptochrome* (*cry*2). A Drosophila-like cryptochrome, *cry*1, also occurs in Monarchs and likely functions as a blue light photoreceptor to entrain the circadian clock (Zhu et al. 2008). The *cry*2 may have a dual role in the brain, that of a core clock element and that of a regulator of circadian activity in four cells of the brain's *pars lateralis*, the brain clock (Zhan et al. 2011). Cryptochromes themselves are evolutionarily ancient blue-light-sensitive flavoproteins associated with circadian rhythms in

both plants and animals. By measuring the relative mRNA levels associated with *per*, *tim*, and the cryptochromes as expressed throughout the day, the pattern of circadian rhythms in antenna and brain may be determined (Figure 8.5).

The co-ordinating role of the antennal clock was worked out in a series of experiments in which the antennae were removed or painted over with black or, as a control, clear paint. (Merlin et al. 2009; Reppert et al. 2010; Guerra et al. 2012). A summary of the results is illustrated in Figure 8.6. Butterflies with antennae intact orient toward the southwest in late summer and early autumn (Figure 8.6A) with the orientation direction tending more southeast as autumn advances, probably representing the fact that orientation must shift in that direction once the monarchs cross into Mexico if they are to reach their overwintering destination (Brower 1995). If the antennae are removed, the butterflies can no longer orient (Figure 8.6B). Ablation of only one antenna does not affect ability to orient (Figure 8.6C), nor does it have any effect on the clock-shifted changes in the direction of orientation that are proportional to the number of hours in the shift (Figure 8.6D). As with ablation of both antennae, covering both with opaque black paint that completely blocks light penetration eliminates orientation ability. What is most interesting, however, is that if only one antenna is blackened, rather than removed, the result is the same, that is, no orientation (Figure 8.6E). The clock in the single blackened antenna no longer displays a circadian pattern (Figure 8.5A), and so the input to the brain will no longer be synchronized with that of the opposite light-receiving antenna covered with clear paint and functioning normally. Thus the discordant timing between the two antennae seems to disrupt orientation by the time-compensated Sun compass (Guerra et al. 2012). When the black-painted antenna is removed, the clear painted one is sufficient to re-establish orientation (Figure 8.6F). The circadian rhythms in the brain continue to function normally even when there is no input from the antennae (antenna-less) or when one antenna is black with no rhythm so that input to the brain is desynchronized (Figure 8.5B). Because the brain rhythm does not respond to rhythmic antennal inputs, it is unlikely that brain clocks are part of the time-compensated orientation mechanism.

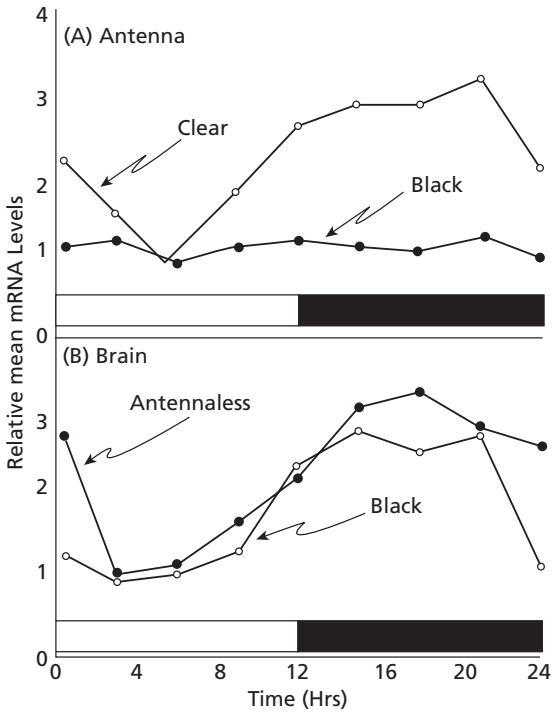


Figure 8.5 Daily rhythms in the antennae and brain of Monarch Butterflies as shown by the relative levels of RNA associated with the *per* gene. (A) When an antenna is covered with clear paint, the circadian rhythm functions normally. The rhythm is eliminated in an antenna painted black. (B) In the brain the circadian rhythm is unimpeded in butterflies either without antennae or with the antennae painted black, demonstrating a rhythm separate from the one in the antenna. The bar on the time axis indicates the light/dark cycle under which the butterflies were maintained; open portion indicates light, filled bar is dark, with each equaling 12 h of the 24 h "day." Modified from Merlin et al. (2009) and Guerra et al. (2012).

In addition to information provided by its position, the Sun provides information via the plane of polarization of light or the e-vector. The e-vectors of the polarized light of the sky create a pattern in the celestial hemisphere (visible as dark–light patches viewed through two polarizing filters such as sunglasses and a car windscreen). There is a band of maximal polarization 90° from the Sun's position (Figure 8.7); this band is visible through the twilight period for up to 45 min after sunset or before sunrise. Thus considerable information is available from the polarization pattern if an organism can

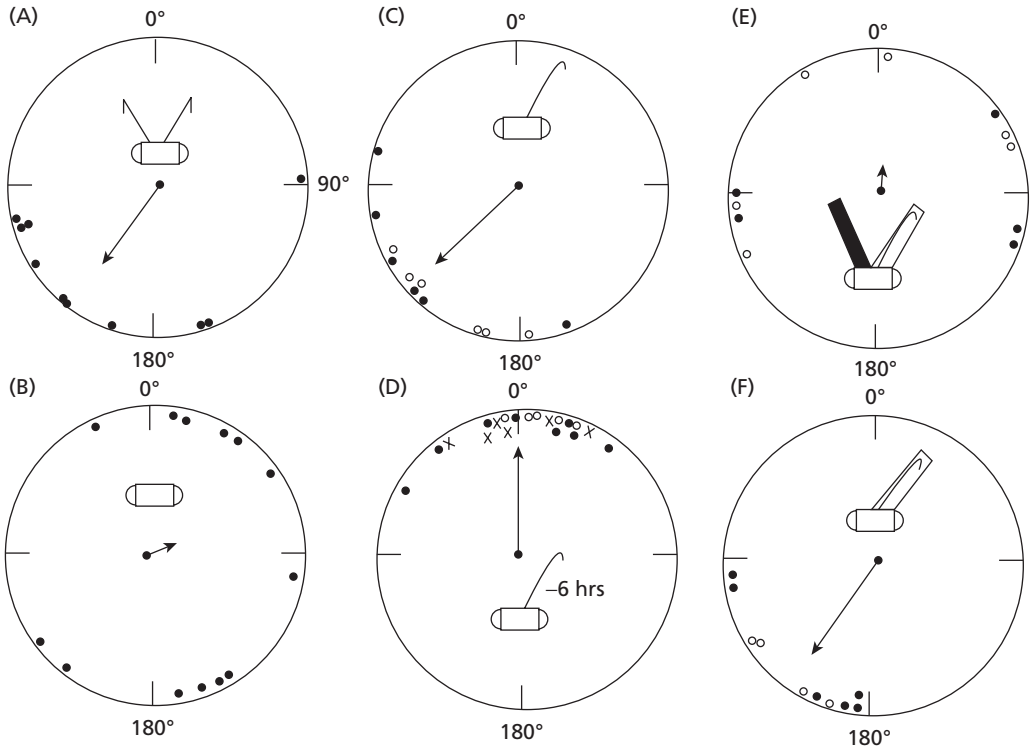


Figure 8.6 Role of the antennae in the Sun compass of the Monarch Butterfly. The cartoons of butterfly heads in each circle represent the experimental treatment. (A) With antennae intact, autumn migrants orient to the southwest when the Sun is visible. The filled circles represent individual butterflies; the vector arrow indicates the strength and angle of the directional response. (B) With antennae removed no orientation is present. (C) Even with only one antenna, the butterflies could orient. Solid circles right: antenna present; hollow circles left: antenna present. (D) Orientation with a clock shift of 6 h demonstrating a time-compensated Sun compass. Circles as in (C); crosses are butterflies with both antennae present. (E) With one antenna painted black and one with clear paint, orientation is disrupted, suggesting that the Sun compass cannot function with discordant timing. (F) With only one, but clear, antenna the Sun compass functions as in (A) and (C). Modified from Merlin et al. (2009) and Guerra et al. (2012).

detect it. Several organisms can indeed detect polarization including ants and bees, orthopterans, tiger salamanders (*Ambystoma tigrinum*), and bullfrogs (*Rana catesbiana*) in which the pineal is involved, and birds (summarized in Dingle 1996 and references therein). In the desert ant (*Cataglyphuss bombarina*) the photoreceptor system of the dorsal rim of the eye serves as a "hard-wired" representation of a celestial map, the polarization pattern of the overhead sky, and by scanning the sky the ant can use the map as a compass to determine homeward direction after a foraging expedition (Wehner and Wehner 1990). The ants also use a system of landmarks in combination with the celestrial map, but which can be decoupled from the celestial system (Åkesson and Wehner 2002).

As with ants, the ommatidia on the dorsal rim area of the compound eye of other insects, including the Monarch Butterfly, are the part of the optic system that detects light polarization (Reppert et al. 2004). The rhabdoms in these ommatidia are arranged morphologically in a way that more or less matches the e-vector sky pattern and so act as crossed polarization analyzers. The question is thus whether the butterflies can use this pattern for orientation. When butterflies were tested in a flight simulator, manipulation of the e-vector with linear polarizing filters demonstrated that the Monarchs

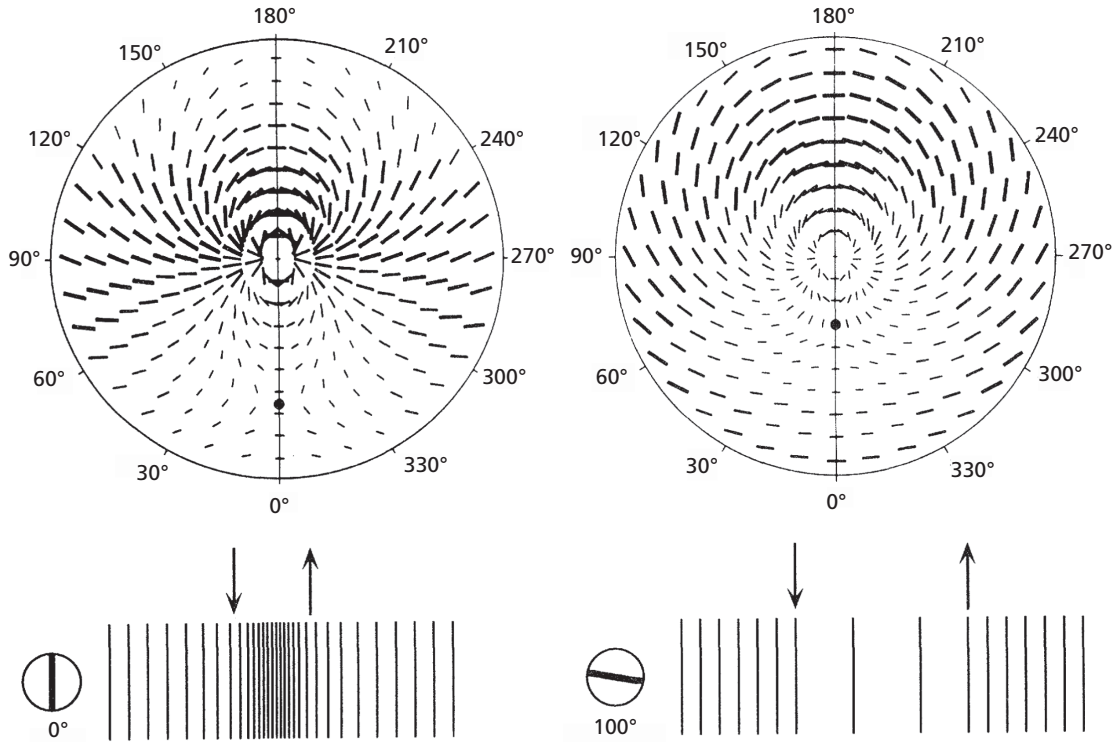


Figure 8.7 (Upper panels) Two e-vector patterns in the sky with the Sun at 24° (left) and 60° (right) elevation above the horizon. The Sun is indicated by the black dot in the central axis. The orientation of each black bar gives the e-vector direction, and the width of each bar indicates degree of polarization. (Lower panels) Responses of an interneuron in the optic system of a cricket to changes in the polarization of incoming light. Arrows indicate onset and end of stimulus. From Dingle (1996) after Wehner (1989).

could indeed respond to plane of polarization by shifting direction appropriate to the changes in polarization (Reppert et al. 2004). This response would be of use to the butterflies under cloudy conditions when the azimuth is not visible but polarization patterns are still apparent. In further tests with a flight simulator, Stalleicken et al. (2005) concluded that polarized light cues were not necessary for the functioning of the time-compensated celestial compass because orientation or clock-shift compensation were unimpeded if the dorsal rim areas were occluded. The Sun's azimuth or light intensity and spectral gradients or a combination are the primary compass cue as long as the Sun is visible.

The various elements of the Monarch Sun-compass system must be integrated to produce a co-ordinated orientation response. A model for how this might be accomplished is illustrated in Figure 8.8 as developed by the Reppert laboratory (Reppert et al. 2010; Heinze and Reppert 2011; Zhan et al. 2011). The Sun and its azimuth are detected by the main parts of the eyes, whereas the polarization pattern is detected by the ommatidia located on the dorsal rim area. These inputs are directed to the central complex (CC) of the brain (Heinze et al. 2013). The photoperiod engendered by the Sun entrains two sets of clocks, one in the antennae and a second set of brain clocks located in the pars lateralis (PL); these latter clocks in turn communicate with the pars intermedius (PI) between the two brain lobes. Although these brain clocks do not seem to be involved with the time-compensated orientation mechanism (Figure 8.5), they may time seasonal changes in reproduction and diapause that accompany autumn migration. The antennal

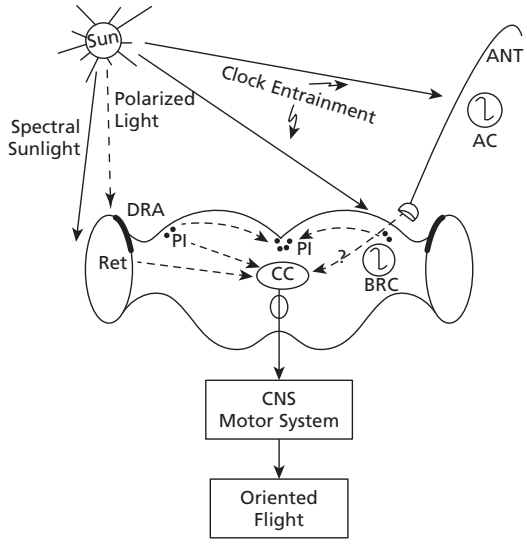


Figure 8.8 Model of the control of the Sun compass of the Monarch Butterfly. Inputs from the spectral sunlight pattern of sky polarization and antennal clocks are integrated by the brain for transmission to the motor system to produce orientation. Further description in the text. ANT, antenna; AC, antennal clock; BRC, brain clock; CC, central complex; CNS, central nervous system; DRA, dorsal rim area of the eye; RET, main retina of the eye; PI, pars lateralis; PI, pars intermedius. From illustrations and data in Reppert et al. (2010) and Zahn et al. (2011).

clocks presumably communicate with the CC to coordinate with visual inputs to that region, although a pathway has yet to be firmly identified. The CC transmits the integrated information from the Sun and the antennal clocks to the motor portion of the ventral ganglia to produce the appropriately oriented flight.

An intriguing aspect of the Monarch life cycle is that summer-reproducing butterflies do not orient, whereas autumn-migrating butterflies in reproductive diapause do. Interestingly if autumn butterflies are stimulated to reproductive activity by topical application of methoprene, a juvenile hormone (JH) mimic, they can still orient. JH activity does not, therefore, preclude orientation (Zhu et al. 2009). Using a microarray analysis of cDNA sequences, Zhu and colleagues were able to identify a suite of 40 genes whose expression in the brain correlated with oriented flight independent of any JH activity. Autumn migrants are thus separated from summer butterflies by molecular activity, including differently regulated clock and locomotion genes. In addition, micro-RNAs and other molecular signatures are associated with the differences between summer and orienting migrant Monarchs (Zhan et al. 2011).

Autumn migrant Monarchs maintain a southwesterly orientation, but over the winter there is a shift in orientation so that spring migrants leaving Mexico orient toward the northeast which brings them back from Mexico into the southern tier of US states. Guerra and Reppert (2013) first established with clock-shift and antenna-removal experiments that spring butterflies orient using an antenna-dependent Sun compass, as they did in the previous autumn. Temperature at the overwintering sites falls to mean lows around 2–4°C during December to February. Butterflies captured in the autumn in Massachusetts were kept in the laboratory and subjected for 24 days to daily temperatures mimicking those they would experience at the Mexican wintering sites (11°C during light and 4°C in the dark). The regimes were run during increasing daylength and in a constant 12L:12D day. In both cases these autumn-captured butterflies oriented to the north as they would in the spring. Butterflies kept under conditions similar to those of the fall migration route continued their southwestward autumn orientation. It is thus evident that the cold experienced by the Monarchs at the overwintering sites is what triggers the switch from southward fall orientation to northward spring orientation.

In addition to the Sun, the pattern of stars in the night sky provides directional information and information about position on the Earth's surface, that is, information for true navigation. Several migratory birds have been shown to use the stars to ascertain direction, but there is no confirming evidence as yet that any use star patterns for true navigation (e.g., Mouritsen and Larson 2001). The first proof that birds can orient using the stars was by Stephen Emlen who showed with experiments using an Emlen funnel in a planetarium (Figure 4.12) that North American migratory Indigo Buntings (*Passerina cyanea*) used a night sky pattern based on the North Star (summarized in Emlen 1975; Dingle 1996). The experiments took advantage of

the birds' night-time migratory restlessness when they would directionally hop in the funnel, allowing determination of preferred orientation under different patterns that could be manipulated in the planetarium "sky." Mouritsen and Larsen (2001) used a computer-controlled Emlen funnel, which allowed more detailed temporal analyses, in a planetarium to test young European Pied Flycatchers (*Ficedula hypoleuea*) and Blackcaps (*Sylvia atricapilla*) for their use of celestial cues. Three basic hypotheses were tested: (1) true star navigation, (2) time-dependent compass orientation, and (3) time-independent compass orientation. The data were consistent with the time-independent compass hypothesis, indicating that the birds used the rotational center of the night sky as a reference point to guide their orientation. This would be the North Star in the Northern Hemisphere with autumn migrants moving away from this point and so southward. Earlier experiments by Wiltschko et al. (1987) had shown that in Garden Warblers (*S. borin*), the rotational center of the sky was learned prior to migration by young birds. Any rotational center would do; it did not need to be the North Star. Because the star compass is limited to orientation, orthodromic or loxodromic routes (Box 8.2), which require navigation, apparently may not be distinguished by these birds, at least not with a star-based system.

Because starlight is so dim, night-migrating birds must have very sensitive night vision in order to perceive star patterns. Night migrants that have been examined display a tight cluster of brain regions highly active only during night vision (Mouritsen et al. 2005). Studies were done on two songbirds that migrate at night—the Garden Warbler and the European Robin (*Erithacus rubecula*)—and, by using a method to detect sensory-driven gene expression, Mouritsen and colleagues discovered the night vision brain area in both species, designated as "cluster N." This area is located on the dorsal surface of the brain near a known visual pathway and did not display activity when vision was obscured by covering both eyes. The cluster N region likely functions to enhance night vision in migrants. In contrast, two non-migrants, Zebra Finches (*Taeniopygia guttata*) and Canaries (*Serinus canaria*), showed no night-time increase in the activity of cluster N.

Physical cues

Some animals, for example the horseshoe crab (*Limulus polyphemus*), which uses beach slope for orientation, and marine turtles, whose hatchlings use wave action to move away from beaches, make use of relatively simple physical cues. Such cues, however, are of no use for the long-distance travels of many migrants. A much more generally available physical cue is the Earth's magnetic field, and there is now an abundance of evidence that numerous organisms from bacteria to lobsters to whales can use this cue to determine location and routes, from simple homing to intercontinental migration (Wiltschko and Wiltschko 1995; Dingle 1996; Phillips et al. 2010a,b). The Earth itself is a giant magnet with field lines exiting from its surface at the South Pole and extending around the globe to re-enter at the North Pole (Box 8.3). The continuously varying *angles of inclination* relative to the surface are a potential source of reliable directional information if they can be perceived by migrants. In addition to inclination angle of the magnetic field, there is also polarization information directly indicating north and south (see Box 8.3). The evidence suggests that most migrants do not use polarity, but rather rely on the directional information present in angle of inclination which provides distinction between poleward and equatorward directions, but not between north and south (e.g., Deutschlander and Muheim 2010).

Experimental demonstration of the use of magnetic inclination involves manipulating the vertical component of the magnetic field with a magnetic coil that surrounds a test apparatus such as an Emlen funnel. By manipulating the current passing through the coil, the vertical component, but not the polarity, of the magnetic field can be inverted, reversing the angle of inclination. If the subject animal possesses an inclination compass, it will reverse direction of orientation even in the absence of a change in polarity. This was the method used to test for an inclination compass in a Tasmanian population of Australian Silvereyes (*Zosterops lateralis*) that migrate between Tasmania and the Australian mainland (Wiltschko et al. 1998). Control birds tested in the spring just before sunset in the local geomagnetic field preferred the normal southwestward migratory direction expected in the region of New South Wales

Box 8.3 Geomagnetic field of the Earth

The magnetic field of the Earth is produced by the geodynamo of a fluid core moving electrically conducting material across an existing field (Deutschlander and Muheim 2010). Magnetic field lines exit from the Earth's surface at the South Pole and extend around the globe to re-enter at the North Pole (Figure 8.9). These lines provide two kinds of information. First is polarity. This is the information contained in the commercial compasses used by humans in which a needle points toward magnetic north from anywhere on the globe. The second information source is the magnetic inclination or dip angle, an "inclination compass." The field lines form continuously varying angles of inclination relative to the Earth's surface, increasing toward the poles and thus decreasing toward the Equator. The inclination angles indicate polarity in opposite directions on either side of the Equator and thus would tell a migrant only which direction was poleward and which equatorward, not a universal north or south. The intensity of the field ranges from about 68,000 nanotesla (nT; 100,000 nT equals the former 1 gauss) near the poles to 23,000 nT near the magnetic equator. The magnetic poles and geographic poles do not coincide, and the angle between them from any point on the globe is the "declination."

There are also local variations in the intensity of the field as a consequence of the properties of the rocks underlying the Earth's surface. The most important variable is the concentration of coarse-grained magnetite (Fe_3O_4) in the rock which may cause "hills" and "holes" in an otherwise geomagnetically "flat" surface. These have the potential to disrupt orientation. Along the Atlantic seashore off the east coast of North America there is a series of magnetic "ridges" and "valleys." Statistical analysis of data from cetacean strandings indicate that some species, e.g., pilot whales (*Globicephala* spp.), are more likely to strand at coastal locations bordering magnetic minima or valleys, whereas others such as the dolphin (*Delphinius delphis*) tend to beach more in the vicinity of maxima or ridges. These cetaceans presumably use the relatively simple tactic of migrating along magnetic valleys (Kirschvinck et al. 1986). Hammerhead sharks (*Sphyrna lewini*) apparently home to seamounts after pelagic foraging by geomagnetic topotaxis using changes in magnetic intensity along slopes (Klimley 1993).

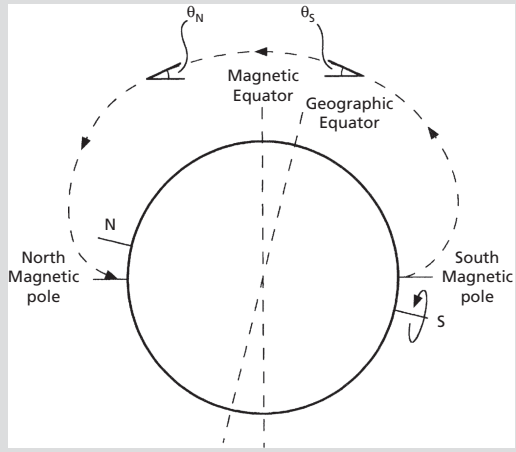


Figure 8.9 Geomagnetic field of the Earth relative to the true north–south axis. Field lines exit from the south magnetic pole and re-enter at the north magnetic pole. They form continuously varying angles of inclination which are indicated north and south of the magnetic equator as θ_N and θ_S. The angle at any place on the Earth's surface between the imaginary lines (equators) connecting the magnetic poles and connecting the geographic poles is the declination. From Dingle (1996).

in which they were captured. When the magnetic field was artificially shifted so that "north" was deflected to 240° WSW, the test birds oriented toward the northeast. When the field was shifted to 120° ESE, the birds oriented northwest, albeit it took them seven trials before they did so, a delay that remains unexplained. Especially interesting was the fact that when tested in a vertical field with no directional information, both experimental groups continued to orient in their previously preferred magnetically influenced direction. Thus they were still able to orient, presumably by using celestial visual cues. This suggests that although magnetic cues predominated when they were present, celestial cues were not ignored, but rather were recalibrated using magnetic information. This experiment is an example of "cue conflict" experiments in which two sources of directional information are present but one is preferred over the other (Muheim et al. 2006a). As we shall see, these Silvereyes are but one example of the interaction between visual and magnetic cues in determining migration direction.

Magnetic field intensities change across the Earth's surface (Box 8.3), and it has been shown that at least some birds can adapt the geomagnetic inclination compass to different intensities. European Robins become disoriented when tested in artificial magnetic fields weaker (16 and 34 μT) or stronger (60–105 μT) than the Earth's field. What was interesting, however, was that after exposure to unnatural fields for an hour, the birds were able to orient in a seasonally appropriate direction (Deutschlander and Muheim 2010). This result implies that the functional range of magnetic field detection is flexible and that the birds can adjust to new magnetic conditions.

In these robins it has further been reported that their magnetic compass is lateralized (Wiltschko et al. 2002). Birds were tested in a magnetic field under monochromatic green light with one or the other eye covered. They were apparently able to orient to the appropriate migratory direction if the left eye was covered but not when the right eye was covered (Figure 8.10), suggesting that the ability to detect the fields was lateralized in the right eye. Further implications are that magnetic compass detection is located in the eye along with visual processes and that the compass joins a number of cognitive functions in humans and other vertebrates (including birds) that are lateralized, with each hemisphere of the brain specialized for certain tasks (e.g., Rogers and Andrew 2002). The lateralization results, however, have been challenged (Hein et al. 2011; Engels et al. 2012). In experiments also with robins, the birds were able to orient using a magnetic compass with either the right or the left eyes covered, indicating that the magnetic compass was not lateralized (Figure 8.10). Wiltschko et al. (2011) replied suggesting three possible reasons why the experimental results might differ. Further (and double-blind) experiments were then done to test each of the three suggestions of Wiltschko and colleagues (Engels et al. 2012), but the birds still displayed a magnetic compass with either eye. There was thus no evidence in the experiments for lateralization. Until the conflict between the results can be resolved, it is probably preferable to accept the more parsimonious explanation of no lateralization of the magnetic compass.

Like birds, sea turtles migrate long distances, in this case between oceanic feeding grounds and nesting beaches that may be on isolated islands such as Ascension or along continental coast lines. We have seen that juvenile sea turtles hatching on Florida Atlantic beaches use light intensity and wave action to move offshore to feeding grounds (Salmon and

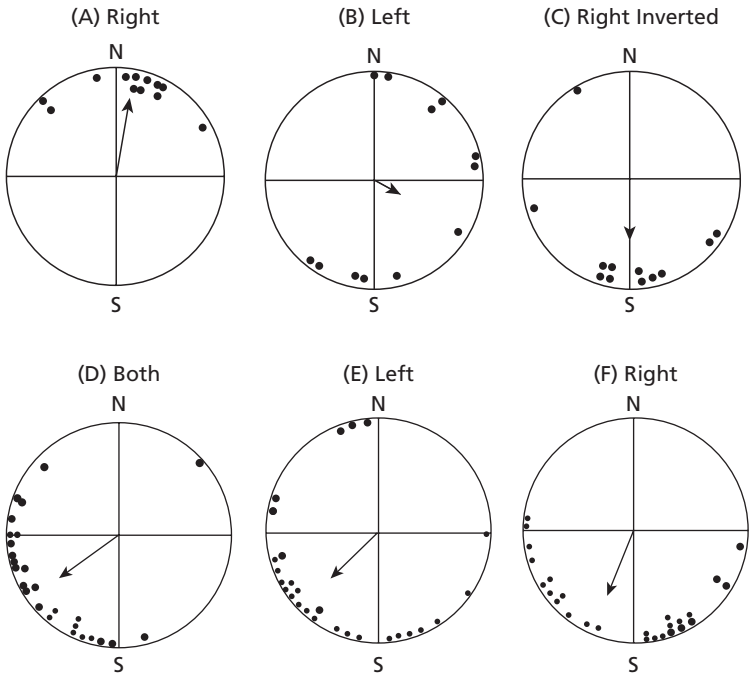


Figure 8.10 Contradictory results regarding lateralization of magnetic field detection in the European Robin. (A–C) Results from the Wiltschko experiments. (A) With the right eye uncovered, the birds oriented in the spring in the appropriate northward direction. (B) With the left eye only exposed, orientation breaks down. (C) With the right eye only exposed and the magnetic field inverted, the birds orient southward as expected. (D–F) Results from the Hein–Engels experiments. (D) With both eyes exposed, orientation in the autumn is in the appropriate southwestward direction. (E, F) Orientation is still to the southwest with either the left or right eye only exposed. (A–C) From results in Wiltschko et al. (2002); (D–F) from Hein et al. (2011) and Engels et al. (2012).

Wyneken 1994; Salmon and Witherington 1995). It turns out that juvenile Green Turtles (*Chelonia mydas*) also possess a "magnetic map" that they can use to position themselves in the ocean (Lohmann et al. 2004, 2007). Turtles in the laboratory were placed in harnesses of soft cloth and attached to an electronic tracking apparatus that recorded their orientation in a water-filled arena. The arena was in turn surrounded by a magnetic coil system that allowed the experimenters to vary the magnetic field. The experiments were done in Melbourne in the middle of the Florida Atlantic coast, which was near the feeding grounds where the turtles were captured. The turtles were then subjected to magnetic fields that duplicated fields occurring 337 km north or south of the capture location. Turtles exposed to the northern field swam southward, and those exposed to the southern field swam northward. Thus the turtles seemed to have a magnetic map that allowed them to "home" to the feeding grounds. The forms of magnetic information used to derive the map are not yet fully elucidated as it is known that sea turtles can detect at least angles of inclination and intensity (Lohmann and Lohmann 1996). Experiments similar to those done on the turtles reveal that spiny lobsters (*Panulirus argus*) also possess a magnetic map (Boles and Lohmann 2003).

An even more sophisticated use of a magnetic map occurs in Loggerhead Turtles (*Caretta caretta*) (Lohmann et al. 2007, 2008a). These turtles undertake one of the longest and most impressive of marine migrations. They hatch on beaches on the Atlantic coast of Florida, migrate offshore into the Gulf Stream which is part of the North Atlantic gyre (Figure 5.6) that circles the Sargasso Sea. The young turtles remain in the gyre system for several years, including crossing to the eastern Atlantic, before eventually returning to feeding grounds offshore from the southeastern USA. Young Loggerheads were exposed to magnetic fields matching those found at different points around the gyre with the following results: (1) turtles tested in fields matching those off Florida swam east-southeast; (2) those tested in a northeastern Atlantic field swam approximately south; and (3) those tested in a southern mid-Atlantic field near the southernmost curve of the gyre swam northwest. These are the directions of swimming that would be predicted to keep the turtles positioned in the gyre if they indeed had a magnetic map that allowed them to maintain appropriate migratory directions. Simulations of turtle movements within an ocean circulation model indicated that directed swimming for as little as 1–3 h per day was considerably more likely (43–187%) to keep the migrants both in the gyre and in warmer waters more suitable for growth and survival (Putman et al. 2012).

The evidence points to migrants such as sea turtles having magnetic maps, but it is not certain how such a map is acquired. One hypothesis is geomagnetic imprinting (Lohmann et al. 2008a). Under this hypothesis young turtles imprint on the magnetic fields of their natal areas, and later use this imprinted information to home in the correct direction. Salmon can also detect magnetic fields (see Quinn 2005 for summary) and could use magnetic information to direct them to the coastal location where water from their home stream empties into the ocean. This is possible because isolines of both magnetic field inclination and total field intensity vary latitudinally (Lohmann et al. 2008a). Experience may also play a role in the use of magnetic information en route. Many migrant birds change course at points along the migratory pathway. The Australian Yellow-faced Honeyeater (*Lichenostomus chrysops*), for example, migrates northeast during the first part of its autumn migration, and then switches to northwest when it reaches the latitude of Brisbane, Queensland, at about the point where the Australian coastline similarly changes direction. European Pied Flycatchers (*Ficedula hypoleuca*) that breed in central Germany until mid-October fly southwest to the Iberian Peninsula where they change course to southeast to parallel the Spanish Mediterranean coast (after mid-October). If birds are held in the magnetic field of Frankfurt, Germany, they do not show this shift in direction ability when tested in the laboratory. If, however, laboratory birds are subjected to magnetic fields matching those they would encounter en route to the Iberian Peninsula, they make the shift to a southeasterly direction at the appropriate time (Beck and Wiltschko 1988; Wiltschko, W. and Wiltschko, R. 2005). Thus the experience of changing magnetic information is necessary for the birds to make the required change in the direction of their pathway.

Migrating insects also use physical cues, probably including magnetism. As we saw in Chapter 5 enormous numbers of moths migrating over Britain fly in a predominantly downwind direction regardless of season. A major question concerns the cues they use to select winds, since they are too high to detect their movement relative to ground features. The fact that migrating swarms are often layered suggests that the insects are using cues associated with the winds themselves and that the relevant cues are associated with turbulence (Reynolds et al. 2010). Turbulent kinetic energy in windstreams aloft is subject to local minima (Reynolds and Reynolds 2009) and migrating insects would tend to concentrate in these with the added advantage of minimizing the energetic costs of flight. Reynolds et al. (2010) analyzed flight paths of "medium-sized" (10–70 mg) nocturnal insects using vertical-looking radar. These migrants, unlike larger insects, did not show compensatory orientation in a preferred seasonal direction, and indeed there was no overall pattern to flight headings. Mean flight headings were downwind, but generally somewhat offset. In the Northern Hemisphere the Ekman spiral (rotation of mean wind direction with height due to the Coriolis effect—see Chapter 5) means that surface winds tend to blow to the left of winds aloft. The effect is greatest when turbulent mixing is low and means that offsets to the downwind direction should be to the right of downwind. In 39 of 48 instances of predominantly downwind flight, offsets were in the predicted rightward direction supporting the notion that the insects are selecting low turbulent flow.

In larger moths, for instance the Silver-Y (*Autographa gamma*), autumn migrants migrate southward and are able to compensate for wind drift when the latter takes them from their preferred course of 205° or roughly SSW (Chapman et al. 2008a). This preferred direction is presumably innate and determined by selection to optimize return to winter breeding sites. In crosswinds where the drift angle (the difference between the track and 205°) was large (>20°), the moths corrected with a mean angle of +27° and always in the expected direction. To achieve this correction the moths must have a compass sense. They fly too high to detect sideslip from ground movement patterns; a lunar compass was ruled out because the moon was not visible on several of the observation nights; and a star compass is beyond the resolution of the moth eye in all likelihood. This leaves the geomagnetic compass as the most likely mechanism. The many species of insect migrant that show appropriate directionality at night suggest that a magnetic compass may be widespread among these windborne species.

There can be a special problem with the inclination magnetic compass of migrants if they cross the Equator. This is because the angle of inclination decreases equatorward, and then for some distance north and south of the Equator the angle is essentially flat before reversing on the other side of the Equator (Box 8.3, Figure 8.9). Under flat conditions birds are known to become disoriented. So what to do? One possibility is that the birds could switch to another source of directional information such as star patterns, and at least some may actually do this. Another possibility is to use the field lines as a cue to switch polarity from migrating equatorward to orienting poleward. One species that migrates across the Equator from Europe to southern Africa is the Garden Warbler (*Sylvia borin*). Wiltschko, W. and Wiltschko, R. (1992) subjected warblers at the beginning of October, when they would be crossing the Equator, to a period of experiencing only horizontal field lines, as they would on an Equator crossing. When tested in the natural northern conditions of field lines directed downward toward the North Pole, these birds oriented to the north or poleward when in nature they would be flying south. In other words the experimental birds switched to a preference—poleward—which in the Southern Hemisphere would mean continuing to migrate south. Control birds not subjected to a horizontal field continued to orient south as they would if still well north of the Equator. Thus the horizontal field lines provide a mechanism for switching direction of orientation from equatorward to poleward. While experiencing horizontal field lines in nature, the birds presumably use other cues to orient.

A further aspect of any compass system is that it must be calibrated to a common reference in order to avoid navigational errors (Muheim et al. 2006a). A celestal compass can be calibrated by star patterns for a nocturnal migrant (e.g., the Pole Star is always in the north) and diurnal migrants can use the position of the Sun combined with an internal

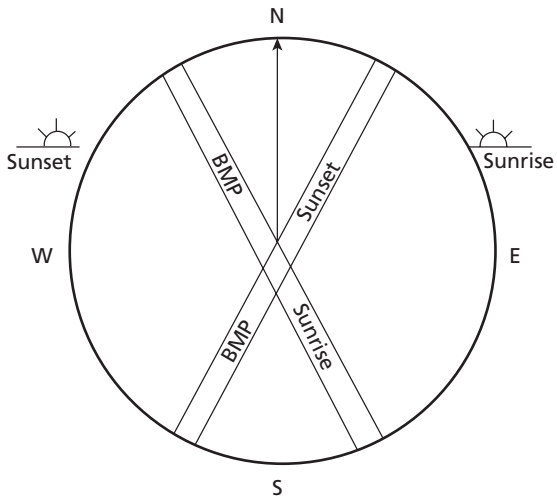


Figure 8.11 Bands of maximum polarization (BMP) of skylight at sunrise and sunset for the Northern Hemisphere at midsummer. The pattern is always symmetrical regardless of season or latitude, as indicated by the vector arrow pointing to geographic north. This geographic reference could calibrate a magnetic compass.

clock. The position of the Sun at sunset can also provide information for a nocturnal migrant departing at dusk. In the case of a magnetic compass, there is a problem because the declination angle between the geographic and magnetic poles changes as one moves from the Equator toward the poles in either direction (Figure 8.9, Box 8.3) and, furthermore, over time the positions of the magnetic poles shift. A pattern that provides reliable information on direction is formed by the bands of maximum polarization (BMPs) across the arc of the sky that occurs at sunrise and sunset (Figure 8.11). This pattern is always symmetrical with respect to geographic north, independent of the time of the year and the latitude (Deutschlander and Muheim 2010).

Experiments with Savannah and White-throated Sparrows (*Passerculus sandwichensis* and *Zonotrichia albicollis*) indicate that both these species calibrate their magnetic compasses by using the skylight polarization patterns that intersect the horizon at sunrise and sunset (Muheim et al. 2006b, 2007, 2009). When this pattern was artificially shifted by 90° as viewed by experimental birds, the direction of orientation was also shifted on average by about 90°. Birds were not observed to recalibrate when exposed to a 90° magnetic shift at solar noon with a different polarizing pattern. In order to use this polarization information birds must be able to see the entire sunset sky; if their view is restricted by the experimental set-up, they use the magnetic compass to recalibrate the celestial systems (Muheim et al. 2006a). Earlier experiments failing to demonstrate recalibration of the magnetic compass by sunset polarization cues had failed to allow birds a full view of the horizon. At least in the case of White-throated Sparrows, the polarization cues used to calibrate the magnetic compass determine the compass hierarchy (magnetic versus celestial) throughout the period of migration in both spring and autumn (Muheim et al. 2009). In fact, star and Sun compass calibrations seem to be secondarily derived from magnetic and polarized light cues in these sparrows and in Australian Silvereyes (Wiltschko et al. 2001; Muheim et al. 2006a, 2007).

Birds in experiments on orientation usually show considerable directional scatter, but field observations usually reveal that birds in nature display little scatter during migration with all individuals following the same course. It is also the case that birds migrate in flocks, and it is flock aggregation that may explain the consistency and accuracy of orientation (Simons 2004). Simons suggests that this accuracy may be a consequence of the "many wrongs principle" first suggested by Bergman and Donner (1964) and further elaborated by Hamilton (1967) and later Wallraff (1978). The idea is derived from the statistical fact that as a random sample increases in size the standard error decreases (i.e., $s/\sqrt{n}$). All else being equal, migrants traveling in larger groups will be more likely to orient correctly and arrive at their destination successfully than will migrants traveling in smaller groups. Simons suggests that this could go a long way toward accounting for the accuracy of migratory navigation and the tendency of many organisms—birds being the best known example—to migrate in groups (flocks in birds). There is an automatic advantage to group cohesion, and accuracy could be further enhanced by following an experienced leader or leaders. In at least one bird, the European Skylark (*Alauda arvensis*), flock size does seem to improve accuracy (Rabøl and Noer 1973), but the possible relation between group size and accuracy of navigation during migration still needs further investigation.

In spite of the decades of investigation of orientation mechanisms and the often remarkable progress made in understanding them, there is still much to be learned. One remaining area of mystery is the detection of longitude. Latitude can be detected readily, at least theoretically, from the height of the Sun at noon or the angle of magnetic inclination or field intensity. To best determine longitude, however, requires knowledge of two times, the one at "home" and the one at the present location (see the excellent book by Sobel 1995). Thus to use celestial cues a migrant would need two internal clocks, one of which is fixed to home time (Chernetsov et al. 2008); no such fixed clock has ever been identified. (Magnetic intensity is a potential map cue, but in many parts of the world its isolines virtually parallel latitudes.) Chernetsov and colleagues displaced Eurasian Reed Warblers (*Acrocephalus scirpaceus*) during spring migration from Rybachy on the Baltic Sea coast eastward 1,000 km to a site near Moscow. At the site of capture these birds oriented roughly northeastward, a course that would take them along the Baltic coast to the southern Fenno-Russian border regions where they breed. The displaced birds oriented roughly northwest, a course which would take them back to the appropriate breeding area. Comparable data for White-crowned Sparrows in North America suggest that they may be able to correct for a 3,000 km longitudinal displacement (Thorup et al. 2007). Magnetic intensities could serve as a cue in the Reed Warblers, but would require an ability to detect a 3% intensity difference. Suffice to say that no certain mechanism has been identified.

Another example of unknown navigational mechanisms is that of Humpback Whales (*Megaptera novaeangiae*). These mammals migrate between low-latitude breeding areas in tropical seas to high-latitude summer feeding grounds in both the Arctic and Antarctic. Their journeys span more than 6,500 km of open ocean. Satellite monitoring of radio-tagged whales has revealed that, in both the South Atlantic and South Pacific, these migrants follow constant-course segments of more than 200 km for several days with a remarkable precision of 1° deviation or less (Horton et al. 2011). This precision occurs in the face of variable currents that require correction for significant deviation. How the whales orient with this degree of precision and with what cues remain unknown. In the Beluga Whale (*Delphinapterus leucas*) of the Arctic social behavior may be a factor in the accuracy of migration routes. Genetic data indicate that these whales maintain associations with a network of relatives during migration (Colbeck et al. 2013). Different groups of whales have different routes and different areas where they spend summer or winter, and the social networks are likely a mechanism that maintains the group-specific routes and locations.

Mechanisms and locations of magnetic detection

Years of study have now led to the conclusion that there are two mechanisms by which migrants and other animals can detect the Earth's magnetic field (Mouritsen and Ritz 2005; Wiltschko, W. and Wiltschko, R. 2007; Zapka et al. 2009; Deutschlander and Muheim 2010; Phillips et al. 2010a). The first of these is a ferromagnetic system based on magnetite (Fe_3O_4) which has been found in a wide variety of organisms from bacteria to birds. The occurrence of magnetite in bacteria indicates that its presence in organisms is phylogenetically ancient. Applying a strong magnetic pulse ("pulse remagnetization") to bacteria to reverse the polarity of the magnetite caused these bacteria to reverse direction in a magnetic field (Blakemore 1975). Several studies have now revealed an iron-based mechanism in the nasal region in fish and birds, in the latter being associated particularly with the upper beak (pigeons and European Robins). In pigeons magnetite- and maghemite-rich nerve-cell endings have been reported in the upper beak, and these structures connect to the brain via a branch of the trigeminal nerve (Fleissner et al. 2003, 2007). Operant conditioning experiments show that pigeons can detect a strong magnetic anomaly (~100,00 nT), but that this ability disappears when the trigeminal nerve is cut, so that it is apparent that this nerve does indeed carry magnetic information concerning intensity to the brain. Naturally occurring magnetic anomalies are of much lower intensity (~10 nT), but the trigeminal neurons seem to have the necessary sensitivity to detect these small changes, allowing for precise geographic positioning (Deutschlander and Muheim 2010).

Recent studies, however, propose that the clusters of iron-rich cells in the upper beak of pigeons are in fact not magnetosensitive neurons but rather are

macrophages which are immune cells that have organelles containing the iron-rich protein ferritin in the cell nuclei (Mouritsen 2012; Treiber et al. 2012). This being the case, the true magnetite-dependent magnetoreceptor in birds (or at least in pigeons) has yet to be identified. The iron-rich dendrites identified by Fleissner et al. (2003, 2007) appeared to occur in six specific locations along the beak. Mouritsen (2012) examined many of the original microscope slides used by Fleissner and colleagues to reach their conclusions, and concluded that the structures they identified occurred in many more than six specific locations along the beak. Furthermore the iron-rich cells are nucleated, which precludes them from being the dendrites of nerve cells. Thus we seem to be left with evidence supporting only a trigeminal nerve-related magnetic sense. The function and sensory origin of that sense are now unknown.

Further experiments indicate that matters are still more complicated. If pulse remagnetization is applied to the upper break, migratory birds will change their direction of orientation as long as the trigeminal nerve is intact. However, bilateral sectioning of the trigeminal in Eurasian Robins did not interfere with their ability to use a magnetic compass for orientation. Thus, even though these beak magnetoreceptors supply magnetic information to the brain, that information is not necessary for magnetic orientation. As we shall see, experiments with the visual processing system indicate that this information is also not sufficient. So how is this magnetic information used? The experiments demonstrating that the magnetite-based receptors are sensitive to magnetic field intensity suggest that they provide information concerning geographic position, rather than direction, and that this serves as a component of a navigational "map" (Wiltschko, W. and Wiltschko, R. 2007).

The second magnetic field detection system is one closely associated with the visual system of animals from insects to birds (Deutschlander and Muheim 2010; Phillips et al. 2010b). In birds the magnetic compass has been shown experimentally to be light dependent (Muheim et al. 2007; Wiltschko et al. 2010). European Robins oriented appropriately in a magnetic field under full-spectrum "white," blue (424 nm wavelength), and green (560 nm) light. Under green light of 560.5 nm robins display seasonally correct migratory directions. A small shift to 567.5 nm resulted in the birds becoming completely disoriented over a range of light intensities. Interestingly when wavelength was increased to 617 nm (red) the birds were still able to orient under lower light intensities, but the direction was shifted relative to the correct migratory orientation. Magnetoreception was thus intensity dependent with apparently two antagonistically interactive spectral systems, a highly sensitive short-wavelength (blue–green) option and a less sensitive long-wavelength one (Muheim et al. 2002).

The establishment of magnetic detection in the visual system raises the question of how such a mechanism would work. The demands on a mechanism are strict (Box 8.4).

Photopigments are widespread among organisms and respond to light in two quite different ways (Mouritsen and Ritz 2005). Visual pigments such as the opsin family of the retina absorb light, undergo a conformational change, and trigger the cascade of reactions underlying normal vision. Other photopigments, for example, chlorophylls or flavins, use light energy to transfer electrons to nearby molecules, so forming pairs of molecules with unpaired electrons, known as a radical pair. Radical pairs are sensitive to Earth-strength magnetic fields that influence the speed of formation or the yield of radical pairs, and such a radical pair mechanism (RPM) could be harnessed in the eye to provide magnetic compass information (Ritz et al. 2000). If an RPM is involved, it should be possible to disrupt orientation by exposure to weak radio-frequency magnetic fields. In the European Robin this is indeed the case, providing strong indirect evidence that magnetic orientation is based on an RPM (Ritz et al. 2004).

Given that magnetic orientation is blue–green light dependent, the photopigments involved in the RPM must be photoreceptive to light in these wavelengths. Cryptochromes are flavins that satisfy this criterion and are implicated in many blue light-dependent signaling pathways in both plants and animals. They are the only known class of photoreceptor molecules found in vertebrates that can form radical pairs upon photoexcitation. Transgenic studies of magnetic reception in *Drosophila* have shown that a UV/blue-receptor cryptochrome is involved (Gegear et al. 2010), and cryptochromes are

Box 8.4 Requirements of magnetic sensory radical pair molecules necessary to detect the Earth's magnetic fields

1. They must exist in the retina of migratory birds.
2. The cells containing the molecules must be active at night when magnetoreception occurs.
3. The radical pair molecules must be at least partly fixed in the cell (restricted motion).
4. The molecules must be excited by light.
5. The absorption spectrum must match the range where magnetic orientation occurs (i.e., blue–green).
6. The initial electron transfer must not randomize the original opposite or parallel spin relationship of the two electrons.
7. The half-life of the excited radical pair intermediate must last long enough to allow the magnetic field to modulate the interconversion of the radical pair.
8. Because the Earth's magnetic field's influence on the putative process is weak, the effect must be integrated over a large area.
9. The molecules must be linked to the visual transduction system.
10. The transduction process must be sensitive enough for the nervous system to detect.

Sources: Mouritsen and Ritz (2005); Liedvogel and Mouritsen (2010).

further implicated in the magnetoreception of other insects and of amphibians (Phillips et al. 2010b). We have also seen that cryptochromes are involved in the orientation of migratory butterflies where they mediate circadian rhythms necessary for proper orientation (e.g., Zhan et al. 2011). Cryptochromes occur in the retinas of European Robins and Garden Warblers and are in all probability the molecules involved with magnetic orientation and its dependence on the visual system, although conclusive, direct evidence is not yet available (Liedvogel and Mouritsen 2010).

The hypothesis that magnetic field detection is a function of sensing by radical pair-forming photopigments (cryptochromes) in the eye further suggests that the magnetic sense would be processed in the visual pathway. Evidence for this notion is provided by neuronal activity in retinal cryptochrome-expressing neurons and in cluster N of the brain when night-migrating songbirds display magnetic orientation (Heyers et al. 2007). The two areas of the central nervous system involved are part of the same visual pathway. Cluster N, as previously discussed, is a specialized region of the forebrain that is active at night. In European Robins bilateral lesions of cluster N eliminate the ability to perform magnetic orientation, but they do not interfere with star/Sun-compass orientation (Zapka et al. 2009). Behaviorally the magnetic field is sensed by head scans so that the magnetic receptors cross the field lines intersecting with them orthogonally (Mouritsen et al. 2004). Furthermore the RPM system so activated would produce a light-dependent three-dimensional pattern that may in some animals be sensed as a pattern of light intensity or even color superimposed on the visual world, allowing the animal to "see" the world in two ways (Phillips et al. 2010a). This could provide a sophisticated spherical coordinate system interfacing distance, direction, and position in space to supplement the directional information provided by the magnetic compass. There is, however, a further complication. Wu and Dickman (2012) report neuronal responses in the pigeon brainstem sensitive to magnetic field direction, intensity, and polarity. Exactly how these are involved in orientation and/or surface location is still unresolved.

Co-ordination of orientation systems

One of the classic experiments on bird migration was that of the Dutch ornithologist A. C. Perdeck (1958). In its conception the experiment was simple enough, but it revealed a great deal about the behavioral organization of migration and orientation patters. Perdek captured European Starlings (*Sturnus vulgaris*) and Chaffinches (*Fringilla coelebs*) in The Netherlands during their southwestward migration in autumn, banded them, and transported them to Switzerland where he released them to continue their journey. Some 10,000 starlings were banded and released, and the subsequent recovery of bands revealed two patterns. Recoveries of first-year birds indicated that they kept going in a southwesterly direction and wintered from southeastern France to northern Spain, about the same distance south of

their usual wintering grounds as the displacement from The Netherlands to Switzerland. Adult birds, in contrast, corrected for the displacement and wintered in their usual areas in western France. After the initial wintering in the "wrong" place, however, the young birds subsequently returned to the breeding area where they hatched. Thus there were both endogenous (genetic) components to migration, such as the southwestern movement direction as indicated by the young birds, and components based on experience, such as the return of adults to their usual wintering area in spite of displacement and possibly the return of the young to their natal area to breed.

In the course of further experiments on endogenous or genetic components of migratory behavior, a navigational model has been developed, largely from birds, known as the "clock-and-compass" or "vector navigation" model (Dingle 1996; Mouritsen 2003 for summaries). The basic notion is that migration combines a time program based on a circannual rhythm (Chapter 6) with a directional program. The time program determines the onset of migration based on fat deposition and molt sequence. Once migration begins, the time program and a genetically based directional component—which can be modified by experience—will determine its pathway and duration. The experience component results in the shorter-duration and more accurate pathways of older birds. Much of the necessary experience is gained during ontogeny when directional cues are learned (imprinted) and calibrated. An example is the determination of the North Star as a reference point for many night-migrating songbirds based on the rotation of stars and constellations around this point during the night. Thus, even though the use of a magnetic inclination compass is acquired genetically, the direction of orientation may be modified based on celestial cues. A role for experience in orientation is also evident in the guidance systems of other organisms from the location of home water bodies in newts, frogs, and alligators to the location of the home hive in honeybees (Phillips 1986; Walker and Bitterman 1989; Phillips et al. 2010b). Perdeck's (1958) starling displacement experiment suggests that indeed young birds were using a clock-and-compass strategy, although a strategy based on guiding by older birds with clock-and-compass as a back-up cannot be excluded.

Guiding is one of three additional orientation strategies to clock-and-compass (Mouritsen 2003 and Box 8.1). This could be a selective factor in favor of flocking, as pointed out by Simons (2004). A third strategy is piloting or the use of fixed terrestrial reference points or landmarks. Inexperienced migrants could not do this, because such landmarks would need to be learned on previous journeys. Studies of long-term memory in migrants and closely related non-migrants suggest that the former may have evolved special cognitive and assessment abilities for learning particular sites and routes (Mettke-Hofmann and Gwinner 2003, 2004; Mettke-Hofmann and Greenberg 2005). Experiments comparing migrant Garden (*Sylvia borin*) with non-migrant Sardinian Warblers (*Sylvia melanocephala*) demonstrated that the former showed a memory for a specific feeding site for at least 12 months, whereas the latter remembered the site for only two weeks. The hippocampus, an area of the brain associated with memory, was larger in experienced adult Garden Warblers than in inexperienced juveniles. No such difference was observed in Sardinian Warblers. Memory of natal site may be at least part of the mechanism used by Perdeck's adult starlings to recognize that they had been displaced and to return to their previous migratory pathway before resuming their journey. The accuracy with which many species return to a natal or wintering area certainly implies some form of piloting, at least in the final stages of the journey.

Finally, migrants may use true navigation or the ability to reach a goal while in unfamiliar territory (Box 8.1). Navigation implies the use of at least two global coordinates (e.g., latitude and longitude) that form a reliable grid, which, in its simplest form, would be an elementary map allowing the migrant to determine position on the Earth's surface. In a more complex form, a migrant would have a complete coordinate map of its route derived presumably from both inheritance and experience. The return of young birds in Perdeck's study to their natal breeding area after wintering in the "wrong" place suggests a navigational component, probably in combination with clock-and-compass in some

sort of hybrid strategy (Mouritsen 2003). The return of Reed Warblers displaced 1,000 km to their breeding grounds also indicates a navigational component (Chernetsov et al. 2008). We still have little idea of how true navigation is accomplished by migrants, and this remains one of the greatest lacunae in our understanding of how migrants find their way (Alerstam 2006).

The complexity of migratory orientation and navigation and the necessity for several sources of information to determine course and track is especially evident in the high Arctic. At these high latitudes orientation by both celestial and geomagnetic cues is a special problem. There are at least four reasons for this: (1) the midnight Sun makes orientation by the stars impossible; (2) the geomagnetic field lines are very steep; (3) the declination angle between magnetic and geographic north is highly variable between nearby sites; and (4) the position of the magnetic North Pole constantly shifts (Åkesson et al. 2005). Following a constant magnetic course can lead to spiraling in to the magnetic North Pole, which certainly limits the usefulness of magnetic compass orientation (Muheim et al. 2003). In spite of these difficulties, huge numbers of migrants breed in the high Arctic and succeed in journeying between these breeding sites and wintering sites at lower latitudes. The routes taken by Arctic breeding shorebirds revealed by tracking radar are inconsistent with magnetic loxodromes (rhumb lines), not unexpectedly (Alerstam et al. 2001). Rather these routes appear to be the result of Sun compass orientation. At these high latitudes Sun compass routes resemble orthodromes or great circles (Box 8.1) and take shorebirds from Arctic Canada to the east coast of North America, where previous studies have shown that the birds fly out over the Atlantic to make landfall in the Caribbean and northern South America (Dingle 1996 for summary). In these latter stages, star and magnetic compasses are probably used, as much of the route is traversed at night. In passerines no single method of orientation predicts migratory routes actually followed (Muheim et al. 2003). In these cases, combinations of orientation mechanisms seem likely with each varying in importance depending on conditions in different parts of the route, possibly including frequent recalibrations of the magnetic compass direction.

True navigation is also a capability of at least one high Arctic passerine, the White-crowned Sparrow (*Z. leucophrys*) (Åkesson et al. 2005). Both adult and juvenile birds captured at Inuvik in western Arctic Canada were transported in an icebreaker both eastward and westward for distances ranging from 266 to 2862 km. They were then tested for orientation direction in a circular cage (Emlen funnel). Birds transported westward selected courses consistent with the expected migratory directions of autumn journeys. Both adults and juveniles displaced eastward to the magnetic North Pole and then across the 0° declination line shifted orientation from the migratory direction to a course leading back to the breeding area at the start of the normal migration route. This suggests that in spite of the complications of magnetic orientation, the birds were using geomagnetic cues either alone or in combination with solar cues to undertake navigation back to "home base" before beginning migration. Since geomagnetic variation coincides closely with longitude in the Arctic, the birds seem able to determine longitude in this way to establish a bi-coordinate map, at least in that area of the world.

Summing up

The past few decades have seen enormous progress in our understanding of the mechanisms that migrants and non-migrants use to find their way about. With our limited sensory capabilities and reliance on technical gadgetry to orient and navigate, the abilities of migrants to transit with great accuracy vast expanses of both land and sea seems to us most astonishing indeed. As we learn more, these abilities tend to become even more astonishing. It is difficult for us even to imagine a migrant being able, for example, to "see" in both magnetic space and the space illuminated by light of visible wavelengths. In addition to magnetic fields, the stars, the Sun, odors, and planes of polarization of light are all used by various migrants, almost always in combination, with each sensory system used according to position on the route or the environmental conditions encountered. The complexity of interacting hierarchical systems in guiding migrants on their journeys is now well established. It is also apparent that there is some sort of genetic program with respect

of timing, distance, and direction, although the latter has received much greater emphasis. This is the case for both vertebrate and invertebrate migrants.

The application of newly developed methods from genomics to satellite tracking has enabled understanding in increasingly greater detail. Genomics has provided information on the extraordinarily sophisticated navigation system of the Monarch Butterfly, including the perhaps unexpected relation between visual inputs and antennal circadian rhythms. Chemical and neurophysiological techniques have begun to elucidate the likely role of cryptochromes in the detecting of magnetism and the location of the processing of magnetic information in cluster N of the brains of birds. Satellite tracking of transmitters attached to migrants has permitted detailed outlines of the routes followed by migrants that must be explained through understanding navigation capabilities. This by no means implies that older methods should be abandoned. Circular cages of the Emlen funnel design are still the method of choice for determining the orientation directions of avian migrants, and the orientation of insect migrants is still done with tethered flight, albeit with ever more sophisticated techniques such as computer monitoring.

As exciting as advances are, there is still much to learn. Alerstam (2006) has outlined several of the unsolved problems in animal navigation. Two of these seem to me to stand out. First, we still know relatively little of the relation between a genetic program, experience, and memory in determining migration routes. How does a sea turtle know to which beach it should home to lay eggs after a migration across the South Atlantic or around the gyre in the North Atlantic? How does a *Urania* moth determine in which direction to migrate in tropical Panama? The problem has been most fully studied in birds, and we know or at least strongly suspect that there is a genetic component to knowing "home." We also have data that show an increase with experience in the success of following the migration route. We are, however, just beginning to appreciate the scope of the problem and how the knowledge of the route is integrated with mechanisms to assure that the route is accurately followed.

The second standout problem is the presence in migrants (and other organisms such as ants and bees) of some sort of "map" (Wehner, R. and Wehner, S. 1990; Chernetsov et al. 2008). In ants the map is relatively simple, based on a preprogrammed celestrial map derived from polarization. In migratory birds, the situation is more complicated because it requires some determination of longitude to indicate a bi-coordinate system in combination with latitude. White-crowned Sparrows and Grasshopper Warblers can return to their usual migration routes after longitudinal displacement. In the sparrows there is a suggestion that recognition of displacement involves differences in the magnetic field, but in some regions the magnetic fields are variable and would provide problematic information. Thus map questions remain largely open ones. In spite of recent broadening of species tested, however, we still have data on orientation and navigation for relatively few migrants. There is a need for studies of a greater spectrum of species employing similar experimental procedures in the pursuit of generality. The increasing sophistication of the methods available should provide opportunities to analyze the performance of a greater variety of migrant diversity to explore in detail both the mechanisms of orientation and navigation and the adaptive nature of guidance systems in an evolutionary framework.

