**Title**
Behavioural Screening and Selection Through Affinity:  The Case of Polygyny in Paper Wasps (*Polistes dominulus*)

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# BEHAVIOURAL SCREENING AND SELECTION THROUGH AFFINITY: THE CASE OF POLYGYNY IN PAPER WASPS (*Polistes dominulus*)

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*ABSTRACT:* An evolutionary model for emergence of polygynous foundation in polistine paperwasps is proposed. Adapted from Hamilton's model, the model is based on selection through affinity, a process of genetic assortment. This would involve selective association of founding wasps on the basis of common possession of a behavioural trait. The model, therefore, invokes a form of behavioural screening in a genetically heterogeneous population. The validity of the hypothesis and the nature of the trait concerned are considered in relation to observations on formation of Polistine polygynous associations and between species comparisons.

*RÉSUMÉ:* On propose un modèle évolutif de l'apparition de la fondation polygyne chez les Polistes. Placé dans le cadre du modèle général de Hamilton, ce modèle, appelé sélection d'affinité invoque un processus actif d'assortiment génétique. Il repose sur un postulat, taxé de postulat d'affinité, selon lequel la réalisation d'une fondation polygyne ne peut se faire que si tous les sujets ont acquis un même trait de comportement qui n'existe pas dans les espèces strictement monogynes. On examine la vraisemblance de ce postulat et on cherche a déterminer la nature de ce trait commun par étude comparée du comportement dans plusieurs espèces.

> *"It is always difficult to draw unambiguous distinctions in Biology, but it is often valuable to try"*
> Maynard Smith, J. (1976).

## INTRODUCTION

The origin of a sterile caste in Hymenoptera societies is most frequently explained by means of the model of Hamilton (1964). More generally speaking, the concept of inclusive fitness, basic for the model, allowed many authors to account for altruistic behaviour in social Hymenoptera despite its apparent selective disadvantage (West-Eberhard, 1969, 1978; Jeanne, 1980; Gadagkar, 1985a, b; Ito, 1987);

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some of these forms can represent steps in the progression of the sociality in the evolutionary process in Hymenoptera.

In Hamilton's model, selection for an altruistic behavioural trait depends on the degree of genetic similarity between helper and helped, in terms of the gene responsible for that trait. Thus, this model has sometimes been called a model of genetic relatedness (Pamilo, 1984) or of genetic similarity (Rushton, Russell, & Wells, 1984; Rushton & Nicholson, 1988; Parker 1989).

In nature, pedigree relatedness is indeed the simplest explanation for genetic similarity between individuals. Thus Hamilton's model uses Wright's coefficient of relationship $r$, a quantitative measure of pedigree relatedness, to measure the degree of genetic relatedness. That means that pedigree relatedness was implicitly considered by most authors as the only determinant of any genetic similarity between helper and helped. For that, the model of Hamilton was often considered as a model of kin selection (Maynard Smith, 1964).

In fact, pedigree relatedness is not the only reason why helper and helped animals can be genetically similar. Dawkins (1976) pointed to a possible model (known as the "green beard" model), by which such a similarity would result from the existence of a clearly recognizable cue (such as a green beard) bound to the possession of the altruistic gene. Thus, any altruistic animal would be allowed to specifically help genetically similar subjects by turning its cooperative behaviour towards other animals possessing a green beard. Nevertheless, this author did not believe that such a model, less economical than the kin selection model, could have a noticeable extension.

Indeed, it meets an objection, proposed by Maynard Smith (1976), claiming that any genetic similarity between helper and helped animals for other reasons than pedigree relatedness is less likely a priori. This is because the evolutionary process would have implied simultaneous adoption of altruistic behaviour per se and active preference for genetic relatives as the beneficiaries (having a green beard in the case stated by Dawkins). In contrast, the classic kin selection model seems to be more simple and more likely.

The point is that, in these models, altruistic behaviour and choice of the helped animal are considered as being distinct traits of behaviour: there is a trend in evolutionary ethology to consider any trait that can be distinguished by observation as related to a distinct unit of selection.

This assumption is not necessary; any interactive behaviour within a population can change the conditions of selection. At a theoretical level, Eshel and Cavalli Sforza (1982) showed that "structural assortment" during association could substitute for kin selection and account for cooperation.

