Title

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Publication Date

2007-05-20

Poster Sessions

Ecological Effects of Road Infrastructure on Herpetofauna: Understanding Biology and Increasing Communication

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Abstract: Roads are the ultimate manifestation of urbanization, providing essential connectivity within and between rural and heavily populated areas. Roads permeate national forests and other established wilderness areas; consequently, no areas in the U.S. are protected from this expanding infrastructure. The ecological impacts roads have on herpetofauna across temporal and spatial scales are profound, beginning during the early stages of construction and progressing through to completion and daily use. Herpetofauna have the potential to be negatively influenced from roads as a consequence of urbanization, either directly from on-road mortality or indirectly as a result of a variety of ecological impacts and enabled human accessibility. The quantity and the potential severity of indirect impacts of roads and urban development on amphibians and reptiles far exceed those incurred from direct mortality of wildlife although our understanding of these indirect consequences is premature. Our objective for this presentation is to: 1) summarize the prevalence of data on direct mortality of herpetofauna, 2) to characterize the diversity of indirect effects from roads, 3) to suggest larger-scale impacts on population and community levels, and 4) to recommend areas of future research for impacts that are undocumented but for which herpetofauna are likely susceptible based on their ecological strategies. Lastly, we present approaches for resolving and preventing conflicts between wildlife and roads. While some on-road mortality can be minimized in some instances for some species with road crossings, the mitigation of indirect effects such as pollution cannot be accomplished with these measures. In light of the many indirect effects that have been identified and the many more that remain to be documented, proactive transportation planning, public education, and communication among the professional sectors of society are the most effective way to minimize and mitigate road impacts and the only effective mechanism for avoidance of road impacts.

Introduction

Human societies, whether urban or rural in population density, depend on transportation networks to establish conduits for people and products. Mass production of vehicles in the 1900s created demand for expansion and efficiency of the road network, particularly in the United States (U.S.); currently, approximately 6.4 million km of public roads span the U.S. (Forman et al. 2003). Roads generate an array of ecological effects that disrupt ecosystem processes and wildlife movement. Road placement within the surrounding landscape is possibly the most important factor determining the severity of road impacts on wildlife because it influences roadkill locations and rates and the observed presence or absence of species.

The combined environmental effects generated by roads (e.g., thermal, hydrological, pollutants, noise, light, invasive species, human access), referred to as the "road-effect zone" (Forman 2000), extend outward from 100 m to 800 m beyond the road edge (e.g., Reijnen et al. 1995). Considered independently, each factor influences the surrounding ecosystem to varying extents and is further augmented by road type and environmental processes, including wind, water, and behavior (Forman et al. 2003). Based on a conservative assumption that effects permeate 100-150 m from the road edge, an estimated 15-22% of the nation's land area is projected to be ecologically impacted by roads (Forman and Alexander 1998), an area about 10 times the size of Florida (Smith et al. 2005). However, some effects appear to extend to 810 m (i.e., 0.5 mi), resulting in 73% of U.S. land area that would be susceptible to impacts (Riitters and Wickham 2003).

Roads enhance connectivity between rural and heavily populated areas, and consequently are the ultimate manifestation of urbanization, which occurs in progressive stages across multiple temporal and spatial scales. Between 1950 and 1990, urban land area increased more than twice as fast as population growth (White and Ernst 2003). As development sprawls outward from the city core, existing transportation corridors are supplemented to support increased traffic volumes (Forman et al. 2003). Alternatively, roads may facilitate future development of an area, increasing use of surrounding habitats by humans for hunting, collection, and observation of wildlife (Andrews 1990; White and Ernst 2003). The extension of the U.S. road system permits vehicle access to most areas, as evidenced by the fact that 82% of all land lies within only 1 km of a road (Riitters and Wickham 2003). The USBTS (2004) defines an urban area as "a municipality . . . with a population of 5,000 or more." By this definition, many national parks and wildlife refuges have daily visitation levels equivalent to populations of small urban areas and during months of peak visitation have traffic volumes comparable to some cities (National Park Service 2004). Therefore, recreational activities in these natural areas may detrimentally impact species that should otherwise be protected (Seigel 1986).

Conflicts continually arise due to the interconnectedness of issues related to roads, wildlife, and adjacent habitats. These conflicts have led experts from multiple fields (e.g., transportation planners, federal, state, and local governments, land managers, consultants, non-profit organizations, environmental action groups, engineers, landscape and wildlife ecologists) to contribute their knowledge in an effort to explain the "complex interactions between organisms and the environment linked to roads and vehicles" in the field of road ecology (Forman et al. 2003). The field continues to grow, as evidenced by the increase in scientific publication (herpetofauna; fig. 1) of reviews, bibliographies, and texts that focus on the general effects of roads on natural systems (e.g., Andrews 1990; Forman et al. 1997; Forman and Alexander 1998; Spellerberg 1998; Spellerberg and Morrison 1998; Trombulak and Frissell 2000; Forman et al. 2003; White and Ernst 2003; NRC 2005). Further, there are also brief reviews that elaborate on the specific effects that roads have on wildlife. These reviews are published online (FHWA [Federal Highway Administration] 2000), in conference proceedings (Jackson 1999; Jackson 2000), as unpublished reports (Noss 1995; Watson 2005), and in a peer-reviewed journal (Trombulak and Frissell 2000). Additionally, some of these focused reviews have dealt specifically with herpetofauna (Maxell and Hokit 1999; Ovaska et al. 2004; Smith et al. 2005); further comprehensive presentations of this information are now available (Jochimsen et al. 2004; Andrews et al. 2006 [www.parcplace.org]; Andrews et al. 2007).