PART 3

Migratory Life Histories and Their Evolution

In Part 2 the focus was on the *how* questions of migration. I now turn to the *why* questions and consider data and theory that may help us understand the evolution of life histories that incorporate migration as a major feature. Chapter 9 considers seasonal migrations, beginning with migration pathways and the selective factors that may favor their evolution. It is apparent from many studies that seasonal migration patterns are resource based, with an abundant, predictable, but temporally restricted food supply the most important source of selection. Depending on location, resource abundance may be a function of latitudinal temperature variation or alternatively of variation in rainfall. The second part of the chapter directs attention to the issue of why some species in a region or taxon migrate whereas others do not. Dependence on a particular set of resources often involving certain types of habitat structure seems to be an important consideration in this case. Habitat structure and foraging mode in some cases interact. Freedom from predation also may play a part. Noteworthy is that in both birds and insects, long-distance migrants to the Temperate Zone belong to taxa that display migration in the tropics. The evolution of migration, however, seems to involve different mechanisms based in the different biology of the two groups.

Chapter 10 discusses some pathways that match the life histories of migrants to special habitat requirements. One such requirement is that of refuges. Waterfowl are often particularly vulnerable during molt and migrate to sites offering protection at this time. Other species require specific breeding sites. Most amphibians, for example, return to water to breed and have evolved sometimes complex migrations to accomplish this. Similarly, many terrestrial crustaceans return to the sea to deposit their eggs. Sea turtles and oceanic birds must return to localized beaches and islands, respectively, for their breeding, requiring the ability to locate what are effectively dots on the face of the earth. I conclude the chapter with an extended discussion of diadromy. Mostly this occurs in fishes, many of which are important commercial species, but it is also present in snails and crabs. It includes many of the most interesting cases of both ancient and contemporary evolutionary pathways to specialized life histories.

If the persistence of habitats is highly variable through time, migration is favored as a strategy to escape deteriorating habitats and colonize new ones. This is a common feature among the denizens of temporary habitats. Among the most variable of ephemeral environments are those of arid regions, and inhabitants of these areas display some of the most highly evolved migratory life cycles. Among these are locusts, among which the Desert Locust of northern Africa and nearby regions displays a highly polyphenic life cycle and migratory behavior. Waterbirds of ephemeral wetlands have developed migratory lifestyles that allow them to exploit these ephemeral, but, when present, resource-rich habitats. Ephemeral resources, however, are not confined to deserts. In northern coniferous forests crossbills have evolved a life history to migrate and breed where there are cone crops providing food for breeding. These "rich-patch exploiters" with

flexible migration are characteristic of ephemeral habitats.

Selection for migration varies in intensity and pattern, with the result that migratory life histories vary considerably both within and across species, as discussed in Chapter 12. Variation may occur among species and among populations within a species, and there can be major life-history differences between migrants, non-migrants, and different degrees of migration. Such differences may be expressed even among individuals, as seen in the Cane Toads of Australia with more vigorous movement in individuals on an invasion front. Partial migration, where some individuals migrate while others are sedentary, occurs in many groups. This phenomenon has been the subject of much theoretical exploration including models based on evolutionarily stable strategies. Some recent theoretical work has begun to explore the relationships between partial migration and reproduction. It is apparent that variation in the occurrence of migration and in its routes and timing supplies conditions for the action of natural selection, with results that include the contemporary evolution of new routes and patterns.

The most extreme forms of migratory variations are polymorphisms and polyphenisms, and these are explored in Chapter 13. They are particularly prevalent in insects where they can take a variety of forms. The variation can include winglessness, wing length, flight muscles, and even traits involving song (in crickets) or trophic apparatus (true bugs). The variation can be the result of genes (polymorphism) or of the environment (polyphenism). There are trade-offs between investment in wings, flight muscles, and reproductive capacity or behavior, and these are influenced by hormone titers and their timing. Comparisons at different hierarchical taxonomic levels consistently suggest that pterygomorphisms are associated with degrees of habitat permanence, with total winglessness more likely in habitats that vary little and that are long lasting. Polymorphisms and polyphenisms, especially the latter, are also found in the seeds of plants, with a partitioning between those germinating near the parent or transported a distance away by wind, water, or in the fur of mammals.

Finally Chapter 14 discusses the genetic basis for migratory life histories. Classic techniques such as common garden experiments and observing the performance of hybrids still have much to reveal, but the modern advances in genetics are allowing the location of migratory behavior in specific genes, such as are involved with aphid wing polymorphisms and changes in the timing of salmon migration. Migration is a complex behavior influenced by many genes so that quantitative genetic methods are often required for its analysis. Heritability estimates indicate much genetic variation, and this variation is confirmed by rapid responses to artificial selection on migratory traits. Selection experiments further indicate the presence of migration syndromes that include genetic correlations among suites of traits encompassing morphology, behavior, and life histories. In all the instances of genetic influence discussed, migration is revealed as a complex adaptation arising from interactions between genes and environments to produce the great variety of migratory syndromes we observe.

CHAPTER 9

Seasonal migration patterns

Seasonal migrations involve movements between two or more areas that are occupied in different seasons during the annual cycle. Classically these are migrations to one location for breeding and to another for the remainder of the year. Annual migrations of birds such as those discussed in Chapter 3 are fairly typical examples that can vary widely in the distances traveled (e.g., the Swift Parrot from Tasmania to mainland Australia versus the Arctic Tern from the Arctic to the Antarctic). Such to-and-fro movements are not limited to birds, but occur also in organisms as diverse as aphids and whales. Furthermore, seasonal movements may be between more than two places. The movements of ungulates between three different regions of the Serengeti ecosystem in East Africa (Chapter 3) and the numerous cases of circuits to at least three areas of ocean—for breeding, maturing of young, and adult feeding—in many marine fishes (Harden Jones 1968; Dingle 1980) are good examples of multipartite migratory cycles. Completion of migratory cycles in species such as the Monarch Butterfly or various aphids can take more than one generation. This theme of variability and its significance will pervade the discussion in this chapter.

Terrestrial migrations

The variety of seasonal migration and the contrast between migrations and other movements that may be seasonal are indicated in Table 9.1, using examples from birds breeding on three continents. Some points are worth noting. First is the fact that seasonal movements are not confined to migration. Both local wandering and local nomadism, rather arbitrarily separated here on the basis of distances moved, occur seasonally, especially outside the breeding season. Australian Fairy Wrens are more likely to wander in the winter or in the dry season, and European tits and starlings and California Tricolored Blackbirds (*Agelaius tricolor*) do most of their wandering in the winter. Lorikeets are somewhat less seasonally restricted in their search for flowering trees because the program for blooming varies seasonally among the three species visited. These wandering and nomadic movements are probably best considered extended foraging or ranging. The second point is that a species is not confined to a single type of movement. Starlings display extensive intracontinental migrations in Europe, as discussed in Chapter 8, as well as nomadic movements, and the Song Sparrow (*Melospiza melodia*) of North America displays sedentary, partially migratory, differentially migratory, and wholly migratory behavior. Partially migratory populations are those in which some individuals remain sedentary (usually males) while others migrate (usually females and juveniles). Differential migrants are populations in which individuals, often of the different sexes or ages, migrate different distances. In western North America the Yellow-rumped (Audubon's) Warbler is primarily an altitudinal migrant, whereas Alaskan, Yukon, and eastern birds (Myrtle Warbler) are intracontinental migrants. Pallas's Sandgrouse (*Syrrhaptes paradoxicus*) irrupts well beyond its usual range as well as wandering widely in western and central Asia, whereas Pintail Ducks (*Anas acuta*) are both north–south migrants and nomadic.

The migrations listed in Table 9.1 all occur within the Temperate Zones or between temperate and tropical regions. It would be misleading, however, not to discuss migrations within the tropics because, contrary to the picture we often receive, intratropical migrations are actually quite common.

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Table 9.1 Types of seasonal bird movements with examples of breeding species from three continents.

Type of movement	Australia[a]	Nearctic	Palearctic
Extended foraging or ranging			
Local wandering (<1 km)	Fairy wrens (Maluridae)	Chickadees (*Poecile*)	Tits (*Parus*)
Local nomadism (1–100 km)	Lorikeets	Tricolored Blackbird	Starling
Migration			
Partial migration	Silvereye	Song Sparrow	European Robin
Altitudinal migration	Olive Whistler	Yellow-eyed Junco	Alpine Accentor
Intracontinental migration	Yellow-faced Honeyeater	Yellow-rumped Warbler	Redwing
Irruption outside normal range	White-browed Woodswallow	Bohemian Waxwing	Common Crossbill
Continental nomadism	Grey Teal	Pintail (?)	Pallas's Sandgrouse
Intercontinental migration	(None; cf. Ch. 3)	Swainson's Hawk	Garden Warbler

[a] Australian examples from Ford (1989).

In Australasia, for example, the Buff-breasted Paradise Kingfisher (*Tanysiptera sylvia*) and the Dollarbird (*Eurystomous orientalis*—a roller) both breed in tropical Australia, and winter in New Guinea (Dingle 2004). Levey and Stiles (1992) indicate some 69 altitudinal migrants among the forest birds on the Caribbean slope of Costa Rica. Among insects several butterflies, *Urania* moths, and several species of locust (Orthoptera) migrate wholly or mostly within the tropics. Finally, migratory fishes are dominant in the faunas of tropical rivers, such as the Congo, the Amazon, and their tributaries, notably to take advantage of annual floods (Lowe-McConnell 1975; Goulding 1980; Dingle 1996).

Given the considerable energetic costs of migration and the hazards that occur en route, it is appropriate to ask why organisms should migrate seasonally at all. A very general evolutionarily stable strategy (ESS) model for the evolution of seasonal migration from an ancestral resident population has been considered by Griswold et al. (2010). They assumed two types of migration pattern. The first was a "shared breeding" pattern in which migrants and residents share a common breeding area, and migrants depart to a separate area outside the breeding season. In the second pattern migrants and residents share a non-breeding area, the migrants breeding elsewhere. The model considered ecological conditions and a single genetic locus determining migratory behavior. This model led to four conclusions: (1) ecologically migration was more easily established in the shared breeding case; (2) the additive effect of the migratory allele influenced its establishment more in the shared non-breeding case; (3) the dominance effect of the migratory allele influenced its establishment more in the shared breeding case; and (4) the migratory allele can invade even when residents are competitively superior to migrants during time spent in either shared seasonal habitat. Partial migration could occur and depended on the interaction between which season was shared and the additive and dominance behavior of the migratory allele. This very general model could serve as a foundation on which variation in habitat quality, population density, and genetic variation can be superimposed to develop predictions about specific taxa or regions. Other models along similar lines are summarized by Holt and Fryxell (2011), and all lead to a result that partial migration can persist. Models will be further discussed later in this chapter.

Other analyses of the evolution of seasonal migration focus on the qualities of habitat, and specifically on the contrast between the abundance of seasonal resources in the Temperate Zones in spring and summer, by contrast with the inhospitable conditions in winter. A major development in this approach was the publication of David Lack's (1954) book on the natural regulation of animal numbers. Lack drew a clear distinction between ultimate evolutionary factors and proximate causes, outlining a

cost–benefit approach that in one form or another has dominated thinking since 1954. Simply stated, Lack proposed that if the benefit-to-cost ratio of migrating exceeds the ratio for staying, then migration will be favored by natural selection. This is true, of course, for all organisms. This basic logic, however, masks a multitude of complexities in trying to assess exactly what constitutes costs and benefits and how best to measure these variables. Explicitly or implicitly Lack's contributions pervade subsequent analyses of the evolution and ecology of migratory behavior and the attempts to determine the appropriate selective forces acting on migration. Much of the earlier literature on the subject is summarized in Dingle (1996; see also Zink 2011).

Much recent effort has concentrated on climatic factors and how they might influence changes in seasonal resource abundance and in turn how that variation may influence migration. Climate changes with latitude, and there have been several studies examining the relation between latitude and the frequency of migrants among faunas. One of the most comprehensive of these is a study of migrant frequency in Europe and eastern North America (Newton and Dale 1996a,b). Their results are summarized in Figure 9.1. On both continents there is a clear trend of increasing frequency of breeding bird species that are also migrants, departing to spend the winter at lower latitudes to return again the following spring to breed. For Europe, similar results had been obtained in an earlier study by Herrera (1978). In these cases latitude presumably acts as a surrogate for factors such as temperature and photoperiod. Temperature variables, such as mean temperature of the coldest month, correlate well with migration frequency. This is also true in southern Africa; when the average temperature of the coldest month is >20°C, 90% or more breeding species are non-migratory (Hockey 2000). Cooler temperatures of course reduce the abundance of both plant and insect food. The explosive increase in resources during high-latitude springs and summers has long been assumed to be a driving selective force behind migrations to breed in the temperate and sub-Antarctic zones (but see Salewski and Bruderer 2007). The long days of high-latitude summers also allow extra hours of foraging for food to feed developing young. Migration to the tropics or subtropics allows migrants to exploit the more abundant resources of these regions during the non-breeding season.

Although general trends are parallel (Figure 9.1), there are some interesting differences between the

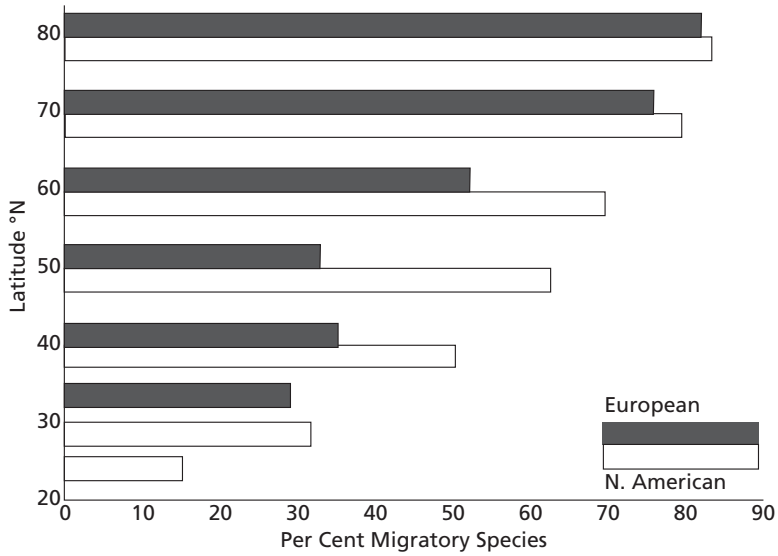


Figure 9.1 Proportion of migratory species as a function of latitude for European and eastern North American migrants. Data from Newton and Dale (1996a,b).

continents in bird migration frequency. At mid-latitude between about 35° and 50°, there is little change in the proportion of migrants among European birds. This difference from North America, where there is a steady increase in proportion northward, is probably a result of warmer average temperatures in Gulf Stream-warmed Europe at these latitudes; European temperatures are also less extreme and variable. The generally milder European winters would likely result in more resources in the non-breeding season and more residency among the breeding birds. A second difference, not apparent in Figure 9.1 which plots data for all birds, is that among land birds the proportion of total migrants among North American breeding species does not increase beyond 50°N. The increase in migrants north of 50° is attributable largely to shore birds and water birds. This apparently is because in the extensive boreal forests of North America several species feed on tree seeds, and can remain as residents at high latitudes in most winters (Newton and Dale 1996a).

Temperature is a factor in bird migration in the Southern Hemisphere (Chesser 1998; Joseph 1996, 1997; Hockey 2000), but the milder temperate climates with less severe winters mean its influence is reduced. It also interacts more with other climate factors such as rainfall (Nix 1976; Dingle et al. 2000; Hockey 2000; Dingle 2004). Furthermore there is far less land area within southern temperate areas; the only significant land area south of 35° is the cone of South America. One of the consequences of the less severe climates is overlap between breeding and wintering ranges. For example, 54 of the 75 or so species of South American migrant tyrant-flycatchers show this pattern (Chesser 2005). The wintering areas of South American migrants can be predicted by the daily mean temperature (DMT) in the months of January and July (Joseph 1996, 1997, 2003). Some 92 migrant passerines breeding in the southern temperate cone of South America divide into two groups. The first, South American temperate tropical (SATT) migrants, travels to warm humid regions of northern South America with DMT greater than ~20°C. These migrants breed in the warmer, more northern temperate regions. The second group, South American cool temperature (SACT) migrants, breeds in the more southerly areas of the cone and spends the winter months in regions where DMT is generally <20°C. The region of DMT between 16 and 20°C is an area of overlap between the two groups. The January and July DMTs tend to be more similar for SATT migrants than for SACT birds. The SACT and SATT patterns mirror similar patterns in North American migrants (NACT and NATT; Joseph 1997).

Northern temperate zone migratory bats, like birds, seem to migrate because of cold winters. The situation in bats, however, is complicated by the fact that many species can enter hibernation in caves or buildings with relatively favorable microclimates. As an apparent consequence, migration is less common in bats than in birds (Popa-Lisseanu and Voigt 2009). In tree-roosting bats, however, hibernation may not be sufficient to allow survival in cold winters because tree-holes are likely to offer little protection against extreme winter cold. Many bat species thus travel hundreds or even thousands of kilometers to warmer latitudes where hibernation in trees is less risky. Some temperate cave bats move considerable distances between summer and winter roosts with no clear geographic pattern. A possible contributor here is roost temperature rather than a difference in seasonal temperatures (Rodrigues and Palmeirion 2007). Because bats in migration are subject to high rates of evaporative water loss, the routes followed may be determined in part by the availability of water during transit (Fleming and Eby 2003).

In addition to hibernation, many bats can undertake overnight torpor which can reduce the energy costs of migration. In a study of silver-haired bats (*Lasionycteus noctivagans*), McGuire et al. (2012) found that most migrants stayed only one or two days during autumn migration at a stopover site on the north shore of Lake Erie. They roosted at a variety of trees and man-made structures such as utility poles and the periphery of buildings, and some foraged apparently opportunistically on rainy nights. Simulations suggested that the bats carried sufficient fuel to reach the probable wintering area without stopover refueling. Thus, in

contrast to many passerine birds, brief sanctuary and short-term rest seemed to be sufficient on a stopover rather than a need for extended rest and refueling.

The situation with regard to seasonal migration in Australia is more complex than in either the Nearctic or Palearctic migration systems. Largely this is a consequence of the varied climatic regimes in Australia, encompassing an arid northwest and interior, a tropical north and northeast, a Mediterranean southwest, and a temperate southeast with much altitudinal variation (Jonzén et al. 2011). The influence of this varied climate on bird migration has been assessed by Nix (1976), who based his analyses on the climatic factors controlling the growth and development of plants (Dingle 1996 for a summary), and by Griffioen and Clarke (2002 and Chapter 3). In both studies the influence of rainfall and moisture patterns was evident.

Rainfall and moisture are particularly important in the migrations of Australian butterflies (Dingle et al. 2000; Table 9.2). For the analysis Australia was divided into a number of phytogeographic regions (Barlow 1985), and the number of butterfly species and the proportion of those that are migrants was determined for each region from data in Dunn and Dunn (1991). The butterfly data were analyzed with respect to several geographic and climatic variables using regression and multiple regression. The more interesting results are summarized in Table 9.2. The first of these is the sharp contrast between the variance explained (r^2) by latitude for all Australia versus that explained when only the regions along the east coast of Australia (Cape York to Tasmania) are considered. In contrast to Temperate Zone birds where latitude explained 82–98% of the variance in migration frequency (Chesser 1998; Newton and Dale 1996a,b), on a continent-wide scale in Australia latitude explained virtually no variance in the proportion of migrant butterflies inhabiting the different regions. Considering only eastern Australia, on the other hand, where rainfall regimes are similar to those in temperate Europe and North and South America, latitude explains 78% of the variance in the frequency of butterfly migrants.

Table 9.2 Results of linear regressions of proportion of butterfly migrants on latitude and climatic variables in natural regions across Australia and along the east coast of Australia.

Variable	All Australia			East coast		
	Sign	r^2	*P*	Sign	r^2	*P*
LAT	–	0.01		+	0.78	*
SOILMOIS	–	0.52	***	+	0.15	
MEANTEMP	+	0.09		–	0.67	*
TEMPSEAS	+	0.01		+	0.79	*
MINTCMON	–	0		–	0.79	*
ANNTRANG	+	0.43	***	+	0.66	*
ANNRAIN	–	0.36	***	–	0.55	

LAT, latitude; SOILMOIS, soil moisture; MEANTEMP, annual mean temperature; TEMPSEAS, temperature seasonality or the standard deviation divided by the mean; MINTCMON, minimum temperature of the coldest month; ANNTRANG, annual temperature range; ANNRAIN, mean annual rainfall.
Values are sign of correlation (+ or –), r^2 values, and levels of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).
Source: Dingle et al. (2000).

The single variable that best explains butterfly migration patterns over the continent is soil moisture which is negatively associated with migration frequency and explains 52% of the variance. Soil moisture is not statistically significant in explaining variance in eastern Australia. Rainfall is also significant over the continent, but not in the east where it varies little from north to south. Temperature variables are significant for the east coast, but not for the continent as a whole, except for annual temperature range where high temperatures will impact soil moisture. Multiple regressions that include soil moisture, temperature, and rainfall improve the proportion of continent-wide variance explained to about 75%. It is thus likely that latitude is a surrogate for temperature on the east coast, but predictions of migration frequency over the entire dry continent of Australia must include soil moisture and rainfall measures that contribute to it. Soil moisture is of course a significant factor contributing to the plant flowering and growth on which the butterflies depend, and variability in plant productivity will select for migration to exploit seasonal or varying resources (Nix 1976; Dingle 1996).

Moisture and its influence on plant growth is a factor in the migration of the wildebeest and other ungulates such as zebra and Thompson's Gazelle in the Serengeti ecosystem of East Africa. When the rainy season begins, grass biomass increases rapidly in both the plains and woodlands. The animals, however, leave the woodlands and migrate to the plains, returning later to the woodlands when the grass on the plains begins to dry up (McNaughton 1979). Holdo et al. (2009) examined this migratory cycle (see also Chapter 3) with a rainfall-driven model of grass dynamics and compared model results with observed distributions of wildebeest over a period of three years. They included in their simulations not only rainfall but also grass biomass, tree cover, nitrogen content (a measure of nutritional quality) and the intake rate of grass consumption. The effect of tree cover was included because migrants leave woodlands for the open plains, and intake rate allows inclusion of various digestive constraints. Other factors included plant sodium levels and "flow accumulation" or the availability of surface water. The chief results of model versus actual data on movement distance are displayed in Figure 9.2. The best fit to the data was a model that incorporated intake, tree cover, and nitrogen content (I,T,N; the column second from the left). Adding flow accumulation did not improve the prediction, and other combinations of factors did not predict distance traveled as well as the I,T,N model. The authors concluded that seasonal rainfall influences fertility gradients—a feature consistent across African savannahs—which drive the lengthy ungulate seasonal migrations.

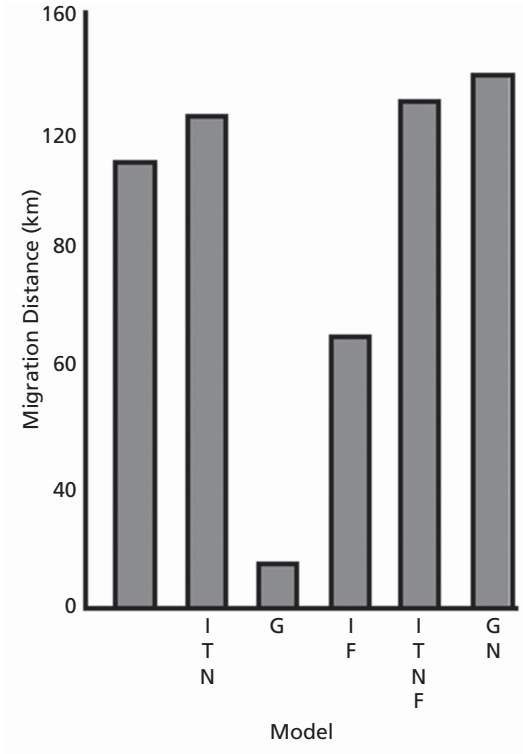


Figure 9.2 Predictions of various models for migration distance of Serengeti Wildebeest as compared to observed distance. The first column is the observed movement distance, and the second is the best movement model which incorporates I (green grass intake), T (tree cover), and N (grass nitrogen concentration). Remaining columns are for predictions from less good models incorporating combinations of I, T, N, and G (green grass biomass) or F (flow accumulation, a measure of rainfall amount). Data from Holdo et al. (2009).

Some Temperate Zone ungulates in both the Palearctic and Nearctic display seasonal migrations covering considerable distances. Examples include the Red Deer or Elk (*Cervus elephas*), the Caribou or Reindeer (*Rangifer tarandus*), and the Saiga (*Saiga tatarica*) (Shuter et al. 2011). Bishof et al. (2012) analyzed the migrations of Red Deer in Norway, asking whether they moved northward in the spring by gradually advancing over new vegetation growth ("surfing the green wave") or whether they moved rapidly to the summer range ("jumping the green wave"). The latter strategy was the predominant one with the migrants moving rapidly from the winter to the summer range. There was little difference between the sexes in spite of different life-history demands, although females were sometimes constrained by calving and offspring care, especially when tracking different degrees of local plant growth. Evidently selection favors a rapid reconnection with the summer range in this population.

In addition to ungulates, several species of bird migrate to the northern limits of the North Temperate Zone and even well into the Arctic to breed. These are primarily shorebirds and seabirds such as skuas and terns. The pattern of migratory route followed in the autumn by many of these Arctic breeders is particularly interesting. Alerstam et al. (2007) used radar aboard an icebreaker to track the paths of autumn migrants departing from Beringia over an area from 64°N in Bering Strait to 75°N to the north of Wrangel

Island, and from 130°W in the Beaufort Sea east of the Alaska/Canada border to 110°E at the Tamyr Peninsula in Siberia. Eastward flights over the Arctic Ocean were made by 79% of the estimated more than two million birds that were tracked with long flights over the sea spanning 40–80° of longitude, that is, 1,400–2,600 km. The flights lasted 26–48 h and followed tracks that traced a great circle rather than a constant compass direction. Birds departing from northern Alaska such as the Semipalmated Sandpiper (*Calidris pusilla*) and the White-rumped Sandpiper (*C. fuscicollis*) connected across Hudson Bay to the eastern North America flyway, whereas birds from northern Siberia connected mostly with the Pacific flyway upon reaching North America. A few species, for example, Barid's Sandpiper (*C. bairdii*) which breeds as far west as Wrangel Island, continued their migration down the central flyway, across the Gulf of Mexico and all the way to southern South America where they are the predominant sandpiper on shallow lakes and pans (personal observations). In following the routes that they do, the migrants seemed to be avoiding the central parts of the Arctic Ocean even if it meant flying over water for a longer distance.

It is likely that these eastward autumn migration routes are the result of historical circumstances (Alerstam et al. 2007). During the last glacial maximum (~18,000 years before present) large ice sheets probably limited northern expansion of North American breeding birds. As these ice sheets retreated, tundra breeders probably expanded into Alaska, establishing the connection to North American flyways. The Bering Land Bridge and Western Alaska also contained much tundra habitat, providing resources both for breeding and for refueling on migration routes eastward from tundra in northern Siberia. There was also colonization eastward into Alaska by Old World passerines such as the Arctic Warbler (*Phylloscopus borealis*), the Yellow Wagtail (*Motacilla flava*), and the Wheatear (*Oenanthe oenanthe*). The Wheatear, like Baird's Sandpiper, retains an ancestral wintering ground, in this case migrating from Alaska to tropical Africa.

Historical circumstances may also play a role in the migrations of birds from tropical to temperate areas. This may be the case with the Chipping Sparrow (*Spizella passerina*) in North America (Milá et al. 2006). This species has migratory populations in the temperate areas of North America and sedentary populations in the highlands of Mexico and Central America. Using a phylogeographic analysis based on mitochondrial DNA, Milá and colleagues suggested that the migratory populations originated in southern Mexico and that the migration evolved as a result of a northward population expansion since the last glacial maximum 18,000 years ago. This intraspecies comparison suggested that historical climate patterns may have been a mechanism driving the evolution of migration, a behavior that shows up and is lost repeatedly in many avian lineages. Salewski et al. (2007) make a similar argument that "chance" events such as glaciation are a major contributor to the evolution of avian migration systems. They argue that the post-glacial spread north of populations that became migratory was to obtain refuge in the non-breeding season rather than to promote taking advantage of new resources for breeding.

Zink (2011) reassessed the conclusions regarding Chipping Sparrow migration proposed by Milá et al. (2006). Zink noted that the Milá study was based on only two areas, temperate and tropical, so that it would not be possible to tell which was ancestral because they are sister areas. This implies the possibility that the species existed just south of the ice sheet as small populations that expanded when the glaciers retreated. Zink used breeding records and a species distribution model based on the statistical model Maxent (Edith et al. 2011) to predict the distribution of chipping sparrows at the last glacial maximum (LGM). The model predicted an extensive LGM breeding distribution in the southern and western USA with little suitable breeding habitat in Mexico. The winter range at LGM was indicated as south of the current winter range. There was thus a strong suggestion that Chipping Sparrows currently breeding in North America came not from Mexico, but are recent (i.e., post-glacial) colonists from the western and southern parts of the USA. Zink's general assessment is that in analyzing the origins of migration and migrating populations more attention must be paid to rigorous hypothesis testing. Because there is no ancestral migration syndrome (Piersma et al. 2005), it is possible to find transitions across the entire sedentary-to-migratory gradient

and the reverse; no one pattern need be consistent across any avian lineage, and no one pattern has received unambiguous phylogenetic support.

Oceanic migrations

Several large marine animals from sharks to whales are seasonal migrants in the ocean basins. These migrations are generally driven by trade-offs between suitable breeding areas and areas of high resource abundance. This is true for the migrations of large baleen whales such as the Blue (*Balaenoptera musculus*) and the Humpback (*Megaptera novaeangliae*) (Corkeron and O'Connor 1999; Rasmussen et al. 2007; Bailey et al. 2009; Block et al. 2010). Polar seas are enormously productive, compared to waters in temperate and especially tropical regions, because of the higher solubility of CO_2 in cold water on which phytoplankton productivity depends. This productivity, however, is largely limited to summer months because of the extreme cold and low light levels of polar winters. In the Antarctic the primary food of whales is the euphausiid crustacean *Euphausia superba*, commonly known as krill, which can reach such extraordinary densities that the sea may appear pink from the hemoglobin in their semitransparent bodies. In the Arctic and the cold waters of the northern Atlantic and Pacific there are also swarming euphausiids with shoaling fish and large concentrations of *Calanus* copepods providing additional major food resources.

In contrast there is little food available in tropical waters, with some notable exceptions to be discussed, but the thermal environment is favorable for energy balance. The result is that baleen whales spend the winter months at low latitude because, with productivity low everywhere, the gain in heat balance becomes a primary factor. Selection for migration thus seems to center on the balance between food availability and heat loss, with the deposition of fat in the form of blubber during temperate and polar summers followed by a period of reduced intake but energy conservation in warm waters.

This selection is further reinforced by the reproductive cycle. Newborn calves have thin blubber providing little insulation; birth in warm waters allows suckling calves to devote energy to growth and deposition of blubber rather than maintaining body temperature against an extreme thermal gradient. Lactation is also very costly, with an energy drain some 12–15 times that of pregnancy (Lockyer 1978) so that during periods of food scarcity, lactating females especially benefit from warm seas and reduced heat loss. There is much age and sex variation in the migratory patterns of mysticete whales; pregnant females, for example, spend the longest time on feeding grounds, and suckling females and their calves are the last to leave warm-water areas. These patterns are a consequence of the balance between warm- and cold-water benefits during the reproductive cycle. Whale populations are more or less confined to one hemisphere, which raises the question of why there are no pole-to-pole migrations. The critical factor may be the birth and suckling of young, possibly both because of the favorable tropical thermal environment and because the stress of long distances and the lack of food in tropical waters mitigate against the extra travel involved.

The recent advances in tagging and tracking large marine animals have produced new insights into baleen whale migrations. Bailey et al. (2009) analyzed satellite tracks of Blue Whales in the northeast Pacific. This population spends the warmer months largely off the coasts of Oregon and Washington, with the extent of the northward migration varying significantly between years, probably because of environmental fluctuations influencing prey abundance. The cooler months are spent off the coasts of Costa Rica and Nicaragua. The whales migrate mostly within 100–200 km of the coast which allows them to take advantage of the high productivity of the cool southward-flowing California Current to forage en route. Humpback Whales also migrate along this coast and even closer to the edge of the continent than the Blue Whales. The wintering area off Central America is in the region of the Costa Rica Dome, a large area of upwelling with a thermocline close to the surface. This promotes rich phytoplankton blooms which are the base of a highly productive whale food chain. The whale tracks in the area of the Dome are concentrated and suggest that they are foraging. Foraging thus probably occurs year-round in the cool, productive waters along virtually the entire migration pathway.

The Costa Rica Dome also appears to be an important component of the migration route of Southern Hemisphere Pacific Humpback Whales (Rasmusson et al. 2007). This population migrates some 8,300 km northward from feeding areas off Antarctica, a track which is the longest movement undertaken by any mammal. The animals tracked on this migration included a mother-and-calf pair, so the high productivity of the Dome is probably important for development of the young. Overall worldwide winter distributions of Humpbacks occur in waters at 21–28°C regardless of latitude or ocean basin. Areas such as the Costa Rica Dome and a similar area in the eastern Atlantic are probably important as suitable reproductive habitat on a fine scale. The Dome provides unique spatial overlap (but with temporal separation) between Northern and Southern Hemisphere populations of Humpbacks.

The California Current system is important to the migrations of several large marine predators in the Pacific, another of which is the Pacific Bluefin Tuna (*Thunnus orientalis*) (Block et al. 2010; Boustany et al. 2010). These tuna are spawned in waters off Japan and migrate to the eastern Pacific as late one- or two-year-olds. The fish remain in the eastern Pacific for up to four years before making a return migration to the western Pacific to spawn. The movements back and forth across the Pacific occur over a region of current conversion known as the North Pacific Transition Zone (NPTZ). The high productivity of the NPTZ means that it is in effect a top predator migratory highway, and it is used by Bluefin and Albacore Tunas, seals, turtles, and oceanic birds (Block et al. 2010). The fact that they are endothermic further allows Pacific Bluefins to roam over huge areas of the North Pacific, including cold temperate and sub-Arctic waters. Other tuna (and some sharks) are more limited in thermal tolerance and so are confined to subtropical regions of the North Pacific. Adult Bluefins when not spawning off Japan have been recorded as far south as New Zealand, giving this species one of the largest home ranges of any animal.

During their years in the eastern Pacific, the juvenile Bluefins migrate up and down the west coast of North America (Boustany et al. 2010). They are found the farthest south in the spring off the southern edge of Baja California, Mexico. This is a region of upwelling and a productivity "hotspot" of the California Current System. The most northerly location occurs in the autumn off northern and central California, another hotspot. Fish distributions were tightly clustered in areas of high productivity and more scattered at other locations along the migratory route. Conditions in the ocean varied from year to year resulting in the migrants also varying their routes and areas of concentration. With the seeming exception of the eastern South Pacific, the Bluefins thus use migration to exploit the resources of nearly the entire Pacific Basin.

The Atlantic Bluefin Tuna (*T. thynnus*), like its Pacific counterpart, makes use of a large ocean basin, in this case the North Atlantic (Block et al. 2001; Teo et al. 2007). These tuna spawn in either the eastern Mediterranean or the Gulf of Mexico and occupy feeding grounds in both the mid-Atlantic or along the east coast of North America. Tuna tagged off the North Carolina coast spent the winter there and moved offshore in the early spring. These offshore excursions were along the Gulf Stream east toward Bermuda or southeast toward the Bahamas. Later in the spring and into early summer the tuna moved into waters off New England and on the Canadian shelf, returning to the Carolinas or the Bahamas by winter. Those breeding in the Gulf of Mexico moved there in the spring and remained for several weeks. Other western Atlantic tuna moved to the eastern Mediterranean spawning grounds in the known breeding season. Data are insufficient to determine the natal origin of individuals in the western Atlantic for certain; evidently this population contains fish from both the Gulf of Mexico and eastern Mediterranean spawning grounds.

Seabirds are additional migrants that exploit the resources of the entire Pacific Basin (Shaffer et al. 2006; Black et al. 2010). Sooty (*Puffinus grieus*) and Short-tailed Shearwaters (*P. tenuirostrus*) breed on islands and coastlines around New Zealand and Tasmania, and migrate to the North Pacific during the southern winter. While in the North Pacific they exploit the high productivity generated by the cool ocean currents along the coasts of both Japan and western North America. Tens of thousands of shearwaters can be seen feeding in regions of upwelling along the California coast (personal observations).

The routes followed can be a circle or figure-eight around the entire Pacific, as first one feeding area and then the other on the opposite of the North Pacific are visited, with birds traveling on average for about 64,000 km in around 200 days (Shaffer et al. 2006, 2009). The pathway allows Shearwaters to exist in what amounts to "endless summer" as they exploit productive resources of both the Northern and Southern Hemispheres.

Evolutionary ecology of seasonal migrations

There is no reason to believe that species with independent evolutionary histories and different ecologies will uniformly respond to a single trigger . . .

Outlaw and Voelker (2006)

The previous examples of seasonal migration illustrate a further point—that among and within various taxa there can be conspicuous differences in the proportion of migrants. A question important to understanding the evolution of migration systems is, then, what are the causes behind these differences? In the case of birds, for example, the *Bradypterus* warblers of the Old World are sedentary with but two exceptions, and the *Basileutrus* warblers of the New World are entirely so. In contrast the majority of Old World *Phylloscopus* warblers and of New World Paruline warblers are highly migratory on a continental or intercontinental scale. Among shorebirds most sandpipers are highly migratory often between hemispheres, while many lapwing and plover species are largely sedentary or make only local movements. Among insects the Large Milkweed Bug (*Oncopeltus fasciatus*) and the Monarch Butterfly are the single long-distance seasonally migrant species from their respective groups, whereas among moths of the genus *Spodoptera*, the Armyworm Moths, most are impressive migratory travelers.

As with most complex behavioral ecologies, migration systems have evolved in response to a diverse set of selective factors that vary in importance in the different taxa, depending on ecologies and life histories. In shorebirds—for example, sandpipers—it is likely that the total area of available habitat, as it influences food and nest site availability, may be the most important consideration in the evolution and maintenance of migration. Most sandpipers breed in habitats that are extensive and rich in food supplies compared to areas where they spend the winter. By far the majority breed in the Arctic and sub-Arctic, which covers a vast area across North America and Eurasia and produces an enormous biomass of potential insect food during the very brief summer-nesting period. Even those species that breed on grasslands or other interior Temperate Zone habitats, such as the Upland Sandpiper (*Bartramia longicauda*), have available an area that is large relative to the wintering grounds. Only a few sandpipers breed in the tropics or on the temperate margins of continents. The vastly increased nutrient and energy demands of breeding are probably difficult, if not impossible, to sustain on the basis of the resources available on the strands, estuarine mudflats, or grasslands of the regions south of the usual northern breeding areas. Those plovers and lapwings that do nest in these habitats do so at low densities relative to the migrant sandpipers. The strands and mudflats on continental margins are frequently inundated during the tidal cycle, making nesting possible only at the margins. They are, however, critical as migratory stopover sites, with a premium placed on sites with rich and abundant infaunas (Wilson 1991; Warnock and Bishop 1998).

Predation may be another factor favoring shorebird migration into the high Arctic. Mammalian predators, for example, increase in abundance and diversity at lower latitudes. In an experimental study, McKinnon et al. (2010) estimated the relative decrease in predation risk along a 3,350 km long transect spanning 29° of latitude in the Canadian Arctic from the Southern edge of Hudson Bay (53°N) to the northern edge of Ellesmere Island (82°N). They monitored the survival of 1,555 artificial nests over two summers at seven shorebird breeding sites along the latitudinal gradient. Shorebird nests are uncomplicated affairs consisting of a depression or scrape in the tundra, so artificial nests are a reasonable approximation of actual nests. The artificial nests provided a "standardized predation risk" with a control for the many factors that would cause variability of survival in real nests—for example, spatial or temporal variation, or behavioral differences in parental nest defense. Nest predation

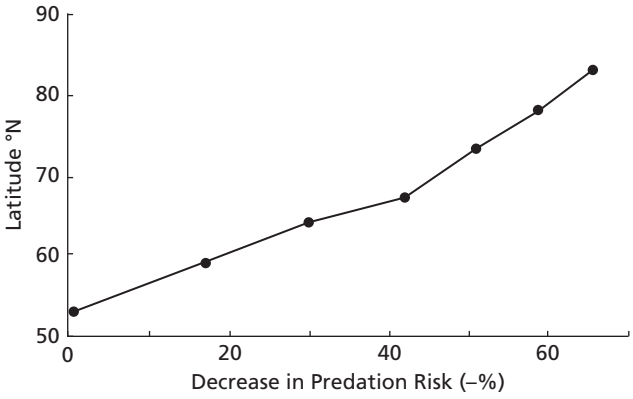


Figure 9.3 Average decrease in predation risk as a function of latitude measured with artificial nests at a series of shorebird breeding sites in the Canadian Arctic. Data from McKinnon et al. (2010).

was negatively correlated with latitude (Figure 9.3), there being a reduction in predation risk of 66% over the 29° latitude of the transect. It thus appears that the extra physiological costs of migration to the very high latitudes could be compensated for by the benefits gained by reduced predation. A latitudinal gradient in nest predation was not detected in temperate breeding Neotropical migrants (Martin 1995), but whether this is a real difference or a result of methodological differences is not clear (McKinnon et al. 2010).

For the Large Milkweed Bug and the Monarch Butterfly, the key to migration—and therefore the ability to exploit the resources occurring in the flush of the temperate summer—seems to center on the development of certain physiological traits. The two insects belong to genera in which they are the sole long-distance migrants (Dingle 1978; Dingle et al. 1980; Ackery and Van-Wright 1984). The adoption of a migratory life history has required the acquisition of the ability to undertake reproductive diapause (Dingle 1978; Tauber et al. 1986), which the non-migrant species are unable to do. For the Milkweed Bug the enabling mechanism has been the ability to shut down the juvenile hormone production of the corpora allata in response to short photoperiod (Chapter 6). Milkweed Bugs of several species can enter a diapause-like state upon starvation; *O. faciatus* has been able to link this response to short photoperiod (summary in Dingle 1996). The development of a photoperiodically induced diapause means that the bug now has a lengthy period to migrate to wintering areas. The relation between diapause and migration in the Monarch is similar (Chapter 5). The requirement for successful migration by these tropically derived species was thus the ability to escape oncoming winter with a reproductive diapause permitting the required lengthy travel.

Does the migration of insects into the temperate zone in the summer represent a benefit that would continue to be supported by natural selection? Chapman et al. (2012c) have considered this question with regard to the massive spring migration into the British Isles and northern Europe (up to 240 million individuals into Britain) by the Silver-Y Moth (*Autographa gamma*). It had been postulated that such mass migrations into temperate regions might represent a sink from which subsequent generations did not return, the so-called Pied-Piper effect (Stinner et al. 1983). Although this made little evolutionary sense and had been discounted (e.g., McNeil 1987) and return flights had been observed (Showers 1997), it remained unclear whether a significant proportion of return migrants made it back to source regions or whether there were reproductive benefits to seasonal migration. There was also little information on population sizes or migration intensities. These were the issues addressed by Chapman et al. (2012c).

These authors tested the hypothesis that autumn migrant moths produced during summer returned to winter breeding regions where reproduction over the winter resupplied return migration the following spring. They used entomological radars (see Chapter 4) to monitor the numbers of moths entering or leaving Britain and a network of light-trapping stations to quantify inter-annual variation

in population size over the years 1976–2009. Results for abundances and the growth rates over the period of the study are shown in Figure 9.4. Light-trap abundances for autumn were consistently higher than for spring, reflecting the growth of the moth population over the summer (Figure 9.4A). A Bayesian state-space model was used to predict abundances before migration at both ends of the route (Britain and North Africa). Figure 9.4B indicates the net population growth rates for the summer population (autumn migrants) and the winter population (spring migrants). The higher growth rates for winter–spring reflect the smaller winter population sizes and vice versa for autumn. Together the results indicate density-dependent population regulation with smaller populations growing at a higher rate. The results further indicate that selection strongly favors migration with breeding necessary at both ends of the route. This conclusion was given further support by (1) breeding summer populations in Sweden, (2) a model suggesting that favorable wind fields carry moths southward in autumn toward North Africa, and (3) breeding and population growth in North Africa in winter, but a complete absence of moths there in summer when hot, dry conditions prevent breeding (Harskly 1975; Zanaty et al. 1985; Pedgley and Yathom 1993).

With respect to birds, there have been various attempts to determine whether the proportion of an avifauna that migrates is a function of the types of habitat in which birds occur. For North Temperate Zone migrants, Bilcke (1984) proposed that the proportions of migrants in different breeding habitats were determined by the proportion and distribution

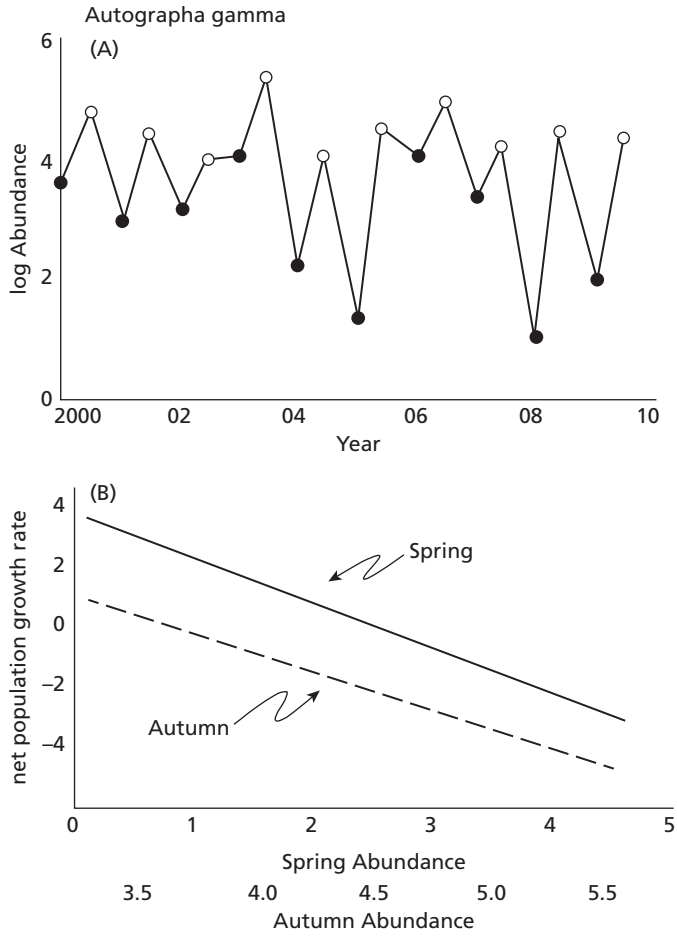


Figure 9.4 The seasonal migration of the Silver-Y Moth into Britain. (A) Spring (filled circles) and autumn (hollow circles) abundances of moths from light trap records. Light traps were run from 1975 to 2009; only data from 2000 to 2009 are shown but are reflective of the total sequence. Abundances are clearly higher in autumn, reflecting summer breeding. (B) Net population growth rates as a function of population size. Slopes are essentially the same but intercepts differ, indicating density-dependent regulation (higher population size, lower growth rate). Individual points for the 32 years of sampling are omitted. Data from Chapman et al. (2012c).

of habitats in the wintering range. His conclusion was based on a comparison of migrants in Europe and eastern North America. In Europe most migrants occur in areas of scrub and open forest with vegetation of intermediate height; few occur in closed forest of trees >10 m in height (Figure 9.5). These migrants winter in Africa, which is dominated by the same sorts of habitats, and it is in these savannas and open woodlands that they spend their time while wintering (Moreau 1972). In one study in West Africa, Palearctic migrants were never observed to enter primary forest during 20 years of studies, whereas they were common in open fields, at forest edges, or in man-made forest gaps (Brosset 1990). By contrast, in migrants from eastern North America that travel to the Neotropics—areas where forests cover a much wider expanse than in Africa—many species do occupy tall primary and secondary forests (Figure 9.5 and papers in Keast and Morton 1980).

Bilcke's analysis was extended by Helle and Fuller (1988) and Mönkkönen and Helle (1989) to include vegetation height and the regions of East Asia and western North America (Figure 9.5). This study confirmed Bilcke's thesis for Europe and eastern North America. Different patterns emerged in eastern Asia and western North America, although the fewer habitats sampled means the results should be interpreted cautiously. In western North America migrants are more or less evenly distributed among habitats with vegetation >1 m in height; this pattern may be the result of a more limited distribution of wintering areas than occurs in eastern North American migrants. These western migrants winter almost entirely in a narrow strip of the Pacific Coast from the Mexican state of Sonora to Guatemala (Hutto 1985), where vegetation diversity is a good fit to the diversity in the temperate breeding ranges. In eastern Asia tropical regions are largely divided between forest and more open areas, with less area including shrub or savanna. This fits reasonably well with the distribution of migrants among habitats prevalent in Japan. Thus the overall correspondence between the breeding and wintering habitats of migrant birds seems to be reasonable based on these comparisons across continents.

A larger sample of 742 landbird species was examined by Hockey (2005) with respect to migrants in the southern Afrotropics (Figure 9.5). Hockey

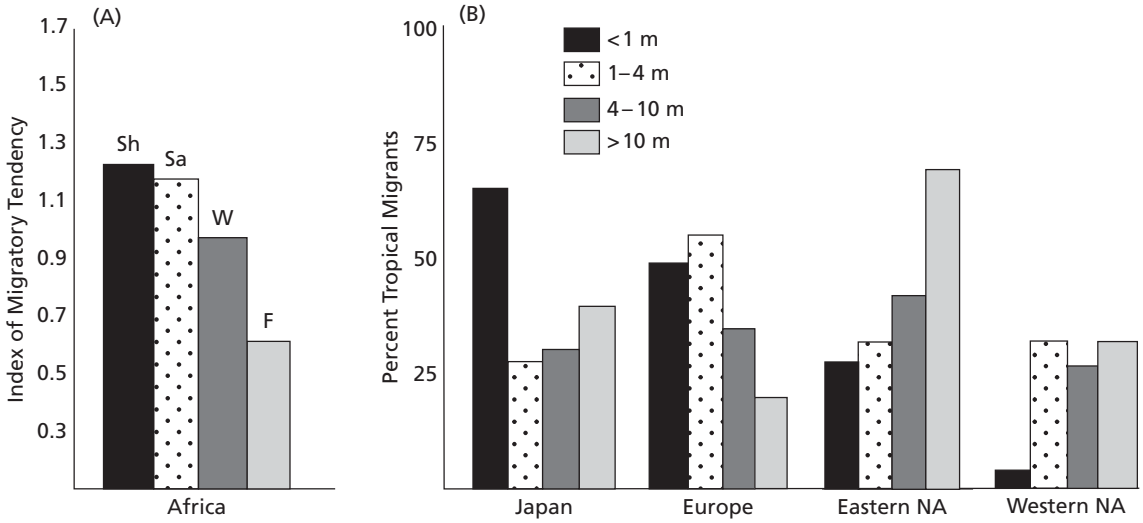


Figure 9.5 Associations of migration and habitat. (A) African data are for 742 landbird species of the southern Afrotropics. The index of migratory tendency is the average for all species from a given habitat ranked from 0 = sedentary to 4 = intercontinental migrant. Habitats are: Sh, shrub/open; Sa, savannah; W, woodland; F, forest. (B) Percentage of breeding birds migrating to the tropics to winter from four northern continental regions. Bars are the indicated categories of vegetation height which correspond roughly to the habitat categories for the Afrotropics. NA, North America.

Sources: Africa: Hockey (2005); northern continents: Dingle (1996); based on data from Helle and Fuller (1988) and Mönkköen and Helle (1989).

plotted habitat against an "index of migratory tendency" which was the average of all species ranked from 0 = sedentary to 4 = intercontinental migrant to the Palearctic. The results are more or less the same as those for Europe and Japan in that the long-distance migrants both within Africa and to the Palearctic tended to inhabit open habitats, in this case shrub and savanna where most vegetation would be <4 m high. There is some local migration by birds living in woodland with semi-open canopy, but in closed forest the great majority of species are resident. For migrants the breeding and non-breeding habitats are similar. Again this contrasts especially with eastern North America, where a large proportion of migrants does occupy forests which are the predominant habitat, at least ancestrally, in both breeding and wintering areas.

The observation that bird migrants may be more prevalent in certain habitats still begs the question of which species occurring in any given habitat are migrants and which are residents. One line of argument is that the division between migrants and residents is at least in part a consequence of competition (Cox 1968, 1985, summarized in Dingle 1996). Cox's model for seasonal migration is based on a presumptive balance between competition and time available for breeding—the 'time allocation and competition theory' (TAC). Because the ratio of juvenile:adult survival in the tropics is low, Cox suggests that there is severe competition for food to feed young and perhaps also for nest sites protected from predators. Tropical birds, however, can breed over a much longer period than their Temperate Zone counterparts. Migration is evolved over four major stages: (1) range expansion to breed due to some combination of competition, climate, resource variability, and predation; (2) retreat back to the original area for the remainder of the year; (3) development of long-distance disjunct migration populations; and (4) further reinforcement of migration mostly by competitive displacement. The TAC was tested on New World parulid warblers and seems to account reasonably well for migration patterns, having originated in the Mexican Plateau, a region of unstable habitats that varied over periods of glaciation and of a varied topography.

Levey and Stiles (1992) use a different approach to migration among New World birds. Their "evolutionary precursor hypothesis" (EPH) posits specific ecological traits that are more likely to promote migration in some species rather than in others with different traits. To address this question they examined the habitat and diet characteristics of Costa Rican land birds, an avifauna that shows seasonal movements within the tropics. The hypothesis tested was that Nearctic migrants shared many ecological characteristics with Neotropical groups displaying high frequencies of migratory movements on a smaller scale. Seasonal movements within the Tropics were postulated to predispose those groups displaying them to migration out of the Tropics. Ecological attributes hypothesized to select for migration were high temporal variation and high spatial variation in the resource base. Such variation was thought to be more likely among species feeding on fruits or flowers, as opposed to insects or vertebrates, and among species living in the forest canopy or on the forest edge rather than in the forest interior. These food habits and canopy and edge habitats would be "unbuffered" against seasonal changes and climatic variation as opposed to "buffered" resources in the vegetation at lower levels of the interior habitats.

The data summarized in Tables 9.3 and 9.4 suggest that both diet and habitat are highly correlated with degree of altitudinal migration, the most common form of migratory behavior in the Costa Rican species. With respect to diet, some 56% nectarivorous species are migrants.

Nectar is likely a resource particularly susceptible to transient fluctuations. Among frugivores, 34% are migrants. These proportions for fruit and nectar feeders contrast sharply with the 9.7% and 6.7% of migrants among predators feeding on either small

Table 9.3 Association between diet and seasonal altitudinal migration in 346 forest birds on the Caribbean Slope in Costa Rica.

Diet	Total species	Migrants	% migrants
Small insects	145	14	9.7%
Fruit/seeds	94	32	34.0%
Vertebrates/large insects	75	5	6.7%
Nectar	32	18	56.3%

Source: Dingle (1996) from Levey and Stiles (1992).

Table 9.4 Association between habitat and altitudinal migration in Costa Rican Caribbean Slope forest birds.

Habitat	Total species	Migrants	% migrants
Understory	88	6	7.3
Canopy/edge	242	62	25.6
Aerial	16	1	6.3

Source: Dingle (1996) from Levey and Stiles (1992).

or large prey. With respect to habitat (Table 9.4), the highest proportion of migrants, about 26%, occur among species that inhabit the unbuffered forest canopy or edge. Both data sets are consistent with the EPH in that specific ecological attributes are associated with increased tendencies toward seasonal migratory movements. Evidently movements are adaptations to track fruit and flower availability, especially in more exposed and more seasonally variable habitats. An exception to the association of frugivory/nectarivory as evolutionary precursors among New World migrants are the parulid warblers analyzed by Cox (1985) which are primarily insectivorous. The best explanation for this exception may be that these species came from highly seasonal habitats with selection acting mostly via seasonality. In this case the TAC model seems a better fit, although the two models (EPH versus TAC) are not necessarily mutually exclusive (Dingle 1996).

The proportions of species partitioned among diets in Tables 9.3 and 9.4 contrast markedly with the division of feeding habits among Old World migrants (Hockey 2000, 2005). Among migrants in sub-Saharan Africa insectivores are disproportionately well represented, whereas frugivores are almost exclusively sedentary. Within the insectivore group the greatest proportions of migrants are found among clades that predominantly or exclusively hunt aerial insects above the canopy such as swallows, sit-and-wait perch hunters that dive down on large active insects (kingfishers and rollers), and taxa feeding on the larvae of flying insects (cuckoos). Smaller birds that glean small insects are largely resident, as are terrestrial gleaners such as coucals (Cuculidae, *Centropus*) and chats (Turdidae). African crakes and rails (Rallidae) are also terrestrial gleaners but are an interesting migratory exception. They are predators of terrestrial arthropods in wet or marshy habitats. In contrast, South American and Australsian rallids are not migratory (16% migratory in South America, 22% in Australia, but 52% in Africa) (Dingle 2008). Likewise New World cuckoos are mostly resident (24% migratory in South America versus 91% in Africa and 92% in Australia).

Why is there a difference between Africa and the other Southern Hemisphere continents in migratory rallids and cuckoos? If rallid migrations were mainly a consequence of ephemeral wetlands, one might expect a higher proportion of migrants in Australia. Australian rallids, however, are distributed primarily coastally and subcoastally where wetlands are largely permanent (Barrett et al. 2003). South American species, too, generally prefer permanent wetlands, and these species that do migrate, like three species of coot (*Fulica*), range far to the south where cold winter temperatures likely come into play. The significantly higher frequency of migration in African rallids is probably a response to variable wetlands, but the even more extreme variability of arid zone Australian wetlands may limit their use on that continent (Roshier et al. 2001). In the cuckoos, African and Australasian species are closely related and of probably Asian origin; the New World species, on the other hand, are an independent radiation. The taxonomic and ecological overlap among the Old World species, which occur mostly in drier open or semi-open habitats, probably accounts for the similarity in migration frequencies (Hockey 2000). In the New World, cuckoos are primarily denizens of forest interiors where migrants are few in any austral group (Hockey 2000, 2005). Ground- or thick scrub-dwelling cuckoos in both South America (e.g., anis, *Crotophaga*) and the Old World (e.g., coucals) are residents. Differences in habitat occupancy seem to exert major influences on migratory propensity in these groups (Dingle 2008).

The evolutionary precursor hypothesis (EPH) was further evaluated by Chesser and Levey (1998). They noted that the Levey and Stiles (1992) analysis had two shortcomings: (1) because data were not independent of the observations that generated the EPH, there was not a true test of the hypothesis; and (2) because the comparative method did not incorporate phylogeny in a way to evaluate transitions

between character states, statistical independence was likely violated. In their analysis Chesser and Levey (1998) used 12 bird families that included austral migrants within South America and compared non-buffered versus forest interior habitats and frugivorous versus insectivorous feeding optimized on phylogenetic trees. The relationship between migration and frugivory was not significant, but when tested in a phylogenetic context the relation to habitat was significant or nearly significant with an association between migration and non-buffered habitats. The EPH was thus only partially supported. These variable-edge, open, or canopy habitats probably select for foraging on variable dietary resources regardless of whether the diet consists of fruit, nectar, insects, or some combination.

Boyle and Conway (2007) further extended the evaluation of the EPH. Their sample was 379 species of New World Tyranni, a large group that includes tyrant flycatchers, manakins, cotingas, tityras, becards, and their allies. These species exhibit a range of migratory behaviors, habitats, and diets typical across a broad spectrum of migratory passerines. They categorized migration both with respect to migratory versus sedentary and a range of migratory distance categories from <100 km (sedentary) to >3,000 km. Species were assigned to six types of habitats and along a four-unit foraging scale from insectivory to frugivory. They added elevation as another habitat variable and included foraging group size and body mass as additional species characteristics. The analyses incorporated phylogenetically independent contrasts.

Consistent with the EPH, habitat and diet were related to migration, but in a more complex way than suggested by previous analyses (Figure 9.6A). A trend toward frugivory and migration was apparent in canopy and understory forest birds, whereas migrants living in more open habitats such as woodland and arid areas were more likely to be insectivorous. There is thus an interaction between diet and habitat in determining the proportion of birds that are migratory.

With respect to migratory distance, habitat was more important than diet, with forest understory species on average migrating shorter distances. Overall there was less difference in migratory tendency across frugivorous birds living in different habitats than there was in insectivorous birds, suggesting that differences in migratory tendency among these birds were a consequence of habitat-specific behavior in insectivores but not frugivores. What is particularly interesting about the Boyle and Conway (2007) study is that foraging group size is consistently and negatively correlated with migration (Figure 9.6B). Birds that are solitary foragers are not only more likely to migrate but also to migrate farther than birds foraging either in pairs or in flocks. In considering the contrast between sedentary versus migratory behavior, habitat was important in interpreting the relation between diet and migration, but when distance was involved in considering diet and migration, the critical factor was foraging group behavior. It may well be that short- and long-distance migrations evolve in response to different sets of selective pressures. Here it could be especially important to distinguish short-distance migration, involving inhibition of at least some "vegetative" or maintenance responses, and extended foraging or ranging (Chapter 2).

In an extension of the EPH, Boyle and Conway propose a "resource variability hypothesis" wherein species encountering large fluctuations in food resources will be more likely to evolve migratory behavior than species depending on resources more evenly distributed or less seasonal. This is similar to hypotheses concerning the evolution of migration in early successional or ephemeral habitats (see Chapter 11), and is consistent with the analysis of Outlaw and Voelker (2006) showing that, in the largely open-country pipits and wagtails (Motacillidae), increasing seasonality promoted migration. Once migration has evolved, a different set of selective factors may influence other aspects of migratory behavior such as timing or distance traveled. An interesting notion further suggested by Boyle and Conway is that group foraging and migration may be alternative strategies, each allowing different approaches to dealing with the vicissitudes of resource variability.

The relation between habitat and behavior in the evolution of migration has been further explored by Bell (2011) using a sample of 272 passerine species breeding in North America north of the Mexican border. He also included phylogenetic comparisons in his analysis. The evidence was consistent with

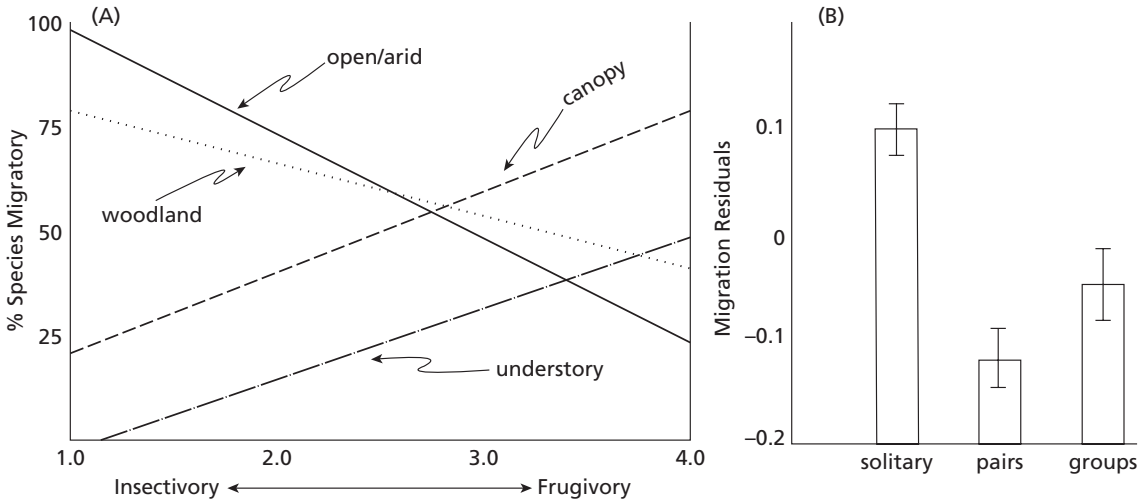


Figure 9.6 (A) The proportions of migratory species among the Tyrranni plotted for habitat along a gradient of diet from insectivory to frugivory. The interaction between diet and habitat is apparent. (B) Relationship between foraging group size and migratory tendency (including migratory distance). Values (±1 SE) are residuals for migration tendency at each group size after habitat, diet, and body mass effects are accounted for. Data from Boyle and Conway (2007).

earlier studies in suggesting that an increased tendency toward migration is associated with greater reliance on food resources that vary in abundance because they are more exposed both to consumers and to environmental fluctuations. In contrast, residency is associated with food resources in more buffered habitats that are less variable. Along with habitat buffering, latitude also explains much of the variance in migration, consistent with Newton and Dale (1996a,b). Bell goes on to suggest that the trend toward migration may be part of a suite of co-adaptations along a scale from buffered to unbuffered habitats. Residents, for example, tend to forage more intensively over an area, to have more robust legs and feet, and larger brains, all adapted to finding and extracting hidden food items. The smaller brains and less robust limbs of migrants may be adaptations for lighter weight (Winkler and Leisler 2005), but may also be a consequence of reduced selection for finding cryptic resources in buffered habitats. Bell proposes that migration arose as a non-directional back and forth seasonal movement following unbuffered resource abundance, and became directional and physiologically adapted (e.g., fat storage, hyperphagia—see Chapter 6) by incorporating pre-adaptations that are general among avian lineages (see also Piersma et al. 2005; Dingle 2006). Bell notes that further analyses of foraging, exploration, and migration tactics are required to test the co-adaptation model.

An extensive modeling approach to the evolution of migration or residency is taken by Shaw and Couzin (2013). They developed a spatially explicit, individual-based model to evolve behavior rules based on (1) the types of ecological conditions leading to maximization of fitness by migration, and (2) the types of information individuals use to guide their movements, specifically information regarding resources, history, or social factors. Individual migratory behavior involved a movement pattern (e.g., large-scale relocation) and an "information use strategy" (e.g., persistent directed movement—see Chapter 2). In the model, behavior rules evolved via simulations of a wide range of ecological conditions, including the degree of seasonality of resources, patch quality, and average patch size. Patch quality served as a measure of how buffered the resources are against seasonality. Simulated individuals moved in two-dimensional space at constant speed, with each characterized by a position, a velocity vector, and a set of weighted information preferences which directed their movements over

the course of a simulation. Because costs and benefits of migration vary across species, the model also incorporated three different fitness functions accounting for different values of resources along the route and at the endpoint of a generation.

Two distinct types of behavior emerged from the simulations. In the first, movement evolved almost entirely on the basis of resource information while ignoring historical and social information, and organisms essentially did not move. In other words these individuals behaved as residents. In the second type, all individuals within a population evolved to rely at least to some extent on historical information and traveled far. These latter thus behaved as migrants, and their behavior was directed and resulted in large spatial relocation. The migrants relied primarily on historical information even when information on resources and social factors was available. Consistent with empirical information on many migrating species, migration was pre-emptive (Dingle and Drake 2007). The modeling results also led to three predictions: (1) highly seasonal environments should select for migration; (2) seasonal non-buffered resources should select for migration; and (3) migration should be more common in seasonal environments with smaller habitat patches. All of these predictions are consistent with most empirical observations on migration. They further provide a basis for examining the causes behind the exceptions that do not fit these predictions.

Additional patterns: double breeding and sexual selection

The pattern of seasonal migration we have seen so far in this chapter consists of travel between a breeding site and a non-breeding (commonly wintering) site under the influence of natural selection. In the studies of avian migrants, only a very few species are known or suspected to breed at both ends of the migratory route, that is, are migratory double breeders (Rohwer et al. 2009). The advent of techniques to identify endpoints of travel, such as stable isotope analysis (Chapter 4), now allow more certain identification of double breeders among migrants. Rohwer and colleagues were able to identify at least five Neotropical migrants that breed at both ends of migration: Yellow-billed Cuckoo (*Coccyzus americanus*), Cassin's Vireo (*Vireo cassinii*), Yellow-breasted Chat (*Icteria virens*), Hooded Oriole (*Icterus cucullatus*) and Orchard Oriole (*I. spurius*). All these species breed in North America in late spring and early summer and all or many of these breeders migrate to coastal western Mexico to arrive after about the middle of July. Using stable isotopes and other methods such as molt patterns, Rohwer and colleagues were able to identify birds breeding in this region of Mexico in the late summer as ones that had previously bred in the north. Coastal western Mexico receives most of its annual rainfall during a July–September monsoon, creating habitat conditions that readily support breeding. After breeding in Mexico, there is a further southward migration to final wintering areas in the Neotropics. The migratory circuit of these five species thus includes two breeding areas hundreds to thousands of kilometers apart and a non-breeding area hundreds to thousands of kilometers farther south of the intermediate western Mexico sites. There is an interesting parallel here to the case of moths such as the Silver-Y that require breeding at both ends of the migration route to maintain populations (Chapman et al. 2012c). This confirmation of double breeding in birds raises the question of how much each breeding event contributes to overall fitness via natural selection.

Natural selection may not be the only selection acting on migrant birds. Life-history trade-offs associated with partial migration have been assessed in the lek-breeding White-ruffed Manakin (*Corapipo altera*) of the Neotropics (Boyle et al. 2011). This species breeds in montane forests, and high-elevation storms can limit foraging success and drive some individuals to lower elevations. By using stable isotopes to identify which males were involved in altitudinal migration, Boyle and colleagues showed that males leaving leks to move to lower altitudes incurred a cost in diminished social status and reduced mating success in the next breeding season. Thus sexual selection is acting on migratory behavior in addition to natural selection acting via variation in the weather. Survival costs of residency are trading off with benefits gained from mating success.

A somewhat different interaction between natural and sexual selection occurs in the New World Orioles (Icteridae: *Icterus*) (Friedman et al. 2009).

In Neotropical resident species both sexes possess elaborate and colorful black and yellow or yellow–orange plumage (Ridgely and Tudor 2009). In species where the sexes are dichromatic with dull females, phylogenetic analysis demonstrates that sexual dichromatism is due to the loss of bright colors in the females. Most of the dichromatic orioles are migratory or breed in the temperate zone, and dichromatism is 23 times more likely to evolve in migratory taxa than in sedentary ones. Apparently the loss of bright coloration in females has been contingent on the evolution of migration. It may be the case that the bright female colors of the resident tropical species serve as an aid in the defense of territories which are held for much or all of the year. These colorful females also have a full song repertoire whereas migratory duller females do not. Selection pressure for territorial defense may be relaxed in migrants, and it is also possible that predation may play a role. Whatever the case, it appears that natural selection in migrants is altering the elaborate sexually monochromatic plumages characteristic of resident orioles so that there is correlated evolution of migration and sexual dichromatism.

Summing up

Seasonal migrations are pervasive. They occur on all continents and in both Northern and Southern Hemispheres. Seasonal variation in temperature and rainfall result in variation in the resources that organisms need to survive, reproduce, and rear their young. When annual temperature variation is high, the frequency of European, eastern North American, and southern African avian migrants increases. The migrations of butterflies in central Australia and of ungulates in the African Serengeti are driven by the respective rainfall regimes that stimulate plant growth. Whether resources vary in time or space or both, a way to exploit them is to travel to where and when they occur. Long-distance migrations allow the exploitation of the rich resources available at high latitudes. The rich food supplies of the vast Arctic and North Temperate land masses or of the far southern oceans, to cite prime examples, are present for only a limited period. To exploit these resources requires not only the ability to reach them, but also to escape the onset of severe winters and to make use of resources en route, for example, rich stopover areas for birds or upwellings for ocean predators. For migratory birds, whales, and other long-lived organisms, their long lives have resulted in repeated evolution of round-trip journeys often accompanied by sophisticated navigation to precise breeding and wintering sites (Chapter 8). Insects such as the Monarch Butterfly have evolved round-trips that occur over several generations. The use of reliable cues, photoperiod especially, allows seasonal changes to be anticipated and thus preemptive migration to occur.

Not all organisms have evolved a movement strategy, and one of the important questions for biologists is to gain understanding of why some organisms migrate, whereas others—even some closely related to migrants—do not. There is no ancestrally embedded migration syndrome; rather migration evolves by enhancing capabilities already present. So what causes this enhancement? The thread that weaves through analyses of the evolution of migration is resource variability, whether based in habitat or feeding mode. Thus species in more open habitats in Africa or Eurasia seem more likely to be migrants. In the New World many migrants are forest species, but occur more often in exposed areas such as canopy or in more open forests. Many are frugivorous. In the Old World, insectivory—especially of the more volant insects flying in the open—seems more common. At least in the New World, habitat and diet also interact. Interestingly social behavior may be a factor, as lone or pair foragers are more likely to be migrants. Overall migrants are more likely to derive from groups occupying "unbuffered" habitats and to use historical information, for instance, the consistency of seasonal change. In a very real sense seasonal migrations may be a well-represented special case of migrations evolved in response to ephemeral habitats. The latter will be treated more fully in Chapters 11 and 13.

Other selective factors are also likely at work in the evolution of migration. Breeding at both ends of the migration route has now been confirmed in lepidopterans and birds. This means that migration connects not only breeding and non-breeding areas but also dual breeding sites. In the Silver-Y Moth of Europe and North Africa it appears that this dual

breeding is essential for the survival of the population; it is not yet clear just how important it is for avian migrants. Migration has furthermore now been seen to interact with sexual selection in some avian species. The general extent of this interaction remains largely to be explored. Predation has been shown to be reduced in high-Arctic breeders, and competition has also been implicated.

New techniques have opened the migration world in unexpected directions, providing many new empirical data, and new and expanded theory is beginning to provide deeper understanding of what these data might mean. There is still, however, much left to do to fully understand the evolutionary ecology of these often spectacular seasonal migrations. This is perhaps particularly true with respect to refining methods. Our classifications of habitats, for example, are still relatively crude. In spite of the efforts of many brilliant minds to characterize habitats, beginning with Robert MacArthur (1959), the problem of how to define habitats in such a way as to have predictive power still persists (Hockey 2005). We have made much progress through the analysis of phylogenies, but there is still work to be done in distinguishing signals due to phylogeny from those deriving from habitat or foraging mode. When phylogeny does influence migration, to what extent does it act independently and to what extent through behavior and ecology (Böhning-Gaese and Oberrath 2003; Boyle and Conway 2007)? The challenges are formidable.

CHAPTER 10

Migration to special habitats

Several migratory phenomena involve movements to sites or habitats that provide specific requirements of resources or refuges. We have seen in earlier chapters some examples of migrations to restricted breeding sites by marine vertebrates of terrestrial origin. Thus albatrosses, shearwaters, and marine turtles wander widely over the world's oceans but return to breed on islands or beaches that are mere specks on the surface of the globe, driven by the need to lay their eggs on land. The opposite need occurs in amphibians, whose young require water in all but a few species. This demand for water leads to migrations that take breeding adults to a variety of aquatic habitats, some ordinary such as temperate ponds, others exquisitely exotic, for example the bromeliad nursery pools of certain tropical tree frogs. Bromeliads may also serve as nurseries for crabs, of which many, like amphibians, spend their adult stages in terrestrial habitats; however, there are some notable exceptions where females carry eggs and young, and must return to water to release their eggs. The many species of crab that release eggs into the sea follow a similar pattern. The most studied of migrations to special breeding sites are those of diadromous fishes, as we have already seen in many places in this book.

Breeding requirements, however, are not all that drive migration to specific sites or habitats. Among the special needs of certain life-cycle stages may be a requirement for shelter or the fulfillment of unusual physiological demands. We have already seen in Chapter 7 the requisites supplied to overwintering Monarch Butterflies by high-altitude refuges in the Transvolcanic Mountains of Mexico. Many kinds of insect seek refuges through migration to and from diapause or aestivation sites. The often spectacular Bogong Moth migrations to aestivation sites in southeast Australia that were noted in Chapter 3 are an example of the latter. Hibernating amphibians, reptiles, and mammals also need refuge, and finding it often involves migration. Likewise many aquatic birds are flightless during the molt and must find places that provide both refuge and the resources for the high energetic demands of regrowing flight feathers.

All the above migrations have in common the fact that they take migrants to places supplying specific needs that cannot be easily met elsewhere. Many are synchronized, at least in part, with seasonal changes, but they are sufficiently different from the usual form of seasonal movements that a separate treatment seems justified. For this reason I consider them apart from the more usual seasonal migrations discussed in the previous chapter. The examples given should illustrate the somewhat special nature of the migrations to restricted sites and habitats and the nature of the selection that may be acting on them.

Refuging migrations

Among the more interesting of migrations to refuges are the molt migrations of waterfowl and some other aquatic birds. These birds are characterized by molts in which all or most of the flight feathers are lost more or less simultaneously, so that for several weeks they are unable to fly. They thus require a location that is both relatively free of predators and provides sufficiently rich food resources to sustain the high energetic requirements of regrowing the major flight feathers (primaries) following the molt. Characteristically these molt migrations occur after the breeding season and are independent of autumn migration, sometimes even

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proceeding in the opposite direction from the latter. Not all age and sex classes are involved, but usually only postbreeding adults. A good example is the shelducks (*Tadorna* spp.) of Australia and Europe. Australian Shelducks (*T. tadornoides*) concentrate on Lake George, a shallow lake in eastern New South Wales, from an area that apparently includes New South Wales, Victoria, South Australia, and Tasmania judging from the recoveries of banded birds that left Lake George following reacquisition of flight capacity (Fullagar et al. 1988 and Figure 10.1). Where refuges have the right conditions of shelter and resources thousands of birds may gather for the duration of the molting period. At the Waddenzee, sheltered behind the West Frisian Islands off the northwest coast of The Netherlands, some 200,000 European shelducks (*T. tadorna*) spend the molt period feeding on the rich resources of the shallow reaches and bays (Dingle 1996).

A particularly interesting and well-studied example of molt migration integrated into a complex annual migration cycle is that of the Eared Grebe (*Podiceps nigricollis*) (Jehl 1997; Jehl et al. 2003). This grebe is an extremely inefficient flyer and avoids flying whenever possible; for the most part it flies only to migrate. In spite of its poor flight capability it migrates as much as 6,000 km per year to reach high-yield habitats that few other species exploit. The lengthy migration cycle occurs in spite of the fact that its annual non-flying periods can total as much as 9–10 months. When these grebes do fly it is primarily after dark. The short, broad wings and rotund body whose dimensions can be accentuated by large fat stores at the start of migration mean that these birds have inherently high drag and wing loading and when flying must flap continuously to remain airborne. It is thus perhaps not surprising that they have a unique life history and migration pattern.

Eared grebes breed over a wide area of western North America roughly from Arizona and New Mexico to the southern tier of western Canada. Beginning around the middle of July, more than 99% of the entire population of adults and young move to two large saline lakes: Great Salt Lake in Utah

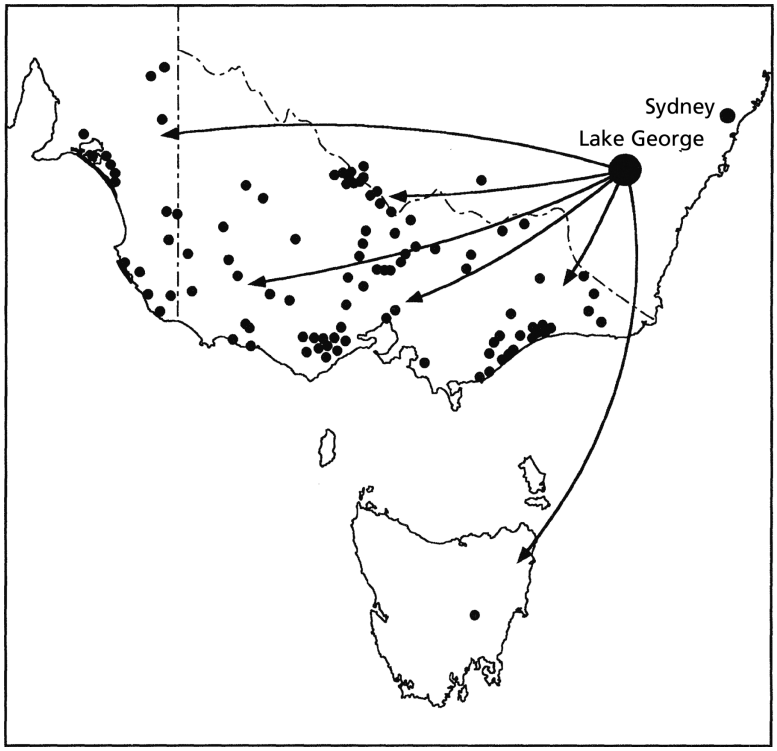


Figure 10.1 Recoveries of Australian Shelducks banded at Lake George in New South Wales during their molting period. The distribution suggests a molt migration to Lake George from a wide area in Southeastern Australia.

Source: Dingle (1996) after Fullagar et al. (1988).

(GSL) and Mono Lake in California (MLC). Here they feed on high concentrations of brine shrimp (*Artemia* spp.) and brine flies (*Ephydra* spp.). The flight to these lakes is direct and probably occurs over a period of 20 h, or two consecutive nights, over a maximum distance of 1,200–1,400 km. After arrival at these staging lakes, the adult grebes molt flight feathers, leaving them flightless for about 35 days. The birds deposit large fat stores, increasing body mass from around 350 to > 600 g, reduce breast muscle mass by more than 50%, and increase leg and digestive system mass (Figure 10.2). Juveniles undergo similar but less extensive changes. The changes extend the flightless period until departure on the next leg of migration in late November and December when the rich food supply markedly decreases. At this time the grebes fast and again change body composition (Figure 10.2).

This winter migration takes the grebes to the Gulf of California. To make the flight requires building flight muscle while reducing the mass of other body organs in order to achieve minimum wing loading and energetic costs and to maximize flight range. To achieve this goal the grebes lose ≥150 g of body mass from ~ 600 g to 410–450 g; this includes a 30% loss of fat stores, indicating the nature of the trade-off between fuel load and flying efficiency. Because of the distance and time (~17 h) required for the flight from either GSL or MLC across the intervening desert with no landing points, the grebes must make the journey in a single night. Jehl suggests that the obesity and pectoral muscle atrophy at the

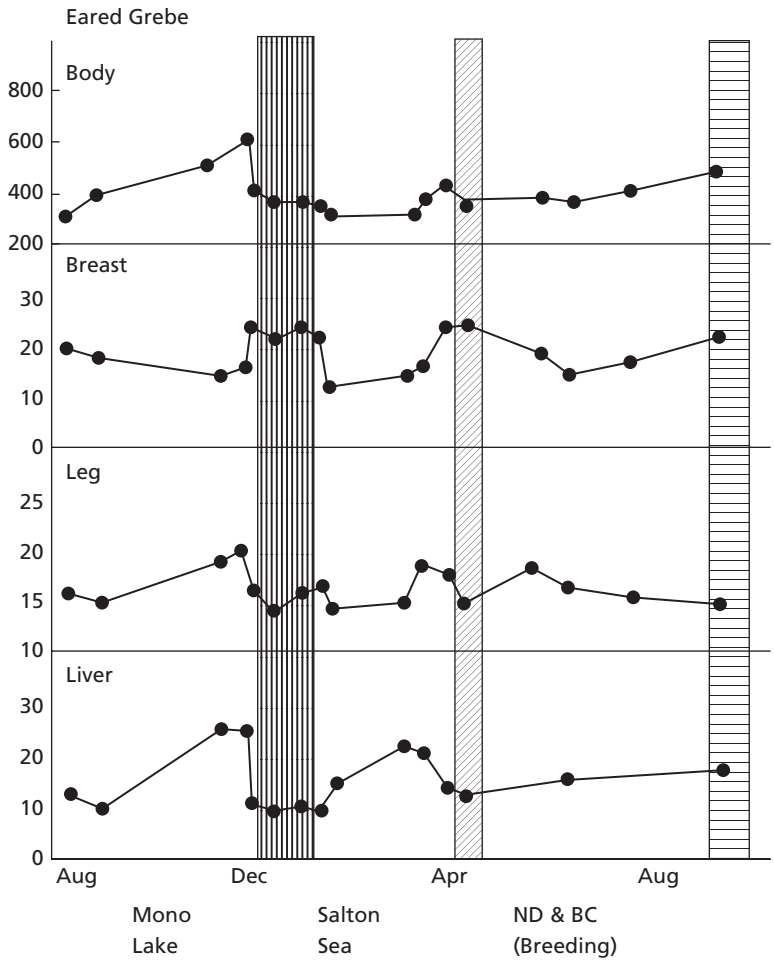


Figure 10.2 Mass changes in Eared Grebes from western North America during their annual cycle. Bars indicate periods of migration. Note increase in body mass during molt and staging at Mono Lake and increase in leg muscle mass during this period. Leg mass declines before migration whereas breast muscle mass increases. Liver mass builds up during staging at both the Mono Lake and Salton Sea staging areas. Breeding occurs in North Dakota (ND) and British Columbia (BC).

Source: Jehl (1997); used with permission of John Wiley & Sons.

GSL and MLC staging areas is a tactic for delaying migration until the long winter nights provide the hours of darkness necessary to reach the Gulf. Once they reach the Gulf, the grebes probably feed on the euphausiid crustacean *Euphausia simplex* which reaches densities of up to 50,000 individuals/m^2 in the early spring. The grebes may move up and down the Gulf by swimming to track these prey, although this needs confirmation.

By late January grebes begin to migrate north to the Salton Sea in far southern California where they reach peak numbers in March. The timing seems to coincide with the seasonal populations of the Pile Worm (*Neanthes succinea*) and is an interesting incorporation into the annual cycle of the grebes, because the Salton Sea is a man-made saline lake extant only since the beginning of the 20th century (Reisner 1993). As at other staging areas the birds first become flightless and then reorganize physiology and body composition before migrating to the breeding grounds in late March and April. Most birds proceed via GSL. They have enough reserves to fly non-stop, but because of the relatively short nights, some probably stop at seasonal wetlands that are the product of high elevation winter snows. Thus these grebes, in spite of clumsy flight and inability to save energy by gliding, have, by using staging areas rich in food, managed to incorporate migration into an annual life-history cycle.

Many insects migrate to diapause or aestivation refuges as described for Monarch Butterflies and the Bogong Moth of Australia (Chapter 3). In a case similar to the Bogong Moth, budworm moths (*Euxoa sibirica* and *Ochroplura triangularis*) of Japan migrate to aestivation sites on Mount Iwake (Oku 1983). Other examples of insect refuging migrations occur in several species of Lygaeid, Rhopalid, and Pentatomid true bugs; in various ladybeetles (*Coccinella*, *Hippodamia*); and in some species of butterfly such as the Mourning Cloak or Camberwell Beauty (*Nymphalis antiopa*). The winter clusters of Boxelder Bugs (*Boisea* spp.) sunning on exposed walls are well known in the American West and Midwest. Most of these refuging movements are on the order of a few hundred to a few thousand meters, but some ladybeetle flights can cover hundreds of kilometers. A summary and further examples of these insect refuging flights are given in Dingle (1996).

Migration to restricted breeding sites

Specialized breeding requirements are among the strongest factors selecting for migration. An interesting example is the desert isopod, *Hemilepistus reaumuri*, which occurs across North Africa, the Middle East, and into central Asia in areas receiving 50–400 mm of annual, largely winter, rainfall (Baker 2004, 2005; Baker and Rao 2004). This is a relatively large isopod (>200 mg) that is semelparous and monogamous with parental care and lives in burrows in the desert floor. They feed on organic matter in the soil. The quality of both burrows and the surrounding habitat determine reproductive success and hence fitness. Young mature in the burrow for about nine months and then depart to seek new burrows, traveling for distances of up to about 1,100 m over the desert. At the Negev Desert site in Israel studied by Baker, the emergence and migration of the juveniles takes place from February into early March. Baker studied these movements by constructing a 300 m long × 3 m wide corridor across the plain with barriers at 25 m intervals so that isopods could be captured, marked, and then placed in the next section of the corridor to continue their journeys. He used both experimental observations and modeling techniques such as dynamic programming to assess the costs and benefits of the timing and lengths of the migration pathways. To examine the possible effect of experience on distance traveled and burrow choice, isopods were kept in priming pens for seven days before testing for settling four days after transfer to new pens.

Not surprisingly several factors were implicated in determining travel distance and probability of settling. The daily mortality rate during the season of travel was 4.2%—higher than the mortality of individuals settled in burrows—so there is a cost to travel although the source of the cost, whether predation or some sort of physiological stress, is not known. There was further a reduced probability of successful reproduction the greater the distance traveled, and, in contrast, slower movement and increased time before settling were associated with a higher probability of successful reproduction. Slower movement would of course allow more time to assess habitat quality that perhaps balances against greater mortality costs of slower travel. In the priming experiments,

settling was a positive function of perceived habitat quality, suggesting that experience with habitats over which the isopods travel is a factor in determining where to settle. Experience may be a factor promoting longer travel (either distance or time or both) because such travel will allow for habitats to be compared. Time of year also had a positive effect on probability of settling, implying that "running out of time" may reduce selectivity and increase costs. Finally, burrow quality clearly influenced decisions. Settling in previously used burrows enhanced reproductive success relative to constructing a new burrow in which to settle. New construction obviously requires more energy, but it is also the case that old burrows may be located in habitats with proven success rate. The study of *Hemilepsis* is particularly interesting because it indicates the costs and benefits of timing, time spent, and distance moved, providing a deeper understanding of what movement entails. The influence of priming and the lowering of thresholds with time and distance imply that these isopod movements are indeed migratory and indicate the contribution of a truly migratory strategy to fitness.

Turning our attention to the migrations of amphibians to and from breeding or wintering sites, Berven and Grudzien (1990) analyzed the migrations of Wood Frogs (*Rana sylvatica*) in Virginia. Adults were highly site specific, returning repeatedly to the same breeding pond. Berven and Gurdzien marked more than 1,000 adult frogs over the course of their study, and every single one returned in the following spring to the pond in which it was marked. Strong homing to breeding ponds has also been observed in several other amphibians (Dingle 1980). Juveniles leaving ponds for the first time, however, sometimes moved to other ponds to reproduce; 21% of marked new metamorph males and 13% of metamorph females were recaptured in ponds other than those from which they emerged, with the longest distance traveled being >2500 m. These juvenile amphibians are analogous to salmon "strays" that return to breed in streams different from where they were born, sewing to colonize, for example, new streams that become available for spawning (Quinn 1985). Selection is likely to favor such straying under dynamic conditions of stream and suitable breeding pond formation or failure. Wood Frogs do not maintain a constant population size but rather exhibit considerable annual fluctuation. They approximate a genetic neighborhood model (Wright 1932) in which populations are linked by gene flow, but can respond to local environmental conditions, including occupation of new ponds by juveniles.

The selective factors acting on Wood Frog migration were assessed by Rittenhouse et al. (2009) for populations in Missouri. The frogs in their study bred in ponds located in relatively dry sites along ridge tops surrounded by moister woodlands of oak, hickory, and understory sugar maple. Frogs were trapped and radio-tagged near the breeding ponds, and for 3 years 117 adults were tracked for 50 days or until mortality occurred. The study indicated a significant cost of migration for these adult frogs moving from ponds to non-breeding habitats. This cost was manifested primarily in predation and desiccation (Table 10.1). A total of 29 deaths could be reliably assigned to predation and another 13 to desiccation, all the latter occurring in the dry year 2005. Eight further deaths could not be assigned a cause, although it was suspected that "old age" and handling stress were involved. Frogs at highest risk for desiccation occurred near breeding ponds; the non-breeding habitats at a greater distance from ponds were moist, cool drainages where desiccation was never observed. Predation risks were also highest near breeding ponds, and Rittenhouse and colleagues suggest that prey capture is easiest where frogs congregate and so are less cryptic. The breeding migrations may thus involve a trade-off between converging to places of abundant resources for the young and the increased survival costs of converging. Migration away from ponds after breeding thus reduces losses from predation and desiccation. While actually moving, predation risk was less during single long-distance movement on rainy nights than during multiple short-distance movements which likely made the frogs more apparent to predators. Of conservation concern is the fact that timber harvesting seems to reduce habitat quality, causing the frogs to evacuate recently harvested stands (Semlitsch et al. 2008).

A frog from a quite different habitat is the high-altitude Columbia Spotted Frog (*Rana luteiventris*) from the mountains of western North America. Pilliod et al. (2002) studied migration and habitat

Table 10.1 Sources of mortality in radio-tracked Missouri Wood Frogs (*Rana sylvatica*).

Year	No. of frogs (males, females)	Deaths	Cause of death		
			Predation	Desiccation	Unknown
2004	42 (36, 6)	9	9	0	0
2005	49 (29, 20)	31	13	13	5
2006	26 (17, 9)	10	7	0	3

Source: Rittenhouse et al. (2009).

use in this species by monitoring 736 marked and 87 radio-tagged individuals at 2,500 m altitude in the Skyhigh Basin of east central Idaho. The frogs made use of three types of habitat: (1) breeding ponds which were usually small, shallow, fishless, and silt-bottomed, although a few rocky deep lakes were used; (2) summer foraging habitats at small wetlands; and (3) wintering sites that were deep (>3 m) lakes with fish and rocky bottoms, which did not freeze to the bottom. Adult males remained near or in the summer breeding habitats with only 6–11% migrating to summer wetlands, and even these remaining within 200 m of a breeding pond. In contrast up to 57% of females moved to summer wetland habitats, and some traveled as far as 1,000 m. Juveniles were more variable with none migrating from some ponds in three of the four years, and from 10% to 60% migrating from other breeding ponds to wetlands. Migrating frogs tended to follow straight-line routes quickly, suggesting orientation, and could cover up to 500 m across dry, upland habitats before reaching summering or wintering sites. The considerable migratory capabilities of these frogs allows movement among distant water bodies several hundred to a few thousand meters apart, even in steep mountain terrain at the upper altitudinal limit of the species. Migration is integrated into a life history that exploits various habitats appropriate to the reproductive and survival needs of the frogs.

Migration to and from breeding ponds also occurs in urodele amphibians with one relatively well-studied example being the Red-spotted Newt (*Notophthalmus viridescens*) of eastern North America. Newts differ from Wood Frogs in their population structure. They are organized into "metapopulations" with high reproductive rates in a few ponds from which some juveniles (the "red eft" stage) migrate to ponds where reproductive success is lower. Movement between ponds of higher and lower breeding success maintains the newt metapopulations at a relatively constant size (Gill 1978). Individual newts may or may not exit the aquatic habitat after the breeding season to return to the terrestrial habitat (partial migration), but in any case the majority of adults moving to the terrestrial habitat return to the same breeding ponds from which they emigrated. Grayson and Wilbur (2009) used enclosures to examine the influences of population density, sex ratio, and gender on the migration decisions of Red-spotted Newts (Figure 10.3). The study demonstrated that the migration response of the animals was plastic.

Density was a major factor influencing migration, with 63% of newts migrating from high-density enclosures as compared to 39% from low-density ones. Females were much more likely to migrate than males. Timing of departure from ponds was also influenced by density, with earlier departure occurring under high density. The sex and density data indicate that migratory behavior in these newts is plastic with both sex and environment influencing timing and frequency. The possible advantage for females using the terrestrial environment may be a richer food source even though terrestrial migrants enter torpor over the winter. Newts in ponds in winter stay active even under the ice, which may confer a mating advantage come spring. These suggestions, however, need confirmation.

Red-spotted Newts are forest-dwelling urodeles, whereas some species and populations of the salamander genus *Ambystoma* inhabit grasslands. One such is the California Tiger Salamander, *A. californiense*, which occupies prairies and oak savannahs in the Central Valley and Coast Range, with some

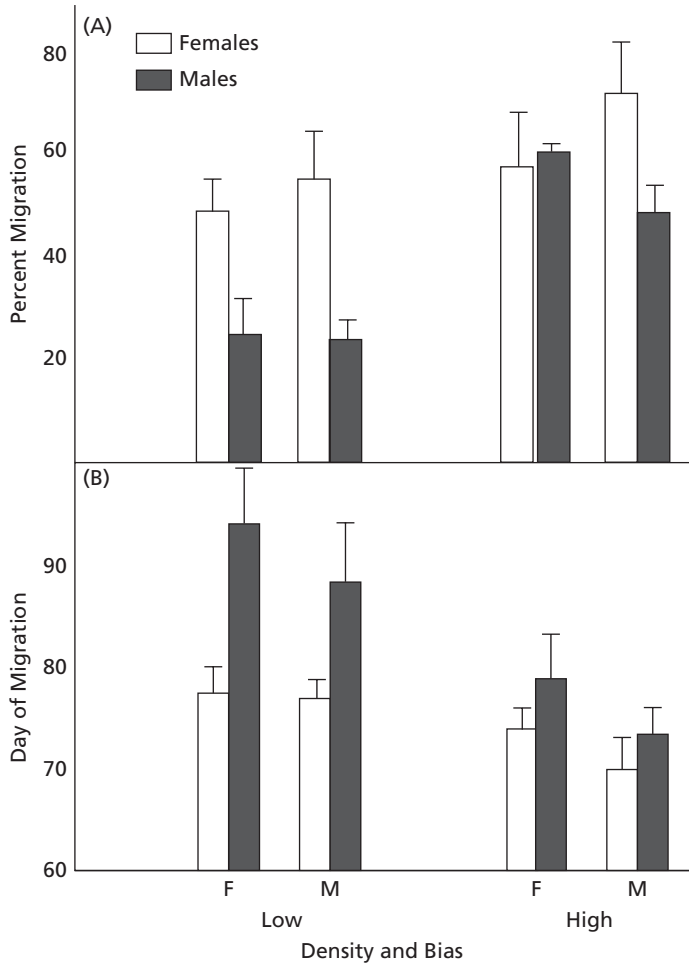


Figure 10.3 Proportion migrating from ponds and timing of migration in Red-spotted Newts in Virginia, USA, as a function of density and sex-ratio bias. F and M refer to female- and male-biased enclosures, respectively. Note that more females migrated (A) and they migrated earlier (B) than males. Density influenced both proportion migrating (more at high density) and date of departure (earlier at high density). There was no significant influence of sex ratio. Data from Grayson and Wilbur (2009).

outlier populations in other areas, and uses especially vernal pools for breeding (Searcy et al. 2013). Like other Ambystomidae, adults spend most of their adult life underground, in this species mostly in the burrows of ground squirrels and pocket gophers (Trenham and Shaffer 2005). With the advent of winter rains, adults migrate on rainy nights to vernal pools to breed, with metamorphosing larvae emerging from the ponds between May and August as these water bodies dry. The movement of the salamanders into and out of vernal pools near Davis, California, was studied both spatially and temporally by using drift fences to intercept the animals (Searcy et al. 2013).

Several interesting results emerged from the study and revealed differences between these grassland inhabitants and the forest-dwelling newts. The densities of adults and metamorphs were negatively correlated with distance from the ponds, presumably reflecting the fact that metamorphs are small and just entering the terrestrial environment and adults are dependent on the pools for breeding, with shorter distances reflecting capture at time of breeding. What was surprising was that higher densities were associated with drier habitats. Juvenile (post-metamorph) densities occurred at higher elevations less subject to inundation during rains, and adult density was higher where there was flood-intolerant vegetation. These higher densities in drier sites presumably reflect better-drained sites where refuge burrows would not flood during the rainiest months. California Tiger Salamanders also migrate

for surprisingly long distances (but not as long as Red-spotted Newts) with median distances of 615 and 667 m for juveniles and adults, respectively—much greater than for other ambystomids. It is not clear whether resource-richer distant habitats or ease of migration through grassland, as opposed to forest floor for other large ambystomids, is responsible for the longer movements, but it is unlikely that they are not adaptive. Grassland amphibians are in general understudied, so whether the characteristics of these Central Valley ambystomids generally apply to other grassland amphibian species or populations remains to be determined. Given the rate of habitat destruction in grasslands, the implications for conservation are apparent.

Migration to breeding sites on a much larger scale is exhibited by the various species of sea turtle (Table 10.2). These animals spend most of their lives at sea feeding in areas where local conditions such as reefs or current convergence (Chapter 5) result in rich resources (Witt et al. 2011), but they must return to sandy beaches for nesting where the females dig nest holes and lay their eggs. Five species have worldwide distributions with nesting, beaches on continental coasts, offshore islands, and in some cases oceanic islands, for example, Ascension or the Seychelles (Table 10.2). Two species have limited distributions; Kemp's Ridley is limited to the Caribbean coast of Mexico, and the Flatback is distributed only on beaches and in waters along the northern perimeter of Australia. In the case of the widely distributed turtles, migrations can be for considerable distances, as we have seen as in the case of the Green Turtle which migrates between Ascension Island and the coast of Brazil. Tracking studies reveal that turtles home to their natal areas, but not necessarily precisely to natal beaches or specific nesting sites (Bowen and Karl 2007; Lohmann et al. 2008b). Beaches are constantly shifting under the influence of storms, erosion, and flooding, so willingness to choose nesting sites over a length of coastline is probably adaptive. This flexibility of choice would further allow colonization of new beaches and expansion of the nesting range, a similar scenario to the "straying" of newts and salmon. Migration allows exploitation of resources scattered and shifting over wide areas of the oceans. The role of straying in new colony formation has also been noted for other large marine vertebrates such as seals and sea lions, which, like sea turtles, must return to beaches to give birth, and in this case also rear their young (reviewed in Dingle 1996).

Table 10.2 Species of sea turtle and some of their major nesting beaches.

Species	Major nesting beaches
Loggerhead (*Caretta caretta*)	Florida, Mexico, Brazil, Cape Verde Islands, Greece, Oman, Burma, Japan, Australia (both coasts)
Green (*Chelonia mydas*)	Hawaii, Marshall Islands, Indonesia, Australia, Diego Garcia, Seychelles, Ascension, Suriname, Galapagos, Mexico (both coasts)
Hawksbill (*Eretmochelys imbricata*)	Caribbean (multiple sites), Brazil, Sinai, Seychelles, Maldives, Sarawak, Solomon Islands
Leatherback (*Dermochelys coriosea*)	Florida, Dominican Republic, Suriname, Gabon, Sri Lanka, Nicobar Islands, New Guinea, Solomon Islands, Mexico, Panama (Pacific coast)
Kemp's Ridley (*Lepidochelys kempii*)	Mexico (Caribbean coast)
Olive Ridley (*L. olivacea*)	Mexico (Pacific coast—multiple sites), Costa Rica, French Guyana, East and West Africa, India
Flatback (*Natator depressus*)	North and northeast coasts of Australia (multiple sites)

Source: Sea Turtle Conservancy (www.conserveturtles.org).

This theme of migratory flexibility, as seen from newts to pinnipeds, also extends to at least some seabirds that use limited nesting sites but exploit vast areas of oceans in the non-breeding season. A case in point is Cory's Shearwater (*Calonectris diomedea*) of the Atlantic Ocean (Dias et al. 2011). Geolocation data from 72 different migrations of shearwaters nesting on Selvagem Grande Island in the Canaries revealed that the migrants showed considerable flexibility from year to year in their destinations in the non-breeding season. Some birds were site-faithful whereas others shifted from the South to the North Atlantic, from western to eastern South Atlantic, and even from the Atlantic to the Indian Ocean. These changes in destination did not reflect either age or sex. Wintering was located in certain areas of the ocean in the Northwest Atlantic, the Canary Current, the Brazilian Current, the

central South Atlantic, and the region of southern Africa along which flowed the Benguela Current in the Atlantic and the Agulhas Current on the Indian Ocean coast. All the areas possessed resources associated with currents and upwellings. Individuals were also flexible with regard to stopover behaviors such as landing on the water while on feeding grounds and the schedule of movements within and between sites. This overall flexibility was superimposed on consistency of departure dates from the nesting island and of fidelity to particular wintering sites by individual birds. The combination of site fidelity but the ability to shift sites allows adaptive exploitation of non-breeding locations over a huge area of ocean.

Diadromy

Diadromy, the movement between fresh water and salt water, is a special case of migration to specific types of habitats. It occurs, for example, in Neritid snails (Chapter 3), in amphipods (Kuribayashi et al. 2006), in several species of crab, and in many fishes (Table 10.3). Diadromy in fishes is by far the best-studied example of this sort of migration, largely because of the commercial importance of many diadromous species, such as eels, sturgeon, trout, and salmon. Diadromy is a general term that includes movements both from freshwater breeding sites to the sea for growth and development (*anadromy*) and from marine spawning and nursery areas to freshwater where maturation takes place (*catadromy*). Anadromy also sometimes refers to species migrating from lakes to streams, for example smelt and some salmonids. A third subcategory is *amphidromy*, which applies to species migrating from either the sea to freshwater or vice versa, but that spend only part of the growth and maturation phase of the life cycle there before returning to the breeding habitat to complete the final stages of growth. All these forms of fish diadromous life cycles are extensively defined and discussed by McDowall (1988, 1997, 2008).

In most cases a substantial portion of the life history is spent in each diadromous habitat. An extreme exception occurs in the amphipod crustacean, *Sternomoera rhyaca*, of Japan (Kuribayashi et al. 2006). The species is biennial and semelparous and spends most of its life in small coastal freshwater streams. For reproduction, however, it undertakes an unusual migration to the sea. During March–June, adults, either singly or as precopulatory pairs, drift the several hundred meters downstream to the sea. Mating and oviposition of eggs into the female's marsupium take place in the brackish water at the stream mouth. The males then die. The now ovigerous females, after only hours or a very few days at the stream mouth, migrate back upstream, and the marsupial eggs develop and hatch in fresh water, a requirement for egg hatching. At this point the females die. Thus the only life-history stages requiring elevated salinity are mating and subsequent oviposition. Closely related species spend their entire lives in fresh water with no requirement for migration to the sea, so why this catadromous cycle occurs in *S. rhyacea* or whether or how it is maintained by selection are unclear.

There has been much speculation and analysis concerning the origins and subsequent evolution of the different forms of diadromy in fishes, where some 250 species display some form of this migration pattern (McDowall 1997). Diadromous fish taxa fall into three broad and informal groupings (Table 10.3). The first includes lampreys, sturgeons and their allies, anguillid eels, and salmonids, with

Table 10.3 Distribution of diadromy among some taxa of fishes.

Taxon	Diadromous species	Total		
		Species	Percentage	Type[a]
Lampreys[b]	9	37	24.3	A
Acipenseridae	11	27	41.4	A
Anguillidae	15	15	100	C
Salmoniforms[c]	44	94	46.8	A
Galaxiidae	8	36	22.2	Am
Clupeidae	32	180	17.8	A, C, Am
Mugilidae	14	70	20.0	A
Goliridae	45	~800	5.6	A, C, Am
Cottidae	6	~300	2.0	A, Am
Scorpaenidae	1	~300	0.3	A
Soleidae	1?	117	0.8	A?

[a] Anadromous (A), Catadromous (C), Amphidromous (Am).
[b] Includes Petromyzontidae (33 species), Geotriidae (1 sp.), and Mordaciidae (spp.).
[c] Includes Salmonidae (68 spp.), Osmeridae (12 spp.), and Salangidae (14 spp.).
Source: Dingle (1996) after McDowall (1988).

the latter including salmon and trout, smelts, and the somewhat bizarre salangids or icefishes of the northwest Pacific region. In most of these taxa the frequency of diadromy is high, and in the catadromous anguillids it is present in all or a portion of all species with the species ranging latitudinally over both hemispheres. It is also worth noting that the relatively low 24% anadromy of lampreys is biased by the fact that in several cases there are species pairs represented by one anadromous species and a very closely related exclusively freshwater species evidently derived from it (Hardisty and Potter 1971; Potter 1980). Thus the brook lamprey, *Lampetra planeri*, is thought to be a non-migratory offshoot of the anadromous river lamprey, *L. fluviatilis*, and in Australia *Mordacia praecox* is evidently a derivative of *M. mordax*. If these species pairs are considered single species units—an assumption that does not result in bias when considering other fish families—the percentage of anadromy in this group increases considerably.

The taxa in the second and third groups in Table 10.3 show decreased frequencies of diadromy among the species represented. Some smaller fish families such as the sticklebacks (Gasterosteridae) may also belong with this broad grouping. The frequency of anadromy is high in the mullets (Mugilidae), but most of the species have not been studied enough to know what proportion of the different species are committed to freshwater breeding. In the gobies and families in the third group diadromy is rare, even in families such as the Soleids that contain several migratory species. Across these taxa diadromy probably has an independent origin as a function of local ecologies, with a diverse subsequent evolution.

An obvious point about the taxa that are included in group one is that they tend to be phylogenetically primitive, with radiations that date back to the earliest radiations of the agnathans and teleost fishes. Therefore, it is probable that diadromy also has an ancient origin (McDowall 1988). It is likely that current spawning habits are also ancient ones. Catadromous eels have a deep ocean origin (Inoue 2010), whereas lampreys, sturgeons, and salmonids reflect a freshwater origin. The argument for a freshwater origin for the salmonids goes back to Tchernavin (1939) and has since been supported by Hoar (1976) and Ishiguro et al. (2003). Given the current distribution of the group and the frequency of landlocking within and among species, a freshwater origin seems logical and is supported by molecular phylogenies (Ishiguro et al. 2003).

Gross (1987) proposed a model for the evolution of diadromy whereby fish species originally confined either to the sea or to fresh water evolved the diadromous habit through a series of steps. Taking a freshwater origin as an example, the first step was becoming a euryhaline wanderer with occasional excursions to feed at the edge of the sea. The next step was amphidromy with regular migrations to the sea, followed in turn by anadromy with both regular migrations to, and completion of adult growth in, the sea. In some cases an exclusive marine existence could evolve from what had been originally a freshwater species. In the case of catadromy, marine species evolved through a similar series of steps via euryhaline wandering and catadromy to an exclusive freshwater existence. The model seems intuitively reasonable, but there is little explicit evidence, and furthermore there is a much wider range of migratory patterns than hypothesized by Gross's model (McDowall 1997). Each of the various types of diadromy clearly has multiple origins throughout fishes, with many taxon-specific idiosyncracies. The latter is true right to the species level where there are both migratory and relatively sedentary forms, and in some species or populations individual fish may choose whether or not to migrate, depending on factors such as growth rate, water temperatures, or mating strategy (Watters 2005). The flexible strategies make multiple origins likely, a situation parallel to other forms of migration where behaviors and physiologies evolved for a variety of purposes are incorporated and modified for migration (Chapter 3 and Dingle 2006).

Phylogenetic origins aside, the evolution of diadromy in a given taxon is most likely a function of the resources available in the marine and freshwater habitats. This evolution is apparently driven by a trade-off between more efficient adult feeding and growth in one environment (or increased winter survival in some cases) and more successful reproduction in another. Diadromy from this perspective is part of a life-history syndrome that allows a fish species to occupy the more favorable

conditions at each stage of its life cycle (Dingle 1980; McDowall 1988). An optimization approach would also stress that the benefits of migration must exceed its costs. It is worth noting in this regard that a strategy of not migrating is not ultimately limiting, as many fishes in predominantly migrating diadromous families or genera and indeed many populations within otherwise migratory species are to varying degrees sedentary. Often this means the evolution of a life-history syndrome different from the migrant (Chapter 12).

Gross et al. (1988) argued for a causal relationship between the higher species diversity of anadromous fishes at boreal latitudes and the generally higher marine primary productivity in the seas of these latitudes. They suggested as a counterpoint to this that fresh waters were more productive at lower latitudes, especially those below about 20°, and noted that at these latitudes catadromy predominates. Like the model for the origins of diadromy (Gross 1987), this idea has a certain intuitive appeal and indeed a plot of the frequency of anadromy shows an increase in boreal regions with a transition between 20° and 40° corresponding to a transition in the productivity of the areas. As McDowall (2008) points out, however, although there is every reason to predict that productivity would influence biomass, there is no particular reason to assume that it would affect species diversity. McDowall notes that all boreal species would have been driven to lower latitudes by the last period of glaciation and that habitats would have opened up as the glaciers retreated toward the poles, especially so in the Northern Hemisphere. These opportunities for colonization would have been more open to species with preference for cooler temperatures, as indeed is the case for the salmoniforms and the sturgeons, for example. That evolutionary and ecological processes generating species diversity are more complex than productivity differences is suggested by the fact that salmonids are more speciose than osmerids, even though both groups are similar sorts of marine predators. It is also the case that there are relatively few anadromous fishes at southern boreal latitudes and none in South America, in spite of the high productivity of marine waters and availability of freshwater habitats. It seems more likely that cold-tolerant fishes that were already anadromous could more easily colonize streams at boreal latitudes in the Northern Hemisphere and that habitat diversity and geographic isolation between river systems could drive allopatric speciation leading to higher diversity.

An allopatric speciation model also seems to fit catadromous species. Molecular studies indicate that in the Pacific the tropical eel *Anguilla borneensis* from waters around Borneo is an ancestral species (Tsukamoto et al. 2003). Every eel species in the Pacific displays its own migration loop incorporating both route and breeding. Spatial and temporal shifts in these loops could lead to isolation of populations and subsequent speciation. The migration of temperate eels thus likely evolved from more local movements of tropical eels, possibly as a consequence of long-distance drift of larvae by ocean currents. Like eels, the tropical family Kuhliidae consists of species, 12 in all, that are partially or fully catadromous, with the latter species basal in the phylogeny. Fishes of the family occupy streams on tropical islands. The ephemeral and isolated nature of these streams, the phenotypic plasticity of migratory traits, and the relative paucity of resources in inshore tropical marine habitats are hypothesized to play key roles in driving the evolution of diadromy and the diversity present in its extent (Feutry et al. 2013).

Summing up

Outlined in this chapter are migrations to meet distinct requirements at specific periods of the life cycle. Among these requirements are shelter and special conditions for breeding. With respect to the former, the unique situation in waterbirds—that molt flight feathers simultaneously and thus enter a long flightless period with a high energy demand for feather growth—means that the birds must seek often quite restricted sites. Where suitable sites occur as at Mono Lake or the Salton Sea in California or Lake George in New South Wales, very large numbers of molting birds may congregate. The hundreds of thousands of Eared Grebes occurring first at Mono Lake and later on the Salton Sea are a case in point. Other examples of sites providing unique combinations of requirements are the high-altitude diapause sites of Monarch Butterflies in Mexico and

aestivation sites of noctuid moths in Australia and Japan. Many frogs and salamanders require lakes or ponds that do not freeze to the bottom to successfully overwinter. The selective benefits of all these shelters are obviously high because the organisms using them make impressive migratory journeys to seek them out.

In the case of many breeding migrations, the movements apparently reflect at least in part the inability to escape from ancestral requirements for reproduction. Thus many amphibians and terrestrial crustaceans must return to an aquatic medium to release their eggs and larvae, and sea turtles, pelagic marine birds, and pinnipeds must return to land to lay their eggs or rear their young. For the remainder of their life cycles these vertebrates forage widely over vast areas of the world's oceans, often displaying considerable flexibility in foraging sites over the period of their journeys. They then exhibit remarkably precise navigational abilities to guide them in their return to the rookeries. The evolution of diadromy in fishes, in all its many variations, may also reflect return to ancestral spawning sites, following the evolution of foraging in the opposite medium. Like other examples of migration, there is considerable flexibility in the incorporation of physiological and behavioral traits necessary to carry out extensive journeys. Diadromy is not confined to fishes, as it occurs in crabs, shrimps, and snails as well.

Many of the migrations discussed in this chapter have a seasonal component, but it is not specific seasonality that defines them. Monarch Butterflies and many true bugs and beetles shelter in diapause sites in the winter. Japanese and Australian noctuids, on the other hand, do so in summer aestivation sites. They are similar, however, in all that involve lengthy flights from breeding habitats to diapause sites and return. Movements of waterfowl to molting aggregations may be in the opposite direction to the usual route of autumn migration even though the two migrations may overlap temporally and spatially. Among diadromous fishes some spawn in the spring with egg hatch in the autumn, whereas others reverse the two events. It is the need for special spawning areas, coupled with the benefits of growth and maturation elsewhere, that provides the selection for the particular migratory patterns. But like seasonal migration, the patterns and processes described reflect the adaptive flexibility of migratory behavior.

CHAPTER 11

Migration under ephemeral conditions

Many habitats are not constant for very long when viewed over either time or space. The most obvious of ephemeral habitats are those that are seasonal, and, as discussed in Chapter 9, migratory life cycles synchronized to the seasons have evolved repeatedly. Changes also take place, however, as a consequence of ecological succession or of unpredictable variations in climate. These two factors contribute to making habitats ephemeral, and the exploitation of those habitats requires that the organism escape by some sort of suspended reproduction or by becoming dormant, often for long periods, or by moving between habitats as occasion demands. The Banded Stilt of Australia (Chapter 3) is an example of a creature that does both, migrating to ephemeral lakes of high productivity when these fill, but otherwise spending periods of reproductive inactivity that may last years. Equally long periods of dormancy are found in desert plants or in the eggs of crustaceans that are denizens on temporary water bodies, such as the brine shrimp exploited by the stilts. Organisms capable of long-distance movement have usually opted for migration in spite of the potential costs at the expense of growth and reproduction. Perhaps even more importantly, they may migrate in spite of the risk of failing to find a new habitat (Farrow 1990) or of the added risks and costs of exploratory ranging excursions, for example, those engaged in by the Australian Grey Teal (Chapter 3). In spite of costs and risks, there has been repeated evolution of extraordinarily successful migratory life-history strategies for exploiting ephemeral, but often rich, resources.

The general hypothesis underlying migration in ephemeral habitats is that it evolves to keep pace with changing habitat structure. The general result of a number of studies can be illustrated with a simple probability model (Roff 1990). Imagine a species with populations in two habitats that persist in their suitability for growth and reproduction from one generation to the next with probability P. The probability that a habitat will persist to the next generation is P^2 and that it will persist for t generations is then P^t. As t increases, there is an ever greater chance that the habitat will be unsuitable for a generation, and the population in it will become extinct. If there is no migration, extinction of the species requires only that each habitat becomes unsuitable at some time during the interval t. With migration between the habitats, species extinction occurs only if both habitats become unsuitable simultaneously, an event less likely to occur (and even less likely with multiple habitats). The probabilities of the species persisting in the two-habitat case for the interval t are given by $1 - (1 - P^t)^2$ without migration as compared to $(1 - [1 - P]^2)^t$ where migration occurs. The significance of this can be seen in a numerical example in which $P = 0.5$ and $t = 3$ generations; in this case the migratory species is almost twice as likely to persist as the non-migratory species. In a more realistic situation with $P = 0.95$ and $t = 100$ generation, the migratory species is 66 times more likely to persist, and this likelihood increases to 6,890 times more likely with a more unstable environment where $P = 0.9$. The likelihood of extinction with migration is even further reduced by the addition of more habitat patches.

One can add more realism to the models by incorporating costs or risks of migration, carrying capacities, population growth rates, and information-use strategies, all of which may influence thresholds and proportions migrating (Kaitala et al. 1989; Roff 1994; Shaw and Couzin 2013). Increasing the cost of migration or decreasing the mean value of the

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population growth parameter λ (= the ratio of population size at time $t + 1$ to that at time t) decreases the proportion of migrants in the population. In general, increasing the mean carrying capacity, K, or decreasing the variances of λ or K, also decreases the proportion of migrants (and flightless morphs—see Chapter 13). Furthermore, as the number of habitat patches declines or the temporal variability increases, there will be increasing selection for migration. In a heterogeneous environment migration will evolve as a function of the costs of travel, the number and duration of habitat patches, and the means and variances of λ and K.

The relation between ephemeral habitats and migration in insects was summarized over 50 years ago by Sir Richard Southwood (1962 and Table 11.1). In his review, Southwood distinguished two categories of habitats, "permanent" and "temporary." The former lasted a relatively long time and had high carrying capacities; they included woodlands and other perennial plant communities, salt marshes, heathlands, and large lakes and rivers and their fringing wetlands. Temporary habitats were ephemeral with relatively low carrying capacities and included early successional plant communities and small or shallow water bodies. Comparisons among taxa revealed that the proportion of migrants was negatively correlated with habitat persistence. The example of British macrolepidoptera is given in Table 11.1; there are more migrants at the temporary end of the scale than in permanent habitats. In woodlands there were even species where females had extremely short, non-functional wings (brachyptery); the Gypsy Moth, *Lymantria dispar*, is a classic example. Subsequent statistical tests indicate a significant correlation in the predicted direction (Roff 1990). In a later summary and analysis Southwood (1977) expressed the relation between migration and habitat as H/τ where H = length of time a habitat is favorable and τ = generation time. When the ratio approaches unity migration is favored; short habitat durations also select for a rapid life-cycle turnover and relatively high fecundities ("r selection"). A more recent theoretical analysis by Roff (1994) produces similar conclusions. With this background we can take a look in more detail at some of the migrants occurring in ephemeral habitats.

Migration in arid environments

Among the most ephemeral of all habitats are patches of rainfall-induced new plant growth occurring within the arid regions of the world. Deserts and savannas themselves remain stable over long periods, but the growth, reproduction, and survival of organisms within them depends almost without exception on the distribution of rainfall. This is very likely to be erratic, although often with a long-term tendency to be seasonally correlated. Migrants often evolve to exploit this erratic rainfall with movements between patches a part of the exploitation strategy. The central Australian butterflies discussed in Chapter 9 (Dingle et al. 2000) are an example, as are many Australian birds (Griffioen and Clarke 2002), and more will be discussed here. Monitoring of rainfall at several desert locations over the surface of the globe reveals that, in

Table 11.1 Number of species of British Microlepidoptera displaying migration or female brachyptery according to habitat.

Permanent			**Temporary**	
Habitats (host plants)	Woods (trees)	Moors, marshes, heaths (bushes, perennial climax plants)	Hedgerows, gravel pits (non-climax)	Arable land (annuals, weeds)
Species	310	273	116	58
Species with female brachypters	13	–	–	–
Migrants	None	1	22	17

Source: Dingle (1996) after Southwood (1962).

general, the less rainfall there is at a site, the greater is the positive skewness in a plot of rainfall amount against frequency (Barry and Chorley 1987). In other words the lower the average precipitation, the more likely will there be many years of little or no rainfall for every year of above-average rainfall. When the latter do occur, a few will provide large amounts of rain leading to highly favorable conditions. Across years there will be a major spatial component, with different parts of large desert regions receiving highly variable amounts of moisture. The theoretical arguments in the previous section predict high frequencies of migration under these circumstances; indeed, many desert and dry country species, such as the Australian butterflies, have adopted migratory life cycles.

Because most of the dry and desert areas of the world occur in tropical and subtropical regions, what rainfall there is becomes subject to the passage of the Inter-Tropical Convergence Zone (ITCZ; see Box 5.1). Rainfall occurs as the advancing fronts of this zone pass over a region, with greater amounts occurring when the front has recently passed over moister areas such as rainforest or even ocean. In several species of both bird and insect in West Africa, migrations are determined by the rain fronts of the ITCZ (Dingle 1996; Cheke and Tratalos 2007). Blackflies of the *Simulium damnosum* complex (vectors of onchocerciasis or "river blindness") travel north with the advancing rain fronts for up to 500 km to breed in rivers that flow only in the wet season. Their descendants later return south to reinvade perennial rivers during the dry season. Birds are also subject to the passage of the ITCZ. The Grey-headed Kingfisher (*Halcyon leucocephala*) follows the same pattern as the blackflies moving north with the rains of April and May and retreating southward in October for winter breeding. The opposite pattern is followed by the White-throated Bee-eater (*Merops albicollis*) which moves south with late-year rains, and then migrates north to breed in the dry season after the rains have passed. These cycles in both the kingfishers and the bee-eaters are synchronized to the emergence and abundance of the (large) insects that form a primary food source, especially to feed the young.