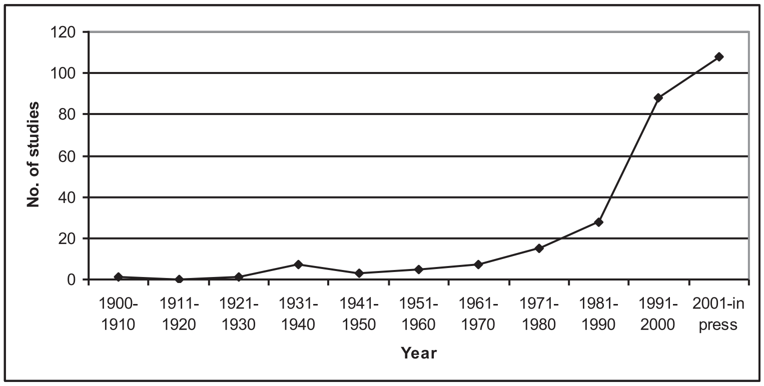

Figure 1. The number of published studies represented within this document that involve herpetofauna and road issues displayed in 10-year increments. Literature includes publications specifically on herpetofauna and road issues, vertebrate studies on roads that include herpetofauna, and herpetofaunal research that includes roads. Note that the final decade (2001-2010) includes only 6 years, yet greatly surpasses the publication rate on roads in previous decades. Figure taken from Andrews et al. (2006).

The extent to which roads are linked to the widespread decline of amphibian and reptile populations (Gibbons et al. 2000; Stuart et al. 2004) is unresolved. Nonetheless, the prospect of mitigating and, even more ideally, reducing the adverse effects that can be attributed to roads seems attainable. A better understanding of how roads affect herpetofauna and the subsequent application of this knowledge will minimize detrimental effects on these taxa. Our objective here is to discuss how roads and vehicles directly and indirectly affect amphibian and reptile individuals, populations, and communities through direct mortality, habitat loss, fragmentation, and ecosystem alterations. We present effects for which there are data in addition to identifying biological characteristics of herpetofauna that increase their susceptibility to roads and are areas in need of research. In a sister paper in this volume (Jochimsen and Andrews), we provide examples of post-construction mitigation and long-term solutions of pre-construction transportation planning and public awareness.

Direct Mortality

Researchers have conducted surveys along roads in an effort to quantify the most conspicuous effect that roads impose on wildlife--mortality inflicted by vehicles. Direct effects involve injury or mortality that occurs during road construction (e.g., inadvertent burial or death from blasting and earth moving), or subsequent contact with vehicles associated with increased development. Direct mortality of herpetofauna has been documented since the beginning of the 20th century, the some effects of roadkill were not observed until decades later (e.g., amphibians, Puky 2006; snakes, Fitch 1999). While urban areas present obvious concerns for roadkills, road mortality has been considered the greatest non-natural source of vertebrate death in protected areas (Bernardino and Dalrymple 1992; Kline and Swann 1998).

Amphibians (Salamanders and Anurans)

Studies investigating road effects specifically on amphibians have been conducted in Europe perhaps longer than in any other region, and mitigation efforts have been in place since the 1960s (Puky 2004; Schmidt and Zumbach 2007). The highest rates of road mortality for amphibians occur where roads located in the vicinity of a wetland or pond disrupting the spatial connectivity of essential resources and habitats across the landscape (e.g., Ashley and Robinson 1996; Smith and Dodd 2003). Mass movements triggered by rainfall and warm weather may result in excessive rates of road mortality for salamanders and anurans (e.g., Turner 1955; Clevenger et al. 2001; Ervin et al. 2001). Many species fall victim to roads in great numbers during mass migrations of breeding adults and later as emerging metamorphs. Road mortality is likely substantially higher for some species of anurans relative to most salamanders due to higher reproductive output and tendency to breed in roadside habitats. In addition, anurans possess a delicate body structure that may make them more vulnerable to the high pressure wave created by a passing vehicle, which researcher Dietrich Hummel found can result in death even without experiencing a direct hit from a vehicle (Holden 2002).

Several studies have focused strictly on the probability of individual amphibians being killed on the road. The estimated survival rate of toads crossing roads in Germany with traffic densities of 24-40 cars per hour varied from zero (Heine 1987) to 50% (Kuhn 1987). Hels and Buchwald (2001) calculated that the probability of individual mortality while crossing a road ranged from 0.34 to 0.98 across traffic volumes, depending on various attributes of a given species. Their model has been adapted to assess mortality probabilities for turtles (Gibbs and Shriver 2002; Aresco 2005a) and snakes (Andrews and Gibbons 2005). However, all are based on individual deaths presented as proportions, so the extrapolations to true population levels are equivocal.