Among the organisms that have adapted migratory movements to the patterns of rainfall in arid habitats, none has done so more successfully than the diverse group of grasshoppers known as locusts. A list of species with major economic impact is provided in Table 11.2. Five species have been the focus of most studies of locust biology and migration because outbreaks of high-density swarming populations often result in considerable crop damage over wide areas (Figure 11.1). These five are the Desert Locust of the drier regions of Africa and the Middle East; the Migratory Locust, roughly sympatric with the Desert Locust, but extending to eastern Asia and more likely to occur in wetter areas such as oases or flood-plains; the Red Locust and the Brown Locust of Africa; and the Australian Plague Locust (scientific names in Table 11.2). The other species in Table 11.2 sometimes occur in high densities but not with the frequency or (usually) with the swarming characteristics of the more economically important locusts.

Particularly interesting is the now apparently extinct Rocky Mountain Locust. This species formed huge, devastating, sky-darkening swarms in the Rocky Mountain West of North America during the 19th century (Lockwood 2004). It is famous still for the masses of dead locusts found in the "grasshopper glaciers" of Montana and Wyoming, but has not

Table 11.2 Species of locust that show density-dependent polyphenism and have major economic impact.

Species	Common name	Habitat
Schistocerca gregaria	Desert Locust	Northern Africa, Western Asia, and the Middle East
Nomadacris septenfasciata	Red Locust	Sub-Saharan Africa
Anacridium melanorhoden	Sahelian Tree Locust	West Africa
Locusta migratoria	Migratory Locust	North Africa to East Africa
Locustana paradalina	Brown Locust	Southern Africa
Chortoicetes terminifera	Australian Plague Locust	Australia
Oedalus senegalensis	Senegalese Grasshopper	West Africa
Melanoplus spretus (extinct)	Rocky Mountain Locust	Western North America



Figure 11.1 A high-density swarm of the Desert Locust, *Schistocerca gregaria*. A swarm such as this can cover an area of several square kilometers and move hundreds or thousands of kilometers, consuming virtually all vegetation as it proceeds. (Photo by G. Tortoli; reproduced by permission from the FAO Photo Library, Food and Agriculture Organization of the United Nations.)

been seen alive since the turn of the 20th century. The reasons for its extinction remain obscure in spite of the fact that during the "dust bowl" years of the 1930s conditions were ripe for swarming. Indeed, at this time there were devastating swarms of the related species *M. sanguinipes* and *M. femur-rubrum*, but, as damaging as these were, even to the point of calling out the National Guard in attempts to control them, they remained local and did not travel the hundreds of kilometers seen in the earlier swarms of *M. spretus*. Thus, the mystery of the apparent extinction of the Rocky Mountain Locust remains unsolved.

Locusts display in extreme form a process known as *gregarization*, originally worked out in the early 20th century by the Russian-British entomologist Boris Uvarov (1966, 1977, and recently reviewed by Pener and Simpson 2009). This transformation from a solitary to a gregarious form occurs as a response to the increased contacts among individuals that occur with rising population densities. The conditions promoting high densities tend to occur after rains resulting from the passage of the ITCZ wind fields (Chapter 5). The most extreme cases of gregarization as described here occur in the Desert and Migratory Locusts, but it is apparent in all locust species. When locusts (the Australian Plague Locust is an exception) grow and develop under crowded conditions, their nymphs become darker because of increased melanin deposition, and they become patterned in brightly contrasting yellow and black (see the various locust web sites). The trigger for this change is primarily contact along the hind leg (Simpson et al. 2001). When at low densities and not in contact, on the other hand, nymphs are pale green or fawn-colored with an increasing green tendency at higher humidities. Morphology is also affected. Crowded adults, the so-called *gregaria* phase, are larger and of different body proportions from their uncrowded or *solitaria* counterparts. Desert Locust wings, for example, are twice the length of the femur of the hind leg in the *solitaria* form but 2.3 times the length in *gregaria* individuals. Other differences include a wider head, shorter pronotum with a depressed crest, reduced sexual dimorphism, and higher metabolic rates in the *gregaria* form. Life-history differences in Desert Locusts include reduced fecundity, slower nymphal growth, but earlier adult reproductive maturation (Cheke 1978).

These differences between crowded and uncrowded locusts are great enough in the Desert Locust that they were at first considered separate species. The fact that the crowded and uncrowded forms were the same polyphenic species was recognized by Uvarov in 1921 when he developed his theory of "phase polymorphism" and identified the two phases as products of degree of crowding. ("Polymorphism" now usually refers to forms due to gene differences, with "polyphenism" referring to environmentally induced differences.) The full

ramifications of the polyphenic differences are extensively covered by Uvarov (1966, 1977) and Pener and Simpson (2009).

The most conspicuous differences between the *gregaria* and *solitaria* nymphs, however, occur in behavior. The former are more active and display mutual attraction whereas the solitaria are more sedentary and tend to avoid conspecifics. In the Desert Locust differences may become apparent immediately after hatching in the offspring of parents that have been crowded during rearing; these offspring are more active than those from isolated parents (Harano et al. 2012). Crowding of the nymphs can further increase activity, but not until the second day after hatching. This maternal control over the polyphenism is apparently influenced by egg size; larger eggs are more likely to produce the melanized offspring characteristic of the gregarious phase (Tanaka and Maeno 2010). These authors could not produce evidence supporting an earlier claim that the foam encasing the eggs had a gregarizing effect (McCaffery et al. 1998; see also Pener and Simpson 2009). The difference in behaviors is not fixed. Tanaka and Nishide (2012) found that the attraction/avoidance behaviors could be reversed in either direction in final-instar nymphs if appropriately reared, but the transformation required at least three days to accomplish.

Once attraction among individuals occurs in the nymphs ("hoppers") they assemble into bands that may contain many thousands, or even, in the Desert Locust, up to millions of individuals, thus reinforcing the mutual attraction. These bands of hoppers are characterized by a behavior called "marching" in which the entire band moves off across country, with the cohesiveness of the band maintained by the attraction among the hoppers composing it. The distances moved by hopper bands can be tens of kilometers during the second through fifth instars. Streams of hoppers that are diverted from the main body by objects or uneven terrain are soon attracted back toward it and again merge primarily through visual attraction. Once started in a given direction, course may be maintained by moving at a fixed angle to the sun. Interaction among individuals synchronizes activity levels, and these can be further mediated by resource distributions (Despland and Simpson 2006). To synchronize, individuals must be close to each other, within approximately five body lengths. Hunger levels seem to determine when the bands stop to feed; they will continue to move when guts are full, but stop to feed when guts are half empty. A further difference between the two phases of the Desert Locust is that the *solitaria* phase has a broader host-plant range and a different macronutrient balancing physiology in keeping with the probably less selective feeding opportunities while marching (Simpson et al. 2002).

The marching swarms of hoppers appear to have two advantages. The relatively straight-line movement means that the locusts are more likely to encounter fresh food because they do not backtrack over already denuded areas. Reynolds et al. (2009) postulate that in addition selection pressure from predation encouraged the evolution of swarm formation because the switch to an extremely clumped distribution disrupts predator/food-patch networks. There may also be an element of predator "swamping" whereby individuals are protected by their inclusion in huge numbers, as postulated for periodical cicadas (Karban 1982). There may also be disadvantages to swarming. Diseases, for example, are more likely to spread, although the gregarious form appears to display more resistance, at least to fungal infection (Wilson et al. 2002). Individuals in swarms are also more subject to cannibalism, and in fact the continued marching reduces the risk that individuals will be attacked and eaten by those approaching from behind (Bazazi et al. 2008 and see the discussion of Mormon Crickets in Chapter 1).

When the nymphal *gregaria* locusts eclose to adulthood, the extreme mutual attraction among individuals continues, and the insects form into enormous swarms (Figure 11.1), displaying a form of social behavior (Kennedy 1951; Rainey 1989; Farrow 1990). These swarms may cover an area of several square kilometers and can move hundreds or even thousands of kilometers overland. Swarm cohesiveness is maintained by the attraction mechanisms of the locusts within. Locusts that leave the edges of a swarm soon turn and re-enter it, and those left behind on the ground as the swarm passes over them take off and catch up to it; thus the integrity of the swarm is sustained by the responses of individual locusts. Although the headings of flying individuals within the swarm may be in a number

of different directions, the overall swarm will move primarily downwind in the case of a high-flying swarm. A low-flying swarm will move upwind so long as wind speeds are not excessive; high winds will cause flight to cease altogether. To an observer viewing a swarm from outside, the movement is thus a rolling one in a more or less constant direction (Figure 11.2). At the leading edge of the swarm, locusts settle and feed. As they do so the remainder of the swarm passes over and in turn reaches the leading edge and settles. At the trailing edge the locusts take off, overfly feeding compatriots, and once more settle to become the leading edge. In good habitat the swarm moves slowly, and the behavior of individuals is best considered extended foraging (Farrow 1990 and see Chapter 1) because feeding responses are not suppressed as they are in migration. Feeding by swarms can strip the vegetation to the bare ground, leaving a path of devastation so aptly described in the King James version of the Book of Exodus (10.13–15): ". . . the east wind brought the locusts . . . they covered the face of the whole earth . . . and there remained not any green thing."

If green vegetation is unavailable, a swarm will lose contact with the ground and continue downwind for a considerable period and distance (lower panel in Figure 11.2). Swarms moving in this way probably consist of truly migratory individuals, although the extent of inhibition of "vegetative" responses is extremely difficult to test. The rise to higher altitudes, however, suggests that such inhibition is likely. Eventually fresh flushes of vegetation caused by local rainfall results in a swarm settling again. The odor of fresh or damaged vegetation will attract locusts in the laboratory, but it is not clear how much odor is involved under field conditions as vision (in response to green or yellow wavelength?) could also be involved. It is known that locusts respond to polarized light from reflective surfaces and may use this information in some cases to avoid flying over water (Shashor et al. 2005). Fresh vegetation provides not only energy and nutrients, but also the plant hormone gibberellin, necessary for egg maturation in locust females (Ellis et al. 1965). By accelerating reproduction, fresh vegetation could inhibit migration (cf. the oogenesis–migration syndrome, Chapter 6). In addition to its influence on locust reproduction via plant growth, rainfall influences egg development via soil moisture because the eggs, which are oviposited just below the soil surface, require moisture to develop.

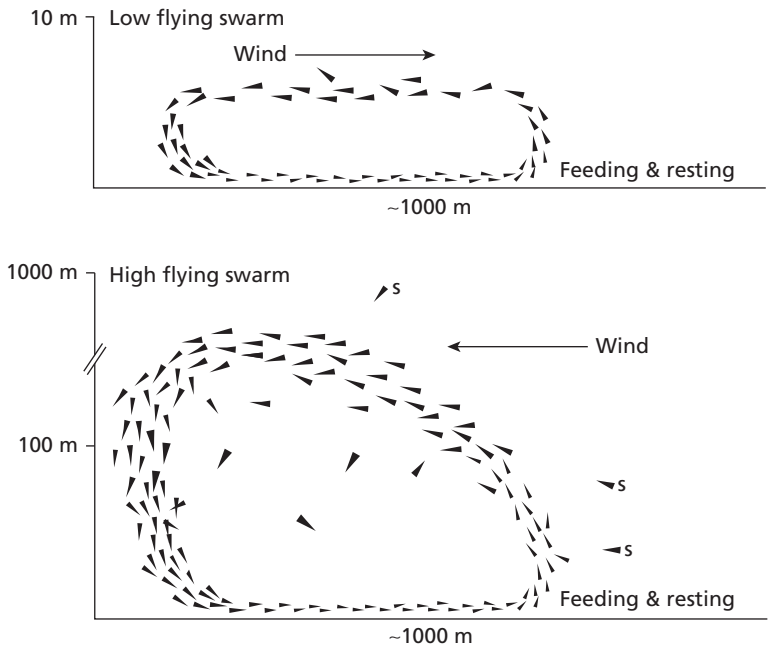


Figure 11.2 Characteristic patterns of movement and orientation in high- and low-flying locust swarms. Low-flying swarms move mostly upwind so long as wind speeds are not too high (upper panel). When green vegetation is not present, swarms may lose contact with the ground and fly at considerable heights downwind (lower panel). S, stragglers orienting back into swarms. From Dingle (1996) after Farrow (1990) and Uvarov (1977).

The relation between meteorology and outbreaks of the Desert Locust was the basis of a pioneering model of locust behavior produced by R. C. Rainey (1951, 1989) whose unique contribution was relating locust outbreaks and weather patterns. In Rainey's theory the gregarious phase was an adaptation for long-range migration to new habitats. Swarms were carried downwind to areas of wind convergence along the ITCZ where rainfall was likely providing the ecological conditions necessary for reproduction and subsequent growth of the locust populations. In this scheme the swarming behavior was seen as an adaptation to ensure that the locusts were carried downwind to areas of wind convergence and rain. An all-out international effort to study Desert Locust dynamics in the plague years of 1954–1955, when aircraft followed swarms over much of the northern two-thirds of Africa and related movements to meteorology, seemed to confirm the Rainey theory.

Subsequent studies have confirmed a relation between locust outbreaks and behavior and meteorology, but the relation is more complicated than originally implied. Furthermore, radar studies have shown that *solitaria* individuals also migrate, but they do so primarily at night along with moths and other acridoids (Shaefer 1969; Dingle 1996). In many cases these migrations are even longer than those undertaken by the *gregaria* swarms. For this reason, the *gregaria* phase can no longer be considered a form specialized to carry out a migratory portion of the life cycle. In the case of the swarms, migratory routes bore complicated relations to weather systems and wind fields with no particular relation to the ITCZ. In fact there was more likely association with synoptic weather disturbances (Chapter 5). There are even periods when migrant locust swarms appear to fly *upwind* to suitable breeding sites so that they exert control of their movements above and beyond simple wind transport. When transported by winds at night, radar has revealed that the migrants exhibit considerable mutual alignment and collective orientation (like the *Autographa gamma* moths over the UK, Chapter 9), strongly suggesting that they are influencing their own track or, in other words, navigating. The control of track by the locusts themselves was specifically excluded by Rainey's model. There is no question, however, that Rainey pointed the way to current understanding of the biology of the Desert and other locusts.

An example of the considerable complexity of Desert Locust movements is illustrated in Figure 11.3, taken from Farrow (1990) for populations in West Africa. In these populations most migration occurred with individuals rather than swarms. From May to July emerging adults fly south with the prevailing northeast tradewinds toward light rainfall areas at the leading edge of the ITCZ, which is shifting northward at this time. The heavier rains of the southwest monsoon behind the ITCZ are unsuitable for locust breeding, because they create soils too high in moisture and high humidities in which the locusts become increasingly susceptible to pathogens. Following breeding in July, there is a reverse migration to the north, this time with the northernmost prevailing winds of the monsoon. In October and November there is a hiatus in breeding as the ITCZ retreats southward, and the locusts again come under the influence of the northeast trades. There may be some population displacement at this time, but whether this constitutes migration is uncertain. From January to March cold fronts bring storms with rainfall in from the Atlantic to the northwest, again providing suitable breeding conditions. The locusts now migrate to the north against the prevailing trades to their spring breeding areas, and the cycle begins again. Note that the cycle depends on rainfall from two sources: the ITCZ and the monsoon in the south and winter storms from the Atlantic in the north.

Desert Locust swarms form infrequently in West Africa, but they can have serious consequences for crop production when they do. In order to enhance the forecasting of swarm formation, and so give warning, the conditions leading to upsurges in the locusts were assessed by Vallebona et al. (2008). They used long time-series climate data to see whether climatic anomalies could account for the upsurges over the period 1979–2005. Their analysis suggested that two factors occurring in spring contributed significantly to locust upsurges. The first was a stronger westerly mid-latitude circulation in March. This was then followed by a weakened African Easterly Jet (AEJ) and increased moisture advection from April to May. (Jets are ribbons of air in the lower levels of the atmosphere and differ from

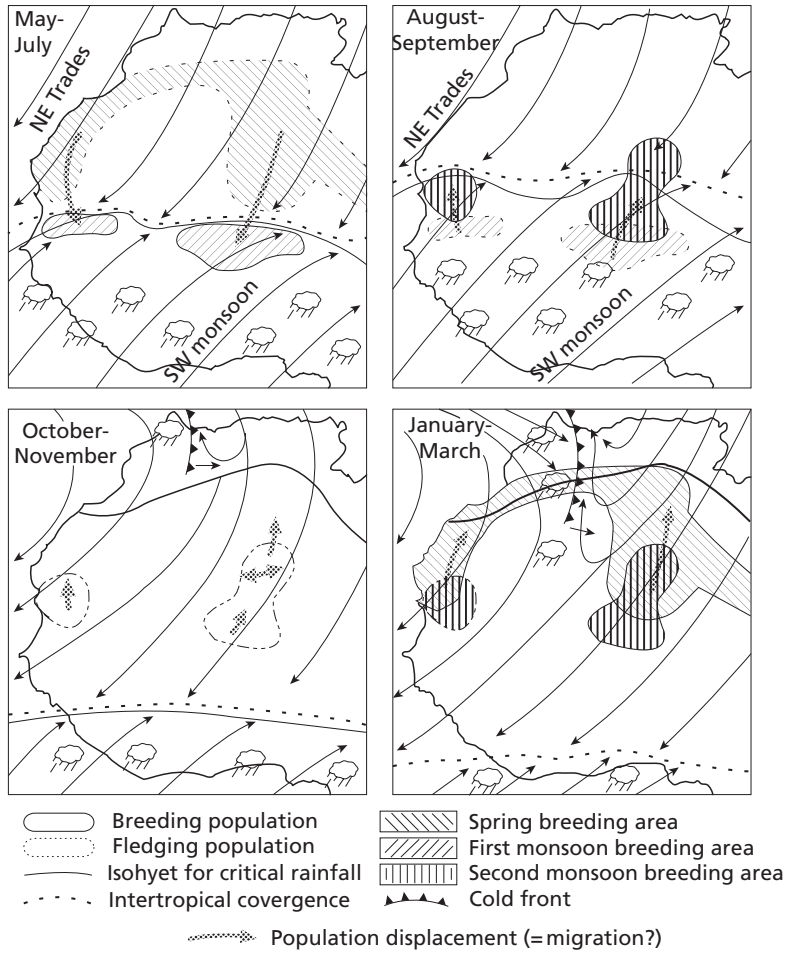


Figure 11.3 Seasonal movements of different generations of the Desert Locust, *Schistocerca gregaria*, in West Africa, showing the complexity of the migration patterns in relation to the Inter-Tropical Convergence Zone and the monsoonal and winter rains. From Dingle (1996) after Farrow (1990) and Popov (1965).

high-altitude jet streams.) The AEJ is a major atmospheric feature in tropical circulation over Africa and is an important link between large-scale and local dynamics of rainfall distribution that would synchronize just the right conditions for locust outbreaks (not too little or too much rainfall and with just the right timing).

Conditions that lead to outbreaks of locust swarms have also been analyzed over a much wider area using data on swarms from 1930 to 1987 (Cheke and Tratalos 2007; Tratalos et al. 2010). These authors took as their data the number of 1° grid squares infested with swarms over the entire range of the Desert Locust over northern Africa and western Asia. Cheke and Tratalos (2007) divided locust populations into four broad regions over the range of the locust (Figure 11.4): western, north–central, south–central, and eastern. The four regions had similar peaks and troughs of locust plagues and recessions in overlapping time-periods, and cross-correlation analysis indicated that there was connectivity between regions. Cheke and Tratalos suggest that the Desert Locust is one large "metapopulation" (Hanski 1999) stretching from the Atlantic coast of northern Africa in the west to Bangladesh in the east.

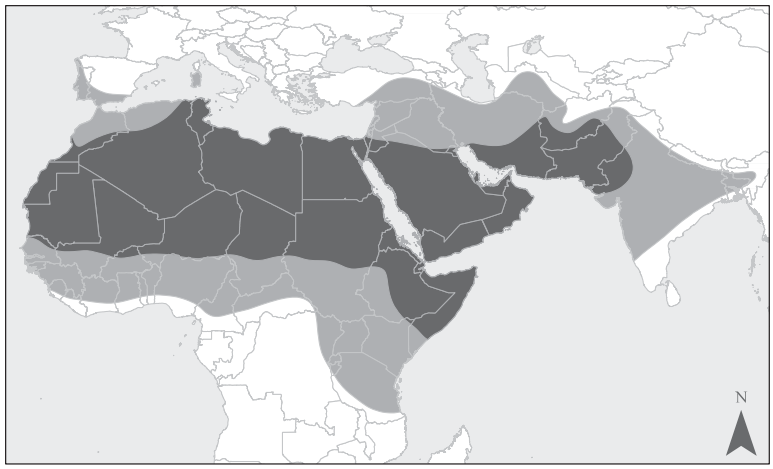


Figure 11.4 Distribution of the Desert Locust. Locusts occur year round in the solitary form in the dark shaded area. Outbreaks extend the range as far as southern Europe and India (light shaded areas). From a map in Cheke and Tratalos (2007).

Tratalos et al. (2010) employed autocorrelation analysis and modeling using moving averages across grid squares to assess the conditions that might lead to locust outbreaks. Endogenous components of the outbreaks predicted much of the variability present, but adding rainfall data improved models considerably and added much more realism to forecasts of locust swarms. Because it is very difficult to obtain data on solitary locusts which often go unnoticed, the models and their forecasts were developed without information on the solitary phase. The models performed relatively poorly during periods of upsurge and this may be because information on the presence of *solitaria* locusts is lacking. Nevertheless it is possible to forecast plagues with some success using data on rainfall and endogenous factors in the population dynamics. Chance, rainfall patchiness, variable wind speeds and directions all contribute to the biology of the Desert Locust and other locusts as well (Farrow 1990; Dingle 1996). The complexity of locust ecology and population dynamics, however, means we still have much to learn about the action of natural selection on the adaptive strategies of these highly successful arid land inhabitants.

Migration and ephemeral wetlands

Many of the world's freshwater wetlands are temporary in nature, and so can be exploited for only short durations. We saw some examples of temporary exploitation by amphibians in Chapter 10. In the case of Wood Frogs and California Tiger Salamanders, breeding ponds are available only in the spring and usually dry up over the summer. These seasonal wetlands can be used by migrants on a regular, predictable basis. The situation with wetlands in arid regions is usually quite different. In this case their presence can be variable and unpredictable, although when they are present they can supply rich resources to support breeding. Because these rich wetlands are usually both spatially and temporally variable, and often some distance apart on both scales, a strategy of flexible migration is often necessary to successfully exploit them (Jonzén et al. 2011).

Nowhere is the temporary nature of resource rich-wetlands more apparent than in the dry interior of Australia (Puckridge et al. 2000; Kingsford et al. 2010). This region covers some 70% of the continent and contains a variety of wetlands that derive from different flow regimes. The two major sources of water are local rains and a flood pulse that results from monsoonal rains occurring across northern Australia in the austral summer; the former are temporally extremely variable in occurrence and the later are extremely variable in intensity. There are four basic types of wetland: (1) floodplains of major river systems that end in interior basins, (2) claypans and saline lakes, (3) lakes, and (4) channels and waterholes. The claypans and smaller saline lakes are filled primarily by local rainfall events which are rare but can be intense when they occur

(cf. Barry and Chorley 1987); they are usually present for only a few months after filling. Some freshwater lakes, such as the deep Coongie Lakes in the Queensland/South Australia border region, usually retain water, even though irregularly re-supplied from river channel flooding or local rainfall. All the water bodies, but especially the flood plains, channels, and waterholes are supplied by irregular floods that distribute water from the monsoonal rains of the tropical north down the river channels, often braided, to the interior of the continent. The discharge rates of these flooding events may vary by three orders of magnitude over 30 years (Reid 2009). In the extreme cases this flooding can fill large interior saline basins to form lakes, as occurred with Lake Eyre in South Australia in 2009. This basin had been essentially dry since the early 1970s, but the 2009 inputs from the Warburton River (part of the Cooper Creek system) filled it to depths of >4 m in places with a surface area >9,000 km^2.

In response to the rains and floods, more than 20 species of waterbird breed in the productive wetlands (Kingsford et al. 2010); some examples are given in Table 11.3. The Grey Teal and the Banded Stilt movements were described in Chapters 1 and 3. The Grey Teal is a dabbling duck which feeds largely on the margins of wetlands large and small. As a generalist forager it takes advantage of those aquatic invertebrates that respond most rapidly to flooding. As a result Grey Teal are among the first migrants to arrive in newly inundated habitats. Waterbirds that rely on the more slowly germinating and developing plants, for example Black Swans, or on larger food items like frogs, yabbies (crayfish), or shrimps such as the White-faced Heron, tend to lag in response to the flood because their food items take longer to increase in abundance and size. Black Swans with their long necks can feed in deeper water and prefer lakes and wetlands with large expanses of open water (Kingsford et al. 1999). These waterbirds face making a decision as to when they escape once drying starts, requiring an assessment of the ongoing availability of food resources. Failures do occur, with some individuals dying before escape. These failures are presumably balanced by the enormous breeding successes possible by exploiting these ephemeral habitats.

Once of the more interesting nomadic migrants breeding on ephemeral wetlands is the Australian Pelican (Reid 2009). This species is piscivorous and relies on the larger fish species that are brought into the lakes by the floods arriving down river systems. The breeding colonies of these pelicans can be impressive. The 1990 breeding event at Lake Eyre South, for example, consisted of 100,000 birds which successfully fledged 90,000 chicks. The clustered floods of 1989–1991 resulted in a boom of native fish in the Coongie Lakes, and a pelican colony of 30,000–50,000 pairs formed on an island in one of the lakes supported by the massive fish populations. The pelicans (and Black Swans) also successfully breed in small colonies of usually tens to hundreds on islands associated with wetlands in coastal and subcoastal Australia, so that the species is a regular annual breeder as well as following the "boom-and-bust" strategy of massive breeding on ephemeral wetlands. This behavioral flexibility seems to be a defining characteristic of the pelicans

Table 11.3 Australian waterbirds with nomadic migration patterns.

Species	Breeding behavior	Food habits	Habitat
Grey Teal (*Anas gracilis*)	Solitary	Generalist, small invertebrates, plants	Shallow water, littoral zone
Black Swan (*Cygnus atratus*)	Solitary, occasionally colonial	Herbivore	Large area shallow water, littoral zone
Australian Pelican (*Pelicanus conspicillatus*)	Colonial	Fish	Open shallow water
White-faced Heron (*Egretta novahollandiae*)	Solitary	Fish, amphibians, large invertebrates	Littoral zone
Banded Stilt (*Cladorhynchus leucocephalus*)	Colonial	Small invertebrates, especially brine shrimp	Littoral zone, open shallow water

Sources: Pizzy and Knight (2007); Kingsford et al. (2010).

and other Australian waterbirds. Ephemeral wetlands are virtually always available *somewhere*, with great benefits to those species that can find and exploit them (Roshier et al. 2001).

Migration in other ephemeral habitats

One of the more prominent ephemeral habitats outside of deserts is the crop of cones occurring on conifer trees in the boreal and high-altitude forests of the Northern Hemisphere. Cone production is seasonal and occurs in the autumn; seeds last over the winter and sometimes until late spring or summer. Most conifers are erratic in the production of cones and seeds over periods of years, but in any given year there is likely to be high seed production somewhere (Koenig and Knops 2000), a situation paralleling the availability of wetlands in arid Australia. Crossbills (*Loxia* spp.) are finches that have evolved to exploit the seeds available in conifer cones. The upper mandible of the beak crosses over the lower mandible, allowing these birds to extract seeds from conifer cones (Figure 11.5). Two species in particular, the Red or Common Crossbill (*L. curvirostra*) and the White-winged Crossbill (*L. leucoptera*), are considered nomadic breeders taking advantage of successive but often widely separated cone crops (Adkisson 1996; Benkman 1996). Different populations of Red Crossbill specialize on cones of different sizes (pines, firs, spruce) and have evolved races differing in body and beak size and calls (e.g., Benkman 2003). There is debate about whether some of the forms might be distinct species (Benkman et al. 2009). In years of cone shortages crossbills can be highly irruptive with populations migrating southward especially, far beyond their normal rages. An invasion of the British Isles apparently resulted in the allopatric evolution of the large-billed Scottish Crossbill (*L. scotica*) feeding in the large cones of local conifers (Newton 1972).

Because cone crops occur only once every few years in any given area, crossbills must move between cropping sites. In irruptive years the birds can move considerable distances, and tagging records indicate that they do not return to previous breeding sites in the same calendar year (Newton 2006). Eurasian Common Crossbills banded in Germany did not return to boreal forests in Russia the same year but did so in later years when there was a new Norway Spruce crop. These birds are also apparently capable of breeding in localities in different years that are as much as 3,170 km apart and on occasion up to 2,950 km from their natal sites. Most American Red Crossbills can move similarly long distance to breed in new cone crops (Cornelius and Hahn 2012). These movements are therefore as impressive as those of Australian waterbirds transiting among wetland sites. Many of the crossbills



Figure 11.5 The Red or Common Crossbill (*Loxia curvirostra*); a bird captured in Russia for banding and study. Note the bill adapted for extracting seeds from conifer cones. Photo by Jamie Cornelius. (See also Plate 3.)

trapped on irruptions had high fat scores, indicating that they were in fact nomadic migrants.

The climate of boreal conifer forests is highly seasonal and so too is the temporal pattern of cone development (Hahn 1998). Cones develop from May through August in western North America, are mature from September or October through October or November, and release seed from November through the winter and spring, and even into the following summer in some *Pinus* species. In keeping with the temporal and spatial patterning of their food resources, crossbills are nomadic migrants on a landscape scale but with a seasonal pattern superimposed (Hahn 1998; Newton 2006; Hahn et al. 2008; Cornelius and Hahn 2012). The seasonal cycle of the birds is controlled by an integrated response to photoperiod and food (Hahn 1995). Captive birds kept in a natural photoperiod, at constant temperature, and with *ad libitum* food expressed annual cycles of physiological function (e.g., gonadal development, fat deposition, and molt). Freely available food alone does not stimulate winter reproduction; the opportunistic winter breeding in the wild seems to require social interactions as well (Cornelius et al. 2010). Changes in food availability may, however, modulate the seasonal pattern because reduced food attenuates luteinizing hormone production and testicular growth in long-day birds; it is stimulated by increased but not continuous food availability.

The seasonal cycle of the Red Crossbill is illustrated in Figure 11.6. Birds frequently breed in the winter when cone crops are mature, and the high fat scores at this time reflect the need to cope with winter cold; gonads indicate breeding condition (testis length around ≥4 mm). Fat declines through early spring as temperatures rise, but increases in May–June which is the primary migration period. Breeding does occur at this time, but less so than in winter and later summer. Major breeding occurs again in summer and is followed by a marked regression in the gonads. Autumn is a time of reduced conifer seeds and is the time that molt occurs. There is almost no breeding. Following molt the birds begin to breed again as the next cone crop matures, and there may be some migration to locate the new crop. Crossbills are thus nomadic migrants with migration superimposed upon a seasonal cycle in response to the phenology of the major food resources.

An interesting response occurs in the hormonal stress system of these birds (Cornelius et al. 2012). The capricious conditions hypothesis (CCH) predicts that, during periods of stress occurring simultaneously with breeding, birds will reduce secretion of the stress hormone corticosterone (CORT). A strong CORT response in a harsh environment such as winter could trigger nest abandonment and so should be avoided. Crossbills breed both winter and summer and so provide an opportunity to test

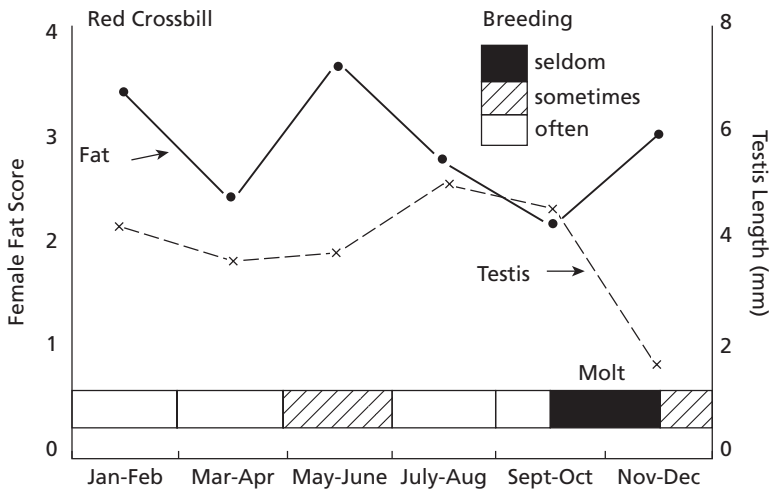


Figure 11.6 The annual breeding, fat, and testicular growth patterns of Red Crossbills. Means are shown, but there is considerable variation. Fat scores are highest in winter and in conjunction with spring migrations. Gonads are at highest development during months when breeding is most frequent. Molting occurs in the October–November period when almost no breeding occurs. Data from Hahn et al. (2008) and Cornelius and Hahn (2012).

the CCH. As predicted by the CCH, stress induced by 30 min of handling in captured birds results in less CORT secretion in winter-breeding birds than in summer breeders, a pattern that should enhance winter reproductive success. Because crossbills breeding in summer do not downregulate the stress response, it is likely that reduced CORT secretion in winter breeders is a consequence of harsh winter conditions. The CCH was thus supported and indicates that birds integrate a modulated stress response into the annual pattern of migration and opportunistic breeding.

Crossbills are not the only inhabitants of boreal forests that are dependent on ephemeral resources. Species of forest back beetles (Coleoptera: Scolytinae) depend on trees that are in a particular stage of development or are in a weakened condition as a consequence of drought on other forms of stress. Many forest bark beetles are notorious pests in forests or to the timber industry because they attack both standing trees directly and even lumber in sawmills. Their lifestyle is to construct extensive galleries beneath the bark where larvae develop, and then to emerge as adults and migrate to new host trees. These latter they find either by the odor of the trees themselves or by detecting pheromones released by other beetles that have already located trees and begun to construct galleries. Once a suitable host tree or log is located, large aggregations of beetles can develop. The beetles feed primarily on the phloem tissues of the inner bark with the results that nutrients can no longer flow from leaves or needles to other parts of the tree, and large infestations of the beetles can cause the death of the tree. In some cases fungi introduced by bark beetles can also cause tree mortality (e.g., Dutch Elm disease).

The best studies of forest bark beetles, because of their economic impact, are those of the conifer forests of the Palearctic and Nearctic regions. Two examples are the Mountain Pine Beetle (*Dendroctonus ponderosae*) of the Nearctic and the European Spruce Bark Beetle (*Ips typographis*) of the Palearctic. The Pine Beetle was studied in British Columbia by Jackson et al. (2008) during an outbreak that was unprecedented in its size and intensity and doing considerable damage to its primary hosts, the Lodgepole Pine (*Pinius contorta*). They used both radar and airplane-towed drogue nets to assess flights of these beetles above the forest canopy. During migratory flights large numbers of the beetles range up to altitudes of ≥800 m above the canopy, and were estimated to fly 30–110 km in a day. These impressive flight performances were undertaken at mean densities of about 5,000 beetles per hectare with a maximum recorded density of about 18,600 beetles in a hectare. Needless to say, migrations of this magnitude and distance can have considerable impact on a forest. In British Columbia pine mortality from beetle damage nearly doubled in the years from 1999 to 2005, apparently as a consequence of greater climatically suitable habitat and changes in forest resulting from management practices.

Mark–release–recapture experiments were performed on the European *Ips typographis* to assess the ability of pheromone-baited traps to capture migrating beetles (these beetles locate hosts via pheromones released by beetles already present) (Duelli et al. 1997). At least 12% of newly emerging adult beetles were found to undertake an adaptive migratory flight, and it was possible that some 50% did so if it was the case that beetles not caught in the pheromone traps left the area. A delay in response to pheromones by migrating beetles is reminiscent of the delayed response of Black Bean Aphids to suitable host leaves as found by J. S. Kennedy (Chapter 2). Electro-antennograms indicated that the delayed response in *Ips* was not due to delayed maturation of antennal chemoreceptor cells. Rather, as Kennedy pointed out for the aphids, the delay in response was controlled by the central nervous system. Migrants of other bark beetle species show a similarly delayed response to host volatiles or pheromones (summarized in Dingle 1996). In three species of forest beetle examined—*D. pseudotsugae*, *Hylobius abietis*, and *I. typographis*—there is inhibition during migration of responses that usually arrest flight, and a clear sequence of characteristic behaviors from take-off to landing. Selection has thus generated a response that takes a beetle away from a deteriorating or otherwise unsuitable location to a new one where resources are suitable. This programming of a long duration into the migratory flight greatly increases the area over which the search for new resources can take place, as so clearly demonstrated by the rapid expansion of the Mountain Pine Beetle in British Columbia (Jackson et al. 2008).

Fugitives or exploiters?

The migratory capabilities of crossbills and forest bark beetles allow these species to take advantage opportunistically of resources that are widely and variably distributed over space and time. Such dynamic environments require that opportunists adjust their physiology and behavior so that fitness is maximized over evolutionary time. The nature of such opportunism has been considered by Cornelius et al. (2013b) based on a comparison of the biology of crossbills with that of non-migratory Zebra Finches (*Taenopygia guttata*) breeding in the arid regions of central Australia.

Zebra Finches occur across much of Australia in both arid and more mesic regions (Zann 1996). In the arid "Red Center" they occur in large home ranges, but like other Australian finches, their movements are restricted by their need to access water. The longest recorded movement is 24 km (Blakers et al. 1984) as compared to the 3,000 km movements recorded for European Common Crossbills (Newton 2006). In the unpredictable rainfall regimes of central Australia, breeding can occur in any month, and breeding bouts have continued for as long as 15 months with non-breeding extending as long as 12 months (Zann et al. 1995). These finches seem in addition to have adjusted molt to the arid conditions. Wing molt of flight feathers, which are energetically costly to produce, is extremely slow and can co-occur on occasion with breeding. In contrast, seasonal breeders, or semi-seasonal breeders such as crossbills, have a relatively brief and rapid molt temporally distinct from breeding (Figure 11.6). The limited movements of Zebra Finches and their irregular reproductive patterns represent a strategy of obligate opportunism (OBO). This strategy is a response to limited reproductive opportunities resulting from pulsed, scarce, and unpredictable resources necessary for breeding and restricted movement, limiting opportunities to explore further afield. As a consequence current reproductive value is inflated relative to residual or future reproductive value, and brood value is high (Box 11.1). Under the OBO strategy reproduction will be favored over long-term survival, and reproduction may occur even under suboptimal conditions.

Unlike Zebra Finches, crossbills are quite capable of moving long distances to locate resources (conifer cones) necessary for their successful breeding. They are opportunistic, but, because of their movement capabilities, they are less restricted in their breeding opportunities because they can usually find breeding resources somewhere. Opportunism is superimposed on an annual seasonal cycle that includes a short period of molting when little or no breeding

Box 11.1 Reproductive value and brood value

The concept of reproductive value was developed by the great British-Australian evolutionary geneticist and statistician R. A. Fisher (1930). It is defined as the "age-specific expectation of future offspring" (Pianka and Parker 1975) and increases from a value of unity at birth (the individual instantaneously contributes itself to the future) to a maximum at the age of first reproduction (the individual has lived to produce its initial and most valuable offspring with respect to fitness). It then declines until the individual dies (post-reproductive individuals may still have some reproductive value if they contribute to the survival of offspring or grandoffspring). The rate of decline will depend on relative investments in reproduction during a given time-interval (long-lived, slowly reproducing individuals will show a slower decline in reproductive value, in contrast to short-lived, rapidly reproducing individuals).

Brood value describes the value of offspring to an adult's lifetime reproductive success, in other words the contribution of a single brood to the total number of offspring produced during a lifespan (Bókony et al. 2009). Life-history characteristics that increase residual reproductive value (e.g., long lifespans, iteroparity, exploitation of predictable abundant resources) typically decrease brood value, whereas characteristics that typically decrease residual reproductive value (e.g., short lifespan, high mortality, semelparity, unpredictable or rare resources) will increase brood value.

Reproductive value is expressed mathematically as:

$$\frac{V_x}{V_o} = \frac{e^{rx}}{l_x} \int_x^\infty e^{-rt}\, l_t m_t\, dt$$

where V_x is the reproductive value at age x, V_0 is the value at birth (= 1), l and m are the survivorship and birth rate, respectively, r is the "intrinsic rate of natural increase" (analogous to instantaneous rate of increase in a compound interest problem), e is the base of natural logarithms, and t is the time. In addition to Fisher (1930) a full discussion can be found in Slobodkin (1961).

occurs (Figure 11.6). This strategy of migrating between sequentially suitable habitats was labeled the "rich-patch fugitive" strategy by Ford et al. (1993) and described for the sequential breeding of Australian Regent Honeyeaters (*Xanthomyza phrygia*) in the same season but at locations many kilometers apart in box tree (*Eucalyptus* spp.) woodlands where the trees were flowering. Like crossbills (and queleas in Africa; Chapter 3) these honeyeaters move between productive breeding sites that are temporally variable and spatially heterogeneous.

The mobility of crossbills, queleas, and Regent Honeyeaters with the capacity to travel long distances to discover patches of resources implies that these species are not fugitives with a "best of bad job" strategy, but rather display adaptive life cycles with flexible migration pathways. For this reason "rich-patch exploiter" (RPE) seems a more appropriate designation (Cornelius et al. 2013b). In this strategy, current reproductive value is not inflated relative to residual reproductive value because exploitable resources can usually be found and investment in processes producing enhanced survival may occur even if reproductive opportunities are suboptimal. Thus brood values may be reduced.

Endocrine profiles and reproductive physiology differ between the two strategies and reflect differences in the breeding opportunism (Cornelius et al. 2013b). The OBO strategy requires birds to maintain a state of reproductive readiness or near-readiness to exploit opportunities to breed. Non-breeding Zebra Finches in arid regions maintained larger testes and higher luteinizing hormone levels than non-breeders in seasonal mesic habitats, suggesting that they are able to initiate breeding quickly when rains produce the seeds on which they breed (Perfito et al. 2007). Although not so clear, the gonadotropin-releasing hormone cycle also seems to differ between the two strategies with a "downstream" regulation of the hiatus in breeding activity in the RPE crossbills. Stress responses also seem to differ. The OBO strategy predicts that high current brood values mean that stress responses should be attenuated (less CORT) in order to avoid nest abandonment. Variation in stress responses across Zebra Finch populations in arid and mesic habitats does provide indirect support for the OBO strategy. Reduced stress responses do occur in nesting crossbills but only in winter when nest abandonment would likely be catastrophic in the prevailing cold temperatures. These endocrine data are thus suggestive of predicted differences in the two opportunistic strategies, but clearly more data are needed to confirm or refute clear distinctions.

The repeated demonstration that opportunists such as crossbills and forest bark beetles display defining characteristics of migratory behavior—for example, initially bypassing suitable resources and gearing up by storing fat, and appropriately regulating the reproductive system—indicates that these species are nomadic migrants. Defining migrants and nomads as separate categories—as proposed by Jonzén et al. (2011)—confounds the process, migration, with its outcome or product, a nomadic pathway. Selection acts on individuals to produce responses allowing the flexibility to exploit resources over a wide area, but not always in the same place. In the case of strongly seasonal migrants, resources are ephemeral but predictable in time and space. In the extreme case of resources random in time and space, nomadic movements (or temporal escape as in the case of brine shrimp in drying desert pans) are a necessity. They can also be superimposed on seasonal cycles, as with crossbills, in which nomadic migrations are programmed both by the temporal regularity of seasons and the spatial unpredictability of cone crops. Nomadic migrations are the solutions for these rich-patch exploiters.

Summing up

Simple theoretical modeling yields the general result that migration should be incorporated into life histories when habitats are transient in time or variably patchy in space. The more ephemeral the conditions the more natural selection will favor migration—this will also be the case as the number of habitat patches or the overall carrying capacity of the environment declines. Selection for migration will be further influenced by the means and variances of the population growth parameter λ. All this leads to an increasing tendency to evolve migratory life histories with an increasing degree of environmental uncertainty (or variability in the case of seasons).

Uncertainty is highest in arid environments, and the greater the aridity the higher the variance in rainfall amounts when rains do occur. This means that on those rare occasions when habitats are productive, they can be very productive indeed. The organisms that have perhaps most characteristically adopted a nomadic migratory lifestyle to successfully cope with desert conditions are certain species of locusts and grasshoppers. The elaborate phase polyphenism of the Desert Locust, *Schistocerca gregaria*, is an outstanding example, but other acridoids have adopted similar lifestyles. The extremely gregarious swarming crowded-phase *gregaria* is behaviorally and morphologically distinct from the solitary form and is superb at exploiting concentrated flushes of green vegetation because its extreme social attraction (congregation) keeps it concentrated where resources exist. Large swarms move over the habitat in extended foraging mode, but when resources are no longer available, the swarms change to migratory mode and can travel long distances beyond their normal range. The solitary phase develops under uncrowded conditions and is asocial, generally avoiding attraction and contact with other individuals. This form also migrates, but it does so at night as radar studies have revealed. It is the form that allows these locusts to exploit the more patchy or transient habitats characteristic of the extensive deserts comprising the core range of the species.

The wetlands of arid areas, especially those of the dry center of Australia, are a rather special example of ephemeral habitats. They epitomize habitats of rare occurrence, but extremely high productivity when they do occur. They are further interesting because many are connected via an elaborate system of rivers and flood plains with the monsoonal rains of the tropical north of Australia. They may thus receive water indirectly from the downstream flows following the monsoonal rains without themselves receiving any rainfall. Several species of waterbirds can migrate to take advantage of these ephemeral but very rich habitats. Ducks and shorebirds take advantage of the shallow or merely wet margins whereas larger birds such as the Black Swan invade the deeper and more extensive water bodies. Even large piscivores, for example the Australian Pelican, can establish large breeding colonies at the edges of transient lakes because the waterflows from rains in the north, if great enough, may bring large numbers of fish to these water bodies. The mystery that remains is how the birds locate these wetlands and what roles may be played by environmental cues or the memory of the birds themselves.

In addition to deserts, boreal coniferous forests are characterized by transient resources belying their apparently extensive uniformity. For bark beetles these resources are trees in appropriate weakened condition from drought stress or other factors. For crossbills the spatially variable cone crops produced by conifers are necessary for nesting. As a result these species, too, have evolved migratory life cycles. The suppression, during migration, of the responses that usually attract the beetles to trees allows individuals time to explore a wide area in search of suitable hosts, rather than stopping at a nearby host that may, like the one from which they emerged, be declining in suitability as a result of previous infestation. Crossbills store enough fat to allow them to migrate distances of hundreds or thousands of kilometers to exploit a new cone crop. As with the birds exploiting ephemeral desert wetlands, the mechanism by which newly available resources are found remains unknown, but it is known that crossbills can use information from social interactions with conspecifics.

In all the above cases migration is at least an advantage and usually a necessity if an organism is to survive in transient and ephemeral environments. The problems presented by these habitats have been solved in various ways from the pheromones produced by bark beetles to the overlapping mandibles of crossbills, but all the solutions occur in concert with the incorporation of a migratory interval as a fundamental part of a successful lifestyle. Because migration allows the nomadic species to buffer the vicissitudes of resources ephemeral in time and space, they are not fugitives to the whims of their environments but well-adapted "rich-patch exploiters" with highly successful lifestyles.

CHAPTER 12

Behavioral and life-history variability in migration

Migration is rarely a unitary phenomenon even in those species usually regarded as classic migrants. Rather, there is much variation in performance not only among species, but also among populations and even individuals. Broadly this variation can be divided into three types, but with overlap between categories. First, there are those species and populations that show behavioral or life-history variation associated with migration in the absence of any overt qualitative morphological or physiological differences. A bird species with populations migrating to different wintering areas would be a case in point. Second, there are species and sometimes populations within species that to varying degrees retain the morphological or physiological capability for migratory movement only during the migration period, often remobilizing energy and materials into reproduction at the termination of this period. Insects that migrate only during reproductive diapause or histolyze wing muscles at the termination of migration are good examples. The most extreme form of variation is the third type, occurring in species that are polymorphic (genetic variation) or polyphenic (environmental variation) in the morphology directly associated with migratory activity. This form is exemplified by those insects in which populations may fluctuate in the proportions of winged and wingless individuals and in many plant species with heteromorphic seeds. In this chapter I shall concentrate on variation of the first type, deferring discussion of morphological contrasts between migrants and non-migrants to the next chapter.

Among species that show no qualitative variation for migratory capability expressed in morphology or physiology, the variability observed may take several forms. These may be manifested in threshold, timing, pathway, or distance traveled, and may be phenotypically or genetically based or involve genotype × environment interactions. Variability is apparent across the full range of taxa and often provides useful insights into the way that natural selection is acting to mold migratory life histories. Here I focus on the phenotypic expression of differences involving migration-related traits; a full discussion of gene influences is presented in Chapter 14.

Population and species differences

Differences among populations and species occur with respect to the presence or absence of migratory activity and in the amount or type of activity that takes place. For example, when New World milkweed bugs (*Oncopeltus* spp.) are tested for tethered flight in the laboratory, species and populations that are migratory show flights of much longer duration than those that are non-migratory (Dingle 1996). The same is true for the North American grasshopper *Melanoplus sanguinipes* (McAnelly 1985). Differences can occur in the orientation of various migratory birds when tested in Emlen funnels. Cases of species differences in orientation response were examined for three European migrants by Marchetti and Baldacini (2003).

Some of the results of the Marchetti and Baldacini experiments are given in Table 12.1. The birds tested were the Pied Flycatcher (*Ficedula hypoleuca*), and species from two warbler families, the Willow Warbler (*Phylloscopus trochilus*) and the Garden Warbler (*Sylvia borin*). These birds are nocturnal migrants

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Table 12.1 Distribution of headings of three European migrant birds tested in Emlen funnels under different conditions.

Species	Vectors of orientation			
	Clear sky Sunset	Clear sky Stars	Clear sky Moon	Moon Direction[a]
Pied Flycatcher	319[b]	288	242	35–215[c]
Willow Warbler	344	327	45–225	14–194
Garden Warbler	Scattered	324–144	328	177

[a] Direction of orientation with respect to the Moon, which is set at 0°.
[b] Numbers indicate vector orientation in degrees where 0° (360°) = N, 90° = E, 180° = S, and 270° = W.
[c] Two vectors in opposite directions.
Source: data from Marchetti and Baldacini (2003).

between Europe and sub-Saharan Africa, and they were tested under various conditions that might be expected to influence their orientation, in this case during spring migration. Data from various migratory birds has suggested that direction of orientation is calibrated by the use of sunset cues (Chapter 8), so the first test placed the birds under clear skies under sunset conditions to see whether orientation later in the night would be affected. In the case of the Pied Flycatcher and the Willow Warbler orientation vectors were statistically significant and were to the west of north. This was also the case when these two species were tested under a clear night sky with stars visible but no sunset cues. Sunset thus seems to exert no influence on the orientation abilities of these two species. When tested under a clear sky with a Moon, the Pied Flycatchers displayed a significant orientation to the southwest. If the data were replotted with the Moon set at 0° (rather than north at 0°), these flycatchers displayed bidirectional orientation, although the vectors were not statistically significant. The Willow Warbler displayed non-significant bidirectional vectors with orientation plotted either with respect to north or to the Moon.

The Garden Warbler's behavior was rather different from the other two species. Under the clear sunset sky the orientation was completely scattered with no directional vector discernible, whereas with a clear starry sky there was a non-significant bidirectional vector. With the Moon present there was a strong and significant orientation to the northwest (328°), and an even stronger significant vector directly away from the position of the Moon. The Garden Warbler can navigate by using information from the magnetic field preferentially, and this may account for some of the differences from the other two species. In addition to the vector orientation differences observed among the species, there were also differences in activity levels among species and among both the conditions discussed here and others such as tests under overcast skies. Differences such as these are usually treated as experimental error, but it may be worth considering that the variation reflects true differences among the subjects and also what that might mean.

Species differences in migratory behavior have also been observed in plants. For example, weedy species of composites (Asteraceae) produce seeds that are small, hard, achenes to which are attached a parachute-like pappus for aiding in wind transport, as so aptly revealed by the children's game of blowing at the seed head of the common dandelion. Andersen (1992) studied the "settling velocity" of the seeds of several species in the laboratory to obtain an estimate of the relative lengths of time these seeds would remain airborne (Table 12.2). A higher velocity would indicate more rapid settling and hence less time spent aloft and a shorter distance traveled. Whole achene–pappus units were dropped down a Plexiglas tube, and their descent timed. The fall times were then converted to settling velocities by dividing by the length of the tube.

Andersen found statistically significant variability at all levels of the analysis that included differences among species, among plants within species, and even among inflorescences and seeds within plants. The variation in settling velocities among species likely reflects difference in the importance of migration and the ability to disseminate seeds widely to the life histories of the plants studied. A glance at Table 12.2 reveals a tendency for introduced annual species to produce seeds with lower settling velocities and hence a proclivity to remain airborne longer as a consequence. The ability to produce seeds capable of a longer migration by these classic weedy colonizers of open ground allows dispersal over a wide area of heterogeneous habitats and is probably in part what allows them

Table 12.2 Settling velocities, coefficients of variation (CV), and ecological characteristics for eight species of weedy composites from North America.

Species	Origin	Life history	Mean settling velocity (m/s)	CV
Heterotheca grandiflora (Telegraph weed)	Native	Biennial	1.02	0.420
Picris echioides (Oxtongue)	Introduced	Annual/perennial	0.702	0.450
Chrysops villosa (Golden ester)	Native	Perennial	0.514	0.140
Aster exilis (Slim aster)	Native	Annual	0.373	0.434
Taraxacum officinale (Dandelion)	Introduced	Perennial	0.307	0.207
Coryza bonariensis (Horseweed)	Introduced	Annual	0.291	0.250
Sonchus oleraceus (Cow thistle)	Introduced	Annual	0.251	0.246
Senecio vulgaris (Common groundsel)	Introduced	Annual	0.248	0.289

CV, coefficient of variation.
Source: from Dingle (1996) after Andersen (1992).

to compete so successfully with native species. The annual life cycle places a premium on high brood value (Box 11.1), and indeed these species do produce very high numbers of semelparous seeds per plant. Dandelion is interesting because it is a perennial. It is also a species of dense grasslands (as any homeowner with a lawn well knows) where open colonizable patches are likely to be rare, putting a premium on staying-power once colonization is successful. It is perhaps worth noting in this regard that perennial milkweeds (*Asclepias* spp.) similarly display "parachute" seed migration. The common *A. syriaca* of northeastern and midwestern North America was an inhabitant of prairies in precolonial times. In remnant prairies it is a colonizer of badger and gopher mounds (personal observations)—like bare patches in lawns, a relatively rare habitat in densely vegetated prairies. Here again a perennial life history would provide staying-power further provided in *A. syriaca* by extensive vegetative underground growth.

Among species with similar migration habits there may be variation across species in exactly how migrating individuals use different habitats. A case in point is habitat use by catadromous eels (*Anguilla*) as indicated in Table 12.3. Eels making a complete catadromous cycle would pass from the sea through brackish estuaries to freshwater rivers with maturation taking place in the latter habitat. There is, however, considerable variation among species and often within species (Arai and Chino 2012). The European *A. anguilla* usually makes a full transition between ocean and the rivers of Europe, perhaps because there are relatively few extensive estuaries on the Atlantic or Mediterranean coasts of Europe. In contrast, on the other side of the Atlantic, a large portion of the American Eel (*A. rostrata*) population spends much of the maturation period in the extensive estuaries of the east coast of North America (Helfman et al. 1987; Lamson et al. 2006). Other individuals apparently never leave the ocean while many more proceed far upstream in the various rivers. A pattern similar to that of the American species occurs in the Pacific *A. japonica* on the coasts of Japan and Taiwan, whereas the two New Zealand species more closely resemble the habitat use pattern of *A. anguilla* of Europe in that they tend to transfer directly from the ocean to fresh water to mature before returning to the sea to breed (Table 12.3). Finally two tropical species from waters around Indonesia and the Philippines, like the species of North America and the northwest Pacific, make extensive use of both estuaries and fresh water to complete the maturation phase of their life cycles. There have been assorted attempts to explain the different patterns of habitat use based on latitudinal clines of food abundance. It seems more likely, however, that the ability of eels to transit waters of all degrees of salinity allows them to best exploit whatever local conditions are most suitable for completing their life cycles.

Table 12.3 Diadromous eels (*Anguilla* spp.) and their patterns of migration and habitat use as adults.

Species	Distribution	Habitat use
Temperate		
Anguilla anguilla	Europe	Rivers, ocean
A. rostrata	North America	Rivers, brackish estuaries, ocean
A. japonica	Japan, Taiwan	Rivers, brackish estuaries, ocean
A. australis	New Zealand	Rivers, ocean
A. dieffenbachia	New Zealand	Rivers, ocean
Tropical species		
A. marmorata	Indonesia	Rivers, brackish estuaries
A. pacifica	Indonesia, Philippines	Rivers, brackish estuaries, ocean

Source: Arai and Chino (2012).

An interesting view of habitat use by eels is provided by Helfman et al. (1987) with respect to American Eels. They note that females mature at a length >45 cm, whereas males seldom exceed this size. Length and age at maturity are positively correlated with latitude and distance from the spawning area of the Sargasso Sea. This means that it is the larger females that predominate upstream in rivers and their headwater lakes, the more so the farther north one samples. Males on the other hand are the more abundant sex in the southeastern USA, where they are generally restricted to estuarine habitats. The precise mechanism for this differential migration is unclear; the earlier settlement of male larvae, differential mortality, and even a sex change to female in larger or older larvae have all been proposed as possible, not mutually exclusive, explanations. Helfman and colleagues further propose that selection may be acting differently on the two sexes. Males may be selected for early maturity in highly productive habitats that promote rapid growth; they are time, energy, and risk minimizers, forgoing upstream migration to minimize risk and energy costs because they have little to gain from achieving more growth by migrating farther. Females benefit (or at least experience reduced costs) from achieving large size, even at the expense of slower growth in less productive freshwater habitats, because larger size means higher fecundity.

Differential migration by sex would have the further potential advantage of contributing to panmictic (random) mating because it would reduce the chance for assortative (non-random) mating between individuals maturing in the same place or even the same year. Panmixia is an advantage as a bet-hedging life-history syndrome, that is, one where parents are selected to produce offspring of mixed genotypes to "cover all bets" in unpredictable habitats. This is the situation faced by drifting eel larvae where place of settlement and maturation are largely determined by the vicissitudes of currents that can vary in their precise course. There seems to be little information on the habitat use by sex of other eel species, but it is a potentially important contributing factor to the evolution of migratory eel life histories. Other aspects of differential habitat use could also contribute to panmixia and most likely interact with other aspects of eel ecology to produce successful generalist species. Given current understanding of eel biology and the difficulties of studying species of such extensive habitats, these ideas are still speculative (and see Helfman et al. 1987), but they may help to explain some of the more puzzling aspects of eel biology.

In addition to intergeneric species differences as seen in *Anguilla* eels, much greater differences in migratory behavior can be seen, not surprisingly, between less closely related species. An example occurs among tropical fishes in the Paraná River which forms the border between Argentina, Brazil, and Paraguay (and includes the famous Iguaçu Falls). Migratory behavior of several species was studied by Makrakis et al. (2012) using mark–recapture. In a 10-year study spanning 1,425 km of river, they marked more than 30,000 fish of 18 species and recaptured 1,083 of them. Sample sizes for 11 of these species were large enough for a statistical analysis of migratory behavior. These species were classified according to behavioral characteristics such as upstream or downstream movement, movement into lateral tributary streams, and distance traveled between capture and recapture. The authors performed cluster analysis on the data and were able to group species into roughly four clusters (Table 12.4 and Figure 12.1). The clusters

Table 12.4 Cluster characteristics and fish species sampled from the Paraná River Basin falling into each cluster illustrated in Figure 12.1.

Cluster characteristics	Species
Mainly mainstream longitudinal movements Highest percentage upstream movement Long-distance movement	*Hemisorubin platychynchos* *Leporinus elongatus*
Second-highest upstream movement in main stream	*Brycon orbignyanus* *B. orbignyanus* juveniles
Moved short distances at slow rates	*Schyzodon borellii*
Highest percentage of lateral or no movement	*Piaractus mesopotamicus* *P. mesopotamicus* juveniles
Little downstream movement	*Pseudoplatystoma corruscans* *Pterodorus granulosus* *P. granulosus* juveniles
Farthest and fastest downstream displacement	*Pimelodus maculatus* *Pinirampus pirinampu*
Second-highest downstream and lateral displacement	*P. pirirampu* juveniles *Prochilodus lineatus*
Little upstream movement	*Salminus brasiliensis*

Source: Makrakis et al. (2012).