Reptiles (Crocodilians, Lizards, Turtles, and Snakes)

Few road surveys have documented mortality of crocodilians and lizards, and most observations have been recorded incidentally (e.g., Klauber 1939; Fitch 1949; Dodd et al. 1989). Traffic deaths have been suggested as the major known source of mortality for some large, endangered species, including the American Crocodile (*Crocodylus acutus*; Gaby 1987; Kushlan 1988; Harris and Gallagher 1989). Crocodilians also present a safety concern for drivers and can result in human death (Associated Press 2005). Lack of evidence for high mortality of lizards could be a detection issue due to small size and rapid deterioration of road-killed specimens of many species (e.g., Kline and Swann 1998), or a lower mortality rate due to their ability to cross roads faster than other reptiles (but see Kline et al. 2001). Also, most species of lizards do not migrate seasonally and exhibit high site-fidelity within small home ranges, potentially limiting their encounters with roads (Rutherford and Gregory 2003).

Slow-moving turtles, especially species that retreat into their shells when vehicles pass, are long-lived species that likely experience irreparable population impacts when adult females are killed (Congdon et al. 1993). Studies report seasonal peaks in road mortality correlated with the migration of nesting females and hatchling dispersal (e.g., Ashley and Robinson 1996; Fowle 1996; Haxton 2000). Spatial concentrations of turtle mortalities tend to be associated with movement between wetland habitats (Dodd et al. 1989). In a seven-year census (1989-1995), Wood and Herlands (1997) reported the roadkill deaths of 4,020 Diamond-backed Terrapins (*Malaclemys terrapin*) along a road that bisects a marsh in coastal New Jersey. Along a highway dividing Lake Jackson in Tallahassee, FL, Aresco (2005a) never observed a single individual survive a road crossing, and subsequently has documented the highest turtle road mortality rate yet reported (pre-fence data; n=343; 95% killed when entering highway, remaining 5% killed in first two lanes).

The most thorough, long-term records of direct road mortality have been provided for snakes. Since the 1930s, herpetologists have driven U.S. roads to document snake occurrence and collect specimens (e.g., Klauber 1931; Scott 1938); therefore, documentation of traffic fatalities with this taxa are not novel. Reports in which the majority of specimens are already dead are not uncommon. The highest road mortality of snakes to our knowledge has been documented along U.S. Highway 441 in Paynes Prairie State Preserve in Florida (1.854 individuals/km surveyed, 623 snakes killed, 336 km surveyed, Smith and Dodd 2003). Episodic weather events may trigger mass movements of snakes that result in high levels of mortality over fine spatial and temporal scales (e.g., Hellman and Telford 1956). Movement patterns influenced by weather are not always exhibited immediately as evidenced by the summer flooding of the Mississippi River that later triggered a pulse in snake movement across a bordering highway in October (Tucker 1995).

Summary

Ample evidence suggests that road mortality of herpetofauna results in significant loss of individuals and in some situations threatens the sustainability of populations. Reed et al. (2004) concluded that road mortality is substantial, exceeding the damage incurred by other anthropogenic sources such as illegal collection for trade. Quantitative effects on populations have mainly been estimated using models or based on mean mortality rates determined by surveys (e.g., Rosen and Lowe 1994), estimates that must be interpreted with caution due to biases associated with road sampling (see Table 1 in Andrews et al. 2006). As the research on road impacts has been disproportionately focused on mammals and birds, we are still learning about some of the more straightforward direct effects of roads on herpetofauna. However, it is apparent that roads are unequivocally a major source of mortality for many amphibians and reptiles in many areas, and likely pose risks to population viability.

Indirect Effects

The manifold effects of roads extend far beyond encounters between wildlife and vehicles (Andrews 1990; Forman et al. 2003); multiple effects occur across various spatial scales that extend beyond the road. Roads are designed to serve as travel corridors for humans, usually without regard for the environmental needs of wildlife. Therefore, problems may arise when wildlife use road systems for their own movement. Unlike natural corridors, roads frequently cross topographic and environmental contours, thereby fragmenting a range of habitat types (Bennett 1991) and affecting many wildlife groups that possess a diversity of ecological and life history strategies. The transformation of physical conditions on and adjacent to roads eliminates areas of continuous habitat while simultaneously creating long-lasting edge effects (Forman and Alexander 1998). When discussing indirect road effects on herpetofauna, the information base becomes sparse because indirect effects are more pervasive and more difficult to quantify than direct effects, and documenting indirect effects due to roads often requires extensive and long-term monitoring.

The Road Zone as Habitat: For Better or Worse

Reproduction

Roads and roadside areas can provide habitat for reproductive behaviors. Amphibians, especially frogs, are known to breed in roadside ditches, but successful egg and larval development may be rare (Richter 1997), as ditches often dry before larvae can metamorphose. Some anurans use water-filled tire ruts for breeding and moisture when traversing long distances (e.g., Reh and Seitz 1990), which can lead to adult and larval mortality (D. M. Jochimsen, pers. obs.). The road zone can also serve as an attractant for reproductive behaviors for reptiles (Hódar et al. 2000), an occurrence that can result in high mortality when reproductive activities coincide with peak traffic densities (Caletrio et al. 1996). Lastly, these behaviors result in differential mortality due to increased roadside exposure, as seen with roadside nesting by turtles that may result in reduced survivorship of both adult females and hatchlings (Guyot and Kuchling 1998; Aresco 2005b; Szerlag and McRobert 2006; Brisbin et al. 2007).