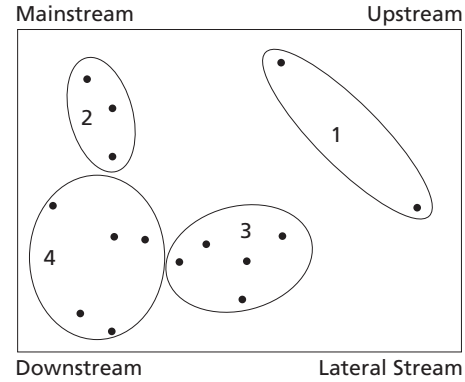


Figure 12.1 Non-metric multi-dimensional scaling ordination of 11 migratory fish species from the Paraná River in South America. Enclosures indicate cluster numbers corresponding to the numbers and cluster characteristics listed in Table 12.4. Stream characteristics indicated are approximate to indicate directionality; for example, there is a downstream to upstream gradient from lower left to upper right. Superimposed are other characteristics such as proportion transiting dams. Data from Makrakis et al. (2012).

followed a general pattern of fishes that undertook long-distance movements upstream in the main river, through to predominately downstream movement or movements into lateral tributaries of the main river. The authors stress that there is considerable variability in performance that is not readily captured by the cluster analysis. Suffice it to say, migration routes in this South American tropical river system are not confined to simple upstream or downstream movements but are a consequence of different migratory tactics depending on species. Understanding the variation is important because the fishes are objects of commercial fishing and the river has already been subjected to a number of dams potentially interfering with fish migration.

A second group of tropical fishes that shows variation in migratory behavior is the assemblage of cyprinids of the genus *Labeobarbus* studied in Lake Tana, Ethiopia, by a group of Dutch and Ethiopian biologists (Anteneh et al. 2012). There are 16 large species in the "species flock" with a maximum fork length of about a meter. With one exception, a species which breeds year round, all species spawn during or immediately following the rainy season when river flows increase and the lake level rises. Studies of two *Barbus* cyprinid species in Lake Chilwa, Malawi, indicated that river flow rate, conductivity, and an increase in suspended solids predicted migration (Jamu et al. 2003), and it is presumed that similar factors stimulate spawning and migration in Ethiopia. Seven of the Lake Tana species form pre-spawning aggregations in the lake, and then migrate up the tributary streams to spawn. Eight other species do not form pre-spawning aggregations and do not migrate into streams, but presumably spawn within Lake Tana, although the location of their spawning grounds is not known. One of these species may also move into rivers, presumably without aggregating beforehand, but reports are conflicting. A single species, *L. intermedius*, as indicated, spawns throughout the year, and there are again conflicting reports, some of which indicate lake spawning whereas others report migration into rivers. Lake spawning is thought to be a derived behavior from tributary spawning ancestors, and it is speculated that it probably evolved to avoid the energy costs of migration and to allow multiple annual spawns. In the present day there is considerable fishing pressure on the riverine spawners, so the lake breeders derive a benefit from their lacustrine

breeding habits. In view of the strong selective pressure that can result from fishing, it will be interesting to see whether contemporary evolution of lake spawning occurs (see Chapter 14).

Much variation in spawning behavior is also seen in salmonids, and this variation can influence fish life histories. A case in point is the Brown Trout (*Salmo trutta*), extensively studied in the English Lake District by J. M. Elliot (1994; see also Dingle 1996). Even within a single stream there can be four types of life cycle:

1. Fish are resident in their natal freshwater stream throughout their lives.
2. After one year, juveniles migrate from the natal stream to the parent river and return as adults just prior to spawning.
3. Juveniles migrate to a neighboring lake and adults return before spawning.
4. Migrations are to and from an estuary or the sea.

The fourth type may itself be extremely variable. In a Norwegian population, for example, the trout exploit stream, lake, and sea habitats, but spawning occurs in tributaries of the lake. The species has a global distribution with a range of life histories that are both qualitatively variable and quantitatively complex.

Some of this variability is revealed by a more detailed study of the trout in two streams of the Lake District differing in important characteristics. The first stream (beck in the local parlance), Black Brows Beck, is on the order of only 500 m long, but it is connected to the estuary of the River Leven some 15 km away by two major streams. Black Brows originates in peat and grassland and flows through woodland until it meets the larger streams leading to the estuary. All altitudes are below 150 m and even at high water discharge velocities do not exceed 60 cm/s, and the stream bed remains stable. Trout inhabiting this stream are migratory and display all forms of migratory travel listed in categories 2–4.

Wilfin Beck is only about 3 km away from Black Brows and has the same temperature and mineral characteristics. In its physical characteristics, however, it is quite different. This stream arises above 150 m and flows steeply for 4 km down to its mouth at Lake Windermere. Its discharge velocities can be close to 100 cm/s, and the rocky stream bed can be unstable at high velocities. At about 1 km from its mouth, a waterfall separates the upper from the lower levels of the stream, and whereas trout are common between the lake and the waterfall, none can breach the falls. The prevention of migration beyond the falls means that trout above this point are resident (category 1 in the scheme of possible life cycles). In contrast, trout in Black Brows spend only two years in the beck before migrating, mostly to the sea. Other differences between life histories are that there is higher survival beyond the fourth year in Wilfin and that eggs in Black Brows are produced by females of only one year class, whereas two and sometimes three or four year classes spawn in Wilfin.

Other differences are apparent. First, the Black Brows migratory fish are larger, as is the case for other migratory/non-migratory contrasts in fishes (Dingle 1996). In the case of Brown Trout, differences are expressed in both length and weight, with migratory fish more robust, being >50 g heavier at 25 cm long than non-migrants of the same length. The larger migrant females produce about twice as many eggs as the non-migrants, and these eggs are larger (although more variable in size) and on average about twice the number and triple the weight of the eggs of the non-migrants (Figure 12.2). The large size of the newly hatched fry translates into larger adults in the migrants, with larger, more numerous eggs and so a greater investment in reproduction

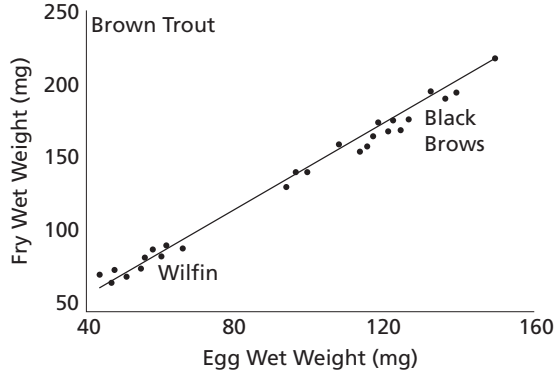


Figure 12.2 Relation between weight of eggs and weight of fry for migratory (Black Brows Beck) and non-migratory (Wilfin Beck) Brown Trout populations from the English Lake District. The great variation in the migrant population is apparent. Data from Elliot (1994).

(16–17% energy to egg production in Wilfin as opposed to 30–37% in the migrant Black Brows trout). Genotype is a major contributor to the population differences because these contrasts persisted even when trout were reared under similar conditions in the laboratory. Access to the sea in the migrants has resulted in selection for larger fish and greater reproductive effort, probably sustained by the great food resources available in the estuary and the sea. Similar sorts of life history variation occur throughout the Salmonidae (e.g., freshwater rainbow and sea-migrating steelhead trout are both *Oncorhynchus mykiss*).

An interesting case of the rapid evolution of migratory behavior (see also Chapters 13 and 14) occurs in the Cane Toads (*Bufo marinus*) of Australia (Phillips et al. 2006; Alford et al. 2009; Llewelyn et al. 2010). The toads were introduced into Australia in the vicinity of Townsville, Queensland, in 1935 with the object of controlling pests in sugar cane fields. These animals are large anurans weighing up to 2 kg and are native to Central and South America. The toads are toxic, emitting poisons from dermal glands when disturbed; are highly invasive, expanding to occupy more than a million square kilometers of tropical and subtropical Australia; and have had a severe negative impact on native fauna and ecosystems. The area occupied by the toads is expanding at an accelerating rate due to the increased rate of movement of the animals at the expanding front (Figure 12.3A).

Studies comparing behavioral and morphological characteristics of toads at an advancing front at Adelaide River in the "Top End" of the Northern Territory with those in the long-established population in Queensland reveal the evolution of a number of traits that contribute to increased migration rates at the front. Toads tagged and radio-tracked at Adelaide River were found to be longer-legged on average than Queensland toads and these longer-legged toads in the population moved farther during 24 h than their shorter-legged conspecifics in the same population (Phillips et al. 2006). As the toad invasion passed over a study site, it was the longer-legged individuals that went through first, followed later by shorter-legged individuals—a morphological difference in passage toads that was highly statistically significant ($P < 0.0001$).

Exactly how longer legs facilitate the greater movement of the toads that possess them, and hence a more rapid expansion of the range, is not entirely clear. In an experimental study, Llewelyn et al. (2010) compared speed and endurance in the resident and expanding front toads (Figure 12.3B). They measured these traits in a 10 m long runway that was 20 cm wide to channel the movement observed. The experimental tests were run in the evening (1800–2400 h) which is the normal activity time for these animals, and all trials were run in Townsville. The trials clearly showed that the hopping speed of toads from the two populations was about the same at ~80–90 s to travel the 10 m of the runway. The big difference between the migrating and resident toads was manifested in endurance. The Adelaide River animals traveled about three times as far at each trial before refusing to move farther (and were presumably "exhausted") than the Townsville resident toads. Thus endurance, but not speed, seems to be a major contributing trait to the rapid expansion of Cane Toad range.

Other traits also made contributions to toad migration and rapid expansion of the range (Alford et al. 2009). For example, the probability of moving on a given night by radio-tracked animals was on average much higher at the invasion front (Figure 12.3C, D). The mean distance traversed per move was greater in migrants, as was the displacement rate. Most interesting from a behavioral perspective, the degree of path straightness was greater at the Adelaide River front, strongly suggesting that movement was indeed straightened out as would be expected of migrants (see Chapter 2). Toads at the advancing front thus belong to a rapidly evolving population that is adapted for movement and that is accelerating the rate at which the total area occupied by these exotic and invasive pests expands.

Migration does not evolve independently of other traits, as shown so well by Australian Cane Toads. Especially important in this regard are traits that have a major influence on fitness such as those associated with reproduction. In birds a long-term discussion of ecological factors relating to clutch size was initiated shortly after World War II, largely by the British ecologist David Lack (1954, 1968). Among the factors considered by Lack was migration, and an exhaustive study that includes migration is that of Böhning-Gaese et al. (2000). They

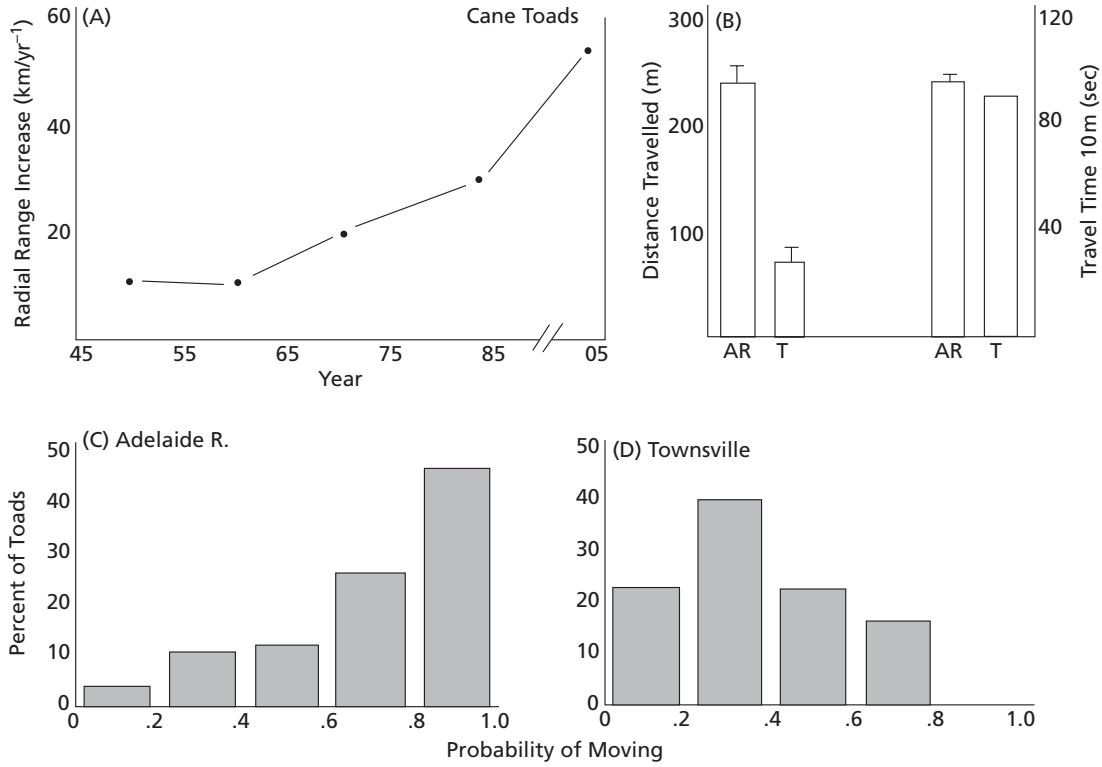


Figure 12.3 Increase in migratory tendency in Cane Toads (*Bufo marinus*) at the edge of their expanding range. Comparisons are between toads at an expanding front at Adelaide River, Northern Territory, versus those at Townsville, Queensland, where they were first introduced. (A) Increase in the radial range since introduction. (B) Endurance measured as distance traveled during observation versus speed in migratory Adelaide River (AR) and Townsville (T) toads. (C, D) Probability of moving in a runway in the two populations.

Sources: (A) Phillips et al. (2006); (B) Llewelyn et al. (2010); (C, D) Alford et al. (2009).

analyzed the life histories and ecology of 373 North American and 252 European landbirds to assess the influence of body size, diet, nest type (e.g., open or closed), nest location, nestling development (precocial or altricial), migratory behavior, habitat, latitude, source continent, and phylogeny on clutch size, annual number of broods, and their product—namely annual fecundity. The data were analyzed using analysis of covariance and multiple regression with similar results and conclusions.

One of the important conclusions of the study is that migratory behavior does indeed seem to influence the three life-history traits considered. The degree of movement was classified into three types—residents, short distance migrants that mostly remained north of the Tropic of Cancer, and long-distance migrants that traveled beyond the Tropics and intercontinentally. The results of the analysis are displayed in Figure 12.4. Clutch size decreases in the progression from residents to long-distance migrants, but the number of broods per breeding season is highest in short-distance migrants. Annual fecundity thus does not differ between residents and short-distance migrants but is significantly lower in long-distance migrants. Other factors also influenced these traits. The most influential factors affecting clutch size were latitude, type of nestling development (precocial birds such as quail and grouse have larger clutches), body size, and type of nest. Migratory behavior was one of the most important influences on brood number along with latitude, nestling development, and type of diet. Annual fecundity was most influenced by body size, diet, nestling development, and migration. Migration is thus an important contributor to the patterns

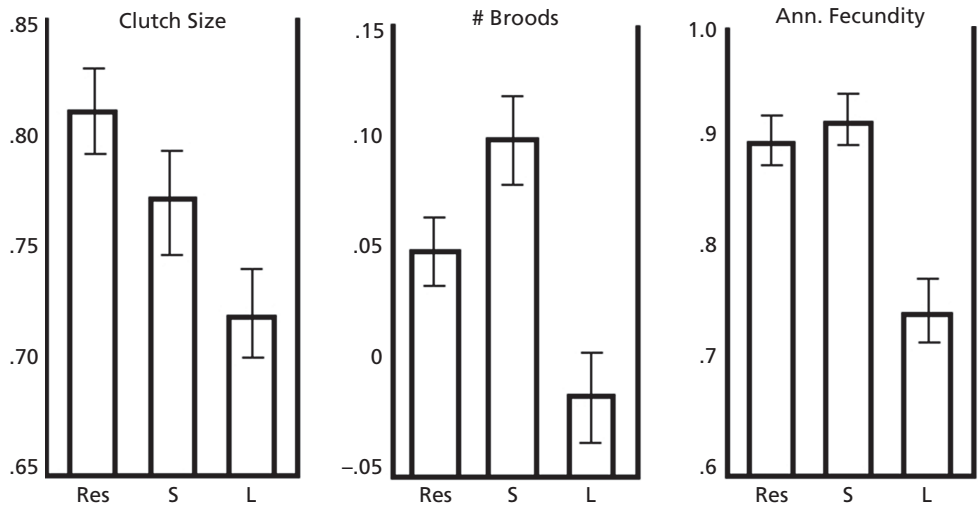


Figure 12.4 Relation between migration and three measures of reproduction in North American and European breeding birds. All values are on a $\log_{10}$ scale. Res, residents; S, short-distance migrants; L, long-distance migrants. Data from Böhning-Gaese et al. (2000).

of reproductive fitness traits, but not surprisingly acts in conjunction with other factors. In spite of the broad range of taxa sampled, the traits occurred independently of phylogeny. It is interesting that the lowest annual fecundity occurs in long-distance migrants, which classical life-history theory would predict would be due to higher winter survival. For whatever reason, the results suggest that one of the benefits of migration may be reduced selection for high reproductive effort. This idea, however, largely remains to be tested (cf. Faaborg et al. 2010).

Intrapopulation variation

In addition to the sorts of variation discussed in the previous section, there is considerable variation seen in the patterns of migratory movement itself. These patterns have been extensively documented for birds and are indicated for New World birds in Table 12.5.

Discussion of most of these patterns is deferred to the next section, but I take up the intrapopulation variation here. In addition to instances where migration and life histories differ between whole populations, there are numerous cases where variation in migratory behavior occurs only in some fraction of the population. In one case, called partial migration, a portion of a population is migratory, while the remainder is sedentary or moves only locally. Within this category there are three subcategories, divided according to the fractions of the population that move and breed in two or more habitats (e.g., wintering and breeding areas) as illustrated in Figure 12.5. A further variant, differential migration, involves the movement of varying distances by different individuals. The two sorts of migratory patterns are not mutually exclusive, and indeed the migratory portion of a partially migrating population is quite likely to move for different distances depending on circumstances. Partial migration occurs in a wide variety of organisms from mammals and birds to fish to insects. Who migrates is often a function of age or sex with (usually) more experienced or more dominant individuals being resident and less experienced or less dominant individuals migrating (e.g., European Robins; Adriaensen and Dhondt 1990), although this need not be the case as we shall see. There is a genetic component to the phenomenon and a great deal of modification by environmental conditions. For a summary of earlier studies see Dingle (1996).

Partial migration is particularly apparent and has been extensively studied in birds. In some species such as the European Blackcap (*Sylvia atricapilla*), migrant and resident individuals are relatively well

Table 12.5 Migration patterns in New World migrant birds.

Pattern	Description
Complete migration	All individuals migrate south in spring and north in autumn.
Interpopulation variation	
Leap-frog migration	Some populations overfly permanent residents; long-distance migrants overfly short-distance migrants.
Post-breeding displacement	Southern populations migrate north after breeding and displace populations migrating further north after breeding.
Breeding displacement	Northern populations displace southern populations that move to higher latitudes.
Population partial migration	One or more populations of a species migrate, other populations resident. Migration may be either to breeding or to wintering areas.
Intrapopulation variation	
Partial migration	Only some individuals migrate to wintering areas. May be leap-frog migration.
Dual partial migration	Some individuals migrate north to breed, others migrate south from resident tropical populations.
Differential migration	Individuals migrate different distances.

Directions (north versus south) are indicated for South American migrants.
Source: partly after Dingle (2008) from Jahn et al. (2004).

defined (Pérez-Tris and Tellería 2002). In other species there may be considerable annual variation both within and between individuals. Such is the case with the Australian Silvereye, *Zosterops lateralis* (Chan 2005). Two subspecies of the Silvereye breed respectively in Tasmania (*Z. l. lateralis*) and in New South Wales (*Z. l. familiaris*) and differ in their patterns of migratory behavior. Birds of the Tasmanian subspecies migrate to the mainland and extensively within the mainland, but some individuals remain in Tasmania over the winter. Furthermore, some birds remain resident in some years, but migrate to the mainland in others, thus being individually partial migrants. Birds that breed in New South Wales appear to be largely resident, although there may be some local movements and even some short-distance partial migration. At the ends of a probability continuum, Tasmanian birds can be considered partially migratory and New South Wales birds mostly resident (see also Chapter 6).

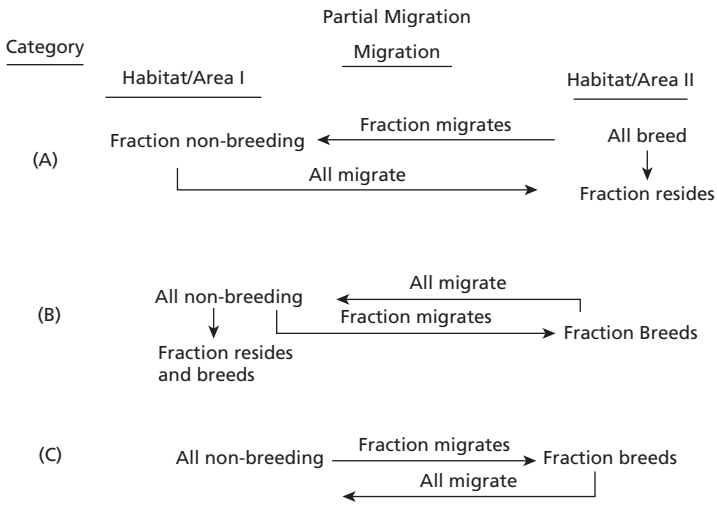


Figure 12.5 Patterns of three types of partial migration. (A) All individuals breed in habitat/area II and a fraction resides there. The remaining fraction migrates to habitat/area I to spend the non-breeding season; all of these then return to II to breed. (B) All individuals spend the non-breeding season in I and a fraction migrates to II to breed before returning. Another fraction does not migrate, but remains to breed in I. (C) As in B, all spend the non-breeding season in I. One fraction migrates to II to breed, but the second fraction remains in I and does not breed.

Source: after a schematic in Shaw and Levin (2011).

Possible correlates of this difference in migratory behavior were assessed by Funnell and Munro (2007, 2010). They tested the ability of birds from the two Silvereye populations to orient and to display migratory restlessness at the appropriate times for migration (spring and autumn). Captive birds were tested in diffuse light in Emlen funnel orientation cages (Chapter 4) in the local magnetic field near Sydney, New South Wales, where the two populations would overlap in the winter when Tasmanian migrants would be present. Birds of both populations were active in the funnels, but only the migratory Tasmanian birds displayed an ability to orient. These birds oriented N or NNW in the autumn (a mean of 26° in 2000 and 356° in 2001) and in spring they oriented SW (217° and 231° respectively in the two years). These are the migratory directions appropriate to season for migrating between Tasmania and the Australian mainland. The New South Wales non-migrants oriented essentially randomly in the Emlen funnel cages in both seasons.

In spite of the fact that they displayed orientation ability appropriate to season and the New South Wales Birds did not, there were no obvious periods of migratory restlessness in the Tasmanian Silvereyes. Both subspecies exhibited a daily activity pattern of a large early morning peak, lower levels during the day, and a lower peak during the 2 h or so preceding sunset. Similarly there was no difference in patterns of activity between subspecies over the annual cycle of breeding, molting, and wintering. In both populations activity was higher during the spring/early summer period when migration (in Tasmanian birds) and breeding take place and was somewhat higher in the migrants, but the difference was not significant.

An interesting partial migration system occurs in Swedish Blue Tits (*Cyanistes caeruleus*) (Nilsson et al. 2008). This species migrates only for short distances with median travel of only 82 km at a median rate of just 13 km/day, and the autumn direction of migration was scattered between south and west. Interestingly northern and southern populations did not differ either in direction or distance. The overall pattern is an example of "chain migration" in which migrants from, in this case, northern breeding grounds occupy the area vacated by southern birds moving still farther south. As is typical of other partial migrants, a larger proportion of adults than juveniles remained in the breeding range rather than migrating. A further characteristic of these Swedish Blue Tits was that 17% of the birds that did migrate remained to breed in the wintering area rather than return to their natal habitats.

In addition to migratory pattern, these Blue Tit partial migrants displayed other distinguishing characteristics. One of these was the way migrants behaved toward novel objects (Nilsson et al. 2010). Average approach latencies were compared among migrants and residents, with the migrants found to have shorter approach latencies. Because migrants must deal with novel situations en route and on arrival, the authors suggest that shortened latencies may have adaptive value. Nilsson et al. (2006a) also compared the partially migrating tits with four species of regular migrants whose routes take them out of Sweden in the winter (Linnet, *Carduelis cannabina*; Chaffinch, *Fringilla coelebs*; Brambling, *F. montifringilla*; and European Robin, *Erithacus rubecula*) with respect to their responses to weather patterns during migration. They examined passage migration at Falsterbo, in southwest Sweden (see Chapter 5). The Blue Tits showed a strong negative correlation between migration and cloud cover; regular migrants were much less influenced. The result is that the Blue Tits "play it safe" by restricting migratory flights to those days with completely or partially clear skies.

Blue Tits evolve changes in patterns of residency as an outgrowth of partial migration. In North America the House Finch (*Carpodacus mexicanus)* has rapidly evolved full-on migratory behavior from a partially migrant population that displayed very little migration (Able and Belthoff 1998). This finch is native to western North America where it is largely sedentary (80% or so resident in southern California), although a very few individuals do migrate for some distance. Around 1940 finches were introduced into Long Island, New York. Since that introduction, the finches have evolved to the point where between 28% and 54% of them are migrants traveling at least 80 km. As the population has expanded into northern New York, for example, the average distance of migration has expanded logarithmically; orientation during migration is appropriate to season, southwest in the autumn and

northeast in the spring. Like Tasmanian Silvereyes, eastern House Finches are partial migrants, and individuals may migrate in some years and remain on the breeding ground in others. The presence of a few migrants in the original western population suggests that migratory capability was already present and genetically based in the birds from which the eastern population was drawn.

Given that there are the alternatives of migration and residency, it is appropriate to ask "Why migrate?" One approach to this question is through the use of models, and one popular model is that of the evolutionarily stable strategy or ESS. The concept of the ESS was developed from game theory largely by John Maynard Smith (see Maynard Smith 1982 for a summary) and is defined as a strategy—the ESS—that when widespread in a population cannot be displaced by any alternative "mutant" (i.e., genetically based) strategy. In this model the various alternatives, here migration or residency, should have the same pay-off or benefit, and if one alternative increases in frequency, its pay-offs should be reduced or, to put in another way, its lifetime reproductive success should be negatively frequency dependent. A mixed ESS is a situation in which the ratio of alternative behaviors is evolutionarily stable because, if the ratio changes, so do the pay-offs and the balance is restored. The classic case of a mixed ESS is the 1:1 sex ratio, because if the ratio deviates from unity, the relative fitness of the more numerous sex declines, i.e., individuals have more competition for mates and so leave fewer offspring. In spite of limitations, such as assumptions of haploidy, ESS models have been quite successful in providing insights into a variety of behaviors.

Partial migration has been examined using mixed ESS modeling and simulation. This approach was used by Kaitala et al. (1993) to consider a population of birds (although the model is not necessarily confined to birds). They modeled a situation in which part of the population winters at the breeding site, while the remainder migrate elsewhere to overwinter and return the following year. The migrants face a higher risk of dying during migration but a lower risk of starving during the winter. Thus they are assumed to suffer density-independent mortality. Sedentary birds do not risk death from migration, but do face a higher risk of starvation, with greater competition for food and so increased risk of death occurring at higher densities. Therefore they are assumed to suffer density-dependent mortality, and this mortality would also be frequency dependent because it would be influenced by the proportion of migrants. Various parameter values were used consistent with known local stable bird populations; for example, it was assumed that birds lay five eggs and that the local population size at which density-independent growth is reduced by half (a measure of carrying capacity) is 100 birds. Other adjustments were made to allow for ambiguity in the model (see Dingle 1996, p. 308ff. for a fuller discussion).

Three major points emerged from the analysis and simulations. First, density-dependent overwinter survival was the single most important requirement for the maintenance of partial migration in the population. This was true over a range of survival values for density-dependent and density-independent conditions influencing mortality. Second, reproductive successes of the two alternative behavioral types do not need to differ in order to result in partial migration. Differential mortality is the critical factor that drives the system and permits the coexistence of the two strategies. However, the magnitude of the ESS fraction of migrants may be affected by relative reproductive success. The model predicts that migration is a "best of a bad job" alternative so that some additional factor should drive it. In at least some birds this seems to be dominance, with subordinate individuals more likely to migrate and suffer consequences of reduced reproductive success. Finally, the third point from the analysis was that environmental stochasticity, in turn affecting density-independent mortality, had very little influence on the ESS solution and certainly not enough impact to influence the evolution and maintenance of partial migration. Any potential influence was effectively overridden by the density-dependent overwinter survival. Density-dependent overwinter resident mortality also overrode other stochastic effects such as those on breeding site or possible genetic dimorphisms.

Kokko (2011) has developed models that relax some of the common assumptions made in producing frequency-dependent models of partial migration. Specifically her models do not assume

that migratory propensity is the only varying trait and that prior residence always operates at maximum strength to assure priority access to preferred habitats. Such previous models had suggested that dominant individuals were likely to be residents and that subordinate individuals were more likely to migrate in a "best of a bad job" strategy, as discussed in the opening paragraphs of this section. Kokko's models did show that there was a prior residency effect; when it was stronger, fewer individuals were migrants, but there was a range of effects over which partial migration evolved. The condition of individuals also affects migration. For example, heavy individuals may be more dominant and have greater access to resources (e.g., food during migration) wherever they are, so it is possible that heavier, more dominant members of a population will be more likely to migrate. This was actually observed in Tropical Kingbirds (*Tyrannus melancholicus*) in South America: dominant birds could enhance survival by migrating and on return take over high-quality territories from non-migrants (Jahn et al. 2010). As Kokko points out, rejecting the specific dominance hypothesis that refers to survival in the non-breeding season favoring (dominant) residents does not mean that "dominance" is not necessary to explain partial migration. In this view, and as suggested by the Kokko models, understanding the dynamics of territory acquisition (and other aspects of breeding success) is crucial to understanding the dynamics of partial migration.

Shaw and Levin (2011) model the situation in which only a fraction of the population migrates and breeds whereas the remainder is resident and does not breed (category C in Figure 12.5). Shaw and Levin give some 30 examples of species with breeding migrations where each year some individuals skip migration and do not breed. The examples cover the gamut from crabs to whales. Existing ESS models cannot be applied to these species where migratory behavior is a function of a trade-off between present and future reproduction (see Box 11.1). Shaw and Levin modeled the ESS probability of migrating, taking into account fecundity, annual survival rates of those that skip versus those that do not, and density dependence.

They first examined an analytical model where all adults migrate and reproduce if the ratio of growth rate to death rate for individuals reproducing immediately is greater than the same ratio for individuals skipping one year and then migrating and reproducing, that is, partial migration where adults skip every other breeding season. The results indicated that partial migration should occur where the migration mortality is high and where fecundity can be greatly increased by skipping a year before breeding. There is support for this conclusion in migratory fish such as salmon and cod. In the Atlantic Salmon (*Salmo salar*), for example, individuals that spawn in smaller rivers where they do not need to travel far upstream have higher post-spawning survival and annual reproduction. Fish that migrate farther up larger rivers have a high mortality cost and spawn biennially (Jansson et al. 1991). The frequency of skipping also increases in sea turtles that forage in less nutrient-rich areas.

The introduction of stochasticity into the models necessitated simulation. In stochastic situations Shaw and Levin assessed the probability and severity of bad years, survival of skipping adults, and the mortality cost of migrations. The results for bad years are illustrated in Figure 12.6 which shows that, as the probability of a bad year increases, the ESS value of annual migration decreases, and it similarly decreases as the quality of years decreases. In a constant environment when the mortality cost of migration is high and when individuals greatly increase fecundity by skipping a year before breeding, partial migration is also likely to occur. Partial migration can thus occur without environmental stochasticity, but stochasticity, including that in fluctuations of population size, does influence the degree of partial migration. Data from various species suggest that the model can be valid in nature, but parameterizing it with actual biological data comparing survival and fecundity of migrants and non-migrants will be far from easy.

Although partial migration is common and particularly well studied in birds—and indeed most of the ESS models discussed have been formulated with birds in mind (although not limited to birds)—it is a common phenomenon among other groups as well. It is very widespread among ungulates (Hebblewhite and Merrill 2011), and among fish it occurs in at least 16 orders, although relatively well characterized in only a few (Chapman et al. 2012a,b). In

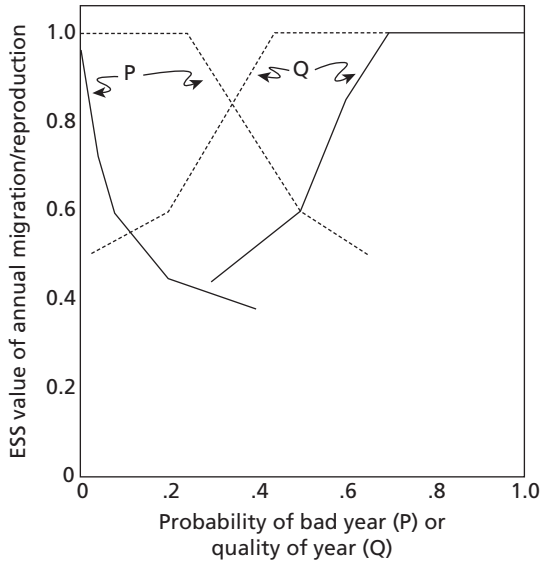


Figure 12.6 Model results for evolutionarily stable strategy (ESS) values of migration with reproduction in the case of partial migration where individuals can skip migrating and reproducing in some years. An ESS value of 1.0 means that all individuals migrate and reproduce every year, and a value of 0 means that all individuals skip every other year. The lines "P" are ESS values as a function of the probability of a bad year occurring for two values of year quality, and the lines "Q" are values as a function of year quality for two probabilities of a bad year occurring. Data from Shaw and Levin (2011).

both ungulates and fish, trade-offs between foraging and predation risk drive resource selection, and the balance between the two aspects of life histories determines the ratio between migrants and residents in partially migrating species.

Hebblewhite and Merrill (2009, 2011) examined foraging–predation trade-offs in the herd of elk or Red Deer (*Cervus elephus*) in Banff National Park in Canada and the adjacent regions of the province of Alberta. This elk herd faces considerable predation from wolves and bears and so it behooves them to find forage that is of high quality while avoiding predation to the extent possible. In their study Hebblewhite and Merrill (2009) examined trade-offs at both a broad landscape scale and a within-home-range scale for both migratory and non-migratory elk. At the landscape scale, migration reduced wolf predation by 70% relative to residents by moving migrants away from areas of wolf abundance. At a fine scale, migrants used areas of 6% higher forage digestibility. Resident elk were subject to higher predation than migrants, but were able to reduce predation risk to only about 15% greater than migrants by using areas close to human activity that were avoided by wolves. Residents also experienced lower forage quality at a landscape scale, but may have gained by using more abundant forage, again near human activity; furthermore they occurred in groups some 20% larger. Migrant females had higher pregnancy rates and winter calf weights as a result of higher forage quality, but survival of both females and calves was lower than for residents (Hebblewhite and Merrill 2011). Residents, however, experienced higher female and calf survival in spite of displaying lower pregnancy rates and calf weight. The frequency of migrants is declining slowly in the region because of higher wolf predation rates, a demographic trend consistent with a trade-off balance favoring residents. It is interesting that human influence seems to have de-coupled the relation between foraging and migration, giving the resident elk an alternative that outweighs the natural advantages accruing to migrants.

Among fishes, partial migration has been particularly well studied in a common European fish, the Roach, *Rutilus rutilus* (Cyprinidae) (Broderson et al. 2008; Skov et al. 2010). These authors studied Roach migration in lakes in southern Sweden and Denmark. These fish and many other cyprinids undertake migrations from lakes into tributary streams and wetlands during the winter, the reason being that the lakes provide better conditions for growth and subsequent reproductions whereas the streams and wetlands provide refuge from predators such as large Perch (*Perca fluviatilis*) and Northern Pike (*Esox lucius*). Broderson et al. (2008) used radio tags to follow the migration of individual fish and experimentally manipulated food supply to study the influence of body condition on decisions of whether or not to migrate. Fish were captured and held in enclosures in which they were supplied with food or were not fed before release back to the lake. The study demonstrated that fed fish of better body condition were more likely to migrate, entered streams earlier and remained longer, and were more likely to return to the lake successfully than unfed fish (Figure 12.7). In addition larger fish were more likely to migrate and to stay longer

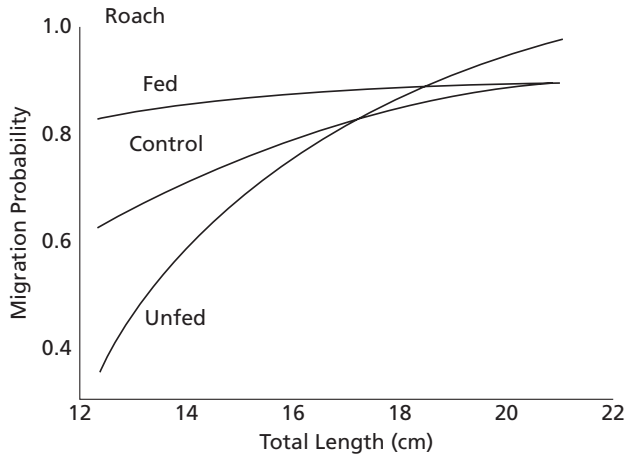


Figure 12.7 The probability of migration in experimentally fed or starved Roach in Scandinavian lakes. Controls are fish that were normally migrating from the lakes. Size and condition both contribute to migration probability. Data from Broderson et al. (2008).

in streams. Evidently fish in good condition were more likely to migrate to streams where not only food was reduced but also predation risk, whereas smaller fish in poor condition stayed in the lake to feed and grow even in the face of greater predation. In contrast to the usual situation in birds where subordinate or younger individuals migrate, here it is the larger individuals in better condition that go. The "best of a bad job" strategy is typical of the non-migrants. Transplant experiments further suggested that migration in Roach is phenotypically plastic (Skov et al. 2010; see also Chapter 14).

Populations of Bream (*Abramis brama*), another common European fish, display a migration system similar to Roach with winter migration from lakes to tributary streams (Skov et al. 2011). These authors also used tagged fish to monitor the migration performance of individuals and monitored the performance in two Danish lakes. Migration was considered in relation to predation vulnerability, which was calculated using an estimate of the numerical proportion of the population of predators (mainly Pike in this case) with gapes large enough to capture and swallow prey fish of given body lengths. The results indicated that predation increased and migration decreased in fish that were smaller. Thus predation still seemed to have a profound effect on migration (correlational in this case), but in Bream it was smaller fish that migrated, unlike in Roach where it was larger individuals in better condition that did so. Migration in these two fish, therefore, depends on the nature of the balance in the risks involved. Across the spectrum of partial migrants this balance can be influenced by a variety of factors including size, age, sex (and the relation between these and condition), predation risk, and resource availability.

Variation in routes and patterns

Populations and individuals vary not only in whether or not they migrate but also in the distances they travel, the routes they follow, the timing of arrival or departure, and the pattern of behavior during the migratory journey (see Table 12.5 for population patterns in New World birds). Across species there may be very large patterns. Newton and Dale (1997), for example, assessed the patterns seen across the migration systems of birds of the western Palearctic. They found that, for these migrants, there was a strong correlation between the latitudinal spans of summer breeding and overwintering ranges; if one range was narrow so was the other and vice versa. This was true even within subdivided groups of the avifauna, for instance, landbirds or waterbirds. Similarly Price and Gross (2005) found a positive correlation in the sizes of breeding and winter ranges in *Phylloscopus* warblers breeding in Central Asia and wintering in India and Southeast Asia. The notable exception to this pattern was shorebirds for whom breeding ranges are latitudinally narrow whereas wintering ranges on

shorelines are latitudinally broad but longitudinally narrow. There were several other patterns in the western Palearctic avifauna ranging from residents to long-distance migrants whose summer and winter ranges are separated by an extensive latitudinal gap which may include much inhospitable terrain such as the Mediterranean Sea and/or the Sahara Desert (Box 12.1).

In addition to these grand avifaunal patterns, the populations of different avian species show different migration patterns (Table 12.5). There are, for example, two major displacement patterns: a breeding displacement where one population supplants another in the lower latitudes of the species' breeding range and the supplanted population moves to higher latitudes to breed; and post-breeding displacement where a higher-latitude population moves to lower latitudes, supplanting a population that moves to still lower latitudes. Perhaps more interesting are "leap-frog" migrations where a population may overfly shorter-distance migrants or even residents. A case in point is the western North American complex of the White-crowned Sparrow (*Zonotrichia leucophrys*) (Clements 2007) that consists of three subspecies, Nuttall's (*Z. l. nuttalli*), Puget Sound (*Z. l. pugatensis*), and Gambel's (*Z. l. gambelii*) White-crowned Sparrows. The Nuttall's population is non-migratory and resident along the coast of California from Mendocino to Santa Barbara. The Puget Sound population breeds from southwest British Columbia through Washington and Oregon to northwest California; it migrates to central and southern California to spend the winter. The Gambel's population breeds in Alaska, the Yukon, and south-central Canada and migrates to the Central Valley of California and as far as northern Mexico. Thus the leap-frogging Gambel's birds migrate over and beyond both the Nuttall's and Puget Sound populations in both spring and autumn. An eastern population and a western mountain population migrate parallel to each other to the Caribbean and central Mexico respectively.

Such parallel migration routes are common among non-overlapping breeding populations of many birds and occur also in insects. In North America, for example, numerous avian species breed across the northern forests from the east coast to the Yukon and southeastern Alaska. These species generally follow a migration route that takes them east of the 100th meridian to wintering areas in the Caribbean, and Central and South America. Western populations of these species migrate west of the 100th meridian and winter in southern Mexico and northern Central America. These species thus show little or no overlap in breeding and non-breeding areas or on migration (see discussion of migratory divides in Chapter 3). The best-known North American insect migrant, the Monarch Butterfly, also displays parallel migration pathways. Most of the eastern population migrates through Texas to Mexico, but a small sample passes through Florida to Cuba (Dockx 2012). The western population seems to travel along three roughly parallel routes: to coastal California, along the Colorado River valley to Mexico, and through eastern Utah and Arizona (Chapter 3 and Dingle et al. 2004).

Different patterns of migratory movement in fish have been observed among both individuals and populations. Such differences have been observed

Box 12.1 Patterns in the migration distributions of birds of the western Palearctic

1. Resident year-round through entire range. Breed in the summer (195 species).
2. Present and breeding in summer only in the northern part of the range; present year-round in south where also breed (22 species).
3. Present year-round but breeding in summer only in the north; part of population winters only in the south (21 species).
4. Present and breeding in summer only in the north; year-round with summer breeding at intermediate latitudes; winter only without breeding in the south (111 species).
5. Summer breeding range immediately to the north of the winter range with no overlap (22 species).
6. Summer breeding range separated from winter range by a latitudinal gap where the species occurs only in migration.
   (a) Migration through largely hospitable habitats.
   (b) Migration across large stretches of sea or desert (107 species; most winter in sub-Saharan Africa).

Source: Newton and Dale (1997).

in tagged Green Sturgeon (*Acipenser medirostris*) in rivers on the west coast of North America. The general migratory pattern of this species is entry into rivers in the spring to spawn and emigration to the sea to overwinter in the autumn. In the Rogue River in Oregon the sturgeon migrated about 40 km upstream (Erickson et al. 2002). Over the summer and into the autumn the fish spent their time in deeper areas (>5 m) with slow-moving water, and after more than 6 months in the river, all tagged individuals returned to the sea for late autumn and winter. The trigger for this outmigration appeared to be increased flows and a temperature drop to below 10°C, both as a consequence of autumnal rains. In the Trinity and Klamath River system of the northwest corner of California the pattern observed was slightly different (Benson et al. 2007). Here four events were observed: (1) a spring upstream spawning migration from April to June; (2) a spring outmigration to the ocean (not observed in the Rogue Rivers); (3) summer residence in deeper areas; and (4) migration back to the sea in the autumn. As with the Rogue River, the autumn migration was apparently triggered by lower temperatures and increased river flows resulting from the seasonal rains. Finally, in the Sacramento River that drains northern inland California, the spring migration into fresh water occurred earlier, in March and April (Heublein et al. 2009). Here individuals proceeded more than 100 miles upriver at least as far as a major diversion dam. Six of the 15 individuals tagged followed the pattern of oversummering in deeper pools and moving out to sea with the lower temperatures and increased flows of autumn. The other nine fish, however, migrated back to the sea before the beginning of September and well before there was any cue from flow rate or temperature shift. Thus in each river the sturgeon seem to have modified patterns to local conditions, but there is still variation that remains to be explained.

Green Sturgeon also exhibit considerable variation during the marine phase of the life cycle (Lindley et al. 2011). The fish spawning in the Rogue and Klamath/Trinity Rivers form a northern population separate from a southern Sacramento River population. Some 355 fish were tagged with acoustic transmitters both on spawning grounds and in non-spawning sites and were monitored in their movements along the coasts of Washington, Oregon, and California. The use of non-spawning aggregation sites in estuaries along this Pacific coast was assessed with fish from the different spawning river populations displaying distinct differences. San Francisco Bay, for example, was used only by Sacramento River fish, whereas the estuary of the Umpqua River on the central Oregon coast was used mostly by fish from the Klamath and Rogue River systems. This difference was evidently not due to Sacramento fish not moving up the coast because these southern sturgeon did make use of the large Columbia River estuary on the border between Oregon and Washington, and some proceeded as far as the Washington estuaries at Grays Harbor and Willapa Bay and were occasionally found in the Umpqua. The data further revealed that sturgeon used non-natal estuaries during the summer, and that they moved among estuaries during the course of the summer—most apparent in the case of the Umpqua estuary.

The larger estuaries such as San Francisco Bay and the Columbia River were important for both northern and southern populations of sturgeon whereas the considerably smaller Umpqua seemed to be particularly important for fish from the Rogue and Klamath/Trinity Rivers. Another observation was that smaller fish made extensive use of the large Washington estuaries, whereas larger fish, although they did occur in these larger sites, also made use of the much smaller estuary of the Umpqua. There were thus both population and individual differences in estuary use. Some of the variation seems to be related to physical differences among estuaries, but it is not clear just which of these might be the more important. Relatively speaking, estuaries are rich, warm habitats likely resulting in greater growth rates for the sturgeon (Moser and Lindley 2007).

Individual variation in the routes and timing of migration is becoming evident in birds with the advent of methods that allow researchers to track birds over their entire migration routes in both spring and autumn. For example, the routes and timing of seven Marsh Harriers (*Circus aeruginosus*) were mapped between Sweden and West Africa over the period 2004–2009 (Vardanis et al. 2011) using satellite telemetry tracking. The routes followed covered a band of longitude that was on the order of 500–1,000 km wide, and in one bird the variation

was over an area almost double that. Variation was considerable both in the same individual in different years and among individuals within and between years. An interesting result was that there was a much stronger repeatability in time than in space. Departure and arrival times varied much less between repeated journeys of the same individual than between different individuals, but there was a great deal of variation in the routes used by the same individual in its repeated journeys.

A major difference in individual migratory behavior in birds is the contrast between performances and patterns during spring versus autumn migration. The long-day photoperiodic cues that trigger enlarging gonads, increased fuel deposits, and poleward migration in the spring are relatively well understood (Chapter 6). The interactions between environment, physiology, and behavior in promoting autumn migration remain largely to be determined (Cornelius et al. 2013b). The changes prior to autumn departure involve a post-breeding decrease in gonad size and often a molt as well. There is some evidence that short days are involved with these changes, because the molt is hastened by short days, at least in some well-studied species like the White-crowned Sparrow, but it is apparent that there is much still to be learned and understood about the migrations of birds to their non-breeding areas.

Recent tracking studies have revealed considerable differences in the speed and duration of spring versus autumn migration and in the routes followed at the two times of the year. Nilsson et al. (2013) surveyed detailed tracking studies of the same individual birds of several species and found consistently higher speeds and shorter durations in birds migrating in the spring as opposed to the same individuals in the autumn. This difference was partly due to flight speeds (including air speed, ground speed, and daily travel speed), but the major differences were the result of longer stopover durations in the autumn. This strongly implied that factors such as rates of foraging and fuel deposition were more important than flight speed in determining these seasonal differences. The further implication is that selection is acting on time of travel for spring migration. For a number of reasons such as territory establishment and nest building, it may be important to travel fast and arrive early in the spring, and this faster travel may be facilitated by greater opportunities to fatten before departure, by contrast with the autumn when breeding has just ended and time before departure may be limited.

Not only are there differences in speed between spring and autumn migration, there are also differences in routes over which the migrants travel. A good example is the Red-backed Shrike (*Lanius collurio*) traveling between Europe and Africa (Tøttrup et al. 2012). Nine shrikes were tracked after capture and tagging between their breeding sites in southern Sweden and Denmark and their wintering sites in southern Africa. The northward spring migration took an average of 63 days and proceeded through East Africa where there were stopover sites, through the Arabian Peninsula, westward across Turkey, and finally northwestward in Europe to the breeding grounds in Scandinavia. The stopovers in East Africa averaged only nine days, whereas the autumn migrations averaged 96 days and took the shrikes south through Germany to stopovers in the Balkans and Turkey, then across the Mediterranean to North Africa and on across the Sahara to a second and major staging area in the Sahel. The stopovers lasted on average for 71 days before the birds proceeded on to southern Africa and so were the major contributors to the much greater duration of the autumn migratory journey. Staging the Sahel took 53 days, almost as long as the time in the breeding area, and should probably be considered a third residence period. The much greater overall speed in the spring occurred in spite of the fact that the distance was 22% greater than that in autumn. Presumably the spring flight path is selected to take advantage of favorable winds, and, like the data of Nilsson et al. (2013), indicates that time selection is likely. The two quite different routes and staging areas further suggest sophisticated navigational systems beyond a simple clock and compass.

Summing up

Variety and flexibility are abundantly apparent in migratory behavior and life-history patterns, and match the variety in the taxa across which

migration occurs. It is not surprising that migration varies among species, reflecting other differences in ecologies and lifestyles and interacting with them in adaptive syndromes. Studies of organisms as contrasting as weedy composites, insects, fish, birds, and mammals reveal migratory patterns among species that reflect responses and adaptations to particular environmental challenges. Birds may orient in different directions, parachuting seeds drift for different durations, and eels in the Atlantic and fishes in South America and Africa use migration to occupy and partition different habitats. Cane Toads at the edge of their distribution in Australia have greater endurance and cover ground more quickly than their counterparts at the center of the range, an example of a rapidly evolving behavioral difference.

Both patterns in life-history traits and patterns in behaviors other than movement itself accompany variation in migration. In English Brown Trout, fish migrating to the sea are larger and produce more and larger eggs than their non-migrant counterparts locked behind a waterfall. Common garden experiments reveal that these are evolved gene differences distinguishing the populations. In migrant birds those that travel long distances produce smaller clutches than either short-distance migrants or residents, but the number of annual broods is greatest in the short-distance migrants. The overall result is lowest fecundity in the longest-traveling migrants, presumably reflecting favorable winter habitats. Among behavioral differences are responses to novel stimuli. Migrant Blue Tits are more likely to approach them than non-migrants, perhaps reflecting the fact that they must continuously respond positively to novelty as they migrate across habitats. Across species, long-distance migrants such as Bramblings are more likely to travel under cloud cover that the short-distance-migrating Blue Tits. In Australian Silvereyes migrants from Tasmania display the ability to orient, whereas non-migrants from New South Wales do not.

Even within a population some individuals may migrate whereas others may not, the condition known as partial migration. Most work on this has been done with birds and fish, but it is a widespread phenomenon. In many cases partial migration seems to be a "best of a bad job" strategy with smaller, less dominant, or weaker individuals migrating, while the stronger or the more dominant are resident. This turns out not always to be the case, however, as there are examples from birds, fish, and mammals in which the dominant or stronger individuals migrate, as they can do well wherever they are. Trade-offs between predation and resource acquisition seem often to be involved. In cyprinid fish, for example, smaller, less robust individuals remain in lakes to feed whereas the larger and more robust migrate into streams to escape predation from voracious pike and other predators. In a Canadian Elk population there are trade-offs between gains in forage and offspring survival by residents and the avoidance of wolf predation by migrants.

There have been several attempts to model partial migration using the notion of an evolutionarily stable strategy or ESS. In one case a result suggests that density-dependent overwinter survival (in birds) is the most important element for the maintenance of a mixed partial migration strategy. Other models indicate that indeed condition dependence is to be expected and that migrants may not be the ones following a "best of a bad job" strategy. In species that migrate to breed there may be times when a migration/breeding episode is skipped. ESS modeling predicts that skipping can become more advantageous as the probability of a "bad year" increases. As with modeling in other situations, the application of ESS models to migration can lead to the asking of more focused questions in designing research approaches to understanding migratory behavior and life histories.

Across species, migration routes of populations and even of individuals vary in pathway, timing, and distance. Within a species some geographically distinct breeding populations migrate parallel to each other, some pass over others (leap-frog migration), and still others replace those that move farther (chain migration). A characteristic of bird migration is that journeys to breeding grounds may be quite different from those to non-breeding areas. In some cases different routes may be involved, with migrants going one way in the spring and another in the autumn, as in Red-backed Shrikes in passage

between Europe and Africa. Time spent in transit can also be different; characteristically journeys to breeding grounds take less time (time selected) than those to wintering areas. In the Shrikes and no doubt other species, the difference is due to time spent at stopovers. There is evidently a premium on arriving in good time at the breeding grounds, especially at high latitudes where the season is short. New tracking methods further reveal that individuals may follow different pathways in the same season but between years. It is evident that space and time are both important to the migratory journey, and variation in space may well increase the efficiency of time.

CHAPTER 13

Polymorphisms and polyphenisms

Chapter 12 discussed behavioral and life-history variation in migration unaccompanied by distinct qualitative changes in morphology or physiology. In this chapter I consider those instances where qualitative distinctions are apparent, concentrating on phenotypic expression of those distinctions. The analysis of genotypic variation will be covered in Chapter 14. The overt differences typically divide forms between migrants and non-migrants with migratory capability retained only for a restricted period, often with remobilization of energy and materials to support reproduction or growth when migration ceases. The first of the qualitative contrasts to be discussed occurs in the planktonic larvae of a marine tube worm. Here the difference between the forms is behavioral with two distinct types—one that settles gregariously where conspecific worms are already present and one that does not, at the termination of the planktonic phase where metamorphosis to the adult form takes place in the substrate (Toonen and Pawlik 2001).

Perhaps the greatest contrasts in form and function between migrants and non-migrants occur in those insects that are polymorphic or polyphenic with respect to the morphology and accompanying physiology associated with migratory activity. In the earlier literature the term polymorphism was used to indicate discontinuities in form without distinguishing between genetic and environmental contributions to the development of differences. Where genetic contributions could be identified, the designation "genetic polymorphism" was sometimes used to distinguish morph differences from those that were clearly environmental such as the production of winged adults in clonal aphids as a result of crowding or maternal age. Current usage restricts polymorphism to cases where differences between morphs are gene based, and the designation polyphenism is applied where distinct forms are produced in different environments (e.g., Shapiro 1976). Both types of variation are common across all kingdoms of life with respect to a variety of traits not limited to migration. Among insects, there is a broad taxonomic distribution with respect to migration in both polymorphisms and polyphenisms, and the differences can be expressed in a variety of ways, as discussed in the next section.

A third set of morphological contrasts occurs in plants. These are the so-called seed heteromorphisms. Plants may produce seeds of qualitatively different shapes that differ in transportability; some seeds have a device that aids in transport, such as a pappus that serves as a parachute or a hook that attaches to mammalian fur, whereas other seeds do not; and some seeds simply drop below the parent plant. There are interesting cases where these heteromorphisms are analogous to the migratory polymorphisms and polyphenisms of insects. The continuous wing-form variation of birds and its association with migratory performance in birds was discussed in Chapter 7.

Settlement polyphenism in a tube worm

As with most marine bottom-dwellers the serpulid tube worm *Hydroides dianthus* releases gametes into the surrounding water where fertilization takes place to produce free-swimming larvae. After a time in the plankton these larvae settle on the substrate, metamorphose into the adult form, and secrete a calcareous "tube" in which the adult life is spent. In common with some 35 species of benthic marine invertebrates representing eight phyla, the larvae of *H. dianthus* are known to

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settle gregariously and to settle preferentially on or near conspecific adults. Toonen and Pawlik (2001) conducted experiments on laboratory-cultured larvae to examine patterns of gregarious and non-gregarious settlement in responses to a biofilm layer on the substrate and to already-settled conspecifics. Larvae settled concurrently in response to both factors beginning at about four days after fertilization, but settlement differed with respect to the two substrates. In the case of biofilm, settlement decreased rapidly after an initial peak and ceased entirely by 14 days after fertilization. Settlement in response to conspecifics continued in assays carried out for a period of 70 days post fertilization, at which point the larvae began to die off. Furthermore, these patterns of settlement did not change if larvae were pre-exposed to either of the substrates, and the differential response to biofilm versus conspecifics did not change if the larval period was prolonged with no substrate exposure.

One hypothesis for the determination of probability of larval settlement in benthic marine organisms is the so-called desperate larva hypothesis. Briefly this postulates that larvae, especially those that carry yoke and do not feed, should show ever more reduced substrate specificity (less discrimination) and hence more willingness to settle on less suitable substrates as their energetic reserves decline with longer durations in the plankton. Toonen and Pawlik (2001) tested this hypothesis experimentally with the larvae of *H. dianthus*. In their study neither changed feeding regimes nor larval starvation led to decreased substratum specificity, as long as larvae were competent to settle and metamorphose. Larvae reared at lower food levels did take longer to reach competency, but they showed no difference in the selectivity of settlement. There was some variation among groups of sibling larvae in responses over time, but these were the result of differences in response to conspecifics, not those in response to biofilm (a food and energy source). These results are consistent with the notion that the planktonic life is a true migration phase with responses to resources (the substrate) a function of the behavioral activity (presumably swimming in this case) rather than simply a response to depletion of available energy reserves (Chapter 2).

Pterygomorphism in insects

Flight polymorphisms and polyphenisms (pterygomorphisms) are but one set of examples of the plasticity present in insect life cycles. Insects pass through several developmental stages from the egg to a nymph resembling the adult in hemimetabolous insects or a larva very different from the adult in holometabolous orders, to a pupa in holometabolous orders only, and finally to the adult. Some life-history events such as diapause may occur at any stage whereas others such as migration occur mostly in winged adults (the exceptions are some cases of ballooning larvae). The number of developmental stages and the number of possible conditions such as diapause, phase polyphenism (e.g., in locusts or army worms), or the presence or absence of wings in adults means that insects may display a huge array of life cycles with 300 or more alternative pathways possible (Dingle 2002). These alternatives, including pterygomorphisms, are programmed by interactions between genes, hormones, and environmental inputs.

Pterygomorphisms are widespread among insects (Table 13.1), and they can take several forms. The outward manifestation is the appearance of the wings which can vary from long (macroptery) to short (brachyptery) to absent (aptery) depending on species and often between populations within species. In ants and termites wing polyphenisms are evident; the special treatment of larvae during development by other members of the colony results in the production of winged adults ("queens" and also "kings" in termites) that fly away from the natal colony to found new colonies elsewhere. They lose their wings by abscission at the termination of flight. Winged parthenogenic aphids are produced by aging or crowded mothers via maternal effects and migrate to new hosts where wings are abscissed (Chapter 2). In many insects, for example, the Gypsy Moth (*Lymantria dispar*), males retain wings and fly actively whereas females are apterous or brachypterous and are flightless. In some midges (Diptera), for instance, *P. perneciosa* in Table 13.1, the males are normal flying adults whereas females resemble slug-like larvae. In crickets, some beetles, and many Heteroptera, flight muscles are histolyzed following migration. In most cases this is

Table 13.1 Major orders of insects in which flight polymorphisms or polyphenisms occur.

Order	Examples
Orthoptera	Crickets (several species)
Isoptera	All termites
Homoptera	Aphids, Leafhoppers
Heteroptera	Many in, e.g., Lygaeidae, Rhopalidae, Gerridae
Coleoptera	Leptinotarsa (Potato Beetle), bark beetles, weevils
Diptera	*Plastosciara perniciosa*
Lepidoptera	Gypsy Moth and others with wingless females
Hymenoptera	Ants (winged queens)

Sources: Dingle (1996); Zera and Denno (1997); Roff and Fairbairn (2007).

irreversible, but in potato beetles (*Leptinotarsa*) and some bark beetles the flight muscles can reform. In the case of *Leptinotarsa* the beetles histolyze muscles before entering diapause in the autumn and redevelop them the following spring. There is thus much variation on the pterygomorphic theme.

Even within a single species pterygomorphisms may take several forms. An example of this intraspecific morph diversity is the North American rhopalid Soapberry Bug, *Jadera hemataloma* (Dingle and Winchell 1997; Dingle 2001; Table 13.2). This true bug occurs across the southern tier of the USA from California to Florida and as far north as central California and Kansas, as well as on some Caribbean islands and into Central America. Hosts are assorted bushes, vines, and trees of the plant family Sapindaceae, where the bugs feed on seeds occurring encapsulated in fruits. Within a given portion of the range, the bugs feed almost exclusively on a single species of native host. The fruits of these different hosts vary considerably in size. In all cases seeds occur at the center of the fruit capsule, but can occur anywhere from one to several millimeters from the capsule wall. In many species the capsule is hollow. An interesting characteristic of the host-specific *Jadera* populations is that the length of the mouthpart stylets (the "beak") is a positive function of the distance of the seeds from the fruit perimeter, a distance across which the beak must reach if the seed is to be penetrated (Carroll and Boyd 1992; Carroll et al. 2003). Beak length is relatively independent of body size.

Table 13.2 Four wing morphs of the North American Soapberry Bug, *Jadera haematoloma*.

Wing form	Muscle condition
Short wing	Flight muscles absent
Long wing	Flight muscles absent
Long wing	Flight muscle histolysis before reproduction
Long wing	Flight muscle retained throughout life

Source: Dingle and Winchell (1997).