Thermoregulation

Research suggests that roadsides and road surfaces attract some reptiles for thermoregulatory purposes. Amazonian lizards may benefit from open patches created by roads, due to increased access to basking sites, which consequently improves foraging efficiency (e.g., Sartorius et al. 1999), and some snakes may be attracted to roads that serve as basking sites (e.g., Klauber 1939; Brattstrom 1965; Sullivan 1981a; but see Andrews and Gibbons 2005). Further research is needed to explore variables (e.g., species, season, and environmental conditions) that would likely be involved if thermal conditions serve to attract reptile species to roadsides and road surfaces.

Foraging

Secondary impacts of roads on herpetofauna can also occur when roads attract prey or predators (e.g., small mammals, Getz et al. 1978; nesting birds, Ortega and Capen 2002). Prey concentrations in roadside ditches (Franz and Scudder 1977), on shoulders, (Leighton 1903; Smith 1969), and forest edges, (Sullivan 1981b; Wells et al. 1996) can trigger an increased presence of predatory species. Terrestrial Garter Snakes (*Thamnophis elegans*) were observed foraging on Western Toad (*Bufo boreas*) tadpoles in ruts on a road in Idaho (D. M. Jochimsen, pers. obs.). Roads also provide simplified foraging opportunities for predators as they increase exposure to animals crossing the road (Vandermast, 1999). Also, dead animals attract frog, turtle, snake scavengers (e.g., Guarisco 1985; Jackson and Ostertag 1999; Jensen 1999; Morey 2005).

Clearly, some species benefit from roadside edge habitat under certain circumstances and the disturbance of urbanization in general, but ultimately this may incur increased risks. Perhaps more commonly, many herpetofaunal populations are intolerant of edge conditions generated by roads and may decrease directly, or indirectly, because of reduced prey levels resulting from reduced habitat quality surrounding roads (e.g., Haskell 2000). Therefore, assessments of indirect road impacts as a consequence of predator-prey relationships must be conducted in the context of individual species and the ecological requirements of predators and prey.

Landscape Pollution

Hydrological and Microhabitat

Hydrological changes occur beyond the immediate vicinity of roads (e.g., Jones et al. 2000). The impervious nature of roads elevates precipitation runoff, fluctuations in flow velocities, and flooding in adjacent wetlands, diminishing suitable habitat for amphibian breeding, foraging, and development (Richter 1997). Abnormal flooding cycles can lower amphibian species richness (Richter and Azous 1995) and increase the likelihood of recolonization by predatory fish in formerly fish-free isolated wetlands.

Skin permeability and vulnerability to water loss also make it difficult for amphibians to maintain optimal moisture levels. Desiccation rates increase during dispersal, particularly in altered environments that do not retain natural moisture levels (e.g., Rothermel and Semlitsch 2002) and may also be accelerated for some species when they must traverse roads in urban areas. Changes in microhabitat surrounding the road can result in reduced cover and leaf litter and therefore drier soils, which could influence the abundances of some amphibian species, particularly woodland salamanders (e.g., Marsh and Beckman 2004). These microhabitat changes are compounded by problems of chemical run-off, erosion, sedimentation, and siltation (Orser and Shure 1972; Welsh and Ollivier 1998; Semlitsch 2000; Semlitsch et al. 2007).

Chemical

Vehicular by-products and compounds associated with road degradation contribute to deposition of pollutants on and around roads (Hautala et al. 1995; Croteau et al. 2007). Exposure to toxic compounds may alter reproduction and have long-term lethal effects on wildlife (Lodé 2000), including endocrine disruption in amphibians that reduces reproductive abilities and survivorship (e.g., Hayes et al. 2006; Rohr et al. 2006). Mahaney (1994) found that water treatments with high petroleum contamination inhibited tadpole growth and prevented metamorphosis. Physiological (i.e., respiratory) and behavioral alterations were observed in lizards and frogs exposed to ozone (Mautz and Dohm 2004). Acid precipitation resulting from automobiles acts as an immune disruptor in adult frogs (Vatnick et al. 2006). Lead levels in soil and vegetation are negatively correlated with distance from roads (e.g., Scanlon 1979), and concentrations are positively correlated with traffic density (e.g., Goldsmith et al. 1976). Chloride from de-icing salt runoff contaminates fresh waters peripheral to road systems (Environment Canada 2001; Kaushal et al. 2005) and can be an agent in reduced survival and reproductive effort (Turtle 2000; Sanzo and Hecnar 2006; Karraker 2007). Forman and Deblinger (2000) suggested that road salts altered aquatic habitats up to 200 - 1500 m from a busy suburban highway corridor. Additionally, research has demonstrated compromised water quality and reduced amphibian survival from herbicides and dust-control agents (Kohl et al. 1994; deMaynadier and Hunter 1995; Wood 2001). Less is known about physiological effects of road-associated pollutants on reptiles. However, it is reasonable that similar issues exist with the uptake of pollutants directly from the environment or from prey items where transferred concentrations vary between sexes and among body sizes (e.g., Rainwater et al. 2005). Scanlon (1979) found higher levels of heavy metals in invertebrate-eating shrews than plant-eating rodents, suggesting that bioaccumulation could be road-related.

Pheromonal

Microhabitat changes may obscure olfactory or pheromonal cues. Olfaction plays a primary role in amphibian migration and orientation (e.g., Duellman and Trueb 1986), and some snakes rely extensively on scent for directional movement cues to locate mates (e.g., LeMaster et al. 2001), prey items (e.g., Chiszar et al. 1990), and ambush sites (e.g., Clark 2004). Some naïve neonate snakes trail conspecific adults to hibernacula (e.g., Cobb et al. 2005). Pheromone scent trailing, observed in a variety of species, could conceivably be altered by some contaminants, such as oil residues on roads (Klauber 1931) or road substrate type (Shine et al. 2004).

Noise

Vehicular traffic alters environmental conditions of habitats adjacent to roads via vibration and noise, which can modify animal behavioral and movement patterns (Bennett 1991). Effects of traffic noise and vibrations on vertebrates include hearing loss, increase in stress hormones, altered behaviors, and interference of breeding communications (Dufour 1980; Brattstrom and Bondello 1983; Forman and Alexander 1998). Road noise and ground vibration may disrupt cues necessary for orientation and navigation during migratory movements of some amphibians (e.g., breeding frogs and salamanders, Dimmitt and Ruibal 1980). Sun and Narins (2004) found that airplane and motorcycle noise reduced the calling frequency of some anuran species but increased the frequency of other species. Background noise from off-road vehicles often results in modification of calling behavior in male anurans and may impair the ability of females to discriminate among call types and to discern locations of calling males during breeding migrations (Schwartz and Wells 1983; Schwartz et al. 2001). Impacts observed in off-road environments would be exaggerated in urban environments, which present even greater noise interference.

Light

Artificial lighting along roads and urban areas alters foraging, reproductive, and defensive behaviors of herpetofauna (Buchanan 2006; Wise and Buchanan 2006). Exposure to artificial light can cause nocturnal frogs to suspend normal behaviors and remain motionless long after light has been removed (Buchanan 1993). More research is needed to assess the overall impacts of lighting in urban areas before informed recommendations can be made (Perry et al. 2007).

Spatial Complexity

Dispersal

Roads can serve as dispersal corridors, facilitating species expansion, an occurrence that is particularly problematic with invasive species. Roads and trail systems facilitated the expansion across Australia of introduced Cane Toads (*Bufo marinus*, Seabrook and Dettmann 1996), which have been estimated to invade new areas at a rate of over 50 km a year (Phillips et al. 2006). Phillips et al. (2003) estimated that *B. marinus* could pose a threat to as many as 30% of terrestrial Australian snake species. Additionally, fire ants (*Solenopsis invicta*) proliferate in roadside areas in the United States (Stiles and Jones 1998) and have been identified as a problematic predator on egg-laying reptiles (e.g., Allen et al. 1997; Buhlmann and Coffman 2001; Parris et al. 2002), reducing reproductive output and hatchling survivorship. Lastly, roads can enable the spread of exotic plant species that subsequently eliminate native flora and fauna (Wester and Juvik 1983; Parendes and Jones 2000) and compromise the quality and availability of habitat and prey bases (e.g., Zink et al. 1995; Maerz et al. 2005). Jochimsen (2006) found a correlation between Gopher Snakes (*Pituophis catenifer*) mortality and cover of an invasive grass species along roadsides in Idaho.

Fragmentation

As road density increases, species that depend on a non-fragmented landscape to complete their life cycles (e.g., Pope et al. 2000) will be in greatest jeopardy. Resources associated with refugia, mates, and prey tend to be concentrated in distinct habitats that are patchily distributed and seasonally available. When roads bisect these habitats, mortality may become concentrated spatially and seasonally (e.g., Carpenter and Delzell 1951). Landscape permeability and maintenance of movement corridors are critical to ensure metapopulation dynamics of amphibians and reptiles (Marsh and Trenham 2001). Many herpetofaunal species require not only the terrestrial habitat peripheral to wetlands, but corridor linkages with other isolated water bodies (Gibbons 2003). Depending on the mechanisms driving migratory patterns (e.g., genetic, behavioral), deterministic movement patterns and philopatric behaviors may inhibit an individual's ability to readily adapt to a road that interferes with the animal's migratory route In a modeling assessment by Jaeger and colleagues (2006), population persistence was higher if roads were spatially clustered as opposed to evenly distributed across the landscape.