A further interesting aspect of the biology of *Jadera* is that in parts of its range exotic sapindaceous host plants have been introduced, the bugs have transferred to these new hosts, and there has been rapid contemporary evolution in both beak length and life-history characters on the introduced hosts (Carroll and Boyd 1992; Carroll et al. 1997, 1998). This is one example of the now well-recognized phenomenon of evolution occurring in contemporary time (e.g., Hendry and Kinnison 1999). The best-studied Soapberry Bug example occurs in Florida. In the southernmost tip of Florida and in the Florida Keys, the host plant is the native balloon vine, *Cardiospermum corundum*. This vine has a hollow fruit with a papery wall and is about the size of a ping-pong ball with several millimeters between the wall and the seeds which are aligned on a central septum. The resident population of bugs possesses relatively long beaks (~8 mm). In contrast, populations of the bug in central and northern Florida have switched to feed on the seeds of the "flat-padded" goldenrain tree *Koelreuteria elegans*, introduced from Taiwan as a street tree shortly after World War II. The fruits of this tree are flattened such that seeds occur within a millimeter or two of the pod wall. Correspondingly beak lengths of these *Jadera* populations average only about 6.5 mm. The two Florida populations of *Jadera* are more closely related to each other than they are to other species in the range (Carroll and Boyd 1992). Furthermore, the introduction of the goldenrain tree can be dated with precision from horticultural records. Therefore the difference in beak length in northern Florida, and an array of other differences between populations including differences in frequency in the flight polymorphism, has evolved in the 40–50 years since the

introduction of the tree. Goldenrain trees produce enormous numbers of fruit, on the order of thousands of pods with large seeds, and it was probably of considerable advantage to switch to them, the more so since even balloon vine bugs prefer their seeds over those of the native host (Dingle et al. 2009). Balloon vines are scattered, seldom produce more than 100 pods at a time, and the seeds are hard and small. Museum specimens of bugs produce a sort of "fossil record" and clearly show a trend to shorter beaks in northern and central Florida after about 1950. Thus the combined evidence indicates that the shorter beaks are a result of contemporary evolution. Interestingly in Texas, Oklahoma, and Kansas there has been evolution in the opposite direction from short to long beaks. This has been driven by a switch from the native Soapberry, *Sapindus sapindaria*, where the large seed is only about a millimeter from the fruit wall, to another species of goldenrain tree, *K. paniculata*, which has larger and more inflated fruits with seeds farther from the periphery than the fruits of the native host.

What is of interest here is that the Soapberry Bug is pterygomorphic, and differences in the biology of this pterygomorphism have evolved along with other life-history differences in the Florida populations feeding on different host plants. The pterygomorphism in *Jadera* consists of four distinct morphs (Dingle and Winchell 1997; Figure 13.1 and Table 13.2). The differences between morphs involve both the length of the wings and the presence or absence of flight muscle. The variation extends from a short-winged form absent flight muscle, through long-winged forms that never have flight muscle, histolyze flight muscle after several days of feeding and before reproduction begins, or retain flight muscle throughout life. The pterygomorphism has a genetic basis (Chapter 14) and is also modifiable by environmental variation. The only visible difference in phenotype is the length of the wings; the differences in the three long-winged forms are revealed only by experiment (flight reveals the presence of flight muscle) and dissections (which confirms absence of flight muscle if not present in eclosing adults or is a result of subsequent histolysis after flight).

That morph phenotype could be due to environmental effects was demonstrated with a series of experiments in which samples from both host populations were subjected to varying densities, food levels, and photoperiods (Dingle and Winchell 1997; Dingle 2001; Table 13.3). Nymphal bugs were reared in full sib families to see whether there were genetic (i.e., family) influences in the response to the three treatments. The levels of significance (*P*-values) from analysis of variance tests are given in Table 13.3. There were both treatment effects influencing the frequency of wing morphs and population × treatment



Figure 13.1 Two mating pairs of Soapberry Bugs *Jadera haematoloma* showing wing dimorphism. The upper pair are short-winged, whereas the lower pair are long-winged. The matches are by chance and are not due to assortative mating. Photo by Scott Carroll. (See also Plate 4.)

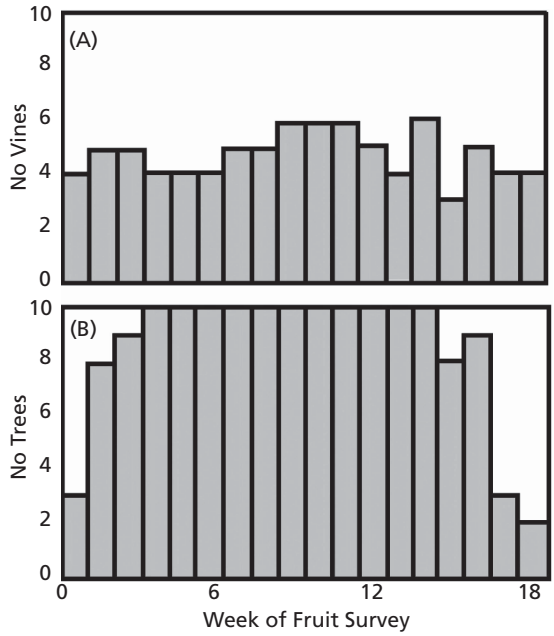


Figure 13.2 The phenology of fruiting in (A) balloon vines and (B) goldenrain trees in Florida. Bars indicate the number of plants out of 10 sampled that bore mature seeds. The samples were taken during the 18-week fruiting season of goldenrain trees. The pattern shown for balloon vine continues throughout the year; there is no fruiting in goldenrain trees outside the sampled period.

Source: Carroll et al. (2003).

interactions in the responses. An example of a treatment effect occurred with photoperiod in which there was an overall decline in frequency of macropters with shorter days (L:D 14:10 to 10:14; $P < 0.0001$). Similarly there was an overall decline in macroptery when bugs were fed more seeds, but in this case there was also a population × seed supply interaction ($P < 0.018$) because the ancestral Keys host race responded more strongly. Perhaps most interesting was the response to rearing density. There was no overall response to experimental variation in density ($P = 0.33$), but the interaction effect was significant ($P < 0.046$) with no change in wing morph frequency in ancestral bugs as rearing densities increased from 15 to 45 individuals per rearing container, but an increase in macroptery in the derived host race with this increase in density. In nature, density variation on host plants is much greater in the derived populations, so the effect may reflect an adaptive response

Table 13.3 Summary of statistically significant sources of environmental effects (*P*-values from analysis of variance) contributing to adult wing morph in the Soapberry Bug.

Treatment	Source			Interaction P × T
	Population (P)	Family	Treatment (T)	
Density	0.004	0.0002	0.33	0.046
Photoperiod	0.004	0.0001	0.001	0.317
Food level	0.008	0.0001	0.0001	0.018

Populations are ancestral (South Florida) and derived (North Florida).
Source: Dingle (2001).

to leave overcrowded goldenrain trees. The significant family effects indicated that gene differences contribute to the degree of response to environmental inputs (further discussed in Chapter 14).

Variation in pterygomorphism in response to the environmental treatments indicated in Table 13.3 are common among insects displaying the phenomenon (see Table 13.1 in Dingle 1996). In northern European water striders (Gerridae) increasing spring daylengths produce a largely brachypterous summer reproductive generation, whereas increasing summer temperatures increase macroptery characteristic of the autumn generation that diapauses and migratesto overwintering sites. In various aphid species crowding of mothers with increased contact among individuals causes them to produce winged offspring, and crowding of offspring may cause them to mature to winged adults (Braendle et al. 2006). Crowding, temperature, and photoperiod all influence morph frequency in various crickets (e.g., Zera and Harshman 2001).

As the flight muscle variation in Soapberry Bugs indicates, pterygomorphisms involve more than simply the presence or absence of wings. In aphids, for example, fully winged morphs are more heavily sclerotized in the head and thorax with a larger thorax to support flight musculature, have more fully developed compound eyes and ocelli, have longer antennae, and vary in other morphological traits (Braendle et al. 2006; Brisson 2010). Life-history traits also differ. The winged phenotype requires longer nymphal development, a longer adult prereproductive period, and a longer reproductive

period while producing fewer and smaller offspring. Shorter photoperiods lead winged parthenogenic females to produce mainly sexual females whereas wingless parthenogenic females produce both sexual females and males. The morphologies indicate adaptation to migration in the winged females with more elaborate sensory systems to control flight and location of new host plants. In contrast, the life-history differences suggest that apterous forms are adapted for rapid reproduction—the "vegetative" responses of J. S. Kennedy (1985 and Chapter 2). A further aspect of the aphid system is that females are polyphenic whereas males are polymorphic (see Chapter 14).

In Soapberry Bugs the frequencies of the different wing morphs differ between the ancestral balloon vine population and the derived goldenrain tree race (Table 13.4). This difference is apparent in the presence of wing muscles among virgin macropters, i.e., before histolysis can occur. A much lower proportion of bugs derived from winged individuals have flight muscles present. It is interesting that the frequencies of the short-winged form, which lacks wing muscles in both populations, do not differ much; the evolution of a higher frequency of flightlessness has apparently occurred more conservatively by eliminating flight muscles but not necessarily by shortening wings, probably because little further is gained in energetic savings by relatively small differences in wing morphology. By far the highest cost to flight is the maintenance of flight muscle; the development of wings is a relatively very small cost (Zera and Harshman 2001). In crickets the flight muscles of the flight-capable morph respire at 300–350% greater rates than the vestigial flight muscles of the flightless form.

Table 13.4 Life-history contrasts between long-winged (LW) and short-winged (SW) morphs of *Jadera* from ancestral long-beaked South Florida and derived short-beaked North Florida populations.

Trait	Ancestral	Derived
Percentage of virgin macropters with flight muscles present	76% females 84% males	53% females 61% males
Age at first reproduction	23.0 days LW 4.8 days SW	7.3 days LW 5.1 days SW
Eggs in first 5 days	142 LW 127 SW	264 LW 288 SW
Egg weight (mg)	7.2 LW 6.8 SW	5.6 LW 5.4 SW
Flight muscle enzyme difference between flyers and non-flyers	Yes	No

Sources: Winchell et al. (2000); Dingle (2001).

In addition to differences in flight muscle frequency, there are differences within and between Soapberry Bug races in the life-history traits and in aspects of flight physiology (Table 13.4). As with other insects displaying pterygomorphisms, the reproductive output of brachypters is higher, but the contrast between morphs is much greater in the ancestral host race. In the ancestral population there is a large difference in age at first reproduction with brachypterous females initiating egg-laying much earlier; the much smaller difference between morphs in the derived bugs is not statistically significant. The proximate cause of this difference between races is probably a higher proportion in the derived bugs of winged females that lack flight muscles and therefore reproduce early. Additional differences between populations occur irrespective of wing morph. In ancestral bugs, egg mass is greater but egg production is lower than in the derived bugs. These differences are consistent across various sampled subpopulations within each of the two host races (Carroll et al. 1997, 1998), indicating that life-history differences have evolved in concert with differences in beak lengths and wing-morph frequencies. These differences demonstrate physiological differences in the nature of trade-offs between flight morph and reproduction, in particular because of the contrast in the reproductive performance of the morphologically identical short-winged morphs of the two populations with much higher egg output in the bugs derived from short-winged individuals. The genetic basis of these trade-offs is discussed in Chapter 14.

Physiological differences in the pterygomorphisms between ancestral and derived populations of Soapberry Bugs are further expressed in the metabolic enzymes of flight muscle and in the response to topically applied analogues of juvenile hormone (Dingle and Winchell 1997; Winchell et al. 2000). In

enzyme analyses, activities were measured for key enzymes in oxidative metabolism (citrate synthase), glycolysis (hexokinase, pyruvate kinase), and fatty acid oxidation (β-hydroxyl CoA dehydrogenase or HOAD) in long-winged bugs. Individuals were first tested for the ability to fly by the simple criterion of tossing them into the air; flight-capable individuals would open the wings and fly, whereas the remainder simply fell to the floor. In all four of the enzymes analyzed, there were significantly higher levels of activity in flying individuals of the ancestral population compared to non-flyers; in the derived bugs there was no difference in activity between flyers and non-flyers. Ancestral and derived populations thus differed not only in life-history traits, but also in the levels of enzyme activity present in active flight muscle.

To examine the influence of insect juvenile hormone (JH) on the *Jadera* pterygomorphism, the JH analogue methoprene was applied topically in the middle of the 5th instar (Dingle and Winchell 1997 and see discussion of JH and wing morph in Chapter 6). In this experiment mating pairs were drawn from full-sib families that had displayed a high proportion of long-winged individuals in the expectation that their offspring would be genetically programmed also to be long-winged. These full-sib offspring were then treated with methoprene and compared to untreated controls after scoring for long or short wings. In some but not all families methoprene treatment produced a higher frequency of short-winged bugs than in controls, and families from the derived population produced significantly more short-winged adults than their ancestral counterparts, suggesting a lower threshold for JH action. Thus JH does appear to have a role in determining wing form consistent with results from other insects, but there is genetic variability both within and between populations in response to exogenously applied JH analyses. The correlates of pterygomorphism in these *Jadera* Soapberry Bugs thus include beak length, life-history traits, the physiology of flight muscle, and JH sensitivity during development (Table 13.4).

To complete the picture of pterygomorphism in Soapberry Bugs, we must ask if there is anything in the ecology of the ancestral and derived populations that would account for the extensive differences between them in flight morph frequencies and life histories. Insight into the evolution of these differences comes from the fruiting phenologies of the host plants (Figure 13.2 and Carroll et al. 2003). The balloon vine hosts of the ancestral population are scattered in their distribution and produce relatively few fruit capsules per plant at any one time (on the order of 50–100 depending on vine size), but they produce fruit and seeds throughout the year. Any given vine may or may not have fruits with seeds upon which the bugs can feed and reproduce, but at any given time seeds are available somewhere. This distribution would select for bugs that could migrate between hosts, but with reduced reproductive output probably because of both energy devoted to flight muscle maintenance and selection against overproduction of young on vines with relatively few fruits. There would be some selection favoring non-flyers with early age at first reproduction (Table 13.4) because seeds may be available on vines for more than one bug generation. Delaying reproduction would be disadvantageous to bugs staying on the host rather than migrating.

In contrast to balloon vine, goldenrain trees fruit massively (thousands of seeds) and synchronously in the late summer to autumn period. In this case the early production of large numbers of eggs would be favored, as seen in short-winged individuals and those with long wings but no flight muscle. There is probably still some selection for flight to new hosts or to move within a tree, but in general once a bug arrives on a tree there is little point to moving because all trees are in more or less the same stage of fruiting phenology. The complex pterygomorphism of Soapberry Bugs can thus be seen as the outcome of the varying balance of selective pressures due to variation in the seed production and phenology of the host plants.

This difference in Soapberry Bug host races is a variation on the theme of habitat duration and its relation to migration. It also mirrors the fact that, as the frequency of long wings increases in a population, the tendency for long-winged forms to migration also increases (e.g., Fairbairn and Butler 1990 for gerrids, Roff and Fairbairn 2007 for crickets, and Dingle 1996 for summary). Both frequency of long wings and frequency of migration increase in

habitats of shorter duration. With respect to wing morph frequency, Denno et al. (1991) examined from the literature the relation between form and habitat in 35 species, representing 41 populations, of delphacid planthoppers (Homoptera) and determined how long, in terms of number of generations, different populations were able to persist in the habitats they occupied. From the data obtained, they plotted percent macroptery as a function of habitat duration (Figure 13.3).

The results show that in habitats of short duration, the frequency of macropters is much higher, as would be expected if the insects had to migrate frequently between habitats. Furthermore, a direct comparison of two species, one from a temporary habitat (*Prokelisia marginata*) and one from a more persistent habitat (*P. dolus*), demonstrated that the species from the temporary habitat developed macropterous individuals much more readily when crowded, suggesting a greater sensitivity to habitat deterioration (Denno and Roderick 1992). Increased macroptery with crowding, as occurs in Soapberry Bugs and these delphacids, is a common response in pterygomorphic insects (Dingle 1996), and may be a response to decreasing frequency of potential mates, who will also be escaping, as well as deteriorating resources (Denno et al. 1991). Other examples of the relation between habitat and wing form, including some of the subtleties resulting from geographic and other types of variation in habitat, are given in Dingle (1996).

Over a larger geographic area, Roff (1990, 1994) has examined the relation between habitat persistence and flightlessness on a global scale. Speculation on the subject goes back at least to Darwin who noted that beetles on the Atlantic island of Madeira displayed a high frequency of flightless forms; he postulated that a flightless morph would have greater fitness on an oceanic island than a winged form because the latter would be more likely to be blown out to sea to perish (Darwin 1859, p. 104). Darwin's hypothesis, however, did not account for scale. For a small winged insect an island is a large place with plenty of opportunity to take off and land elsewhere. Roff (1990) looked for a relation between aptery and insect occurrence on islands and found there was none when comparing island and mainland comparable groups at similar latitudes.

There was, however, a strong tendency toward a higher incidence of aptery at both higher altitudes and latitudes. For example, when carabid beetles are compared across both high and low islands, there were more wingless species in highland areas (true also of mainlands) and increased aptery at higher latitudes on both high and low islands (again true also of mainlands). Roff interprets these results to mean a greater tendency to evolve flightless morphs

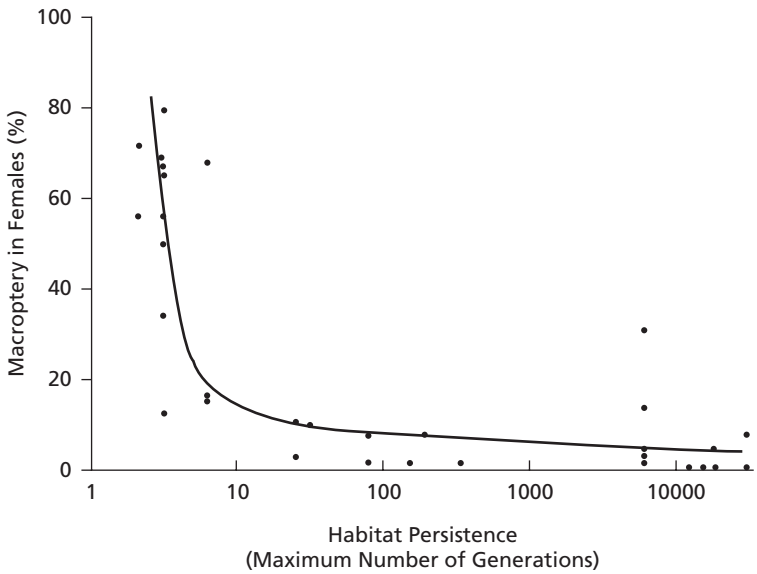


Figure 13.3 The relation between macroptery in female planthoppers and habitat persistence measured in generations for 35 species representing 41 populations. The proportion of long-winged forms declines markedly in persistent habitats.

Source: from Dingle (1996) after Denno et al. (1991).

in more temporally stable habitats, because successional habitats of the same type persist longer at higher altitudes and latitudes, a conclusion supported by simulations (Roff 1994). Studies of succession along altitudinal and latitudinal gradients further support the tendency toward habitat persistence. These conclusions are similar to those of Southwood (1962 and Table 11.1) regarding habitat persistence; woodlands, for example, contained more short-winged forms than early successional fields. An interesting exception is the tendency for species living in trees (like derived Soapberry Bugs) to retain more flight-capable forms than otherwise expected, presumably due to the advantage of being able to move with alacrity in large volumes of tree space (Waloff 1983; Denno et al. 2001a). Holometabolous insects are also less likely to evolve flightlessness. These species can change habitats between the sedentary larva and pupa and the adult, making the retention of flight capability in the adult a distinct advantage to allow movement to the new habitat.

At the smaller scale of a single group of islands, Denno et al. (2001b) examined the effects of habitat isolation, persistence, and host-plant structure on the incidence of macroptery in delphacid planthopper (*Toya venillia*) populations in the British Virgin Islands. This planthopper inhabits salt grass either in undisturbed salt flats or in small patches of sparse vegetation on dunes, and also disturbed lawns. Males were more likely to be macropterous than females, but both sexes were more macropterous in disturbed versus persistent habitats (77% versus 19% in males; 12.5% versus <1% in females). The frequency of macroptery was also density dependent, as is true of many pterygomorphic insects. There was some influence of host-plant structure, at least in males, with 37.6% macroptery in the short grass on dunes as opposed to only 7.6% in the tall grass of salt-flat margins. Consistent with the comparative studies of Roff (1990), there was no evidence that frequency of macroptery was influenced by the degree of isolation of islands; the persistence of the salt-grass habitats best predicts the evolution of the degree of flight reduction.

Seasonality can be a further influence on the ratios of wing morphs. In the *Prokelesia* planthoppers studied by Denno et al. (2001a) on the Atlantic coast of North America, populations that experienced low winter survival in their primary habitats were more likely to produce migratory macropterous offspring. In the Oriental Chinch Bug (*Cavelarius sacchivorous*), a subtropical species living in sugarcane in Okinawa, there is a seasonal interaction between morph frequency and diapause (Fujisaki 2000). This true bug produces three generations per year. The first generation invades sugar cane in the spring and early summer. The offspring of these are the second generation whose nymphs experience long days and warm temperatures, both of which result in more nymphs becoming macropters. Higher densities also increase macropter frequency, but the second generation is more sensitive to density than the first. This interaction between photoperiod, temperature, and density results in the highest frequency of macropters in these second-generation bugs reaching adulthood in late summer. These macropters have a higher total fecundity than brachypters reared at the same densities (although not as high as low-density brachypters) and so are effective colonizers that migrate to fresh hosts. They also live longer than brachypters, a further advantage in finding and exploiting new habitats. Brachypters maturing at low density reproduce earlier, and at low densities are more fecund than macropters, thus having an advantage in early summer before densities become high.

Macropters are more likely to survive as the season changes to winter when they produce diapause eggs that are slower to break diapause than those laid by brachypters. The adults can survive through the subtropical winter while continuing to lay eggs. As spring approaches non-diapause eggs are produced. Macropters have an advantage over brachypters in most winters because they can move more readily to favorable habitats, because of better survival as adults, and because they produce eggs with more intense diapause. Brachypters, however, may have an advantage in the occasional milder winters because of earlier egg-laying and a less intense diapause in their offspring. A similar "bet-hedging" diapause strategy is known in other insects, for example, the grasshopper *Melanoplus sanguinipes* along an altitudinal gradient in California (Dingle and Mousseau 1994).

Returning to the issue of traits phenotypically correlated with flight morph, there have been extensive

studies on various species of cricket (Orthoptera: Gryllidae). One such species is the Sand Cricket (*Gryllus firmus*) which occurs coastally and subcoastally along the east and Gulf coasts of the USA from New Hampshire to Mexico and in Bermuda. Like the Soapberry Bug, this cricket has long- and short-winged morphs with the former sometimes histolyzing the flight muscles and sometimes with flight muscle absent. And as with Soapberry Bugs, there are life-history traits correlated with the flight morph (Roff and Fairbairn 2007). Consistent with other Orthoptera, the long-winged form develops faster (the reverse is true in many other insects) even though there is no difference in body size between the morphs. In female crickets there is a trade-off between reproductive capability and the size of the dorsal longitudinal flight muscle (DLM) (Figure 13.4). In the brachypterous females the DLMs are very small or absent, and the ovaries are large and produce large numbers of eggs. The same trade-off occurs in macropters lacking DLMs. In contrast, in the macropters with large DLMs and capable of flight, the ovaries are small and eggs few. Within these macropters, however, ovary weight varies inversely with the size of the DLMs, with the change in the size of the latter reflecting the degree of muscle histolysis. This flexibility of the flight/reproduction trade-off allows these crickets to "hedge bets" with respect to placing offspring in the current habitat or a new one, with the cost expressed as the magnitude of egg production.

In the dimorphic Japanese cricket, *Modicogryllus confirmatus*, variation in food supply can influence the trade-off between flight and reproduction. Starvation for five days after adult eclosion resulted in reduced but still-occurring egg production in short-winged or de-alated long-winged females, but no egg development in fully flight-competent long-winged individuals. Thus the two forms use stored energy for different functions: reproduction in the brachypters or de-alated macropters, and flight muscle maintenance in the functional macropters (Tanaka 1993). Commitment to reproduction in the brachypterous females results in generally higher food consumption in early adult life (Tanaka and Suzuki 1998; Tanaka et al. 1999).

Although the trade-off between flight muscle and reproduction is most apparent in females of *G. firmus*, it also involves males. In crickets, males

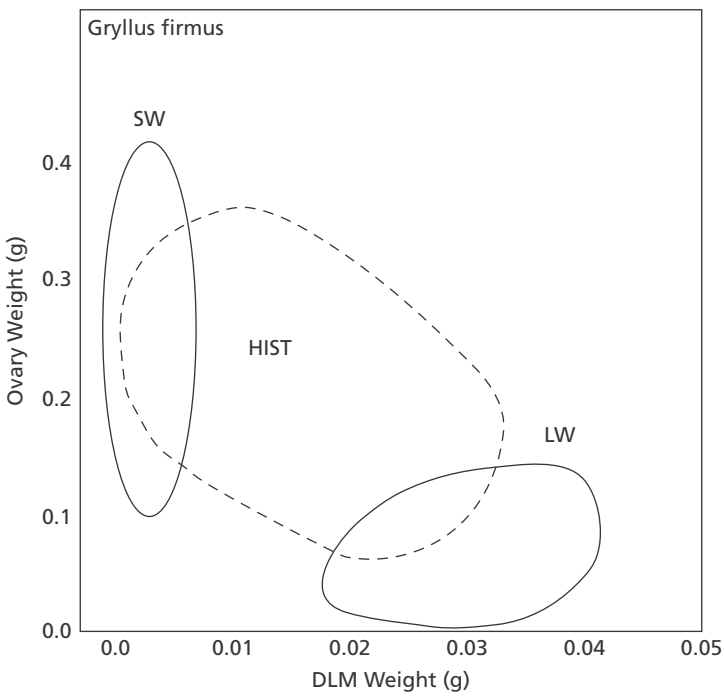


Figure 13.4 The relation between ovary weight and weight of the dorsal longitudinal muscles (DLM) in the cricket *Gryllus firmus*. Points for long-winged (LW) and short-winged (SW) females fall within the respective ovoids. The ovoid enclosed by the dashed line encompasses most points representative of females that histolyze (HIST) the DLM.

Source: data from Roff and Fairbairn (2007).

produce a calling song to attract females by stridulating with a comb-and-file apparatus located on the two forewings or tegmina. This is true of both long- and short-winged morphs. Stridulation is energetically costly, requiring up to an order of magnitude increase in metabolic rate (Forrest 1991), and we thus might expect a trade-off between the two energetically demanding functions of song and migration. Such indeed seems to be the case. In *G. firmus* this trade-off occurs between macroptery and time spent calling. Over a 24 h period macropterous males spent less time calling and attracted fewer females than did their brachypterous counterparts (Crnokrak and Roff 1995, 1998a). In several species of hemipterans, there seems to be a mating advantage for short-winged males (Fujisaki 1992; Kaitala and Dingle 1993; Fairbairn and Preziosi 1996) and in the homopteran *Prokelesia dolus* macropters sire only half the number of offspring as brachypters (Langellotto et al. 2000) so there appears to be a fitness advantage to short wings with respect to mating as well as with respect to habitat permanence. In *M. confirmatus* there is no difference between morphs in testis size at eclosion, but after 5–10 days those of the brachypters are significantly heavier, paralleling the ovary/DLM trade-off in *G. firmus* females (Tanaka 1999).

In a further analysis of the pterygomorphism in *G. firmus* males, Crnokrak and Roff (1998b) examined the influence of food limitation on the trade-off between song and wing morph. They restricted food intake by the male crickets to the minimum amount required to keep them alive for 20 days in order to compare the trade-off between stressful (food-limited) and non-stressful (food-abundant) habitats. There were two observed differences between wing morphs. First, the brachypters called longer on average than macropters on 18 of the 20 days in the test group and on 17 of the 20 days in the fully fed control group, and in both groups the brachypters attracted more females with the songs. There was a decrease in call duration between the stressed and unstressed groups, but the relative difference (longer calling in brachypters) remained the same. Second, the brachypters called at about the same level throughout the test period, whereas the macropters did little calling after 10 days of their adult life. The relative advantage to brachyptery remained with food stress even though overall calling was reduced. This latter reduction suggests that if different individuals of either morph experienced different levels of stress, the variance in calling duration would increase. Under these circumstances the strength of selection would diminish more readily, allowing for the continued appearance for both morphs. A further issue with respect to the trade-offs between flight apparatus and reproduction is the influence of flight itself. Most studies of migratory flight in insects have involved species that are not pterygomorphic (Dingle 1996). In these species that are migratory and bear wings throughout life, selection has frequently acted to reduce the physiological cost of migration. In species such as migratory grasshoppers these costs can be surprisingly small (Rankin and Burchsted 1992). In wing monomorphic species flight enhances oviposition in migratory populations of the grasshopper *Melanoplus sanguinipes* (McAnelly and Rankin 1986), accelerates reproduction in the Milkweed Bug *Oncopeltus fasciatus* (Slansky 1980), and enhances mating behavior in the wing-monomorphic cricket *Gryllus bimaculatus* (Dyakonova and Kurshinsky 2008). In the pterygomorphic *G. texensis* males observed flying in the field displayed stronger calling behavior relative to field-captured brachypterous males (Bertram 2007). There is thus reason to believe that flight might influence the short- versus long-wing trade-offs.

This notion was directly tested in *G. texensis* by Guerra and Pollack (2009). They had previously shown that flight-capable males of this species had a lower courtship propensity than brachypters, similar to *G. firmus* (Guerra and Pollack 2007). And as with other crickets, the female brachypterous *G. texensis* had larger ovaries and greater egg production. Guerra and Pollack (2009) tethered 3–5-day-old macropters and suspended them in front of a fan to promote flight; they were allowed to fly for 5 min. Controls were similarly tethered but given a Styrofoam ball to hold which allows walking but prevents flight. Two days after the flight tests, both experimental birds and controls were dissected to assess the condition of flight muscle and ovaries in females. Long-winged males were tested for courtship behavior by placing them with females 7–9 days after their eclosion to the adult stage. The

short bout of flight essentially eliminated the trade-off between wing morphs in flight capability and reproduction. Flown macropterous females rapidly developed their oocytes such that, two days after flight, ovary weight was almost the same between the flown females and their short-winged counterparts. Flown males reached the same level of courtship activity as the brachypters. The major trade-off would thus appear to be the earlier *in situ* reproduction of brachypters whereas macropters must fly to accelerate reproduction, but readily reproduce on reaching a new habitat. The physiological cost is attenuated by the flight as long as food is readily available.

In *G. firmus* males wing muscle histolysis in the macropters influences the trade-off in mating (Mitra et al. 2011). Both brachypters and histolyzed macropters of this species sang more than flight-capable morphs, but females preferred the songs of the macropters whether or not flight muscles had been histolyzed. The males that have histolyzed their muscles may have a higher mating success than the brachypters because not only do they sing just as frequently but they also produce more attractive songs. There are thus many subtleties involved in the flight/reproductive trade-offs of pterygomorphic crickets and still much research to be done to work out the details of the ecology and the physiology (Chapter 6) of these trade-offs.

Finally with respect to the trade-offs between flight morphs and life-history traits, Guerra (2011) has assessed these trade-offs across multiple species and higher taxa of insects with a meta-analysis of many studies. A summary of the results is given in Table 13.5. Some significant trends are apparent. First, the trade-off in females, as we have seen in Soapberry Bugs and crickets, is expressed largely in earlier reproduction, greater investment in mating, and greater reproductive success (primarily expressed as higher fecundity). More rapid development by larvae or nymphs programmed for short-wings may also occur; in any event, except in the Orthoptera, long-wing development time is not less than that of short-wings, although it may be equal. A very similar set of trade-offs occurs in males, although the trade-offs may be expressed in different ways. For example, in males mating investment may include investment in weapons or other aspects of agonistic behavior that assure access to females or investment in behaviors, such as cricket song, that attract females. The usual later onset of reproduction in long-winged morphs leads to greater longevity. Mitigating factors in the trade-offs are flight muscle histologies and the stimulation of earlier reproduction by actual flight (Figure 13.5). As Guerra also points out, most assessments of trade-offs are based on laboratory studies where food is plentiful, temperature is constant or nearly so, and predation is absent. There is thus a need to evaluate trade-offs under the exigencies of field conditions.

Table 13.5 Overall trade-off trends derived from a meta-analysis across flight polymorphic insects.

Trait	Females	Males
Development time (egg to adult)	LW ≥ SW	LW ≥ SW (except Orthoptera)
Age at first reproduction (post adult eclosion)	LW > SW	LW > SW (N = 1 only)
Mating investment[a]	SW > LW	SW > LW
Mating success	SW > LW	SW = LW
Reproductive success[b]	SW > LW (except Thysanoptera and Coleoptera)	SW = LW
Longevity	LW ≥ SW	LW ≥ SW

SW, short wing or apterous; LW, long wing.
[a] Includes, for example, gonadal investment, mating propensity, and in males competition or weapons.
[b] Includes fecundity and offspring quality in females and siring success in males.
Source: Guerra (2011).

Seed heteromorphisms

In many groups of plants there is discontinuous morphological variation in seeds, known as heteromorphism, that in many ways is analogous to the pterygomorphisms of insects, including similarities in trade-offs between travel and life-history characteristics. In most cases heteromorphisms are associated with differential capabilities to range or migrate ("dispersal" in the plant literature). These differential migratory capabilities are often correlated with germination times; seeds with high migratory capabilities generally germinate more quickly than seeds that fall below or near the parent

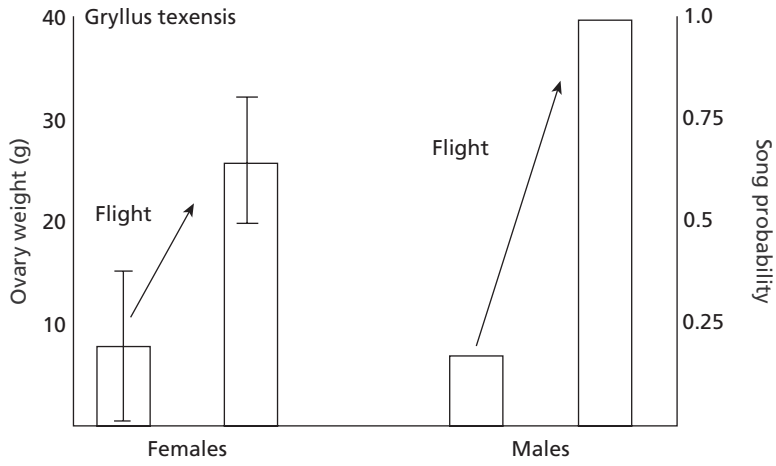


Figure 13.5 The influence of flight on ovary development and male song frequency in the wing polymorphic cricket *Gryllus texensis*. The upward-pointing arrows indicate the direction of change in ovary weight (± SD) or song probability after 5 min of tethered flight.

Source: data from Guerra and Pollack (2009).

plant (e.g., Venable and Lawlor 1980; Imbert 1999). Another characteristic of seed heteromorphisms is that they often occur in taxa with flowers that are also heteromorphic, so that where different evolutionary possibilities exist with respect to flower form, they can be further influenced by variation in seed morphology (Venable 1985). The two most common ways in which this further effect on evolutionary possibilities is realized occur in the heteromorphic ray and disk flowers and seeds among the composites (Asteraceae) and in the contrasting seeds produced by the generally cryptic, often selfed, cleistogamous flowers and the generally showy, outcrossed chasmogamous flowers of species like the jewelweeds (*Impatiens*: Balsaminaceae). The traits associated with seed heteromorphisms are largely maternally controlled, with the maternal environment determining ratios and characteristics of the seeds. This is in effect a form of habitat selection with the ratio of traveling to sedentary seeds determined by conditions in the maternal environment (Donohue and Schmitt 1998; Imbert and Ronce 2001).

Flower and seed heteromorphisms are very apparent in many familiar composites. The flower heads consist of a central disk of small, cryptic florets surrounded by a ring of much more conspicuous flowers bearing showy petals. The central disk and peripheral ray flowers are often differently colored, with the disk darker. The sunflowers and Black-eyed Susans are good examples with blackish or dark brown disks and bright orange–yellow "eyelashes" consisting of the broad petals of the ray flowers. Most composites are less showy, but nevertheless produce two main types of seed with, in many cases, seeds of intermediate form in the transition zone between ray and the disk center. Each floret produces a hard-coated achene or one-seeded fruit. The seeds deriving from the disk often bear a feathery structure or pappus that serves as a parachute. In contrast, ray flowers usually produce an achene with no pappus and a much heavier seed coat. This coat may be smooth or in some cases covered with spines and hooks that result in transport attached to the fur of mammals (Figure 13.6). In some cases it is the central achenes that possess a barb or hook that facilitates transport by fur-bearing mammals (Venable et al. 1995).

The European annual composite, *Crepis sancta*, is an example of a plant that produces heteromorphic seeds from disk and ray florets. The achenes produced by the two sorts of florets differ in mass, color, morphology, and the presence of a pappus (Imbert 1999). The peripheral achenes are heavier than central ones due to a thicker seed wall or pericarp and a taller embryo and are fewer per seed head than the lighter central achenes. The latter bear a pappus and are dark-colored. The presence of the pappus allows these central achenes to travel farther upon release from the plant with some 28% of them traversing distances >2 m as opposed to <2% of peripheral achenes doing so (Table 13.6).

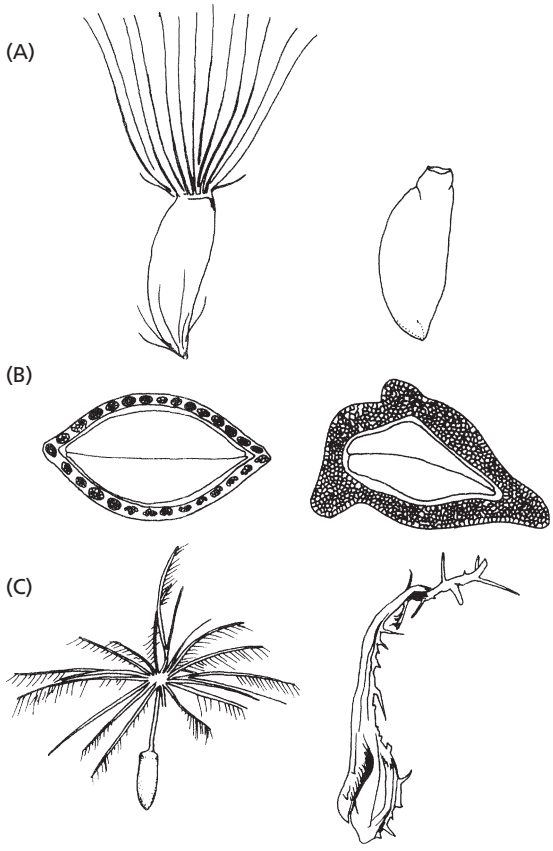


Figure 13.6 Seed heteromorphisms in two weedy composites, *Heterotheca latifolia* (A and B) and *Picris echioides* (C). Disk seeds in each case bear a feathery pappus; ray seeds are thick-walled in *H. latifolia* and bear assorted spines and hairs in *P. echioides*.

Source: Dingle (1996) after Sorensen (1978) and Venable and Levin (1985).

This greater travel distance is a consequence of the greater buoyancy of the pappus-bearing achenes, which, in experimental tests, fell to the ground at only one-fifth the rate of the pappus-absent and heavier peripheral achenes.

Both types of achene are released from the parent *Crepis* plant after the spring flowering season and remain dormant during the dry summer period. The species occurs in habitats such as Mediterranean old fields that are frequently subject to disturbance by mammals and ants, so they may remain buried for periods of years. It is therefore of interest to assess their ability to survive for long periods. In this the more robust peripheral achenes have an advantage. For example, they germinate at a rate of 20.5% compared with 11.1% for the pappus-bearing central achenes. Their seedlings also survive better after germination (Table 13.6). There is thus in *Crepis* a trade-off between greater horizontal movement by wind transport especially, and the ability to germinate better and survive better after germination. In this and other annuals the parent dies after releasing seeds, providing space for "self-replacement" by seeds falling in the vacated space. Until succession becomes too far advanced, the more robust peripheral achenes would have an advantage in colonizing vacated space whereas the greater travel distance of the central achenes enhances colonization of new areas.

There is also an advantage to the heavier peripheral achenes in competitive situations (Imbert et al. 1997). When plants derived from both types of achene were grown at low and high nutrient levels there was no difference between seed morphs in reproductive biomass produced so long as there was no intraspecific competition among plants. When there was competition, however, as manifested in high plant density, the individuals growing from the more robust peripheral achenes had an advantage. In competition with other annual species such as *Bromus* grasses, the plants developing from peripheral achenes were also at an advantage. Finally when plants were subjected to experimental herbivory, nutrient depletion, or both, the proportion of achenes with a pappus increased and would thus lead to an increased travel distance for the seeds (Imbert and Ronce 2001). There is thus an

Table 13.6 Characteristics of pappus-bearing central achenes and pappus-absent peripheral achenes in the European composite *Crepis sancta*.

Trait	Achenes	
	Central	Peripheral
Falling rate	0.23 m/s	1.21 m/s
Fall beneath plant	21.7%	70.9%
Traveling >2 m	~28%	<2%
Germination after 3 years	11.1%	20.5%
Seedling survival after germination	61.3%	77.1%

Source: data from Imbert (1999).

overall trade-off in achene morphology, with central pappus-bearing achenes providing a means of escape and colonization of new space, whereas the more robust peripheral achenes are more competitive in situations of "self-replacement" in already established populations.

The composite *Heterosperma pinnatum* is a summer annual plant of the central highlands of Mexico, north to southern Arizona and southwestern Texas, and is characterized by highly geographically variable seed morphology (Venable et al. 1995, 1998). The central seeds possess a slender beak culminating in a barbed, awned pappus capable of clinging to mammalian fur for transport away from the parent plant. The peripheral achenes are rounded and do not possess a beak or awn, and there is a gradient of seed shape across intermediate achenes. Despite dramatic differences in seed shape, there are no differences in the biomass of either entire achenes or of the embryos within. Furthermore there is considerable geographic variation in the frequency of the different achene shapes within a single seed head, ranging from no or very few awned central achenes and highly rounded intermediate and peripheral achenes to 100% awned achenes or mostly awned slender seeds (Venable et al. 1995). Nor are there significant differences in seedling size or seedling growth rates among the different morphs.

The differences that do occur between achene types are in transportability and dormancy. The travel-equipped awned achenes germinate more rapidly and will break dormancy and germinate slowly as early as January in the laboratory, although they rarely receive enough moisture in the field to do so. The peripheral achenes will not break dormancy in January and are slow to germinate as late as March when central achenes are germinating and growing rapidly. The adaptive advantage of the awned phenotype seems to accrue in habitats with taller and more closed vegetation (Venable et al. 1995, 1998). *H. pinnatum* will not grow under closed vegetation, but requires more exposed and more ephemeral bare patches to germinate and survive successfully. Taller, closed vegetation occurs where there is higher summer but lower spring precipitation, so the frequency of awned achenes is also correlated with these environmental factors. When conditions are harsh and few seeds survive to reproduce, the deeper dormancies of the peripheral achenes are at an advantage. The geographic distributions of achene morph frequencies reflect the geographic pattern of vegetation and rainfall variation (Venable et al. 1998). Thus escape in time and space interact in *H. pinnatum* to produce a presumably optimal germination strategy. In other desert annuals a different strategy may be favored. In the Sonoran Desert of Arizona, for example, transport distances are short (usually <1 m) and escape in time via delayed germination is likely more important than escape in space (Venable et al. 2008).

Seed heteromorphisms may be associated not only with wind or animal transport but also with movement by water. In a comparative study of seed heteromorphisms in 48 species of the genus *Spergularia* (Caryophyllaceae), Telenius and Torstensson (1991) made several interesting observations. The heteromorphism in these plants is associated with the presence or absence of "wings" on the seeds; in the 11 species in which dimorphic seeds occurred, these winged seeds were on average larger than those of species that were monomorphic. This counterintuitive observation led to the postulate that it was the development of wings that allowed the evolution of larger seeds, facilitating their movement away from the parent plant. The heteromorphism may in this instance reflect seed size variation rather than different criteria for the selection of seed migration. A second interesting observation of the study was that the 11 species with a portion of winged seeds were perennials, which may be a reflection of a trend to larger seeds in perennial plants in which competition may be greater in the longer-lived populations. Finally, the 11 species occupied primarily wet or marshy habitats. The presence of wings may thus have evolved not for wind transport, but rather to facilitate floating and transport by water.

In the case of seed heteromorphisms it is apparent that migratory (or ranging) capability interacts with at least two other important characteristics of seeds: size and dormancy. Migration cannot therefore be considered alone, but must be evaluated as part of a syndrome of traits that includes these other two characters (Venable and Brown 1988). This syndrome serves four population dynamic functions in spatially and temporally varying environments:

bet-hedging, escape from crowding, escape from competition with siblings or parents, and colonization. The exact form the syndrome takes depends on the contributions of each trait to adaptation and survival. For example, increasing heterogeneity by increasing the number of habitat patches and the variance in habitat permanence creates the possibility of reducing risk by continuously colonizing new areas. This would select for the classic strategy of structures promoting high migratory capability, small seeds for ease of transport, and low dormancy for rapid germination in a new habitat as seen in annual weeds. Departures from extreme forms of environmental uncertainty would select for different relative investments in the four traits. Furthermore, an evolutionary breakthrough in one trait may lead to a different evolutionary trajectory in another with which it is correlated. The larger seeds of *Spergularia* in the presence of wings may be a case in point. A consequence of syndromes is that traits do not evolve in isolation, and if they share genes in common, as the notion of adaptive syndromes implies, there will be trade-offs among co-evolving characters (see also Chapter 7). In the evolution of seed heteromorphisms, insect pterygomorphisms, and even planktonic settling dimorphisms, the fact and character of these trade-offs are quite clear. The nature of the genetic "blueprints" underlying migration and migration syndromes, and the interaction of these blueprints in the environments in which the syndromes are evolving, will be the subject of Chapter 14.

Summing up

The most evident and most extreme form of variability in migratory performance is the occurrence of migratory polyphenisms and polymorphisms with the alternatives of migrating or staying and reproducing in place. Migration confers considerable benefits to organisms because it allows them in effect to even out environmental heterogeneities. It permits both escape and colonization, the former when local environments become unfavorable and the latter when new habitats become available. In addition to its benefits, however, migration imposes costs and risks. Energy and materials devoted to the migratory apparatus, its maintenance, and migratory effort are lost to growth and reproduction, and there are risks entailed by departing a habitat and seeking a new one. These risks include both mortality en route and the possibility of failure to find a suitable place to settle. Migratory organisms must therefore strike a balance to optimize the relation between the costs and benefits of departing and staying that is manifested clearly in the ratio and timing between polymorphic and polyphenic forms.

The most basic form of the alternative strategies is behavioral, as seen in the tube worms studied by Toonen and Pawlik (2001) where the forms differentially express gregarious and non-gregarious settling. But it is in the insects that animal heteromorphisms are the most apparent because of the widespread and frequently occurring dichotomy between the presence or absence of wings. The heteromorphisms, however, involve more than wings alone. Where no wing-form variation occurs, there may still be two distinct morphs with one histolyzing flight muscles at the termination of flight and one not doing so. And as we saw with *Jadera hematoloma*, there may be three winged morphs expressing no flight muscle, histolysis of flight muscle, and permanent retention of flight muscle, in addition to a short-winged form without these muscles. The degree of wing reduction may also be variable from only slightly reduced, to brachyptery, to full aptery. The habitats in which the insect live largely determine the flight morph strategy. Where habitats are ephemeral—as with temporary ponds or weedy fields—fully flying morphs predominate as seen in gerrids, ancestral Florida Soapberry Bugs, or salt-marsh planthoppers. Where habitats are permanent or there is otherwise less advantage to migration, there is evolution toward increased frequency of flightless morphs. Extensive comparative studies show that, where habitats are stable for a long time, populations may become fully flightless. Where species remain fully migratory, selection frequently acts to reduce physiological and reproductive costs, so that in some groups the cost of migration may be small.

Insect pterygomorphisms evolve as syndromes with strong correlations among flight, physiological, and reproductive characteristics. Because of the trade-off between flight (especially flight muscle maintenance) and reproduction, flightless morphs

usually display greater reproductive capacity than migrants. This can be expressed as more rapid development, earlier reproduction, and higher fecundity. Differences in flight muscle itself may occur in quantitative differences in the oxidative enzymes supplying the power for flight. Differences in habitats and resource supply can modify the degree to which differences between morphs are expressed, as seen in the rapidly evolving Soapberry Bugs. An interesting aspect of migration is that flight itself can speed up reproduction, an adaptive response that would confer increased Malthusian fitness (a high "*r*" and high early reproductive value—see Box 11.1) upon arrival in a new habitat. Trade-offs may occur in male wing morphs as well as female. Male short-winged crickets may have longer and more attractive songs, although again differences may be attenuated by migratory flight.

Among plants, migratory heteromorphisms occur in the seeds of several families and are especially prevalent in the Asteraceae. Mostly these are polyphenisms (although there may also be a genetic component to the thresholds of induction) with the type of seed determined by the form of the flower that produces it: heteromorphic seeds. In the composites it is often the case that disk florets produce a thin-walled achene that may bear a parachute-like pappus facilitating wind transport, or hooks and spines for transport attached to mammalian fur. Ray florets, however, produce an achene that is thick-walled and usually bears no pappus; it tends to fall near the parent. The achenes may also differ in the extent of dormancy, with the sedentary ray achenes capable of surviving longer before germinating. Thus escape in time may be as important, or even more so, than escape in space. The migratory disk achenes germinate quickly when suitable soil and moisture regimes are encountered. Other adaptations for transport are the extended "wings" in some species of *Spergularia* that facilitate water transport and allow larger seeds with larger embryos to be transported. Seed heteromorphisms provide a bet-hedging strategy that averages out environmental variation in time and space.

The co-evolution of physiological and reproductive traits with migratory heteromorphisms in insects and plants indicates that these heteromorphisms represent migratory syndromes. This means that selection acting on one trait will also influence others, on the assumption that the traits share genes in common. Environments interact with the genomes to influence how the syndromes are expressed. The occurrence of syndromes and the interactions between genes and environments point out the need to examine the selective responses of syndromes that produce the complex adaptations that we see in heteromorphisms and other migratory traits. Genes are responsible for responses to selection, and it is to genetic influences that we now turn.

CHAPTER 14

Evolutionary genetics of migration

The variety of distinct patterns of migration indicates that natural selection has shaped considerable diversity among the responses of migratory organisms. Because migration renders the environment more equable for the individual, one would expect relatively intense selection moulding this important homeostatic behavior. Understanding of the observed pattern diversity requires the analysis of two sources of variation and their interactions. The first is the environment, the "templet" of Southwood (1977), that determines the strengths and directions of natural selection. The extended environment or "arena" in which the lifetime track of the migrant occurs produces several sources of selection acting at the beginning and end of a journey as well as during transit (Dingle and Drake 2007 and Chapter 2). The second source of variation is the genetic structure upon which selection acts (Liedvogel et al. 2011). Without underlying genetic variation traits cannot respond to selection, and the influence of genes is thus fundamental to the evolution of migratory syndromes. On the other hand, environments determine the nature of gene expression, so it is equally important to consider the environment in which a syndrome is evolving (Chapter 2). Because different phenotypes may be produced when a particular genotype experiences different environments, the interactions between genes and environments—known as reaction norms when the expression of given genes or genotypes is measured across several environments (e.g., van Noordwijk et al. 2006)—are a third source of variation that is basic to adaptation and evolution. These three important contributions to the evolution of migration (or any trait) will all be considered in this chapter.

In discussing the analyses of genetic variation underlying migration and its evolution, I have somewhat arbitrarily partitioned them into three different approaches. The simplest of these is the determination of whether a trait or the difference between a trait in two or more populations displays a genetic component. Typically samples of two or more populations (or species) that differ with respect to a trait are reared in a common environment to see whether the differences persist and are therefore due to gene differences. Because these methods were originally most frequently used in studying plants, they are usually referred to as "common garden" experiments. We have already seen some of these in previous chapters. Often the experiments are extended by crossing individuals from two populations and observing the expression of traits in the hybrid offspring.

The second general approach is to search for the effects of a single gene or, at most, a very few genes. Classically one looked for genes segregating at a locus in Mendelian fashion, and a few genes influencing migration have been determined in this way (Dingle 1996). The advent of molecular genetics, and the explosion in recent years of sophisticated means of analyzing the genome, have allowed biologists to locate genes on the DNA double helix and map their influences on the development of traits and the enzymes that produce particular metabolic responses. These ground-breaking achievements in genomics are now ripe for application (Liedvogel et al. 2011). We have already seen, for example, how modern molecular techniques have enumerated the role of cryptochromes in the orientation responses of migrating butterflies (Chapter 9). As we shall see, they have also opened new windows to understanding some flight polymorphisms.

Most complex traits like migratory behavior and its associated syndromes are the consequences of many genes and the relationships among those genes. The

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analysis of polygenic influences requires quantitative genetic methods that allow partitioning of phenotypic variation into sources arising from the genes, the environment, and genotype by environment interactions. A brief primer of the methods is given in Appendix I at the end of this chapter. I shall present examples derived from each of the approaches to the genetics of migration and try to elucidate how each might contribute to our understanding of migratory behavior and its accompanying syndromes. The latter result from the fact that no gene influences one trait alone, but rather all genes are pleiotropic to some degree with the result that both traits and combinations of traits are usually the result of several genes acting in concert to produce the phenotype we observe. Genetic variance, genetic correlations arising because genes influence more than one trait, and genotype × environment interactions will all influence the rate and direction of the evolution of migration syndromes.

Population differences

Common garden experiments are frequently used to assess genetic contributions to differences between populations using measurements on parents drawn from each population and on their F_1 and backcross offspring. Examples of migration responses in the F_1 generation for insects, a mammal, and a bird are given in Dingle (1996; Chapter 14). A bird example that includes a backcross was analyzed by Derégnaucourt et al. (2005) using European and Japanese subspecies of the Common Quail (*Coturnix coturnix*). The European population is a partial migrant, but has been declining. As a result, non-migrant domestic Japanese Quail have been released into the wild as game birds. These authors were interested in the potential impact of hybridization between these birds and those of the native, partially migratory, European population.

Captive stocks of both subspecies were maintained in the laboratory and provided the parents for birds used in the experiments. European birds were descended from wild migratory birds that had been captured in France, Spain, and Portugal. Japanese quail were from a population selected for meat and egg production. The parents of experimental birds were 62 European quail and 28 from the Japanese strain which were then used to produce F_1 hybrids and backcrosses to the parental lines. Birds tested for migratory activity were the F_1 individuals from Japanese mothers crossed with European fathers and backcrosses from F_1 mothers and European fathers. Space constraints limited the experiments to this sample. For the tests 22 males and 26 females were randomly selected from the F_1 offspring and 22 males and 22 females were selected from the backcross. After hatching in June and July, quail were kept in groups of ten in laboratory pens under natural daylengths until the short days of December (*c*. LD 9.5:14.5). They were then transferred to individual cages and maintained for 60 days under an artificial LD 14:10 photoperiod and a constant 20°C temperature. All birds were thus reared under the same conditions (the "common garden") from hatching until testing for migratory performance, and the long days stimulated gonad growth and development of migratory behavior.

This quail is a nocturnal migrant. Like many such migrants it displays 'zugenruhe' or migratory restlessness at night during the migration period when held in cages in the laboratory, and measurements of this behavior provide a reliable estimate of migratory behavior in the wild (Pulido et al. 2001). Measurements of migratory restlessness were made by placing the birds in cages criss-crossed with infrared beams. Detectors recorded the numbers of cuts of the beams made by the birds as they moved about the cage, and the signal was then amplified and sent to a computer that totaled the number of cuts during each period of observation. Data were counts of the number of nights of migratory activity (as opposed to the "vegetative" behavior of sleep) during the 60 days of recording, and the number of cuts of the infrared beams per night was a measure of activity level. Results are displayed in Figure 14.1.

The upper two panels of Figure 14.1 show the levels of nocturnal Zugenruhe. In both sexes the behavior of the F_1 individuals was roughly intermediate between that of the European and Japanese parents. The situation is not quite as clear in males because some individuals displayed nocturnal restlessness but not at the levels expected of migrants (these were designated "nomads" by the authors of the study). In the backcross F_1 × European there was a distinct bias toward the European fathers. The

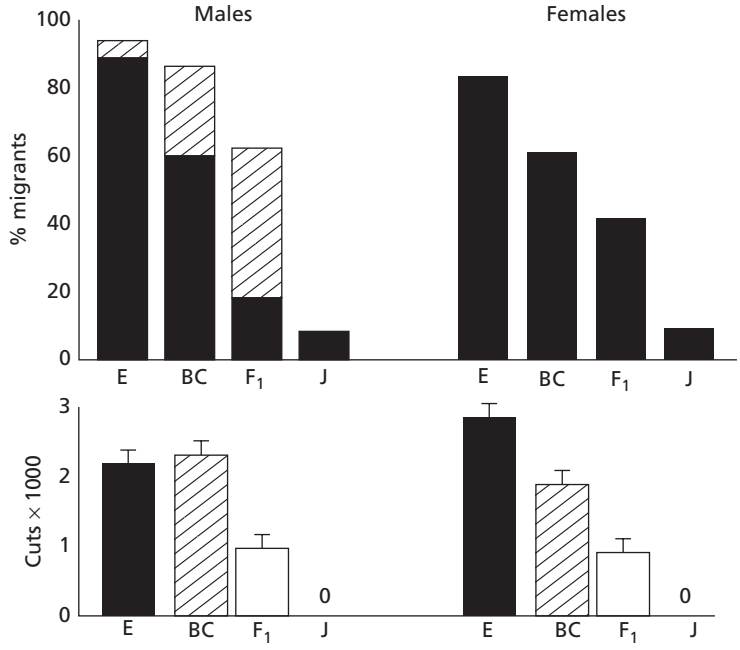


Figure 14.1 Migratory activity in parents and offspring of migrant European and non-migrant Japanese populations of the Common Quail. Top panels display the percentage of birds showing any nocturnal migratory restlessness or 'zugenruhe'. Cross-hatching in males indicates birds showing some restlessness, but not enough to be considered fully migratory. Lower panels indicate movement as determined by the mean ± SE number of times birds cross infrared beams ("cuts") during the night. Absence of bars for Japanese parents reflects lack of activity. E, European; BC, backcross to European; J, Japanese. Data from Derégnaucort et al. (2005).

results are what would be expected of a polygenic trait with no dominance due to major genes. In the lower panels of Figure 14.1, the measurement of migratory restlessness is the number of times ("cuts") individuals passed through the infrared beams. Again the F_1 individuals are intermediate with a bias toward the European fathers in the backcross—in fact in the males the backcrosses showed even more activity than the fathers and were not significantly different from them. This later result is what would be expected from dominance, but the relatively small sample size means that more data would be needed to verify the truth of this. Overall, the results suggest that Zugenruhe and hence proclivity for migration are polygenic traits.

The differences in migratory tendency between European and Japanese quail are the product of evolution over a relatively long period of time. Differences, however, can evolve in contemporary time, as is the case with European Blackbirds (*Turdus merula*), studied by Partecke and Gwinner (2007). There are observations on several species, including the blackbird, suggesting that colonization of urban areas leads to changes in breeding phenology and increased sedentariness. The question asked by Partecke and Gwinner was whether the changes were genetically based—and therefore the consequences of selection—or whether they were phenotypic adjustments to the changed environments. They hand-raised blackbirds in the common environment of the laboratory and measured nocturnal activity and physiological traits such as fat deposition and the timing of gonadal development as a surrogate for the timing of seasonal reproduction; these were determined for two migratory cycles. The populations of blackbirds were urban birds from the city of Munich and birds from nearby forests. The urban birds had been observed throughout the winter whereas the forest birds disappeared at this time due to migration.

The data from nocturnal activity and fat scores for the laboratory-reared birds were combined for a principal components analysis of "migratory disposition" and confirmed that urban birds were indeed more sedentary due to evolved gene differences. Migratory disposition was lower in urban males, especially during the first year, whereas females did not differ. In this partially migratory species, it is males that derive fitness benefits from remaining sedentary because of primary access to preferred breeding habitats. Females differ little in fitness between migratory and sedentary behavior. Therefore

it makes sense that urban habitats that favor earlier onset of breeding conditions, due to a warmer microclimate and other anthropogenic activities such as gardens, would also favor residency in males. Furthermore individuals with low migratory disposition matured gonads earlier which would lead to a longer breeding season and potentially still more fitness benefits. There are therefore good reasons for the evolution of increased sedentary behavior of urban blackbird males.

Laboratory experiments to determine whether gene differences contributed to the differences in wing morph frequencies observed in Soapberry Bugs (Chapter 13) were conducted by Dingle and Winchell (1997). They crossed long-beaked individuals from ancestral populations feeding on balloon vine in the Florida Keys with derived short-beaked bugs exploiting introduced goldenrain trees in central Florida. As discussed in Chapter 13, the derived central Florida bugs not only had shorter beaks, but also displayed higher frequencies of reduced wings and absent flight muscles. For these experiments bugs were drawn from the two populations while still in nymphal stages; both populations had been in a common environment (LD 14:10, 30°C) in the laboratory for several generations, and they and their descendants were maintained in these conditions for the duration of the experiments. Once bugs eclosed to adulthood, they were paired individually before mating with a member of the opposite sex from the same population and with the same externally visible wing morph. The presence or absence of wing muscles was not determined because this requires dissection. Thirty full-sib offspring of each pair were reared together and at the time of adult eclosion were scored as either short-winged or long-winged. The data recorded were the percentage of each morph in each family (Figure 14.2).