Behavioral Responses

As landscape features that alter and fragment natural habitats, roads may impede movements of amphibians and reptiles via alteration of size, shape, or spatial arrangement of habitat patches (e.g., Fahrig and Merriam 1994). Barrier effects are defined as occurrences when 1) animals are killed on roads in numbers that functionally prevent genetic exchange between populations; 2) surrounding habitat quality is reduced such that animals cannot persist; or 3) animals behaviorally avoid roads, contributing to isolation and habitat fragmentation. Vehicles can force wildlife to adapt their behavior either by posing an impenetrable barrier, in which animals selectively avoid the road due to awareness of traffic as suggested by Klauber (1931) or through other little-understood influences on crossing behavior (Andrews and Gibbons 2005).

Road Avoidance

Behavioral avoidance of roads by herpetofauna is poorly documented, and species differences are less understood than is species-specific mortality on roads. Road avoidance may occur as a result of several road characteristics, such as traffic, noise, road substrate, openness, and others not yet determined. Models show that differing catalysts for avoidance can influence differing levels of vulnerability at the population level (Jaeger et al. 2005), therefore indicating a need for species-level considerations. Roads can hinder amphibian movement (e.g., Gibbs 1998), and reduced permeability can even occur on low-use forest roads (e.g., Marsh et al. 2005). Barrier effects from roads may vary depending upon the specific type of movement being made. For example, a greater proportion of natal dispersal movements occurred across roads in Maine (22.1%) than either migratory (17.0%) or home-range movements (9.2%; deMaynadier and Hunter 2000). Road avoidance has also been documented in salamanders (Madison and Farrand 1998), lizards (Klingenböck et al. 2000; Koenig et al. 2001), and tortoises (Boarman and Sazaki 1996).

A variety of researchers have noted road avoidance by snakes (e.g., Weatherhead and Prior 1992; Fitch 1999; Goode and Wall 2002; Sealy 2002; Laidig and Golden 2004; Shine et al. 2004; Plummer and Mills 2006). Avoidance rates can vary with road substrate where paved roads have typically catalyzed higher resistance (Hyslop et al. 2006). Andrews and Gibbons (2005) performed experiments that revealed significant levels of variation among species in road avoidance rates where a positive correlation was found between crossing frequency and body length, likely due to natural behaviors of smaller snakes to avoid open spaces (e.g., Klauber 1931; Dodd et al. 1989; Fitch 1999; Enge and Wood 2002). The propensity to cross roads can also vary within a species where juveniles and adults do not cross proportionately to ratios in the surrounding environment (Seigel and Pilgrim 2002) Some snakes attempt to cross, but deter and retreat (Andrews and Gibbons 2005), ultimately not crossing, a behavior that has been observed in the field (Holman and Hill 1961; Franz and Scudder 1977). Individuals that enter a road but do not cross are exposed to both direct mortality and road fragmentation.

Increasing awareness of the prevalence of behavioral avoidance of roads within and among species suggests a topic of interest from both ecological and evolutionary perspectives. Beyond considerations of road avoidance as a learned behavior, genetically-inherited avoidance of roads has not been directly documented, but if a genetic component for response to roads and traffic exists within species, behaviors that increase survival would be under selection. For instance, in areas of greater habitat connectivity, organisms that tend to avoid roads would survive and breed successfully, whereas in fragmented landscapes, organisms that risk crossing roads might be the effective breeders.

In-Road Behaviors

Behaviors such as movement speed and predator responses influence susceptibility to road mortality and fragmentation. Slow-moving animals, or those that cross the road at a wide angle, increase their mortality risk. Slow movements of amphibians (Hels and Buchwald 2001), turtles (Gibbs and Shriver 2002; Aresco 2005a), and snakes (Andrews and Gibbons 2005) while crossing roads have been documented. While road-crossing speeds of amphibians and turtles may be fairly consistent within and among species in each group (but see Finkler et al. 2003), crossing speeds of snakes vary significantly among species, suggesting that snakes may suffer a greater range of road mortality rates than other taxa (Andrews and Gibbons 2005). Although correlations of age, reproductive condition, or sex with road crossing speed have not been documented or studied, natural differences in speed exist (Plummer 1997). Lastly, little is published regarding crossing angles for herpetofauna. Two studies on snakes found that individuals consistently move perpendicularly across the road, taking the shortest route possible (Shine et al. 2004; Andrews and Gibbons 2005) suggesting that the road is an area that animals are simply passing through and not a selected habitat.

Immobilization behaviors that are likely derived from predator responses (Andrews and Gibbons 2005) may lead to responses to oncoming or passing vehicles that could significantly influence crossing time. Mazerolle et al. (2005) found that the strongest stimuli for immobilization behavior across six amphibian species were a combination of headlights and vibration. Andrews and Gibbons (2005) found high rates of immobilization in response to a passing vehicle among snake species that would greatly jeopardize some from successfully crossing a busy highway.

Summary

In summary, indirect impacts from roads on herpetofauna vary considerably within and among taxonomic groups. Many indirect effects of roads are poorly understood and some have yet to be considered, posing unknown challenges for investigators to determine their ultimate impacts on herpetofauna. Potential discoveries of the indirect effects of roads on amphibian and reptile biology promise a wealth of opportunities to conduct meaningful behavioral and ecological research applicable to herpetofaunal conservation on a global scale.

Effects on the Higher Levels of Ecological Organization

Population-Level Impacts

The difficulty in monitoring road impacts at the population and community levels is reflected in the lack of available data, although larger scale repercussions of road impacts on herpetofauna are probably underestimated (Vos and Chardon 1998). Roads may affect population size and demography of amphibians and reptiles in a variety of ways, but understanding the full effect of roads on herpetofaunal populations may be delayed and could take decades to elucidate (Patla and Peterson 1999; Findlay and Bourdages 2000). Despite early evidence by Klauber (1939) that a California highway resulted in the local decline of snakes, documentation of amphibian and reptile population declines as a result of roads, directly or indirectly, has been limited and often speculative. In many instances, effects on population density and structure from traffic-related mortality and continued loss of individuals can only be inferred. However, declines and lower population estimates associated with increased road densities and traffic levels have been documented in frogs (e.g., Fahrig et al. 1995), turtles (Boarman and Sazaki 1996; Fowle 1996; von Seckendorff Hoff and Marlow 2002), and snakes (e.g., Rudolph et al. 1999; but see Mazerolle [2004] for amphibians and Sullivan [2000] for snakes]). Gibbs and Shriver (2002) simulated movement patterns for pond and terrestrial turtles against road density and traffic volumes that indicated mortality of >5% of the populations of land and large-bodied pond turtles, a percentage that they suggest is likely unsustainable for long-lived species.

Many amphibians and reptiles exhibit intraspecific variation in ecological requirements and strategies between sexes, across life history stages, and seasons. Variation in movement patterns and abundances may consequently result in differential road mortality rates (e.g., Rudolph and Burgdorf 1997; Titus 2006); often, mortality rates are highest in species and individuals that exhibit the greatest vagility (Bonnet et al. 1999; Carr and Fahrig 2001; Brito and Álvares 2004; Roe et al. 2006). This attribute can lead to skewed population structure in amphibians and reptiles via altered sex ratios and composition of age classes (Fukumoto and Herrero 1998). Female turtles are more likely to be killed on roads (Wood and Herlands 1997; Marchand and Litvaitis 2004; Steen and Gibbs 2004; Aresco 2005b), due in part to nesting activities (e.g., Gibbs and Steen 2005; Steen et al. 2006). Conversely, a higher proportion of male lizards (e.g., Rodda 1990) and snakes (Bonnet et al. 1999; Sealy 2002; Jochimsen 2006; Andrews and Gibbons 2007) die on roads because males disperse further than females in some species. Further, sex bias in road captures can be seasonally variable (Sherbrooke 2002; Moeller et al. 2005). Intraspecific variation in road impacts can often be linked to spatial and temporal attributes of dispersion, which can most often be correlated with mating systems. For instance, males of polygynous species are often the more risk-prone sex as they are responsible for courting and defending multiple females within a territory (Goodman et al. 2005). Further studies designed to explore the variation of sex bias in road captures driven by ecological behaviors are needed to investigate influences on population sustainability. Some long-distance movers, such as Eastern Indigo Snakes (*Drymarchon couperi*) are particularly sensitive to edge effects and therefore could be an ideal umbrella species to look at the effects of landscape fragmentation (Breininger et al. 2004).

Many herpetologists still consider road surveys valuable for monitoring amphibian and reptile occurrence despite obvious biases with this survey method (e.g., Case 1978; Enge and Wood 2002; Steen and Smith 2006). Road surveys are occasionally used to monitor the status of populations (Seigel et al. 2002; Weir and Mossman 2005); however, we urge caution in the interpretation of these data as status cannot be considered independent of the myriad impacts of roads on herpetofauna.

Genetic Effects on Populations

Amphibian and reptile species often have restricted or patchy distributions and small effective population sizes. Roads may serve as barriers that restrict gene flow and decrease genetic diversity through a combination of direct mortality and inbreeding. In functionally-small populations, these effects may significantly increase the probability of local extinction (Rodriguez et al. 1996). Few studies have empirically documented genetic effects on herpetofauna due to roads, but those that have support the hypothesis that roads reduce gene flow and decrease genetic diversity in amphibians (e.g., Reh and Seitz 1990; Hitchings and Beebee 1998; Lesbarrès et al. 2003), especially when populations are constrained within urban areas (Hitchings and Beebee 1997; Rowe et al. 2000; Scribner et al. 2001; Vos et al. 2001).

Virtually all genetic studies of road impacts on herpetofauna heretofore have focused on amphibians, although reptiles could sustain comparable genetic impacts from roads. Further, the same life history traits such as long-life spans, low reproductive rates, and delayed maturity of many reptile species that could result in more severe genetic effects from roads than that observed with amphibians also increase the difficulty in discerning the role that road and urban fragmentation has on genetic isolation. Nonetheless, modern genetic approaches offer great potential for providing insight into how roads affect populations of both amphibians and reptiles and future research should be informative. For instance, landscape genetics is a new discipline that aims to assess population substructure at fine taxonomic levels across varying geographic scales, which is achieved by detecting genetic discontinuities (i.e., distinct genetic change within a geographic zone) as they are correlated with environmental features, including barriers such as mountains, temperature gradients, or as applicable in this discussion, roads (Manel et al. 2003). This increase in technological ability will allow for more accurate genetic investigations of populations surrounding roads, thereby permitting impact assessments within populations as applicable to an evolutionary time scale.