For the ancestral Keys population comparisons of the progeny resulting from each cross type (short × short or long × long) revealed no significant differences in adult wing morph ratios. Regardless of parental wing type, the chance of eclosing into a long-winged adult was equal, no matter which cross occurred. Thus even in short-winged bugs, genes for the development of long wings were clearly preset and penetrating. Unfortunately we do not know the ratio of flight morphs among the long-winged offspring. The results for the derived population contrasted markedly. Here the short × short crosses produced significantly fewer macropterous offspring than the long × long parents, well below 50% macroptery. However, even some long × long crosses produced a high proportion of brachypters, in one case even 100% short wing. Comparisons between the two populations revealed significant differences in the wing morph ratios resulting from analogous cross types. These results suggest that differences in the genetic control of wing morph have evolved as part of host race evolution on fruit capsules of different sizes, as with the European blackbirds a case of anthropogenic change (in this case exotic host plants) leading to contemporary evolution. The complexity of wing morph frequencies in the progeny of analogous crosses suggests that we are dealing with a polygenic trait, and the contrasting results reveal differences in the genetic basis for wing morph in the two contemporaneously evolving populations.

In a variant of controlled environment experiments individuals from one contrasting population are transplanted into the habitat of the other. This was the method used by Skov et al. (2010) for assessing genetic contributions to the migratory behavior of the partially migrating Roach (*Rutilus rutilus*) in Danish lakes (see also Chapter 12). Translocated fish from a migratory population tended to behave like the local population when transferred to a lake where migration was not present. In the reverse translocation the non-migrants displayed migration. Thus migration in these populations seems to be phenotypically plastic. However, in the case of previous non-migrants migrating when translocated, the pattern of migration differed from that of the local migrants. These fish migrated less frequently and were not as sensitive to low temperature (which triggers migration) as their previously migrating counterparts. This implies some genetic influence on the syndrome accompanying migratory behavior and indicates a degree of local adaptation.

A common garden experiment on migratory timing was conducted by Quinn et al. (2011) on Chinook Salmon (*Oncorynchus tshawytscha*) in New Zealand. These salmon were descended from a population that had been brought from the Sacramento River

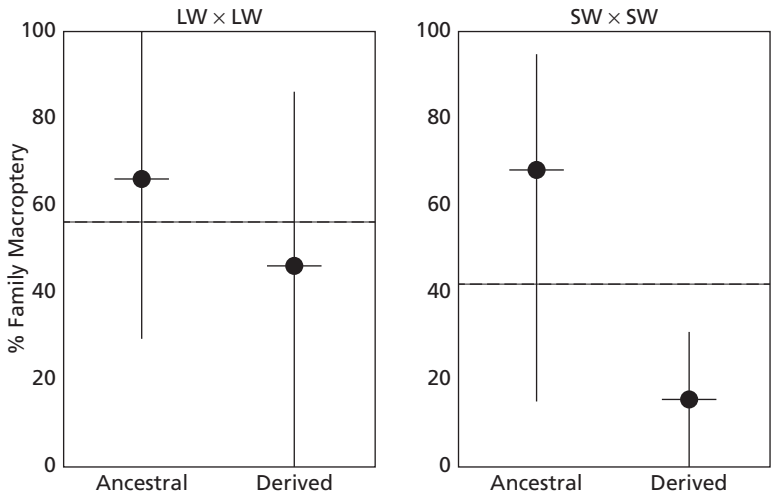


Figure 14.2 A recently evolved contrast in the genetic control of wing morph in Soapberry Bugs (*Jadera*). Data are from families of full-sib offspring of the flight morph crosses shown. Filled dots are medians across families and solid lines indicate full range of responses. Horizontal lines are overall means for each cross type. Populations differ significantly in each cross type. Data from Dingle and Winchell (1997).

system in California and released into streams on South Island between 1901 and 1907 (MacDowall 1994); within 10 years they were spawning in several South Island river systems. Salmon from two streams in separate river systems were sampled for the experiment. A Poulter River population breeds about two to three weeks later than a population from Glenariffe Stream. The former fish also usually spend a year in freshwater before migrating to the sea whereas the latter usually depart for the sea during their first year. Full-sib families from each population were reared in the common environment provided by the Silverstream Fish Hatchery and when sufficiently mature were tagged and released into the sea. This hatchery was near the mouth of the Waimakariri River of which the Poulter River is a tributary, so all released fish were conditioned to return to this river (see Chapter 9). Variation in the timing of the return to breed was determined from dates of capture by anglers fishing the Waimakariri. Anglers captured 114 Glanariffe fish and 31 from the Poulter River. The mean date of entry for Glanariffe fish was 23 February whereas it was 18 days later in the Poulter fish which had been spawned on the same day (18 May). This earlier return by the Glenariffe fish was consistent with the earlier natural spawning of this population. The results are another example of contemporary evolution with the difference in the timing of upstream migration and spawning evolving in about 95 years (1901/1907 to 1997 which was the brood year tested) or about 26 generations. Divergence in egg size, morphology, age of maturity, and growth rates are additional diverging correlated traits (Kinnison et al. 2008, 2011).

Genes and genomics

Major differences among individuals with respect to migratory performance attributable to the effects of single Mendelian loci are relatively rare, which is hardly surprising considering the multiplicity of factors that enter into migration. Even in wing polymorphisms where the distinction between migrant and non-migrant is clear, control seems to be primarily polygenic, as in the Soapberry Bugs in Figure 14.2. Roff (1986) surveyed 23 examples of wing dimorphisms and found only eight to be controlled by a single-locus, two-allele system (five dimorphisms involved beetles). In all but one possible exception, the brachypterous allele was dominant. An additional example of dominant brachyptery was found by Solbreck (1986) in the lygaeid true bug, *Horvathiolus gibbicollis*, a Mediterranean species dimorphic in the wild. The dominance of brachyptery was revealed by controlled laboratory crosses. The gene differences in the pterygomorphism also resulted in a syndrome of correlated responses in life-history traits. First, the brachypters reached adulthood more rapidly, and second, they began to oviposit earlier and finished ovipositing

later than macropters, whereas the latter display a peak oviposition associated with wing muscle histolysis following flight. The short-winged females also produce larger early eggs. These types of differences between the morphs parallel many of the differences—in crickets, for example—that were discussed in Chapter 13.

The use of molecular techniques has allowed investigators to identify individual genes associated with migratory behavior. One case is that of a gene in the Blackcap Warbler (Mueller et al. 2011). As discussed in earlier chapters, migratory birds undergo a number of physiological and behavioral changes that are preludes to migration or that sustain the journey. One important change is a shift in circadian activity to nocturnal restlessness (Zugenruhe) that can be measured in the laboratory, and there is a good deal of information on the "clock genes" that regulate this circadian rhythmicity. A personality trait that seems to be associated with migration is dominance, which, among other characteristics, may lead to exploratory behavior that is manifested to a greater degree in migrants than in non-migrants (e.g., Mettke-Hofmann and Greenberg 2005; Nilsson et al. 2010). Based on the fact that nocturnality and exploratory behavior are associated with migration, Mueller and colleagues examined nine polymorphic loci in six candidate genes, reported as microsatellites and single-nucleotide polymorphisms (SNPs—see Chapter 4), in birds that are known to be involved with circadian rhythms and exploratory behavior.

The Blackcap is a well-studied migrant, so it was possible to take advantage of the geographic variation in behavior by using birds from 14 different sites in Europe, the Canary and Cape Verde Islands, and wintering grounds in Kenya. The association between allelic variation and migratory behavior was studied both among individuals within populations and among populations varying in the proportion of migrants and the average distance traveled. Behavioral measurements were levels of nocturnal activity in registration cages under identical controlled laboratory conditions. In the two populations chosen to examine individual differences, in France and Southern Germany, migratory restlessness was associated with genotypes of the *ADCYAP1* (*adenylate cyclase-activating polypeptide 1*) gene. Individual allele length (the number of tandem repeats in a nucleotide sequence) correlated positively with migratory restlessness in both populations, further supporting the involvement of this gene. The mean genotypes explained 2.7% and 3.5% of the variance in restlessness in France and Germany, respectively, so it is obvious that there is also a great deal of variation deriving from other genes. The between-population variation in migratory tendency was strongly correlated with the variation at the *ADCYAP1* locus, but not at any of the other loci examined. There is thus a real possibility that this gene is associated with migration.

A locus with two alleles located on the X chromosome determines wing polymorphism in aphids (Caillaud et al. 2002). Aphid pterygomorphisms involve both polymorphism and polyphenism (Dingle 1996; Braendle et al. 2006; Brisson 2010; and see Chapter 2). Aphids are primarily associated with temperate regions and produce several generations a year. In the summer, reproduction is asexual with the parthenogenic females producing both winged and wingless young via live births (Figure 14.3).

Upon reaching maturity females usually begin reproduction by giving birth to apterous young,



Figure 14.3 The parthenogenic (summer) long-winged and wingless morphs of the Rose Aphid (*Macrosiphum rosae*). Note that in addition to wings the flight morph has a somewhat different morphology, especially of the head and thorax. Photo by Kathy Keatley Garvey. (See also Plate 5.)

but several factors may cause them to produce polyphenic winged forms which then migrate to new hosts (Chapter 2). These factors include crowding with the immediate cause being tactile contact among individuals, senescence of the host plants, and aging of mothers with older mothers producing winged offspring (a maternal effect). There is also a "grandmother effect" because reproduction is so telescoped that females can influence the outcome in their grandoffspring. Aptery is evidently a derived state, and wing development seems to be the default pathway as wing buds appear in the first two instars of wingless forms, but then disappear. Correlated traits in the winged forms include heavier sclerotization of the head and thorax, in the latter case presumably to support the wings, and also more fully developed compound eyes, ocelli, and antennae that would aid in flight control and host plant location. These correlations presumably interact with the central nervous system in controlling the flight and settling responses outlined in Chapter 2.

As days shorten in late summer and autumn the parthenogenic females switch to producing sexual forms which migrate to overwintering sites, often on different host plants, where they produce zygotic eggs that overwinter. In some species such as the pea aphid, *Acyrthosiphon pisum*, both winged and wingless males are produced; this is the polymorphism controlled by a single locus on the X chromosome called *aphicarus* (*api*). The males are haploid for the X chromosome (i.e., they are X0) so that one allele (w) of *api* produces winged males while the second produces aptery (wl). Clones vary in their response to stimuli, causing females to produce winged offspring, so the question arises as to whether the *aphicarus* locus contributes to the genotype × environment interaction resulting in the winged phenotype. This possibility was tested by deriving F_2 clones from a cross between parental clones homozygous for the two *api* alleles (Braendle et al. 2005a). This randomized the alleles that were not closely linked to the *api* locus. The different genotypes were then subjected to a crowding/starvation stimulus known to cause females to give birth to the winged morph. Results are shown in Figure 14.4A. The wingless form (wl) of *api* that resulted in apterous males had the opposite effect in the polyphenism of females; it resulted in the production of winged offspring in stimulated females. Clones whose females bore only the *api* form (w) that produced winged males produced apterous forms almost exclusively. Clones bearing the wl allele in either homozygous or heterozygous combinations produced winged morphs, but the frequency was variable (Figure 14.4B). Molecular techniques have now allowed mapping of the gene to its position on the X chromosome (Braendle et al. 2005b). Furthermore, in spite of the difference in the control of the switch to aptery between polymorphism and

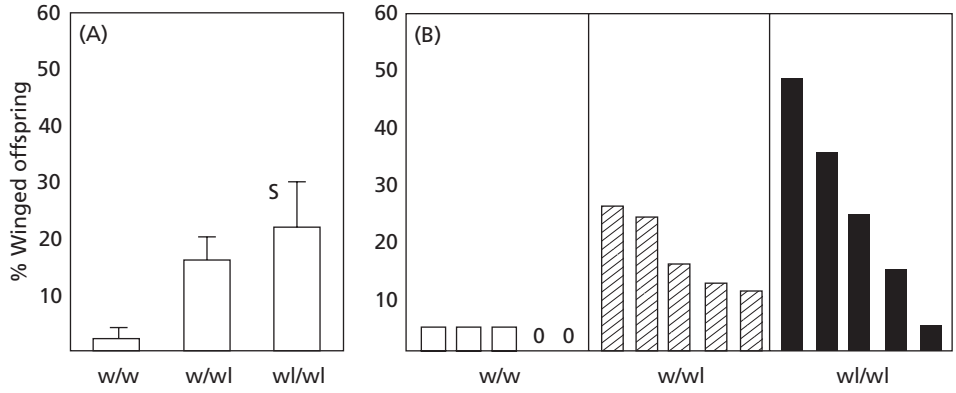


Figure 14.4 The genetic control of male wing morph in the Pea Aphid, *Acyrthosiphon pisum*. (A) Effect of a crowding/starvation treatment on wing morph genotypes of F_2 crosses of female aphids. (B) Clonal variation in female wing morph production clones bearing designated genotypes. w: *api* gene that produces winged males; wl: the form producing wingless males. Note that these alleles have the opposite effect on the polyphenism of females. Data from Braendle et al. (2005a).

polyphenism, the downstream events such as transcription are fundamentally similar (Brisson 2010). The wing development genes found in *Drosophila* and other insects are also present in the aphid genome (Brisson et al. 2010), opening up many possibilities for the analysis of the genetic control of wing development, flight, and migration using molecular methods.

At a finer scale, genes that control muscle or metabolic functions can change expression when migration begins. In the Christmas Island Red Crab, for example, migrants sustain locomotion aerobically for up to 12 h per day, in contrast to the sedentary phase when leg muscles are almost exclusively anaerobic (Chapter 3). Some sort of transition to a phenotype of endurance muscle must therefore be taking place. Transcripts of genes coding for different proteins associated with muscle contraction turned out to be significantly different between the migratory and non-migratory states (Postel et al. 2010). A transcript of tropomysin turned out to be more abundant in migrating crabs. Two other protein-coding genes, *pax* and *mlp*, were more upregulated in migrating crabs. This upregulation is consistent with "remodeling" of leg walking muscles to sustain migration by increasing the number of aerobic endurance fibers in these leg muscles. Genes can thus be appropriately "turned on" to enhance migratory capacity.

Another case of genes influencing metabolic activity associated with migration occurs in the Yellow-rumped Warbler complex of North America (Toews et al. 2013). This warbler is divided into four subspecies or species depending on the authority. Of interest here are the two largest groupings, the Myrtle Warbler (*Setophaga coronata*) of eastern North America and the Audubon's Warbler (*S. c. auduboni*) of the American west. The Myrtle Warbler is a migrant, and in the west the Audubon's Warbler is a migrant north of the Arizona/Utah border but non-migrant to the south. The mitochondria in the flight muscle of migrants to the north show a higher frequency of mitochondrial DNA (mtDNA) that has evidently introgressed from the eastern Myrtle group (the two groups meet along a contact zone). To the south of the Arizona/Utah border there is much less Myrtle mtDNA present in the population; rather the mtDNA is the same as that in the non-migratory Black-fronted Warbler (*S. c. nigrifrons*) whose range is along the northern cordillera of Mexico. The Myrtle mtDNA has a higher acceptor control ratio, a measure of the energetic efficiency of the mitochondria. This greater efficiency should be advantageous for a migrant and may account for the greater introgression of the Myrtle mtDNA into the more northern and migratory population of the Audubon's Warbler.

In addition to influencing metabolic aspects of migration, genes can influence its timing. Such is the case with Alaskan Pink Salmon (*Oncorhynchus gorbuscha*) (Kovach et al. 2012). Populations of this species migrate into streams in Alaska, and 32 years of data were analyzed, representing 17 complete generations of migrations into Auke Creek, a stream that empties into a lake outlet near Juneau, Alaska. Over the period of data collection there has been a phenotypic change toward earlier migration into the stream (Figure 14.5). During this period, beginning about 1970, the yearly mean temperature of the stream has been increasing. In 1979 a neutral genetic marker was introduced into late-migrating fish of this population at a fish hatchery as a control for genetic drift, as this marker would presumably not be influenced by any selection that might

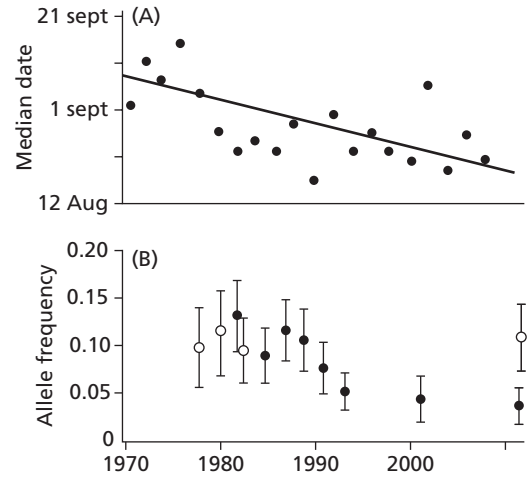


Figure 14.5 (A) Change in migration timing of Pink Salmon in Auke Creek, Alaska. (B) Changes in the frequency of the late migration marker allele (LMMA) for the same period (solid circles) with lack of change in neutral allele (open circles). Error bars are 95% confidence intervals. Data from Kovach et al. (2012).

be occurring for migration timing. Further experiments revealed a genetic distinction between early and late migrants with a "late migration marker allele" (LMMA) specifically associated with later migrants.

Analysis over the years of the study showed a clear decrease in LMMA as the Auke Creek population shifted toward earlier migration (Figure 14.5B). Apparently there was strong selection acting on this locus in the years 1989–1993 as there was a marked shift toward earlier stream entry at that time and little change in allele frequency before or after that period. This change in the allele frequency of LMMA contrasted with the neutral marker which showed no change in frequency, indicating that genetic drift was not involved. There was further no evidence of gene flow between this and nearby populations. The stream temperatures in 1989 were the second highest on record, and since there was a substantial change in the frequency of LMMA at this time, higher creek temperatures are certainly implicated in the selection for earlier migration. Modern genetic techniques have thus demonstrated that selection is causing changes in migration timing. The implications for consequences of climate change are clear.

Migration syndromes as polygenetic traits

Complex traits such as migration are likely to be influenced by genes at many loci for two primary reasons. First, many factors from morphology to physiology contribute to the organization of migratory behavior and its accompanying life-history correlates. Second, polygenic systems allow the generation of many different response patterns to the action of natural selection. Analysis of the polygenic nature of migration thus requires the methods of quantitative genetics specifically designed for this purpose. These are summarized briefly in Appendix I for readers who may not be familiar with them.

The basic quantitative genetic measure of the contribution of genes to the population variability observed in a trait is the heritability which, since it represents the ratio of genetic to phenotypic variance, is symbolized h^2. Heritabilities have now been estimated for various migration-related traits in a variety of organisms (Table 14.1; and additional estimates can be found in Dingle 1996 and Roff and Fairbairn 2001). In all cases listed in the table, heritabilities are significantly different from zero, and often substantially above zero, indicating that a major portion of the variability in the measured traits is the result of (usually) additive genetic variance. This suggested that there is sufficient genetic variation in the respective traits, species, and populations to predict that, were there natural selection acting on any of the measured traits, response would be relatively rapid. Indeed the literature on evolution is now replete with examples, including migration, of such rapid response or "contemporary evolution." Rapid responses are also frequently observed in the laboratory (Roff and Fairbairn 2001). There would seem to be considerable potential for the evolution of migration syndromes, although this too depends on genetic correlations. In birds, there are now numerous examples of changes in migration routes, changes in the timing of migration with climate change, and the evolution of migration from nonmigratory populations (e.g., Canada Geese in Europe, House Finches in the eastern USA discussed in Chapter 12) (Fiedler 2003). In salmon the rapid adaptation of hatchery fish to captive rearing and its subsequent negative impact on wild migratory populations when hatchery fish are released into rivers and streams is a cause for considerable worry (Levin et al. 2001).

A detailed analysis of the role of genetic variation in local adaptation of the wing polymorphism of the water strider *Aquarius remigis* was conducted by Fairbairn and King (2009). This strider occurs throughout California and varies in the frequency of the morphs. Across most of its North American range this species displays a high frequency of the apterous morph, apparently as an adaptation to more or less permanent streams. In California, however, most populations show a frequency of the long-winged morph in the 5–80% range. Fairbairn and King asked the appropriate question: Why do California striders fly? In the Mediterranean climatic regime of central and southwestern California, the macropters breed in temporary streams in the spring and migrate back to permanent streams and pools in the summer, so that the high frequency

Table 14.1 Examples of heritability estimates for migratory and related traits.

Species	Source	Trait	Heritability*
Hydroides dianthus (tubeworm)	Toonen and Pawlik 2001	Settling	0.83 ± 0.31 0.6 ± 0.09
Laodelphax triatellus (planthopper)	Mori and Nakasuji 1990	Wing morph	0.32
Gryllus firmus (cricket)	Roff 1986	Wing morph	0.65 ± 0.08
G. firmus	King et al. 2011	DLM† mass	0.21–0.28 ± 0.05
G. pennsylvanicus	Roff and Simons 1997	Wing morph	0.74 ± 0.19
Dianemobius fascipes (cricket)	Masaki and Seno 1990	Wing morph	0.30 ± 0.04
Melanoplus sanguinipes (grasshopper)	Kent and Rankin 2001	Migratory liability	0.53–0.77
Heliothis armigera (cotton bollworm moth)	Colvin and Gatehouse 1993	Flight duration	0.39
Cydia pomonella (codling moth)	Schumacher et al. 1997	Flight distance	0.37–0.57
Aquarius remigis (water strider)	Fairbairn and King 2009	Wing morph	1.08 ± 0.17
Sylvia stricapilla (blackcap warbler)	Berthold and Pulido 1994	Nocturnal activity	0.37 ± 0.17 0.46 ± 0.02
S. stricapilla	Pulido et al. 2001	Autumn migration timing	0.35 ± 0.16 0.47 ± 0.24
Salmo salar (Atlantic salmon)	Páez et al. 2011	Migration propensity	0.46 ± 0.20
Heterosperma pinnatum (Asteraceae)	Venable et al. 1995	Number of traveling achenes	0.58
Crepis sancta (Asteraceae)	Cheptou et al. 2008	Proportion of traveling Seeds	0.25

*Value or range of values plus standard errors were given.
†DLM = dorso-longitudinal flight muscles.

of the flying morph is an adaptation to this habitat mosaic. Throughout California, however, the proportion of macroptery is positively correlated with altitude, in contrast to the usual situation where aptery correlates with altitude (Roff 1990). The high frequency of macroptery in high-altitude streams evidently results from selection to maintain flight, especially in the face of highly seasonal precipitation and the need to move from downstream to upstream habitats. The heritability for wing morph is high, on the order of 1.0 (Table 14.1), and this heritability is not altered by rearing temperature. This means that wing morph frequency has the capacity to respond rapidly to selection on local scales, as we have seen in the examples of rapid adaptation in other migrant organisms.

Estimates of the heritabilities of migration-related traits get at only part of the important genetic variation affecting migration. This is because migration and other important behavioral traits do not occur in isolation, but often show correlations with other traits, including morphology, physiology, and life histories. The patterns of these correlations (in quantitative genetics the G matrix) are expressed in the form of syndromes or "strategies." A particular migratory syndrome may involve wing length, fat deposition, and timing of reproduction as we have already seen in many organisms. The causes of correlations between characters can be either environmental (phenotypic correlations) or genetic, and, if we wish to determine how natural selection acts on a syndrome such as migration, it is necessary to distinguish once again among sources of variation. Variations on the methods used to estimate heritability (Appendix I) may be used to estimate genetic correlations that represent the degree to which traits share genes in common (usually) or whose genes are linked.

In my laboratory we have used selection to examine the genetic architecture of the flight polymorphic migration syndrome of the Soapberry Bug, *Jadera haematoloma*, described in Chapter 13

(Dingle et al. 2009). The trait we subjected to selection was beak length, and both the ancestral long-beaked population feeding on the native balloon vine in the Florida Keys and the derived short-beaked population feeding on goldenrain trees in central Florida were included. Two replicated lines selected for long beaks, two replicated for short beaks, and two randomly mated control lines were established for each of the populations. Selection was carried out for six generations using a within-family selection design to slow inbreeding (Falconer and McKay 1996). In this design the longest- or shortest-beaked individuals in each family, in the respective selected lines, were chosen as the parents of the next generation, rather than selecting some proportion of the longest or shortest irrespective of family, so that each family in the line is represented in the next generation. This design reduces selection intensity but minimizes loss of genetic variation due to chance. The results of selection on the beak lengths of females of the two populations are summarized in Figure 14.6 which shows the responses in all lines. Both populations responded strongly, with marked changes in beak length even in the within-family design. These results show not only that there was considerable genetic variation for beak length (Table 14.2) but also that reverse or forward evolution of the trait was possible in both populations. The trait is presumably an ancient one in the ancestral population, but

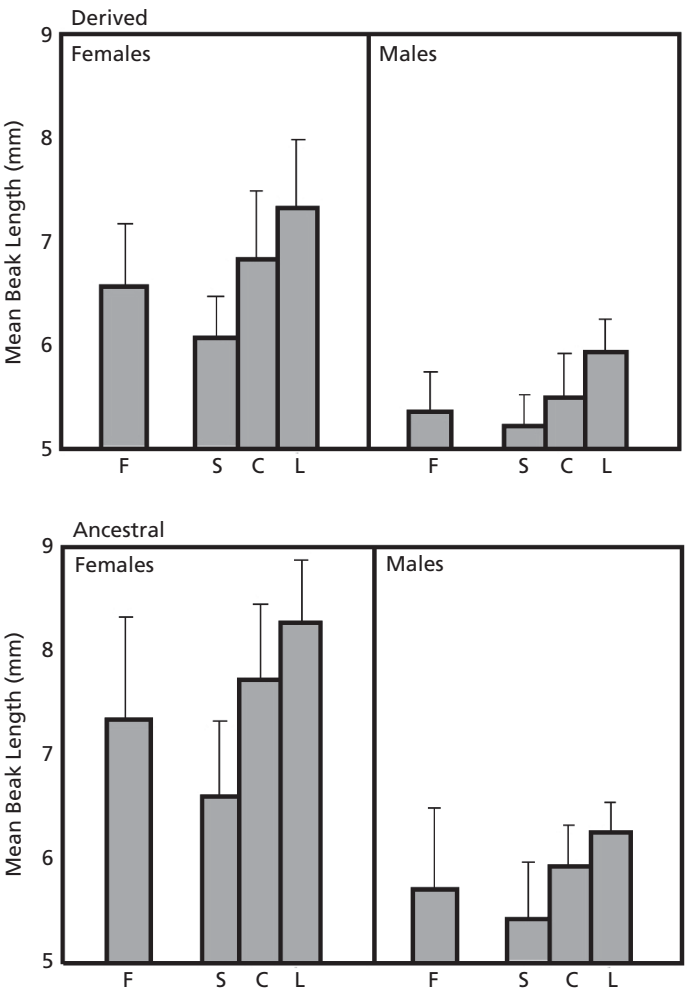


Figure 14.6 Summary of responses to laboratory selection on beak length in Florida populations of the Soapberry Bug, *Jadera haematoloma*. Ancestral bugs from the Florida Keys feed on balloon vine and have long beaks; derived bugs from central Florida feed on goldenrain trees and have short beaks. Plots show mean ± SE beak lengths of founder bugs (F) and mean beak lengths ± SD of bugs selected for short (S) or long (L) beaks and unselected control (C) lines. For derived bugs results are for six generations of selection. For ancestral bugs control and short beaks are for six generations of selection. Ancestral long-beak lines displayed progressively longer generation times, so results are for four or five generations of selection. Note that both forward and reverse responses to selection occurred in each population. Data from Dingle et al. (2009).

Table 14.2 Parameter estimates with standard deviations calculated from the results of selection for beak length in Soapberry Bugs (*Jadera*).

Population	Heritability LW[a]	Heritability SW	Genetic correlation[b]
Ancestral	0.51 ± 0.023	0.60 ± 0.03	–0.68 ± 0.03
Derived	0.68 ± 0.02	0.87 ± 0.02	–0.84 ± 0.01

[a] Because both short-winged (SW) and long-winged (LW) individuals appeared in the selected lines, heritabilities for beak length were estimated separately.
[b] Genetic correlations are between beak length and wing form.
Source: Dingle et al. (2009).

has evolved in roughly 100 generations in the derived population (Chapter 13). The respective beak length changes were comparable to those occurring over the 100 generations in the field.

The results of the selection experiments indicate considerable additive genetic variance for beak length, with heritability estimates ranging from 0.51 to 0.87 (Table 14.2). What is more interesting from our perspective here, however, is the relation between beak length and flight morph. In natural populations there is a phenotypic correlation between beak length and flight morph, with a higher frequency of both long beaks and long wings in the ancestral population (Chapter 13). A question regarding the selection on beak length was whether beak length and flight morph frequency were genetically correlated and so would evolve together. The answer is indeed affirmative, with strong genetic correlations in both populations between beak length and flight morph (–0.84 in the derived bugs and –0.68 in the ancestral), indicating that as beaks become longer the frequency of brachypters declines. The genetic architecture thus indicates that beak length and flight morph frequency evidently share genes in common and will evolve together as a beak length–migration syndrome with selection on beak length from host plant fruit size also generating a response in flight morph. We were unable to determine the correlation between beak length and the condition of the flight muscle because to do so would have required destructive sampling and a highly complex and labor-intensive experimental design.

The migration syndrome in Soapbury Bugs may also include aspects of reproductive output, although the data are less clear. Two measures for which genetic correlations were determined were egg mass and number of eggs laid during the first six days of oviposition. These were determined at the end of the last generation of selection, so a value for genetic correlation could not be estimated—only whether or not a significant genetic correlation was present. In the case of egg mass, a statistically significant genetic correlation was present only for the lower egg mass of the short-beaked lines, as would be predicted from the observation that natural short-beaked bugs laid more, but smaller, eggs (Chapter 13). There was, however, no change in egg mass in the long-beaked lines. With respect to egg number, the only statistically significant result was the lower egg production of long-beaked (and hence likely long-winged) bugs, again consistent with observations of populations in nature. There is thus some indication of a migration–reproduction genetic correlation, but the evidence is not strong.

Genetic correlation between migratory traits and traits associated with physiology or life history have now been found in several organisms. A sampling is presented in Table 14.3. In the hemipteran *Oncopeltus fasciatus*, like *Jadera* a seed feeder but preying on the seeds of milkweeds (Asclepiadaceae), selection on the frequency of migratory flights results in bugs with longer wings and higher fecundity (Dingle 1996). The higher fecundity would be an advantage for migrants invading "empty" habitats as these milkweed bugs do in the spring in North America. Populations that are non-migratory, such as those from Puerto Rico, have lower fecundities and presumably invest more energy in survival.

Among insects the most comprehensive studies of genetic correlations between migratory traits and those associated with other functions are on crickets (*Gryllus*) and especially the Sand Cricket, *G. firmus*. Several examples are given in Table 14.3. In crickets, and likely in other insects, high titers of juvenile hormone (JH) in the penultimate larval instar lead to the development of the brachypterous morph, and these titers are regulated by the enzyme juvenile hormone esterase (JHE) (Chapter 6). Fairbairn and Yadlowski (1997) demonstrated a twofold effect on JHE with selection on wing morph. First, they showed that JHE activity is, as expected, higher in penultimate nymphs in individuals destined

Table 14.3 Examples of genetic correlations between migratory and related traits.

Species	Sign[a]	Source	Migratory trait	Correlated trait
Oncopeltus fasciatus (Milkweed Bug)	+	Dingle 1996	Frequency of migratory flights	Wing length
	+			Fecundity
Jadera hemataloma (Soapberry Bug)	–[b]	Table 14.2	Wing length frequency	Beak length
Gryllus firmus (Sand Cricket)	+	Fairbairn and Yadlowski 1997	Wing morph	Mean JHE activity[c]
	+			Threshold JHE activity
G. firmus	+	Zera 2006 and Figure 14.6	Wing morph	High-amplitude JH titer cycle
G. firmus	–	Stirling et al. 2001	Wing morph	Early fecundity
G. firmus	–	King et al. 2011	DLM mass	Ovary mass
G. firmus		King et al. 2011	Flight allocation	Reproductive allocation
Sylvia atricapilla (Blackcap Warbler)	+	Pulido 2007	Migration frequency	Nocturnal activity
S. atricapilla	+	Coppack et al. 2001	Migration onset	Timing of egg laying
S. atricapilla	+	Pulido and Coppack 2004	Migration onset	Timing of juvenile molt

JH, juvenile hormone; DLM, dorso-longitudinal muscle.
[a] Indicates whether correlation is positive or negative.
[b] Higher frequency of short wings = lower frequency of long beaks.
[c] Juvenile hormone esterase (JHE) activity in penultimate instar.

to eclose as macropters. Second, they demonstrated a significant influence of the selection regime over and above JHE activity alone, indicating that the functional relationship between JHE activity and morph in adult crickets has changed in response to selection acting on wing form frequency. In particular, even though the incidence of microptery decreases with reduced JHE activity, a given level of JHE is least likely to produce micropters in lines selected for long wings and is most likely to produce them in the predominantly short-winged lines. Thus, there are changes in both mean and threshold JHE activity with selection on wing morph.

High JH titers in the penultimate instar lead to short-winged adults, but JH also occurs in the adults where it promotes reproduction and, in at least some insects, migration (at intermediate titers) (Chapter 6). In *G. firmus* adults there is a morph-specific circadian rhythm of JH production associated with long wings (Zera 2006, Table 14.3 and Figure 14.7). In these adults there is a daily cycle of JH titers with a low titer early in the day and a high titer in the evening just before nightfall. The cycle occurs in both long- and short-winged adults, but the amplitude is much greater in the morph capable of flight. It is likely that the high JH titer is involved with flight for the following reasons. First, the high-amplitude titer occurs only on the flight-capable adults; second, the maximum amplitude occurs just before nightfall, which is the time of flight in this species. Third, long-winged females that histolyze the flight muscles lose the JH titer cycle. Finally, as we have seen in Chapter 6, there is evidence that JH promotes migratory flight. Since JH also promotes reproduction in the adults and this coincides with cessation of migration, there must be a fine balance between the migration and reproductive functions of JH, a balance which is best studied in vivo where titers and potential interactions with other hormones (and, one hopes, the central nervous system) may be assessed (e.g., Zera 2006).

Further, in *G. firmus* there is a phenotypic correlation between wing morph, early fecundity, and the relation between flight muscle mass and ovary mass that reflects a negative genetic correlation between these traits (Table 14.3). What is interesting about the flight muscle/ovary mass genetic correlation, however, is that it occurs only at low food levels. When crickets are fed ad libitum, the negative genetic correlation disappears, that is, the correlation is environment dependent and so is the trade-off between these traits (King et al. 2011). These

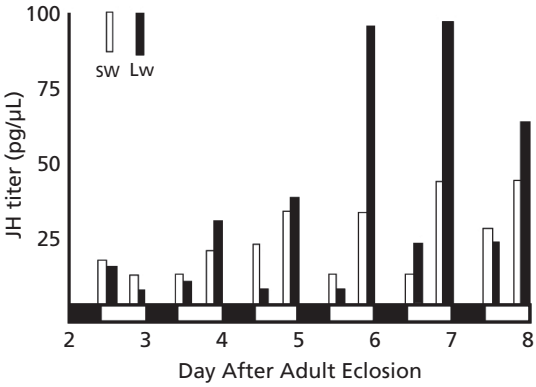


Figure 14.7 The development of the circadian rhythm of juvenile hormone (JH) titer in short- and long-winged *Gryllus firmus*. Periods of light and dark are indicated by bars on the abscissa. Titers are low in the morning and high in the evening in both morphs, but the amplitude is much greater in the long-winged morphs which in this experiment were all flight capable. Data from Zera (2006).

authors investigated the energy allocated to flight and reproduction in addition to the measurements of the masses of flight and reproductive structures. In this case the genetic correlation between flight allocation and reproductive allocation was high, negative, and highly significant in all food-level environments, reflecting a strong trade-off between these functions. Genetic correlations and their standard errors were –0.67 ± 0.09, –0.69 ± 0.08, and –0.69 ± 0.08 for the low, 50%, and ad-lib food environments, respectively. These correlations indicate that the two functions of flight and reproductive allocation compete for resources. The results of King and colleagues demonstrate three important points: (1) there is substantial genetic variation in a migratory trait (flight muscle mass, Table 14.1); (2) genetic parameters can vary with environments, an observation whose importance is becomingly increasingly recognized (e.g., Sgró and Hoffmann 2004); and (3) genetic correlations can be present when allocation of resources is estimated, even when they are not evident when the mass of the traits themselves is measured.

When it comes to vertebrates such as birds, issues of rearing space and labor make the estimation of genetic parameters much more difficult. Nevertheless some data are available especially on the Blackcap Warbler, *Sylvia atircapilla*, a common European migrant. Heritabilities for nocturnal migratory activity and for the timing of autumn migration indicate levels of genetic variance sufficient for relatively rapid response to selection (Table 14.1), and indeed there has been the recent evolution of new migratory routes (Sutherland 1998). Genetic correlations involving migratory traits have also been estimated (Table 14.3), especially with regard to timing of migration and life-history events. Blackcaps vary in migration frequency, notably among populations, and frequency is genetically correlated with nocturnal activity or Zugenruhe measured in laboratory flight cages (Pulido 2007). Birds with a high probability of migrating are likely to be more active migrants when they do so. The onset of migration is genetically synchronized with molt and egg-laying, as the timing of these activities is genetically correlated with the timing of migration (Coppack et al. 2001; Pulido and Coppack 2004). The importance of synchronization lies in the allocation of resources to the various activities. Molt and migration, for example, are both energetically demanding, and it is advantageous to separate them temporally as natural selection presumably has. Migration by flight would also be more difficult with missing flight feathers.

The recent advances in molecular genetics have allowed biologists to specify the genes for quantitative traits. These quantitative trait loci (QTL) are stretches of DNA that contain or are linked to genes that underlie quantitative traits such as those associated with migration. By using molecular tags such as amplified fragment length polymorphism, or usually single nucleotide polymorphism (see Chapter 4), regions of the genome that contain QTL can be mapped to specific chromosomes and regions of chromosomes. Knowing the number of QTL influencing a trait can reveal much about the genetic architecture of the trait, such as whether it is influenced by many genes of small effect (the classic quantitative genetic model) or by a few genes of relatively large effect. Candidate genes underlying a trait can be identified with mapping and can be sequenced and compared with DNA databases of genes of known function. (The Wikipedia web site <http://en.wikipedia.org/wiki/Quantitative_trait_locus> and Lynch and Walsh 1998 provide more information.)

The genetics of migratory traits in salmonid fish has drawn attention because of conservation and hatchery rearing issues regarding these commercially important migrants. Migratory anadromous salmonids hatched in fresh water start life as dark-colored parr, and prior to migration to the sea transform into saltwater-adapted silvery smolts. In crosses between Chinook Salmon (*O. tshawytscha*) varying between first year and later smolting, the early smolting was dominant and apparently controlled by only a few loci (Clarke et al. 1994). Not only the timing but also the propensity of smolting is under genetic control. Hybrids were generated between anadromous Steelhead and freshwater Rainbow Trout, both *O. mykiss* (Johnsson et al. 1994). These hybrids were intermediate between the freshwater and migratory forms in their ability to osmoregulate in sea water, suggesting that in this case the propensity for smoltification was under additive control by multiple genes rather than genetic dominance.

In further studies on *O. mykiss* Nichols et al. (2008) used QTL analysis to assess the genetic architecture of smoltification. They assessed a number of morphological and physiological traits associated with the change from freshwater adaptation to migration using clonal lines of fish. The findings regarding QTL were particularly interesting because they indicated that only a few genomic loci contributed to variation in individual smolt-associated phenotypes and that there is one genome region strongly associated with multiple smolt-associated traits. There were possibly loci of small effect that were not detected because of the relatively small sample size, but the fact that significant differences between life-history characteristics are located within a common genome region suggests that either a single locus or linked multiple loci have an important role in migration versus residency in this salmonid species. There was also evidence that the genes for being Steelhead or Rainbow were mostly fixed in the respective lines, but there was still some evidence for Rainbow genes in Steelheads and vice versa, presumably providing some of the flexibility for migration observed in these lines. The one QTL region associated with multiple traits, however, provides insight into how a "major gene" can work to organize multiple correlated traits. In the absence of direct tests of migratory behavior, the roles of smoltification genome regions in the ultimate decision to migrate still remain to be assessed.

Further analysis of QTL in Rainbow and Steelhead has been carried out using wild populations, in this case from Alaska (Hecht et al. 2012). These authors assessed the relative genetic contributions to 27 physiological and morphological traits associated with the migratory Steelhead life history. They were able to localize 37 QTL to 19 unique chromosomal positions. These explained between 4% and 13.6% of the variance for 19 of the traits measured. As with the earlier study (Nichols et al. 2008) QTL seemed to be acting as master genetic control for important aspects of the migratory life history. In this case there were two such regions located on different chromosomes from the single major region localized in the earlier study. This suggests the possibility that locally adapted gene complexes could play a significant role in the evolution of the smoltification process. It should be noted, however, that several studies on life-history variation and migration-related traits in *O. mykiss* have localized QTL, explaining portions of variance in these traits on at least four additional chromosomes (Hecht et al. 2012). This implies some conservation of genetic mechanisms controlling the traits across populations of the species. The differences in the two studies of smoltification and the location of QTL on a number of chromosomes support the notion of a complex polygenic architecture underlying smoltification and migration in salmonids. We now have a foundation for the understanding of these complex genetic mechanisms contributing to the migration syndrome.

Genes and environments

The phenotype produced by a given genotype depends on the environment experienced by that genotype, and this fact is incorporated into quantitative genetic models with a covariance term (2covG,E—see Appendix I) to indicate genotype × environment interactions. The differential responses of a genotype can be assessed by rearing it in several environments to observe the resultant phenotypes; the patterns of response produced are known as reaction norms. A single genotype can be studied in

this way only in clonal organisms, but a reasonable alternative is to consider siblings of a single family as genotypes and divide broods across the environments to produce the reaction norms. Populations of different provenances or samples from selected lines can also be treated as "genotypes" of individuals sharing at least some genes in common.

Reaction norms yield a great deal of information about potential for response to selection when selective regimes include more than one environment, as indeed occurs with selective regimes in nature. For example, genetic correlations can be computed for the performance of the same trait in two or more environments. If negative, the correlation means that good performance in one environment may be offset by poor performance in another, so that it may not be possible to evolve optimal performance in both. A genetic correlation across environments significantly less than unity indicates a genotype × environment interaction and thus significant variation for plasticity. If the genetic correlation between environments is equal to one, it indicates that the genetic basis for the trait is the same in the two environments and independent evolution in the environments is constrained. This was the case for migration-associated traits in the wing-dimorphic cricket, *G. firmus* (King et al. 2011). In traits such as flight muscle (DLM) mass (Figure 14.8), flight allocation, and reproductive allocation no genetic correlations between pairs of treatments from low to 50% to ad-lib food provision were significantly different from one. Genes for these traits thus produced near-identical performance across food environments, suggesting a low evolutionary potential for phenotypic plasticity in the traits as a function of food level.

Four examples of reaction norms for migratory traits are illustrated in Figure 14.8. In *G. firmus* there is little difference in the expression of the long- or short-wing genotypes across food levels, with genetic correlations between environments close to one, as we have seen. In the African Armyworm Moth (*Spodoptera exempta*) there is a strong interaction between genotype and environment. Like locusts, these moths display phase polyphenism that, in this case, is expressed in the larvae. Under crowded conditions caterpillars are black and highly active, often crawling to the tops of grasses. In uncrowded conditions caterpillars are green, sluggish, and cryptic. In adults there are two genotypes expressing long flights (LW) and only short-distance flights (SW), respectively. When assessed with tethered flight the LW genotype displayed a high proportion of long-duration migratory flights, but only when reared as larvae at high densities. The SW genotypes flew for only short bursts at both rearing densities, so there was a significant genotype × environment interaction (Woodrow et al. 1987).

In the Water Strider, *Aquarius remigis*, and the Blackcap Warbler reaction norms were determined for groups of siblings. For *A. remigis* the families consisted of half sibs all of which had the same father (sire) but were offspring of different mothers (dams). These Water Strider families were split and reared at two temperatures to see whether there was an effect of temperature on the proportions of adults with long wings (Fairbairn and King 2009 and Figure 14.8). There were significant sire and dam effects, indicating that there was genetic variation for long-wing development. Furthermore there was a statistically significant sire (genotype) × temperature (environment) interaction. This interaction is illustrated in the various family reaction norms in Figure 14.8 by the crossing and diverging lines connecting the family proportions at the two temperatures.

In the Blackcap the families consisted of full sibs (Coppack et al. 2001). The treatment was an artificial photoperiod which matched that of early spring six weeks before the actual hatching date of the Blackcap chicks. The control photoperiod was that actually experienced by chicks when they hatched. Again families were split and reared at each photoperiod, and the age of onset of migratory restlessness was recorded. In this case both treatment and family effects were significant, indicating both genetic and environmental effects on the onset of migration. There was, however, no significant genotype × environment interaction, so that apparently the cross-environment genetic correlation was close to one, as in the case of *G. firmus*. The sample size was small (five chicks in each of six families) so it is possible that interaction effects were too small to detect; the fact of genetic variation is nevertheless apparent.

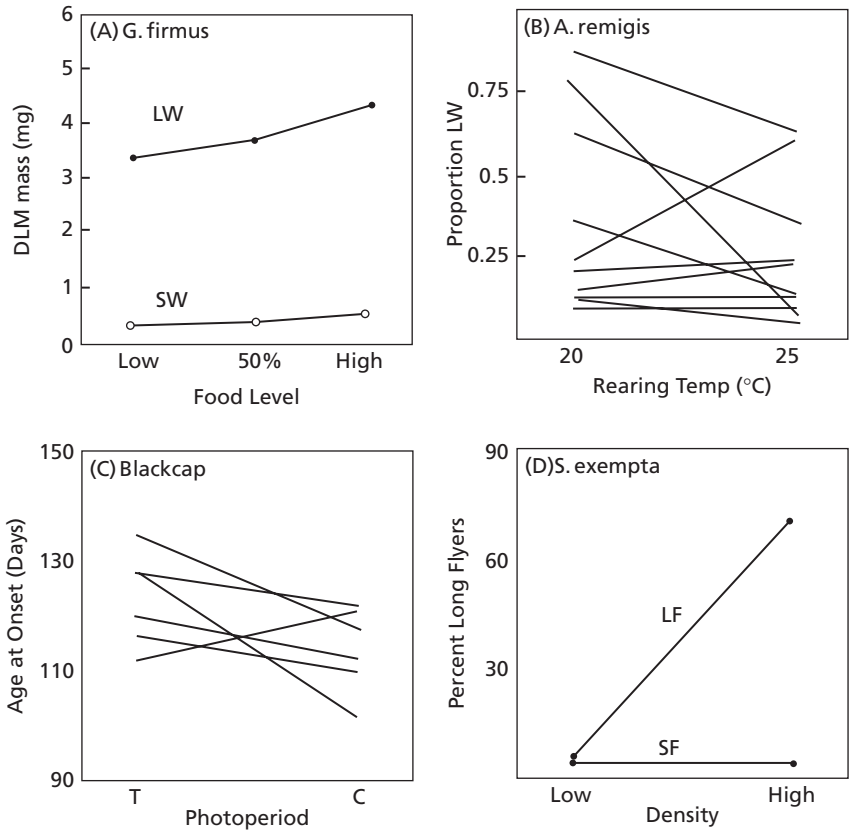


Figure 14.8 Norms of reaction and genotype × environment interactions for migratory traits in four species. (A) DLM (dorso-longitudinal muscle) mass in the cricket, *G. firmus*, as a function of food level. LW, long-wing genotype; SW, short-wing. (B) Proportion of long-winged (LW) adults of the water strider *A. remigis* eclosing from half-sib families reared under two temperature regimes. This is a sample of families drawn from the full complement studied. Crossing and diverging lines connecting points from the same family indicate presence of genotype × environment interactions. (C) Five Blackcap (*S. atricapilla*) full-sib families split and reared at two photoperiods with age at onset of migratory activity recorded. T, treatment photoperiod matching photoperiod six weeks before hatch; C, control photoperiod at hatching; genotype × environment interaction not significant. (D) Responses of long-flying (LF) and short-flying (SF) genotypes of Armyworm Moths eclosing from larvae reared at different densities. Diverging lines indicate that genotype × environment interaction is present.

Data sources: (A) King et al. (2011); (B) Fairbairn and King (2009); (C) Coppack et al. (2001); (D) Dingle (1996) after Woodrow et al. (1987).

Summing up

Studies of the genetics of migratory behavior and migration syndromes have revealed much in the way of genetic variation underlying the traits in question. This variation is often considerable and frequently leads to rapid evolution, local adaptation, and differentiation between migratory and sedentary populations of the same species. Common garden analysis and examination of hybrids resulting from population crosses reveal that rapid contemporary evolution of divergency between sedentary and migratory behavior is a common phenomenon. Urban European Blackbirds are largely sedentary whereas their rural cousins migrate. Rearing under common laboratory conditions and measuring migratory activity confirm that the two populations differ in their genes. Similarly transplant experiments using New Zealand salmon recently introduced from North America demonstrate a genetic basis for, and hence evolution of, differences in migratory timing between streams. Crosses between populations of Common Quail from Europe and a

domesticated line from Japan produce hybrids revealing that migration is polygenic and with rapid evolution of sedentary tendencies in laboratory birds. Anthropogenic influences are also at work in Soapberry Bugs. Crosses between short-winged morphs of populations originating from introduced goldenrain trees or from native balloon vine reveal evolved gene differences contributing to the development of the flight morphs in the two populations. Migration is clearly genetically complex, but equally clearly it can evolve rapidly.

In spite of complexity, there are many instances of single gene contributions to migratory traits. Single genes seem frequently to control wing polymorphisms, and the brachypterous allele is usually dominant in one-locus, two-allele systems. The development of molecular techniques has furthered the identification of genes contributing to migration. A single gene has been identified that contributes to differences in migratory populations of the Blackcap, although it is apparent that much of the variation derives from additional genes. In aphids a gene on the X chromosome controls wing form, and molecular methods have been used to locate its position on the chromosome. One allele of the gene produces long-winged males, but interestingly it is the male short-wing allele that produces the polyphenic long-winged female aphids when there is appropriate environmental stimulation. Genes have also been identified that alter metabolic processes in the muscles of migrating Christmas Island crabs and that change the timing of migration in salmon. Thus genes are clearly involved at all physiological and behavioral levels of migratory performance.

Because many genes are usually involved in producing migration syndromes, the methods of quantitative genetics have been valuable in elucidating the nature of control and constraints in the design of these syndromes. Numerous studies have now produced heritability estimates for migratory traits, and it is apparent from all of these that much genetic variation is present. This variation has resulted in both contemporary evolution and local adaptation in migratory life histories. A good example is the variation in wing-morph frequency seen among populations of the Water Strider *Aquarius remigis* in California. In the Florida populations of the Soapberry Bug, *Jadera haematoloma*, there is intimate association between host plant, beak length, flight morph, and probably reproductive traits as revealed by the pattern of genetic correlations. Selection on one trait thus affects the others as well. Genetic correlations occur between migration distance and migration activity (zugenruhe) in Blackcaps and between wing-morph frequencies and the hormone titers regulating the wing form of crickets. The analysis of acquisition and allocation in crickets reveals genetic contributions to the organization of migratory syndromes in the face of competing energetic demands of migration and reproduction. Molecular methods have now been introduced into quantitative genetics with, for example, studies of quantitative trait loci (QTL) and the smoltification process in migratory salmon. Not surprisingly these further reveal complex relationships, but offer exciting prospects for understanding the contribution of many genes and their genetic correlations to the organization of migration syndromes.

Finally, genes and interactions among genes are expressed as a function of environments; the answers to important evolutionary questions concerning migratory adaptations will involve genes, environments, and the shapes of reaction norms. Variation among environments in the expression of migratory traits as seen in Water Striders, Armyworm Moths, and Blackcaps are examples. To truly understand the evolution and function of any trait we must understand the genes, the environments in which they function, and the interactions between the two. The increasing sophistication of genetic methods and models is greatly magnifying our understanding of the physiology, behavior, and ecology of migration including the development and evolution of migration syndromes. In spite of the often formidable barriers to studying the genetics of natural populations, the insights gained should be reason enough to persevere in identifying the contributions of genes to migration.

Appendix I. The equations of quantitative genetics

Complex traits such as migration are likely to be influenced by genes at many loci. The analysis of such polygenic systems requires the methods of quantitative genetics. These are covered extensively in

Falconer and Mackay (1996) and Lynch and Walsh (1998). Here I summarize these methods briefly, so that readers who may be unfamiliar with them can follow the logic behind their use and their contribution to understanding the evolutionary genetics of migration.

The basic model assumes that both genetic and environmental effects contribute to individual differences. The mean phenotype of the population (P) equals the mean of genetic (G) and environmental (E) influences. Each individual will have its own phenotype (P_i) in turn subject to genetic and environmental effects (G_i and E_i). The total phenotypic variation present is the sum of the differences between the means and all individual values

$$\Sigma\left(P - P_i\right) = \Sigma\left(\bar{G} - G_i\right) + \Sigma\left(\bar{E} - E_i\right) \qquad (1)$$

Squaring both sides to eliminate negative values and dividing the sums of squares by the sample size gives the respective variances and covariances (as in performing analysis of variance or ANOVA) so that

$$V_P = V_G + V_E + 2\mathrm{cov}(G,E) \qquad (2)$$

This is the basic equation of quantitative genetics and it says simply that the phenotypic variance (V_P) present in a population results from genetic and environmental variance plus a covariance term indicating that genes may be expressed differently in different environments (genotype–environment interactions and correlations).

The genetic variance can be further broken down into its components where

$$V_G = V_A + V_D + V_I \qquad (3)$$

The first term, V_A, is the "additive genetic variance" and represents the degree to which offspring resemble their parents (or other relatives). If a trait were completely additive, its value would be exactly intermediate between the values in the parents (corrected for sex). Usually these traits are polygenic and arise from many genes each of relatively small effect. Because it contributes specifically to resemblance to parents and relatives, V_A is particularly important and usually best describes the genetic basis for the evolution of a trait resulting from natural selection ("Darwinian variance") at least over the short term (selection changes gene frequencies which can complicate matters over the long term—e.g., Barton and Turelli 1989). The V_D term refers to dominance variance or the tendency to resemble one parent more than the other, and V_I refers to the variance resulting from interaction among genes within the genome (epistasis). These sources of variation may be important to evolution under certain circumstances but are usually assumed to be small enough to ignore.

Because of the importance of V_A to evolution, it is important to estimate its proportional contribution to V_P or the ratio of V_A to V_P. This ratio is the *heritability*, symbolized h^2 since it is a ratio of variances. This is the "narrow-sense" heritability; the ratio of V_G to V_P is the "broad sense" heritability. Narrow-sense heritability is estimated in practice by holding the environment constant (as in a laboratory growth chamber) so that V_E and hence $G \times E$ covariance are both nil or nearly so. Estimates of h^2 can use any combination of relatives (but do not eliminate V_D if full sibs are used) with the most straightforward way being the regression of offspring means on parental mid-points with the slope of the regression estimating h^2; if parents and offspring exactly resemble each other, the slope will equal unity which thus sets the upper bound for h^2.

One can also take advantage of offspring–parent resemblances to estimate heritability from the response to selection. The equation for this is the so-called breeders equation, $R = h^2S$, where S is the intensity of selection and R is the response to selection of the trait in question. The heritability in this case is called the "realized heritability." Selection intensity is measured as the difference between the mean of the original population and the mean of the selected parents, and the response is the difference between the mean of the offspring of the selected parents and the original population mean. In cases where a trait is dichotomous, as in pterygomorphism, a threshold model is used to estimate h^2 (Pulido 2007, 2011; Roff and Fairbairn 2007). This model assumes a continuously distributed underlying trait called the *liability* and a threshold that determines the developmental trajectory of the observed trait, e.g., wing morph or decision to migrate. The shift in assumed liability after selection is the response (full discussion in Lynch and Walsh 1998).

In addition to heritability, one may also estimate the genetic correlation (r_G) between traits or the degree to which traits share genes in common. This is analogous to heritability, but instead of just the variance of a trait, the covariance between two traits is computed. Instead of starting from the squares of the individual differences as in Equation (1), we take the products of the values for the two traits which produces the covariances for each source of variation (i.e., additive, non-additive, environmental) and the phenotypic covariance is the sum of the genetic and environmental covariances

$$COV_P = COV_G + COV_E \quad (4)$$

Again in a constant environment COV_E is nil. In practice genetic correlation can be estimated by offspring-parent analysis:

$$r_G = \frac{\mathrm{COV}xy}{\sqrt{(\mathrm{COV}xx\ \mathrm{COV}yy)}} \quad (5)$$

In this equation, COV_{xy} is the "cross-covariance" calculated either from trait X in the parents and trait Y in the offspring or from Y in the parents and X in the offspring and COV_{xx} and COV_{yy} are the offspring–parent covariances for each trait separately.

PART 4

Migration and Human Biology

Humans dominate the planet. As of this writing there are some seven-and-a-half billion of us, and in pursuing our energy, food, and shelter demands we have impacted our planet to the extent that "natural" ecosystems exist, if at all, in only the remotest of areas. This is bound to have an effect on migrants and in turn necessarily affects how migrants interact with humans. Some of these latter effects are readily apparent. Virtually all insect pests that have a negative impact on our agricultural food production systems are migrants. By planting huge swaths of botanical monocultures, we produce near-ideal conditions for the massive build-up of insect migrant pests that exploit these monocultures. *Heliothis* moths, Armyworm Moths, and locusts are but three examples. To address the issue of migrant pests, I briefly discuss forecasting and pest management of locusts and the need to understand the migratory life cycles of locusts as part of successful management strategies.

Some of the impacts that migrants have on humans are perhaps less visible. One such is risk associated with infectious disease, both on humans themselves and on our domestic animals. Migrants may carry diseases, and the risk of disease may be exacerbated by preventing migrants from following their normal course, resulting in unnaturally concentrated populations. Other less-discernible impacts concern ecosystem services such as the protein and fertilizer contributed to the terrestrial environment by migrating salmon transporting these resources from the ocean deep into continental interiors via rivers and streams. Furthermore, migratory birds and bats consume millions of tons of insects during their breeding episodes at temperate latitudes. Salmon are also a human food source, and I shall discuss especially the interactions between humans and salmon in California, and how conflicting interests and poor water management have influenced a valuable commercial resource to the detriment of both the fish and California's human ecology.

As the final topic in Chapter 15, I consider the effects that humans are having on the climate and how this might affect migrants. Most of the attention has focused on migrant birds, but other migrants are also affected. Bird migrations are heavily dependent on the appropriate timing of arrival and departure and the synchronization of those events with the populations of prey, nectar, or seed resources necessary for rearing of young. As a result, climate change has become an important topic in the study of bird migration. In all cases there is an overwhelming need to understand the basics of migration biology and the interaction of that biology with social needs, political realities, and the ultimate state of our planet.

CHAPTER 15

Human interactions with migration

Pest management and forecasting

An extraordinary number of the world's major agricultural pests are migrants, and to successfully solve the problems they generate through economic losses it is necessary to understand the role migration plays in their biology. One thread woven through much of the discussion in this book is the relation between migration and temporary or ephemeral habitats. The relationship goes a long way toward explaining the sometimes overlooked migratory characteristics of most agricultural pests. Some 50 years ago the British ecologist Sir Richard Southwood (1962, 1977) noted that not only are insect migrants likely to be denizens of temporary habitats, but that most of our major crops are descended from ruderal ancestors evolved to colonize open areas and bare ground forming the early stages of ecological succession. These epitomize ephemeral conditions, and so our ancestral crops were likely already to be associated with a group of species well adapted to an itinerant, migratory lifestyle that is now supported by large-scale farming and industrial agriculture. The result has been an explosion of species with itinerant life histories that we now consider pests. These include insects, mites, molds and rusts, nematodes, and vertebrates such as quelea birds (Chapter 3) and house mice (*Mus musculus*). Species of all these groups cause severe crop losses. The greatest economic damage as a consequence of migratory activity is caused by insects, and I shall focus on one of the most devastating groups of insect, the locusts.

An indication of the impact of locusts on crops can be seen with the Desert Locust, *Schistocerca gregaria*, whose biology was discussed in Chapter 11. The scale of invasions by this species is frequently described from biblical verse to the dry statements of pest management reports. Two such descriptions convey the magnitude of populations during outbreaks of this species (Betts 1976). Radar observations near Delhi, India, in July 1962 recorded densities of about one locust per 10 m^3 of air up to an altitude of ~1,500 m and over an area of ~1,400 km^2. When one considers that a single locust eats its own weight of crop in a single day, it is no wonder that a swarm of locusts leaves "not any green thing" as noted so succinctly in the Book of Exodus. One swarm in the Horn of Africa was estimated to have consumed around 80,000 tons of fresh vegetation per day, or enough to feed 400,000 people for a year (Roffey 1985). Left unchecked, the damage caused by locust swarms can reach staggering economic proportions in a very short time.

The Food and Agriculture Organization of the United Nations (FAO) has collated information on Desert Locust Swarms going back to the 1930s (Cheke and Tratalos 2007). The data have been incorporated into a system, the Schistocerca Warning Management System or SWARMS (Magor and Pender 1997) used to examine and correlate locust outbreaks across regions. The time-series can be used to make forecasts of where locusts are likely to cause damage once outbreaks and swarms have been observed, although the vast range of the species and its extraordinary capacity for movement across political boundaries makes forecasting difficult at best. Relatively simple models, however, imply that early interventions and even conservative rates of control may contribute to significantly reducing the size of upsurges and plagues of the Desert Locust (Magor et al. 2008).