Community-Level Impacts

Data on community-level impacts on herpetofauna are lacking in general, although in some instances lower species richness is correlated with road density (Dickman 1987; Halley et al. 1996; Vos and Stumpel 1996; Findlay and Houlahan 1997; Knutson et al. 1999; Lehtinen et al. 1999; Kjoss and Litvaitis 2001). Analyses of road impacts on herpetofauna at ecological scales higher than the individual or species are inherently difficult, because larger, more significant impacts on populations and communities are not instantaneous. As with populations, cumulative effects on biodiversity may take decades to become apparent. Due to natural fluctuations across spatial and temporal scales, effective analyses require long-term research. Unfortunately, long-term initiatives are typically limited by logistics (e.g., time and funding), and trade-offs between ideal experimental designs and resource availability prohibit the larger-scale or longer-term projects. Ecological modeling offers one alternative using numbers collected from short-term surveys to predict long-term effects. However, only through data collection at population and community levels will the full extent of road impacts be realized. This challenge must be met in order for our understanding of road impacts to progress, and issues of scale (both spatial and temporal) should be addressed to enable biologically valid data extrapolations.

The Road Ahead

The formation of road ecology as a field has fostered action by scientists, conservation advocates, and agencies to design various measures to prevent, mitigate, or compensate for road impacts on surrounding habitats and wildlife (Forman et al. 2003). Many methods may be implemented once a conflict between wildlife and infrastructure is recognized, but the most common solution is the construction of crossing structures. The general function of a crossing structure is to provide safe passage for an animal across the road and to provide connectivity between habitats adjacent to the road (Forman et al. 2003). The synthesis by Jochimsen et al. (2004) provides a composite summary of the various mitigation structures based on descriptions provided by Jackson (1996), Forman et al. (2003), and the USFS website - Wildlife Crossings Toolkit (www.wildlifecrossings.info). Further, Andrews et al. (2006) present pre-construction solution assessments and a tabular presentation of post-construction mitigation projects. For a synopsis of this information, see Jochimsen and Andrews in these proceedings.

Ecologists, engineers, government officials, and the general public are increasingly aware that roads create ecological disturbances and destruction at multiple levels. The approach in the U.S. has been to alleviate traffic problems by building new roads, an action that is rarely effective, often generating new traffic instead of reducing existing volumes (e.g., Pfleiderer and Dieterich 1995). As in North America, herpetofauna throughout the world have the potential to be negatively influenced by roads as a consequence of urbanization, either directly from on-road mortality or indirectly as a result of a variety of ecological impacts, particularly increased human accessibility to the landscape.

Knowledge of road impacts on herpetofauna no longer consists only of on-road mortality. The range, quantity and, potentially, the severity of indirect impacts of roads and urban development on amphibians and reptiles far exceed those incurred from direct mortality of wildlife. Huge gaps exist in our knowledge of secondary environmental effects on wildlife. Designing controlled and replicated experiments in urban and suburban settings is challenging due to the complex spatial mosaic and political divisions of ownership and occupancy. Scientists must accept the challenge and proceed with the understanding of the complexity of road impacts and the seemingly immeasurable amount of variation inherent in diagnosing the problem and developing the solution.

Post-construction mitigation measures are being developed globally. Since the construction of the first amphibian tunnels in 1969 near Zurich, Switzerland (Puky 2004), many structures have become viable alternatives for reducing direct effects of roads for some amphibian and reptile species (Jochimsen et al. 2004). However, the minimization of indirect effects, such as pollution, cannot be accomplished with mitigation structures. Additionally, few studies adequately monitor the efficacy of road-crossing structures in reestablishing connectivity (but see Clevenger and McGuire 2001; Dodd et al. 2004), which is most often the purpose of construction. In light of the many indirect effects that have been identified and many more that remain to be documented, proactive transportation planning to maintain habitat connectivity, public education, and communication among professional sectors of society are the most effective way to minimize and mitigate road impacts and the *only* effective mechanism for avoidance of road impacts.

Acknowledgements: We would like to thank Palmetto Bluff Conservancy and the ICOET Conference Program for travel support to the 2007 meetings along with the SREL Education for educational support. We thank the Federal Highway Administration for their financial support in gathering this information and for an increasing interest in the effects of roads on herps. Kudos to Robin Jung and Joe Mitchell for the hectic and substantial task of creating a much-needed volume on Urban Herpetology and including a manuscript from which this paper is a synopsis. Preparation was aided by Federal Highway Administration Cooperative Agreement DTFH61-04-H-00036 between the University of Georgia and U.S. Department of Transportation and by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award no. DE-FC09-07SR22506 to the University of Georgia Research Foundation. Lastly, we thank all of the scientists and members of society that are gaining ground on the understanding of road impacts on herpetofauna. This research supports the goals of Partners in Amphibian and Reptile Conservation (PARC).

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