Locust-forecasting attempts illustrate the necessity for understanding the biology of the migrant

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pest, a point illustrated some 35 years ago by Kennedy and Way (1979) and Wellington (1977). Kennedy and Way (1979) summarized how radar, rather than simply functioning as a monitoring tool, has provided a series of rather profound insights into the behavior of long-distance migrants from locusts to moths. These insights include routine nightly activity, selection of winds of appropriate speed and direction, and the ability to maintain a common orientation even at night (Chapters 4, 5, and 8). The insects are, in other words, not being simply "passively" transported by winds but are very actively engaging in migratory activity and are concentrated at their destinations, not dispersed. Understanding the strategic and tactical bases for that activity and its outcomes is necessary for the design of monitoring programs and interventions to minimize the impact of invasions on to major crops.

In addition to the behavior in flight, it is important to understand the ecology of the migrants on the ground. This is nicely illustrated by studies of the Australian Plague Locust (*Chortoicetes terminifera*) that incorporate breeding ecology, conditions for nymphal development, and radar monitoring of flight (Hunter 1989, 2004, 2010; Drake et al. 2001; Deveson et al. 2005; Drake and Reynolds 2012). Current control programs result from some 80 years of research on this species, first by CSIRO and State Departments of Agriculture, and then by the Australian Plague Locust Commission (APLC) established in 1974. The APLC was initiated to control locusts both at their sources in the arid interior of Australia and in the crop invasion areas. The latter charge resulted in an intense research program to understand the ecology of the locusts, and the results are contributing to preventive control programs.

The Australian Plague Locust migrations arise in the arid interior of the continent and move outward in the spring and summer to the agricultural regions of southeastern Australia (Figure 15.1). The locusts prefer open plains of heavy clay soils along creek lines, usually bearing a stony cover. This knowledge allows concentration of the search for developing populations to about 20% of inland Australia in a region roughly centered on the point where Queensland, South Australia, and New South Wales meet, including most of the Channel County of Southwestern Queensland (so called because of its pattern of seasonal anastomosing stream channels), and the northwestern corner of New South Wales. Important to the survival and growth of the locusts in the region are the presence of green grasses on which to feed, especially Curly and Barley Mitchell Grasses and Annual Button Grass, and which are in turn tied to rainfall. Thus it is necessary to combine locust ecology with regional meteorology. A single fall of about 20 mm of rain and a mean monthly temperature above 23°C allows sustained growth of Barley Mitchell Grass, whereas Curly Mitchell Grass requires about 40 mm of rain. Button Grass grows under these conditions, but goes dry after about six weeks with no further rain. The Mitchell Grasses, however, can last two months without rain, and, even if dry, may allow locusts to complete development so long as they are still somewhat green. A single rainfall event can thus produce a locust outbreak. Knowing these facts of locust ecology allows the APLC to predict where plagues are likely to develop using the data from a widespread geographic information system (GIS)-based Decision Support System in eastern Australia.

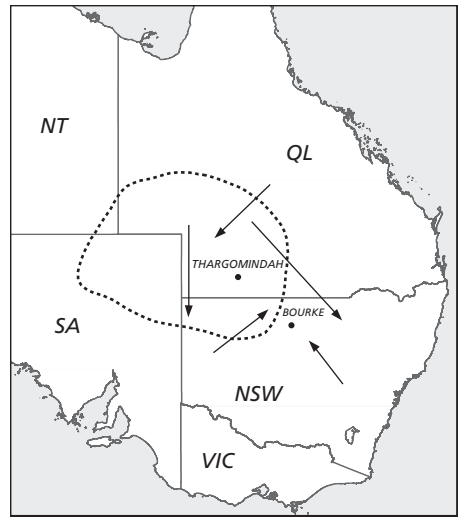


Figure 15.1 Map of eastern Australia showing approximate area where the Australian Plague Locust nymphs develop, the two radar stations for monitoring locust swarms (Thargomindah and Bourke), and the pathways (arrows) of locust swarms detected by the radars. NT, Northern Territory; QL, Queensland; SA, South Australia; NSW, New South Wales; VIC, Victoria. Adapted from data and maps in Drake and Reynolds (2012) after Deveson and Walker (2005) and Drake et al. (2001).

Preventive control involves early intervention using information from the Decision Support System to concentrate survey and control efforts. Bands of locusts are usually visible from overflying aircraft which can then direct treatment efforts to the proper location. The APLC using this information has successfully controlled outbreaks by spraying on average only about 1,000 km^2 per year, a miniscule proportion of the inland range of the locusts. Furthermore chemical use has been reduced by using the lowest effective dose and by using products that can be applied in barriers 300–500 m apart so that only a small proportion of the area is sprayed. Bands of locusts come into periodic contact with these barriers as they march across the landscape. Originally chemical insecticides such as organophosphates were used, but more recently a biological agent derived from *Metarhizum* fungi has been used effectively, the first large landscape-scale use of a biopesticide anywhere in the world to control a major insect pest. The combination of narrowly targeted pesticide use with effective biopesticides minimizes the detrimental side-effects of locust control.

Radar has been effectively used to characterize Australian Plague Locust migration once the insects reach the adult stage and swarm (Drake et al. 2001; Deveson et al. 2005; Drake and Reynolds 2012). Two monitoring radars have been operating for some time at Thargomindah in western Queensland and at Bourke in northern New South Wales (Figure 15.1 and see Figure 4.8). The presence of only two radars limits observations, but these have still supplied impressive amounts of useful data. For example, over the locust flight season from November to April displacement distances totaled about 100–200 km, along more or less straight paths—quite adequate for invasions into agricultural areas. Individual nightly distances traveled could be considerably farther, even up to 400 km with flight speeds in the range of 5–16 m/s, higher usually than speeds that would be sustained with only wind transport. There is thus an active component to these swarm migrations with wind and flight speeds additive. A westward directional bias over the flight season means that there is presumably return migration to the breeding areas by the generation(s) produced by the swarms invading areas outside the source regions of the arid interior. The contributions of both behavioral and ecological studies are apparent in developing effective strategies of pest management while minimizing undesirable environmental impacts.

Migration and infectious disease

Because migrants travel over much of the surface of the planet, a recurring concern is the possibility that they may carry and distribute agricultural or livestock pathogens and human infectious diseases. Livestock diseases, for example, co-occur in both domestic animals and in wild migratory ungulates. As a consequence, there are frequently efforts to restrict the pathways of the migrants. An example occurs in the Yellowstone region of North America where a North American Bison herd occurs within Yellowstone National Park. During harsh winters, especially, the bison exit the park following established pathways in the Yellowstone and Madison River valleys to sites at lower elevations where there is less snow cover and so more access to forage (Wilcove and Wikelski 2008). Because of rancher fears that the migrating bison will transmit brucellosis to livestock, the migrants are hazed back into the park or killed when they stray outside the park boundaries. No serious consideration has been given to simply removing livestock from the winter range of bison. Elk migration is less restricted in the region, and the elk are provided with supplemental forage. Ironically these higher-density, non-migratory populations support higher frequencies of brucellosis infection (10–30% versus 2–3% in unrestricted migrants; Cross et al. 2010). Human activities that restrict long-distance migrations and encourage the formation of year-round sedentary populations can increase the incidence of zoonotic diseases in humans (Altizer et al. 2011). This has indeed occurred in the case of flying foxes (*Pteropus* fruit bats), common in Australia and Asia where restriction of movement facilitated outbreaks of human and domestic animal viruses through extra contact with pigs and horses.

Altizer et al. (2011) have examined Monarch Butterfly populations with respect to infection rates of the protozoan parasite *Ophryocystis elektroscirrha*. They assessed rates of parasitism in three populations: the highly migratory eastern population wintering in Mexico, the population wintering on the

coast of California which migrates shorter distances to breed in the interior west, and the resident population in southern Florida (see Chapter 3). Differences in infection rates were clear. Rates in Florida hovered in the 60–70% range over eight years from 1989 to 1997, whereas rates for the California population were consistently around 30% over a 20-year period, and in marked contrast rates in the eastern highly migratory population never exceeded about 3%. In this latter population infection rates were higher at the end of the temperate breeding season than they were for butterflies that completed the migration to central Mexico, probably reflecting shorter distances flown by infected butterflies as shown in experiments. Because of habitat loss the Monarch migration is an "endangered phenomenon" (Brower and Malcolm 1991; Dingle 1996). If climate-related shifts in migration phenology cause reduction in migratory tendency, parasite infection could have a significant impact on an already at-risk population through both increased infection rates and increased virulence, both already noted for more sedentary populations.

In view of the evidence that reduced or suppressed migration may actually increase infection rates of endemic diseases, possibly increasing risks to humans and their livestock, it is worth asking whether transmission of disease by long-distance migrants poses a significant risk. There are very few examples of long-distance pathogen transport by migrants in the literature (Altizer et al. 2011). In recent years there has been concern because wild migrant ducks, geese, and shorebirds are known for being natural reservoirs of various strains of avian influenza viruses, some of which, like the now notorious H5N1 strain, can be lethal when infecting humans. Two studies, however, indicate that these migrant birds have been unfairly blamed for outbreaks in humans. There is, for example, no evidence for frequent virus exchange between Eurasia and North America. Some viruses have appeared in shorebirds and gulls, but the evidence suggests that any intercontinental transmission is rare (Krauss et al. 2007). Studies in China and Mongolia indicated that avian influenza outbreaks were related to latitude and poultry density (!), but did not bear a relation to the wetland habitats of waterfowl and shorebirds nor to the core of the migration corridor (Takekawa et al. 2010). In both these cases understanding the behavior and ecology of the migrants was essential to understanding the risks and non-risks of viral spread.

Based on current evidence it would seem that as negative human impacts on migrants increase, so do the risks of disease transmission between migrants and humans and livestock. It is clear, however, that we have much to learn about the relation between the migratory life histories of pathogen hosts before we can identify ecological and epidemiological relationships between host movement and disease dynamics (Altizer et al. 2011).

Pacific salmon

> . . . every thing that liveth, which moveth, whithersoever the rivers shall come, shall live: and there shall be a very great multitude of fish . . . [and] the fishers shall stand upon it . . . to spread forth nets; their fish . . . exceeding many . . . And by the river . . . shall grow all trees for meat . . . [which] shall bring forth new fruit . . .
>
> Ezekiel 47:9–12 (King James version)

Perhaps no other organisms so epitomize the negative ecological consequences of human activity than the Pacific salmon species of the western USA. As much as the migratory bison characterized the pre-settlement Great Plains, so did the salmon define the rivers of the west coast of North America from California to Alaska. The great salmon migrations that once extended from bank to bank in western US rivers and streams are now reduced to a mere remnant. The causes are many (Table 15.1), but the most obvious is the damming of almost all these rivers south of Canada for hydroelectric power or to supply water for agriculture (Reisner 1993; anyone who wishes to truly understand the relation between water, politics, and the growth of the American West should read Marc Reisner's magnificent book). Not only do the dams impose obstacle after obstacle on the way to breeding sites, but the spawning streams have become silted, polluted, and warmed from the backed-up lakes and agricultural and logged forest run-off.

The history of the Columbia River, which borders the states of Oregon and Washington, illustrates the decline of salmon populations. Prior to the 1930s

Table 15.1 Factors causing decline of salmon populations in California and elsewhere.

Factor	Impact
Major dams	Eliminate access to breeding sites
Agriculture	Reduced river flow, siltation, pollution
Grazing	Trampled stream banks, siltation, reduced flows
Rural residential	Water removal, stream-bed alteration
Urbanization	Stream alteration, rampant pollution
In-stream mining	Stream-bed alteration, legacy effects
Hard-rock mining	Pollution from tailings, heavy metal pollution
Transportation	Confining of stream channel, emissions pollution
Logging	Erosion, stream degradation
Fire	Post-fire erosion, increased stream temperature
Estuary alteration	Habitat degradation
Recreation	Usually minor but can affect flows and sedimentation
Fish harvest	Direct population impact
Hatcheries	Competition for space, loss of fitness
Alien species	Predation, competition disease

Source: Katz et al. (2012).

the Columbia was the greatest salmon river in the world, and the migrations supported Native American tribes along its length. Fifteen million fish migrated upriver to spawn. Grand Coulee Dam was completed in 1941. Today, fewer than two million salmon make the run up the Columbia, and, fish ladders notwithstanding, about half of the watershed's migrations are in danger of extinction. The Snake River, a major tributary of the Columbia, produced 1.5 million or more Chinook Salmon in the late 19th century; by 1960 this migration had fallen to 125,000 and the 1990 count yielded only 26,500 fish (Dingle 1996 and references therein).

The situation with California salmon is even more dire, with several species and populations endangered or vulnerable (Katz et al. 2012); examples from Chinook Salmon are given in Table 15.2. By 1980 there were some 1,250 major reservoirs in California, and *every* major river but one had been dammed at least once (Reisner 1993; Figure 15.2). The Stanislaus River alone, on its short run from the Sierras to the sea, had been dammed no less than 14 times! The Friant Dam on the San Joaquin River singlehandedly wiped out a spawning run of 150,000 fish. The San Joaquin drains the southern half of the Central Valley of California (the San Joaquin Valley) and empties into the Sacramento River Delta which in turn empties into San Francisco Bay. There are no salmon runs remaining in the San Joaquin system (Figure 15.2), and most in the Sacramento River system draining the northern part of the Central Valley have also been eliminated.

The California Central Valley has a Mediterranean climate with wet winters and hot, dry summers, and the flows of the San Joaquin and Sacramento Rivers have been in great demand to support both agriculture and the major cities. The excerpt from Ezekiel at the beginning of this section describes the multiple uses of a river in a Mediterranean climate. The problem now is the excessive demands put on the flows of the Sacramento and San Joaquin Rivers. Perhaps no other single water manipulation has had such far-reaching impacts on salmon as the California Central Valley Water Project (CVP). Water is taken from the Sacramento River and its tributaries in northern California and transported hundreds of miles to irrigate the pastures, cotton, almonds, and alfalfa of the previously dry and barren (in the summer) San Joaquin Valley and to supply water to the sprawling metropolis of the Los Angeles basin after being pumped over the Transverse Ranges at the

Table 15.2 Populations of Chinook Salmon (*Oncorhynchus tshawytscha*) in California and their current conservation status.

Population	Status
Upper Klamath–Trinity River spring run	Endangered
Central Valley late autumn run	Endangered
Central Valley winter run	Vulnerable
Central Valley spring run	Vulnerable
Central Valley autumn run	Vulnerable
Upper Klamath–Trinity	Vulnerable
California coast autumn run	Vulnerable
Southern Oregon/Northern California coast autumn run	Near-threatened

Source: Katz et al. (2012).

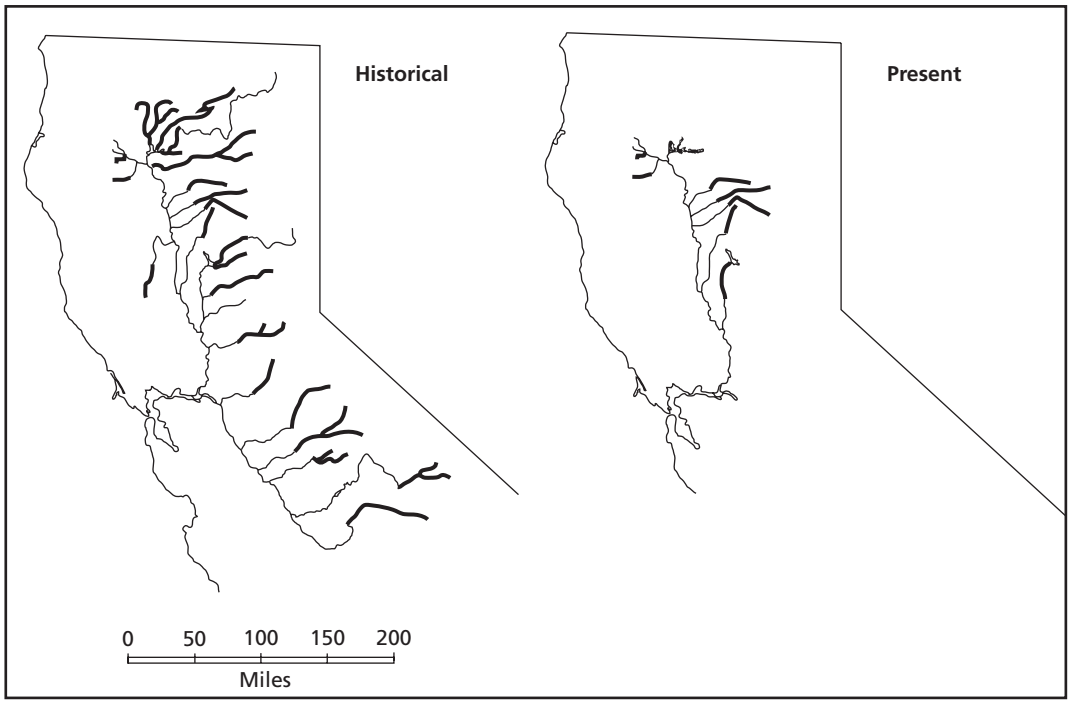


Figure 15.2 Spawning areas (heavy lines) of the Chinook Salmon of California in historical times and present. From Dingle (1996) after a map provided by Peter Moyle.

southern end of the Central Valley. To put this in perspective, more than 70% of California's stream flow originates from north of the Sacramento Delta, where in the northwest rainfall averages >4 m per year, but 80% of the water is used south of the Delta (Börk et al. 2012). The dams and the huge pumps—one State and one Federal—that push water to the south place one impediment after another in the paths of salmon swimming upstream to spawn and of their more fragile offspring returning to the ocean via the Delta. In dry years, especially, untold numbers of juveniles are ground up in the pumps. Supposedly to reduce the impact on fish but increase potential water supplies, there are now (in 2013) plans for two tunnels to deliver water from the Sacramento River by passing under the Delta and depositing "muck" from construction on Delta islands (including a Nature Conservancy refuge for wintering Sandhill Cranes).

The Sacramento River (and formerly the San Joaquin) is unique among world salmon rivers in that there are no less than four genetically distinct annual runs of Chinook Salmon (Moyle 2002 and personal communication) whose combined abundance was once two million fish annually (Katz et al. 2012). These runs reflect the flexibility in salmon life histories (Chapter 12) matched by natural selection to the habitat diversity of the pre-dam Sacramento/San Joaquin drainage (Figure 15.2). At the turn of each new year, the winter-run Chinook migrate up the Sacramento. These fish are still not fully mature; they are silver-sided and their meat is firm, making them the most desirable fish from a commercial perspective. Once the salmon enter the river, they mature rapidly, developing their gonads as they move through the cool water flows of winter, up to the smaller tributary streams. They spawn in the early spring run-off in April and May, and the eggs incubate in the gravel during the summer in spring-fed waters that keep them cool and viable. The young then return to the sea the following year. In 1967 about 200,000 fish entered the river system,

but numbers fell steadily until in 1991 only 191 fish made it upstream to the Red Bluff Diversion Dam (built in 1967) (Dingle 1996). Numbers are somewhat better now, but the population is listed as vulnerable (Table 15.2) and is no longer commercially viable.

The spring run is the second annual run to enter the river, doing so during snow melt from March through May. It may at one time have been the most abundant run in California (Campbell and Moyle 1991). As with the winter run the gonads are immature, and these, too, are excellent eating fish. These salmon migrate into the tributaries and spend the summer in deep pools where water is cool. They spawn from September through October, and the young spend a year in the streams before proceeding downriver and out to the sea through the Delta. Because they must spawn in the upper reaches of the Sacramento drainage these fish, and those of the winter run, are the ones most susceptible to the adverse effects of dams. Because they were still not mature when they entered fresh water, these spring-run salmon were commercially the most valuable. However, they too are listed as vulnerable (Table 15.2), and there is no longer a commercially sustainable fishery.

The two remaining salmon runs in the Sacramento occur in the autumn and late autumn. In contrast to the winter and spring runs, autumn-run fish are fully mature when they enter the river. Because they are almost ready to spawn when they leave the sea, they reproduce quickly in the lower reaches of the drainage as soon as the water cools. These are the big river spawners much favored by fish hatcheries, because as they are mature when caught, holding time in the hatcheries is short. The conversion of energy and materials to gonads, however, means that the meat is already losing firmness when the salmon are caught by either commercial or recreational fishermen. Ironically the autumn run is now the only sustainable commercial fishery, even though vulnerable (Table 15.2). The final and fourth run of the year is the late autumn run which enters the river in October and continues until as late as February. Like the autumn-run fish, they spawn in the main river from January through March. The fry hatch usually in June and spend a year in the river before migrating to the sea. The autumn and late autumn runs are less likely to be blocked by dams, but they suffer greatly from warm, sluggish flows in drought years and from the diversion of water by the Delta Pumps. The late autumn run has suffered so much that not only is it no longer commercially viable, but is also listed as endangered (Table 15.2).

Salmon are cold-water fish, and temperatures suitable for spawning for populations in the lower reaches of rivers, like the autumn-run Chinook, depend on cool flows, nowadays largely from the deep lakes behind dams. In drought years, such as have occurred in some years of the first decade of the 21st century, the problem of sufficient cool water flows becomes acute. California Fish and Game Code 5937 (Box 15.1) gives clear priority to below-dam fish, but it has been little-enforced and never consistently as per intent by water rights agencies (see Börk et al. 2012 for a full discussion). The demands for water by Central Valley industrial agriculture even in drought years has had a severe impact on salmon, with water exports from the Delta doubling over the past 45 years (Yeoman 2013). The ever-increasing

Box 15.1 California Fish and Game Code section 5937

Code 5937 was passed by the California Legislature in 1915 and tried to strike a balance between dams and native fishes and to protect below-dam fish. The Fish and Game Commission of the 1920s never managed to integrate it successfully into water law, and subsequent, popular, vast water projects left the law effectively dead by the 1950s (Börk et al. 2012). The code is as follows:

"The owner of any dam shall allow sufficient water at all times to pass through a fishway, or in the absence of a fishway, allow sufficient water to pass over, around, or through the dam to keep in good condition any fish that may be planted or exist below the dam. During the minimum flow of water in any river or stream, permission may be granted by the department to the owner of any dam to allow sufficient water to pass through a culvert, waste gate, or over or around the dam, to keep in good condition any fish that may be planted or exist below the dam, when, in the judgment of the department, it is impractical or detrimental to the owner to pass the water through the fishway."

demands for low- or zero-cost water have been likened to ". . . giving drink to a drunk. It's never enough." The character of the demand is revealed by the large signs that line Interstate 5 in the San Joaquin Valley—"Congress created desert" (!) and calls to vote out Californian senators and representatives who support more shared and efficient water use. In very dry 2013 a run of around 270,000 salmon was expected in the Klamath/Trinity River system, and the Bureau of Reclamation planned to release 62,000 acre-feet (water one foot deep over one acre) of cold water from Trinity Lake to sustain migration and spawning (65,000 fish died in 2002 when this was not done). San Joaquin Valley farmers in the Westlands Water District 300 miles to the south, however, sued in Federal court to prevent the release and instead transfer the water to them. This is in spite of the fact that the District has only "junior water rights," allowing water access only in extra-wet years with a water surplus (McManus 2013).

To mitigate for habitat loss and the blocking of upstream runs by dams, the State of California has built eight fish hatcheries where returning adult migrants are funneled into holding ponds, and their eggs are harvested and fertilized (Yeoman 2013). The millions of fry produced live in the hatchery ponds until they are released into the river to migrate back to the sea. The problem is that these genetically uniform fish become adapted to hatchery conditions—another example of contemporary evolution (Hendry et al. 2008)—and do poorly in the wild. A 25-year time-series analysis of Snake River Chinooks demonstrated a strong negative relationship between survival and the number of hatchery fish released (Levin et al. 2001). The fish are unable to deal with predators and also are particularly prone to effects of poor ocean conditions as when currents weaken and nutrient-rich upwellings are reduced. The years of hatchery releases have thus substantially diluted the robust genotypes of the original wild stock.

The decline in fish numbers in California has also led to substantial job losses. Associated with commercial and recreational salmon fishing are businesses such as marinas, restaurants, tackle manufacturers, and sporting good shops as well as the boats serving both types of fishing (Yeoman 2013). It is estimated that in 1978 there were some 50,000 offshore and onshore jobs associated with salmon fishing (Dingle 1996); by 1992 there were only about 10,000 jobs left. Recent dry years produced substantial drops in Chinook runs that fell from some 770,000 fish in 2002 to 91,000 in 2007, bottoming out at 41,000 in 2009. Runs have rebounded to 284,000 in the fall of 2012, but 2013 was again a very dry year. The fishery collapsed in 2007, and California officials estimated a cost of $255 million to the economy with job losses at 2,260. More jobs were lost after 2009. Commercial salmon fishing licenses fell from 1,521 in 2003 to 1,149 in 2012, and not all the vessels are active. And San Joaquin Valley agribusiness is in the courts demanding more water, even though water exports from the rivers have doubled over the last 45 years.

I tried to end my 1996 discussion of California salmon on a somewhat optimistic note. I no longer feel optimistic. There will be occasional reprieves in the fluctuating cycle of "boom and bust," but I see little hope of anything but a fringe industry and associated businesses based on salmon. One salmonid, the Bull Trout *Salvelinus confluentis*, is already extinct in California and essentially all other species are endangered, threatened, or vulnerable (Table 15.2 and Katz et al. 2012). Human population growth, agribusiness, and money are a lethal combination with respect to wild salmonids. Attempts to stave off what seems to be inevitable continue, including the formation of the 3,000-member Golden State Salmon Association, but there is real fear that the salmon-fishing industry in California will disappear. That fear is well founded.

Bird migration and climate change

> . . . there is a need to attack the big issues rather than risking affirmative science.
>
> Knudsen et al. (2011)

One of the most important human impacts on world ecosystems is climate change. The increasing amounts of CO_2 entering the atmosphere are having worldwide effects that include increases in annual mean temperatures, changes in rainfall patterns, the melting of high-latitude ice sheets, a rise in sea level, and an increase in ocean acidification. The mean temperature and rainfall pattern changes,

in particular, have been cited as leading to changes in both migration patterns and population trends among birds. There is now a large literature including a book (Cox 2010) on the subject, but a shortage of firm conclusions. General trends seem apparent, but the problems inherent in obtaining reliable data on highly mobile avian species have made the evaluation of claims and trends difficult. For relatively sedentary species with well-documented information on distributions and habitats, such as European butterflies, extension of ranges northward at both north and south limits of distribution is confirmed (Parmesan 2006). This may be accompanied by extinction in the former range. There is still, however, an insufficient understanding of how the impacts of climate change integrate over the life cycle, including that part devoted to migration (Knudsen et al. 2011).

In a useful attempt to assess the various claims of the influences of climate change on migratory birds, a large group of researchers engaged in the subject have co-operated on a combined review of the available evidence (Knudsen et al. 2011). They evaluated ten "claims" regarding climate change impacts, seven of which, with brief statements of the relevant evidence, are outlined in Table 15.3.

Table 15.3 Claims of effects of climate change on bird migration and extent of supporting evidence.

Claim	Evidence
1. Birds advance spring migration	Strong evidence in support, but variability not understood
2. Phenological response a function of migration distance	No firm patterns so far established
3. Migration distance and routes change	Evidence for range changes, more evidence for shortening than lengthening routes
4. Rigid control (e.g., by endogenous rhythms) limits response	Not Clear
5. Responses constrained by annual cycle across space and time	Little empirical knowledge regarding climate change
6. Increased trophic mismatch on breeding grounds	Limited empirical support, few detailed studies
7. Population declines of migrants	Population trends affected, but few studies on multiple factors

Source: Knudsen et al. (2011).

The review weighed the extent of agreement among the authors with respect to the evidence presented.

The first three claims listed in Table 15.3 relate to the timing of migration and the routes followed. The strongest evidence concerns the first claim, that there is a trend toward earlier migration of birds in the spring, a trend that is apparent in Europe, North America, and Australia. Zduniak et al. (2010), for example, examined the passage migration of the Steppe Eagle, *Aquila nepalensis*, through Israel over the years 1977–2008. There was a rapid advance in the date of first spring passage which may have been further reinforced by competition for fewer breeding territories due to habitat deterioration. A possible further effect of habitat deterioration was a declining population of these eagles. Earlier arrival is also seen on a scale across species and localities. In western Europe a survey of 44 localities and 80 species of long-distance migrants found that first-arrival dates advanced on average about 2.2 days per decade across the years 1960–2006, and in England from 1971 to 2000 arrival dates of 17 of 20 trans-Saharan migrants advanced about 8 days (Cox 2010). There is thus good evidence for advancing dates of spring arrivals.

The second and third claims in Table 15.3 concern distances and routes. Long-distance migrants have been said to be less able to adjust to phenological shifts on the wintering grounds, the cause being stronger stabilizing selection (Pulido and Widmer 2005). Evidence, however, is indirect. Studies of the Dark-eyed Junco (*Junco hyemalis*) in North America suggest that this short- to medium-distance migrant is able to adjust phenotypically. When juncos were provided with extra food on the wintering grounds prior to departure, there was an advance in the timing of migration (Bridge et al. 2010). A number of other studies, however, reveal no consistent pattern in short-distance migrants, at least as a function of temperature. Both et al. (2010) studied short- and long-distance migrant assemblages in various habitats in The Netherlands between 1984 and 2004 and found that long-distance migrants declined in forests but not in less-seasonal marshes, whereas residents and short-distance migrants showed no decline in either habitat. Meta-analyses are less conclusive, however, so the case for a phenological response as a function of migration distance

is not clear, even though the assumption is that differences are likely.

With respect to the third claim that distances or routes may change, there is a suggestion that selection resulting from climate change will lead to adaptive responses in pathway or distance (Coppack et al. 2003; Pulido and Berthold 2010). If warming advances the onset of abundant food resources for feeding young, migrants that arrive late will be unable to take advantage; selection should thus favor earlier spring arrival. Coppack et al. (2003) exposed three European migrants, the Garden Warbler (*Sylvia borin*), the Common Redstart (*Phoenicirus phoenicirrus phoenicirrus*), and the Pied Flycatcher (*Ficedula hypoleuca*), to the photoperiods they would experience if they shortened southward migration to winter north of current wintering sites. These photoperiods triggered earlier onset of migratory activity and so would advance migration north if experienced by the birds in nature, a phenotypic response reinforcing any selection for shorter migration distances. Pulido and Berthold (2010) working with the Blackcap (*Sylvia atricapilla*) found that in wild captured birds, migratory activity measured in the laboratory decreased significantly between 1988 and 2001. Furthermore, in laboratory-reared birds, four generations of selection resulted in a significant decrease in migratory activity. The studies by Coppack and colleagues and Pulido and Berthold suggest responses to selection favoring evolution toward shorter migration distances or even residency. This is further supported by well-documented shifts in both wintering and breeding ranges toward the north, in other words toward areas of previously harsher climate (Knudsen et al. 2011).

The fourth claim regarding rigid control concerns primarily the fact that the role of endogenous annual rhythms in programming migration is well documented (Chapter 6). It has been speculated that such programming might limit response to climate change, especially since the rhythms in some species have been shown to be under genetic control (Helm and Visser 2010; Helm et al. 2013), and there are data showing that migration timing can be constrained by the environment (e.g., Bridge et al. 2010). At present it is apparent that there is endogenous control of timing and movement along migration routes, but it is not clear how rigid such control is in nature and how much it might constrain any responses to climate change.

The fifth claim, that responses may be constrained by the complexity of the annual cycle, is an interesting one, but unfortunately there are few data. The idea here is that a migrant experiences many different environments and conditions during its life cycle, and climate can affect these in different ways. This notion has been considered in the case of salmon (Crozier et al. 2008). Salmon experience different environments in different life-history stages so that climate change could produce selection acting in conflicting ways by changing phenotypic optima and distributions. How varying forces of selection would act at different stages is not clear, given the various contributions of the environment, plastic responses, heritabilities, and genotype × environment interactions in different stages, places, and times.

Claims 6 and 7 in Table 15.3 relate to the population ecology of migrants. The claim of a trophic mismatch suggests that climate change influences the phenology of the breeding food source, so that birds arriving on previous schedules may be too late and suffer population declines resulting from insufficient breeding resources. Saino et al. (2011) examined the spring arrival times in Europe of 117 migratory bird species. These birds arrive at a time of higher "degree-days" (number of degrees above a certain threshold each day) and may suffer from a thermal delay causing a mismatch, especially if coming from sub-Saharan Africa. Species with a greater thermal delay showed larger population declines, consistent with a mismatch. There are, however, few other studies and little information on multiple factors. It should also be noted that some species seem to be increasing with climate change. Nilsson et al. (2006b) found that, in parallel with increasing winter and annual temperatures in Sweden, the population of the partially migrating Blue Tit (*Parus coeruleus*) increased, but the proportion of migrants did not change. This latter result contrasts with the way climate change has been predicted to act on migrants (e.g., Pulido and Berthold 2010). The number of migrants observed at Falsterbo was a function of the beech mast crop (the winter food source) and the size of the breeding population.

We can sum up this discussion of climate change and bird migration by noting that there is not a great deal of agreement among ornithologists about the impacts of climate change on avian migrants and their causes (Knudsen et al. 2011). There is agreement that patterns of phenological change in spring migration have been established, at least for birds breeding in Europe and North America, except that little is known about departure patterns of long-distance migrants from their wintering areas. Coping with climate change will depend on adaptive responses, either phenotypic or in response to natural selection. These will need to be evaluated across the entire life cycle in organisms that travel often great distances. The task is obviously not easy and poses significant issues of sampling effort and data reliability, and the problems inherent in searching for general patterns cannot be overestimated. Given the enormous ecological and aesthetic value of avian migrants, however, the challenges cannot be ignored.

Summing up

The four examples discussed in this chapter span the ways in which the behavioral ecology of migratory species may impact our lives. The fact that so many important agricultural pests are migrants makes it imperative that we understand the role migration plays in their life cycles. Movement is an integral part of the population dynamics of these species, and in no group is this more apparent than in the locusts. The migratory abilities of the Desert Locust mean that its range and its potential for crop damage extend over much of Africa and western Asia. The need for widespread international co-operation for monitoring and control has led to the involvement of the Food and Agriculture Organization of the United Nations and the development of a warning system to deal with outbreaks over the entire range. On a smaller scale, our understanding of the biology of the Australian Plague Locust means that control efforts can be highly focused on areas where populations are increasing, and so minimizing the use of pesticides with collateral consequences. The strategic placement of radar units allows migrating swarms to be followed and advance warning provided where appropriate. The control program for the Australian Plague Locust is a prime example of success from the melding of basic and applied science.

The possible relationships between human diseases and their transmission by migrants have received a flurry of attention in recent years because influenza viruses have been associated with species of migrant. Perhaps counterintuitively the existing data suggest that migration may be more of an escape from disease than a means of disease spread. In fact there is evidence from migrants such as large mammals, which share diseases with domestic livestock, indicating that prevention of migration and hence concentration of populations increases disease risk. Here again, it is imperative to understand the basic ecology and behavior of the migrants if we are to fully comprehend their role in the epidemiology of disease. Model migratory organisms including the Monarch Butterfly have important roles in leading to epidemiological understanding.

Perhaps the most tragic outcome of the conflict between the need for water, human populations, and the requirements of economically important migrants is the case of Pacific salmon, most especially in California. One always wishes to be optimistic, but in the case of the salmon of California the battle to save populations to support both a commercial and a recreational fishery may well be lost. There is irony in the fact that much of the water needed to support the jobs associated with a protein-rich food source has been diverted to support cows, a far more ecologically costly source of protein whose overconsumption can have negative consequences for heath. Because they were so valuable yet have been so decimated, salmon epitomize the clash between conservation, competing commercial interests, a misguided water ethic, and just plain greed. Against the past and continuing collusion of government, water law, private interests, and political money, the salmon and those who fish for them have stood little chance. There is perhaps no better example than these spectacular migrating fishes that our stewardship of the planet's biota has not been a particularly good one.

The current direction of climate change is yet another example of a negative environmental trend that we lack the will to prevent. The planet-wide trends are clearly impacting migrants, but we still

lack most of the information we need to make a proper assessment. Birds are the most extensively studied migrants, and it is on them that most effort has been focused. Some trends seem apparent. Many migrants are arriving earlier in the spring, for example. However, we still lack sufficient data to determine whether ecological mismatches between breeding and food supply are having detrimental effects on populations. There is some further evidence that migration routes may be shortening, but again the consequences need investigating. There is a need for studies of multiple factors and their influence on population trends. Determining population trends in nature is never easy, and it is especially difficult for migrants that spend significant parts of their life cycles in regions far apart. Clearly something is going on, but it will take much effort to sort out exactly what. Climate change is a worldwide, unintended experiment, and any understanding we can gain as to migrants' ability to adjust either phenotypically or via genetically based responses to selection will contribute much to the responses we make ourselves.

CHAPTER 16

Summing up and future directions

The ability to move is one of the most important characteristics of living things, and since the publication of the first edition of this book, we have taken major strides in understanding its mechanisms, its forms, and its functions. As our understanding has grown, it has become ever more apparent that migration in all its astonishing variety is the most elaborate expression of movement, and its prevalence in so great a diversity of organisms demonstrates that it has been repeatedly favored by natural selection over alternative lifestyles. Movement away from a familiar habitat as occurs with migration must incur considerable risks, yet time and again in organism after organism migration appears as an element in life cycles. My prevailing theme of this book and its predecessor has been the attempt to understand both the basic mechanisms and the role migration plays in the life cycles of the greatly diverse array of taxa in which it appears. Congruent with that theme I have outlined the forms that migratory behavior and migratory lifestyles can take, and I have tried to illuminate just why, so often, migratory episodes assume such importance in the evolution of life histories and how organisms have adjusted to accommodate those episodes.

In spite of the great variety present, however, three major threads seem to stand out in the tapestry of migratory life histories. First, migration involves specialized behavior that is both qualitatively and quantitatively different from other types of movements. This behavior produces distinct ecological outcomes, but it is not defined by those outcomes. Second, migration is a syndrome integrating behavioral, physiological, morphological, and life-history traits evolved for other functions but modified to support migration. Third, migration is an adaptation to environments that are shifting or patchy in time and space. In this chapter I first summarize the evidence that I see as supporting these conclusions, and then conclude with some thoughts on what I see as some important questions for future research, and what is necessary for students of migration to consider in order to provide answers.

Migration as specialized behavior

J. S. Kennedy's important contribution to the study of migration was to define a set of characteristics that clearly distinguished migration from other types of movement (Kennedy 1985 and Chapter 2). Establishment of these diagnostic features allows specific tests of whether a particular *individual* is a migrant, independently of any knowledge of its previous history. These features include characteristic, persistent, enhanced movement and the temporary suppression or inhibition of responses relating to growth and reproduction (what Kennedy termed "vegetative responses"). These characteristics of migratory behavior mean that environmental inputs that would ordinarily stop movement—say, stimuli signaling food or a breeding site—fail to do so in a migrant. This persistence would be adaptive because it would prevent premature settling in habitats likely to deteriorate, because they are close to the deteriorating or about-to-deteriorate habitat the migrant had just left. A further consequence is that migration is straightened out relative to maintenance movements such as foraging, which increases the chances and the efficiency of reaching a new habitat or refuge. Other specializations include specific behaviors of departure and arrival, with the latter primed by the migratory activity preceding it. Ongoing migration thus lowers the threshold for inputs that eventually stop movement and cause the

Migration. Second Edition. Hugh Dingle. © Hugh Dingle 2014. Published 2014 by Oxford University Press.

migrant to settle either briefly, as at a stopover, or for a longer period at a destination. Because migration often takes an organism for a longer distance relative to the distances it usually moves, it is also likely to be supported by the reallocation of the energy needed to sustain it. Where precise direction and location are important, well-developed orientation capabilities using specific information will also be present. All these characteristics and their co-occurrence provide potential tests for determining whether an observed individual is indeed a migrant.

The underlying assumption in adopting Kennedy's definition of migration both here and in the first edition of this book is that the characteristics that define migration in winged aphids, as so carefully worked out experimentally, will also apply to other migrants with some modifications to allow for noticeable differences in biology. Kennedy did not emphasize fat storage, for example, although aphids do store fat, and one of the characteristics of migrants is their physiological reallocation of resources and modification of biochemical pathways to enhance fat storage as a source of fuel to support migration. Orientation is relatively simple in aphids: attraction to blue sky light when taking off and to yellow light from new leaf growth at landing; it can, of course, be much more complex in the transcontinental migrations of birds. In both cases specific orientation responses identify migrants. It is useful at this point to reflect on the examples of migration analyzed in this book and to examine our assumptions of a generalizable definition as critically as we can. Do other migrants in fact exhibit the same or similar characteristics of behavior as do migrating aphids, or is it necessary to define migration in some other way?

To consider this question, I list some examples in Table 16.1 drawn from the foregoing chapters that seem to indicate specialized behavior consistent with the definition adopted. Some of the species listed in the table have long been considered migrants by criteria other than the ones given by Kennedy and in Chapter 2. Two examples would be the Monarch Butterfly and Great Snipe are classical migrants that travel long distances (which are clearly straightened out) between summer breeding sites and winter refuges. These provide a quasi-independent test of the validity of our criteria for migratory behavior. In addition to the obvious straightening out of their movements, both species deposit fat, display complex orientation, and bypass favorable habits while en route. In *Melanoplus* grasshoppers and other insects, migration primes reproduction, a further characteristic predicted from aphids. Some other examples in the table do not easily fit the classic picture of migration and have been given other designations such as "dispersal" or "nomadism," because they did not display round-trip movements with characteristic destinations. A focus on behavior rather than on outcomes, however, reveals migratory behavior. Spiderlings display characteristic take-off and landing behaviors and some portion of young field mice undertake long straightened-out pathways not exhibited by those settling nearer to their natal area. The distinction between long, straight, migratory paths and more tortuous ranging ones is quite clear in Australian Grey Teals (Roshier et al. 2008a,b). Birds such as queleas (and crossbills) have been considered "nomads" rather than migrants, but both deposit fat like other avian migrants, and quelea do so proportional to the distance they migrate. "Nomadic migrants" better describes their behavior, and Jamie Cornelius, Tom Hahn, and I have argued that their use of migration to reach widespread resources for breeding makes them "rich-patch exploiters" using a specific type of migration strategy (Cornelius et al. 2013). Selection would seem to treat these species in much the same way as it does classic migrants, producing a finely adjusted physiological specialization. The Yellowgreen Vireo and other birds display migratory restlessness at night, suppressing the vegetative activity of sleep, a characteristic also of Australian Silvereyes. These latter birds, when migratory as indicated by their transit from Tasmania to the mainland of Australia, display orientation behavior that residents do not. Among insects, the Desert Locust in its solitary phase migrates at night, whereas non-migrants are quiescent. Finally in tubeworm larvae there is no evidence that starvation increases the tendency to settle by reducing selectivity; rather settlement seems to be primed by the swimming activity of the larvae. In one way or another, the organisms in Table 16.1 all seem to display characteristics that

Table 16.1 Examples of specialized migratory behavior or physiology.

Organism	Migratory behavior
Melanoplus grasshoppers (and other insects)	Flight primes reproduction (Chapter 6)
Desert Locust (*solitaria* form)	Migrates at night when non-migrants inactive (Chapter 11)
Monarch Butterfly	Migrants deposit extra fat and orient (Chapters 6 and 8)
Silver-Y moth	Migrants select appropriate winds and direction (Chapters 3 and 5)
Spiderlings	"Tiptoe" take-off behavior; ballooning promotes landing (Chapter 3)
Tubeworm larvae	Migration primes settling (Chapter 13)
Great Snipe	Bypasses favorable habitats (Chapter 3)
Yellowgreen Vireo (and other birds)	Migratory restlessness at night; sleep suppressed (Chapter 6)
Red-billed Quelea	Deposit fat proportional to distance migrate (Chapter 3)
Grey Teal	Straightened-out migration (Chapter 1)
Silvereye	Migrants orient; non-migrants do not (Chapter 12)
Field mouse (*Peromyscus*)	Migration straightened-out and bypassing favorable habitats (Chapter 2)

define them as migrants (see also Chapter 17 in Dingle 1996), and the list is by no means exhaustive as other examples of specialized migratory behavior occur throughout the book.

In spite of the fact that our behavioral definition of migration does seem to work well in practice in distinguishing migration from other movements, it is the case that in many of the instances cited, presumptive examples of specialized migratory behavior are anecdotal or observations that are a by-product of other studies. There is little direct experimental evidence involving deliberate tests of interactions between migration and settling. This lament is not new (see Gatehouse 1997), but in spite of their utility for leading to predictions, the kinds of experiments the Kennedy definition suggests have generated few studies. Partly this may be due to a tendency to focus on a particular taxon of migrants and so to view migration in that group as general across taxa. The apparency of round-trips in long-lived vertebrates, for example, has perhaps obscured the fact that for most migrants, many insects being cases in point, trips are one-way because of short lifespans, but nevertheless migrants display the characteristics that define migratory behavior. A second consequence is the confounding of behavior with its outcome. A need to examine the relation between flight or other means of travel and settling is not recognized in part because of this confounding.

An example of interactions between activity and settling is that of birds tested in cages in the laboratory. The standard experiment involves treatment with an environmental input such as daylength and recording of activity over a succession of 24 h periods. At the time corresponding to migration, the birds are active at night, a time when they would be sleeping if not in a migratory state. An interaction between activity and settling seems likely because birds in the laboratory maintain this restlessness over a longer period than birds freely migrating in nature. A reasonable interpretation is that active flight reduces restlessness and renders the birds more likely to cease migrating (and show less restlessness) and settle, but there are no experiments involving repeated exposure to appropriate habitat inputs without allowing settling to ascertain whether such inputs would prime restlessness as a surrogate for migratory flight. The experiments revealing that in some insects flight primes reproduction by accelerating oviposition indicate that appropriate interactions occur, but the reciprocal experiments of priming flight with settling responses have yet to be performed. The required experiments will take considerable ingenuity and patience, but that should not diminish the need to perform them.

Whether or not the definition of migration used here is correct in its details, I would argue that it makes one very important conceptual contribution to notions of migration. This is in making explicit a hierarchical distinction between migration as a behavior with a physiological basis subject to natural selection acting on individuals and its outcome as part of the population ecology of the species (Kennedy 1985; Gatehouse 1987). It seems to me that much of the confusion surrounding studies of migration and the lack of communication between workers studying different taxa has been the consequence of the failure to distinguish between

individual migrants and population outcomes. The recognition of the distinction should open the way to experimentation, more focused observation, and more biologically sophisticated modeling, all being necessary for a more comprehensive understanding. The behavioral taxonomy and definition of migration I have proposed (Chapters 1 and 2) will have been especially valuable if they lead to the asking of new and important questions about movement.

Migration as a syndrome of traits

Implicit in the definition of migration in this book is the notion that migration is not a unitary character but rather a syndrome of interacting physiological and behavioral traits. There are two uses of the term "syndrome" when applied to migration. The first is that of an ancient, deeply embedded, and genetically consistent set of traits that has been passed down through lineages (Piersma et al. 2005). As Piersma and colleagues have shown, a syndrome of this sort is not present in migrants. The second use of "syndrome" as a phenotypically consistent set of traits that appears across taxa of migrants (Dingle 2006) is the one I use here. The traits may be genetically correlated within a population or species of migrants, but are not necessarily so across taxa. It seems that similar migratory syndromes have been gained and lost via selection many times and in many groups.

Migration requires the mobilization of resources and energy in support of travel that is not interrupted for foraging or feeding, and so it demands that considerable extra energy be available before such travel is undertaken. Across a taxonomically diverse array of migrants energy pathways are redirected so that, instead of mobilizing to favor growth or reproduction, fuel usually in the form of energy-rich fat is mobilized for movement. In some migrants such as birds this may involve a dietary switch to high-energy food, for instance, fruit rich in sugars. In any case migrants universally incorporate hormonal mechanisms to ensure storage of energy reserves and often the generation of higher levels of nervous activity. Frequently hormone "capture" is involved where a hormone evolved for another purpose such as reproduction or water balance is used to support the remobilization required for migration. Behavioral mechanisms include complex orientation or navigation, incorporating circadian rhythms as biological clocks, and the ability to select the appropriate winds or currents to optimize travel efficiency. Because of the often extraordinary capabilities migrants possess for finding their way, and their ability to use information from, say, magnetic fields that are outside human perception, the mechanisms they evolved to orient or navigate have drawn more attention than any other aspect of migratory behavior.

Migration syndromes incorporate not only behavior and physiology, but they may also involve morphology. In the most extreme cases migrants and non-migrants may be distinguished by the presence or absence of a transporting apparatus. Polymorphic and polyphenic insects are a case in point. The forms are themselves syndromes with various combinations of wing morph, flight muscle development, reproductive timing, and in Soapberry Bugs variation in the mouthparts (beaks). In many cases traits are correlated via genetic mechanisms. Other cases involving morphology may be less dramatic. It is apparent, for example, that in many birds and insects selection acts repeatedly to make the wings of volant migrants longer than those of their sedentary counterparts. Detailed studies of birds, however, show that wing morphometrics are subject to constraints. Birds use wings for many functions besides migration and whereas, for example, long narrow wings are best for migration, shorter, more rounded, wings are better for maneuvering in forests. Trade-offs are therefore an inevitable part of migration syndromes, the syndromes we observe being the result of interaction between selection and constraint.

The allocation of metabolic resources between migration and reproduction—as is so apparent, for example, in flight polymorphic insects—means that migratory syndromes are a consequence of life-history evolution. Indeed this is virtually guaranteed by the fact that one consequence of migration is the determination of where and when to breed, and so life-history traits will be influenced. Thus it should be no surprise that the reciprocal interaction between migration and reproduction, as seen in the Black Bean Aphid, is a key element in how Kennedy defined migration. We have seen in other insects as well how migration primes reproduction

and so determines the key life-history trait of age at reproductive onset. A second key trait, fecundity, is a function of the resources devoted to reproduction relative to those devoted to the energetics of migration, such as the maintenance of flight muscle or the production of silken threads in ballooning spiders. In birds there must be appropriate synchronization of migration (usually twice a year), reproduction, and the costs of the molt and replacement of feathers. Life-history traits and their interactions with morphology, physiology, and behavior are therefore major elements of migration syndromes. Some important modeling studies are now incorporating reproductive effort and timing and their influences on choice of whether and when to migrate.

We are now gaining a greater understanding of the genetics underlying migration syndromes, and the potential of these syndromes to evolve. The determination of the amount of genetic variation and covariation underlying migratory phenotypes allows assessment of how much and how quickly the traits may evolve under natural selection. Important to our understanding is the interaction between genes and phenotypic plasticity, for it is apparent that some of the variation we see is due to environmental variation—contributing, for example, to insect polyphenisms—as well as to genetic variation as seen in insect polymorphisms. Environmental variation also contributes to phenomena such as partial migration among species of bird.

Measures of heritability indicate that there is ample genetic variation for rapid evolutionary change ("contemporary evolution") in migration syndromes. In birds not only have new routes evolved within human lifetimes, but both migratory and sedentary behaviors have appeared where they did not occur before in response to anthropogenically induced changes in the environment. Laboratory studies of migration syndromes using methods such as artificial selection have revealed not only rapid responses to selection, as predicted from heritability estimates, but also significant genetic correlations among traits such that selection on one trait produces responses in those with which it is genetically correlated. The traits in migration syndromes thus evolve together with natural selection acting on traits simultaneously. Still largely unanswered questions are: which traits are likely to be genetically correlated and why? Presumably some of the important genetic contributions involve the structure of trade-offs like those already observed between flight and reproduction in polymorphic insects. The rapid advances in molecular genetics are now allowing the assignment of specific loci to migratory behavior or morphology, as have been identified in aphids and salmon. What is apparent from these studies, however, is that even when specific loci or quantitative trait loci (QTL) are identified, there is still a great deal of the genetic variation for the trait that remains unspecified. There are some exceptions where specific Mendelian loci are the major contributors to migration as in some instances of Mendelian control of wing form in insects, but these are the exception. Studies on both birds and insects indicate hormonal mediation of the interactions among genes, environment, physiology, and migratory syndromes. It makes little sense to view single elements of migratory performance in isolation from other aspects of the syndromes of which they are a part, because natural selection is most likely acting on all the traits simultaneously and on the strengths and signs of the correlations among them.

Migration as an adaptation to shifting or patchy environments

Migration is an adaptation that has evolved to allow organisms to cope successfully with environmental heterogeneity in both space and time. It is an effective means to avoid environmental extremes and to take advantage of resources that are abundant but temporally limited. In the case of long-lived migrants individuals pursue a lifetime track through a sequence of habitats no one of which is available for more than part of the life cycle. Those with short lifespans pass through habitat sequences over the course of succeeding generations. Thus long lifespans permit round-trip migrations, whereas short-lived organisms have time to travel in only one direction within a generation. The entire arena will influence migration, including the responses at each end of the route and the feedback from the pathway itself.

Perhaps the most apparent of shifting environments are those associated with the seasons. Changes in temperature and rainfall regimes produce

flushes of resources exploited by migrants over a wide spectrum of habitats from Arctic tundra and seas to the inundation zones of tropical rivers. In the terrestrial habitats of temperate zones there is explosive production of new vegetation and the insects that accompany it. The exploitation of these resources by migrant birds is the best known of migration phenomena, but some insects such as certain butterflies and moths—like birds capable of long-distance flight—are also migrants between temperate and tropical regions, as are the great whales. Seasons are regular and predictable, and photoperiod is a reliable cue permitting preemptive departure before resources collapse. In the oceans the extraordinary abundance of life in Arctic and Antarctic seas in summer is a rich resource for whales, but they must move to warm waters to give birth to cold-intolerant young. These various factors produce the natural selection leading to the enormous abundance and diversity of seasonal migrants.

The seasons are not the only source of environmental variation. Other habitats that change regularly, if over a longer time-period, are those associated with the early successional stages of ecological communities, and it has been noted, going back more than 50 years, that denizens of these habitats are often migratory, especially among plants and insects. Indeed one of the traits characterizing plant species as weedy is their enhanced ability to migrate as seeds and colonize newly opened germination sites. There is also a practical side to the relation between migration and succession. By converting large areas to agriculture, we create extensive tracts of exactly the sorts of habitats colonized by generalist migrants that we then designate as pests. We then compound the problem by establishing continuous monocultural stands of ruderal plants. It is thus no wonder that a significant proportion of the world's crop pests are migrants, including fungi, insects, and birds such as the Red-billed Quelea. Forecasting the movements and population dynamics of migrant pests has become a significant issue, although it is unfortunate that much more effort goes into controlling pests with pesticides or genetic manipulation of plant resistance than goes into understanding the biology of the migrants.

Deserts and masting boreal cone crops are further ecological conditions that are conducive to the evolution of migration. Rainfall in deserts is not only scarce, it is also likely to be highly erratic in amount and location, producing some of the world's most variable habitats, and cone crops tend to occur widely separated in space and time. These conditions produce a great diversity of migratory species that can take advantage of conditions that, although rare, produce a huge flush of resources when they occur. Migrants that have evolved the ability to exploit these resources are the "rich-patch exploiters" that often breed multiple times in a season or across seasons, and the breeding events can occur in places considerable distances apart. Crossbills and Budgerigars are avian examples, and the various migratory locusts seem to exhibit this strategy among insects. Other habitats that are especially patchy are those which provide special needs. Many birds, for example, must find refuges in which to undergo a protracted molt, and diadromous fishes such as salmon and eels migrate between spatially restricted habitats that provide the necessities for breeding and those that provide the resources needed for growth. Multifactorial aspects of the temporal and spatial patchiness of fresh waters have produced a variety of migratory life cycles among the species and populations of salmonids.

If it is true that shifting or patchy habitats select for migratory life histories, then the converse should also be true: denizens of relatively permanent habitats should be sedentary. That this is indeed the case is perhaps best indicated by wingless insects. In long-lasting habitats, for example the tundra or deep lakes, a disproportionate number of insect species lack wings and so conserve energy otherwise necessary to support flight muscle. Among birds, stable, long-lasting habitats such as tropical rainforests are home to fewer migrants than occur in habitats with infrequent or erratic rainfall such as dry forest or savanna. When migrant birds do occur in rainforest, they are likely to exploit resources that are more patchily distributed such as fruiting or flowering trees or to occur in more exposed and variable habitats of forest edge or canopy.

Within and among migrant species, there is variation in the ways movements are adapted to environmental heterogeneity. Routes can change as a

result of changing conditions, and over the longer term permanent alterations can evolve. Some variation reflects the different interests of the organisms concerned. Differential migration of the sexes, for example, may reflect different reproductive strategies. Male birds may migrate less far and so return earlier to breeding grounds to establish territories; male eels may travel less far because they gain by maturing at a smaller size. With temporal variation in conditions, a given individual may migrate in one year but remain sedentary the next. Whether to move or stay will involve the assessment of the risks contingent upon each behavior and the various trade-offs between migration and other life functions such as reproduction. In some instances variability in migration may reflect environmental uncertainty or situations where a mixed evolutionary strategy may be stable. The very fact of environmental heterogeneity introduces chance and uncertainty into the lives of migrants; migration can reduce the risks, but it cannot eliminate them and will introduce some additional risks associated with travel. Natural selection will reduce the negative effects of trade-offs, and one of the results of this evolution is likely to be migration as an effective means of reducing the variances and net risks that organisms will face.

Future directions

Throughout the course of this book and that of its predecessor I have tried to point out areas where there are gaps in our knowledge or where our understanding is cursory. Perhaps even more so than before, I advocate a much broader approach to the analysis of migration based on a clear perception of the difference between the behavior of migrating individuals and the outcomes of the behavior in terms of both pathways and the ecology of populations. The clear recognition that natural selection acts on individual behavior allows analyses of the distinctions between the various types of movement and—at least as important—on the transitions between them. An implication of the definition of migration I have used is that although migration forms a continuum with other movements (see also Börger et al. 2011), there is a dramatic transition from these other movements. Under what conditions do the transitions occur, and how do genetics, physiology, and ecology interact to produce them? Inhibition is an important part of the definition, yet notions of inhibition seem to have disappeared from analysis of migratory physiology (and indeed from analysis of behavior in general). Perhaps it is time to consider what an animal is not doing as well as what it is doing if it is indeed the case that one aspect has important implications for the other. The ingenuity required for such analyses will be considerable, but the reward should be considerable as well. It also seems apparent that considerations of transitions and of inhibitory/excitatory interactions would be ripe for approaches based on theory and modeling. Integration of theory and hypothesis testing with pattern description would make major contributions to our understanding (Milner-Gulland et al. 2011). It should be kept in mind here that, as Kennedy pointed out, how one defines a behavior goes a long way to determining how one analyzes it.

Concomitant with clarification of concepts, there is still a need to examine a greater diversity of the planet's biota. To some extent studies have been driven by practical and economic considerations. These have largely accounted for the numerous data on pest insects such as locusts and Armyworm Moths, and on commercially important diadromous fishes, to cite conspicuous examples. Migrant songbirds and whales, for example, have attracted attention because of their visibility and esthetic appeal. It is still true, however, that a distressingly small number of the world's great diversity of migratory organisms have been studied and these mostly from the perspective of pattern description. My hope is that in the future we take much greater advantage of what comparative studies of diverse migrants can tell us. I am not alone in this hope (Milner-Gulland et al. 2011). Too often we tend to focus on our "own" group with little regard for what other organisms may do. Thus the repeated emphasis on annual round-trips in the vertebrate literature ignores the fact that even vertebrates that are migrants by all other criteria, including some small mammals, do not make round-trips nor do a multitude of migrants from other taxa. The important relationship between round-trips and lifespans is also missed. My plea is to study migration as a general biological phenomenon modified in important ways to fit

the lifestyles of many different kinds of organisms. The differences superimpose on a common theme, but they are important indications of evolutionary trends, ecological diversity, and biological richness.

There is also room for much more cross-fertilization among biological disciplines for the analysis of migration. There are basic physiological mechanisms underlying the behavior, distinct ecological consequences, and, acting via the genome, evolutionary responses to the natural selection arising from the ecology. Given this sequence, disciplinary boundaries, unless crossed with appreciation of what each can contribute, are likely to hinder progress. Much greater understanding will be forthcoming if students of migration can manage to cross disciplinary boundaries, because the importance of migration extends from the genome to community and ecosystem ecology. Ecological interactions are likely to be profoundly affected by, for example, the transfers of nutrients from the ocean inland by salmon and the arrival of millions of migrant birds at temperate landscapes in the spring. These interactions will feed back to the evolution of migration syndromes. Thus a full understanding of migration should encompass biological disciplines from molecular and quantitative genetics to biochemistry (energetics) to ecosystem dynamics. Behavior and evolution are the threads that tie the approaches together.

As with most fields of science, recent advances in technology have provided both gains in understanding and new perspectives. Two impacting studies of migration are advances in tracking technology and in molecular genetics. The development of cheap, miniaturized geolocators has provided us with exciting data on the capabilities of migrants. We now know that Bar-tailed Godwits migrate nonstop across the Pacific and that shearwaters include whole ocean basins across both hemispheres within their ranges. Specially developed tags transmit data that permit the tracking of sharks and whales on their entire routes over vast areas of ocean. Satellite transmitters are providing intriguing insights into the variability and flexibility of raptors and storks traveling between Europe and Africa. We can expect more to astonish and delight us as technical advances in miniaturization continue. I hope to see the day when we can follow the lifetime movements of a Soapberry Bug! Genes can now be precisely located and associated precisely with parts of the migration syndrome. These can involve morphology such as wing production in aphids or physiology such as the muscle energetics of migrating Red Crabs. There is still much to learn, however, from traditional quantitative genetics and artificial selection, especially concerning the nature and extent of genetic correlations among the traits of migration syndromes and the trade-offs that occur. Important questions remain concerning which assemblages of traits are best adapted to which migratory life cycles in which environments. A wise application of methods, both old and new, should produce exciting and interesting results from studies of migration within the framework I have provided. Let us hope that we have the wisdom of good stewardship of our planet and its migrants so that such results can be realized.

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