In previous papers (Pratte & Gervet, 1980; Gervet, 1986) we

claimed that association of females may result from behavioural screening during the establishment of a society, so that only individuals carrying the behavioural trait under selection can indeed associate. Members of these societies will then be genetically similar, but this will not be because of genealogical relatedness. A process of this kind has been called selection through affinity or "pal" selection; we consider as "pals" individuals that tend to associate together on the basis of common possession of a same behavioural trait.

In the present paper we discuss the possible evolutionary emergence of Polistine polygynous societies in this theoretical context.

## POLISTINE POLYGYNY

In some Polistine species, several foundresses may associate to form a polygynous society (Pardi, 1942). It is well known that this is followed by behavioural differentiation, one individual becoming specialised as the main egg-layer, while others, the auxiliaries, either suspend laying, or their eggs are destroyed by the main layer (differential oophagy, Gervet, 1964 b).

Such societies are interesting for students of evolution for two reasons. First, this condition may illustrate a stage along the evolutionary route to semi-sociality (Lin & Michener, 1972), or to eusociality in insects. In fact, it has been stated (Ross & Carpenter, 1991) that the situation of polygynous Polistes does not represent a remaining ancestral situation but only a selective response to peculiar ecological circumstances, which is compatible with structural constraints present in the Polistine. But West-Eberhardt (1978) suggested that selection acting on behaviour expressed by members of polygynous societies could be similar to that which had led to primitive sociality, with its incipient interindividual behavioural differences. Second, polygynous societies raise the general problem of altruistic behaviour. How can there have been selection for the auxiliary or helper condition, which would seem to imply a lowered fitness?

In answer to that question, West (1967, West-Eberhard, 1969) proposed a model inspired by Hamilton (1964).

West (1967) showed that a female will "benefit" from joining a founder as an auxiliary, and in ceasing laying in the resulting digynous society, if the condition:

$(P_{(f+j)} - P_{(f)}) / P_{(j)} > 1/r$ is satisfied, where:

$P_{(f)}$ = productivity of the founder (if it were to remain solitary)

$P_{(f+j)}$ = productivity of the digynous colony in founder's offspring

$P_{(j)}$ = joiner's productivity had it reproduced alone

r = coefficient of relationship (fraction of shared genes) between the founder and the joiner.

These conditions are quite strict, but, according to West, could be satisfied by the combination of three conditions:

First, productivity of the polygynous group is significantly greater than that of a solitary founder;
Second, the joiner's own productivity is low, so that it loses only a small number of descendants in return for a surplus ensured through the founder's increased production with the aid of the joiner;
Third, associated wasps are closely related.

The first condition is the most easily satisfied: the dominant member lays more eggs than if it were solitary and most of the eggs laid by auxiliaries are destroyed by differential oophagy (Gervet, 1962, 1964), the colony is more resistant to destruction (Gibo, 1978), predation (Ito, 1986), and usurpation (Gamboa, 1978). It also exploits the habitat more efficiently (Gamboa, 1980). It may be that the main advantage of polygyny is more closely related to increased chances of nest survival than to any increase in daily laying. In other words, the important feature is not the increase in egg-laying as such, but the improved survival of colonies, which naturally results in greater overall egg production. If so, any such advantage would be closely linked to local ecological conditions such as prey or predator abundance. These in turn could depend on latitude (Jeanne, 1979).

If monogynous founding has only a very low probability of producing offspring, an advantage to polygyny will persist, even when colony-member kinship is low. Hence, predictions of kin and individual selection models will no longer differ whenever a subordinate has any probability at all of replacing an alpha as main-layer (Queller, 1989).

Intrinsically lower fecundity of wasps which assume auxiliary status is less certain. Social relationships established between wasps meeting for the first time do reflect fairly accurately their respective laying rates (Gervet, 1964) and endocrine states (Röseler, Röseler, & Strambi, 1980; Röseler, Röseler, Strambi, & Augier, 1984; Röseler et al., 1986). But, such directly detectable physiological traits do not seem to be of much value as measures of their potential fecundities.

Finally, measures of the degree of kinship between nest companions vary. They are sometimes such that they could confer a genetic

advantage on the helper (Metcalf & Whitt, 1977). However, more ex-
tensive studies have often shown that these relationships may often
be no closer than a wasp would have had with its own offspring (Quel-
ler, Strassmann, & Hugues, 1988; Strassmann et al., 1989). Where
this is so, there would be no selective advantage to polygyny, unless
benefit in terms of offspring produced were to exceed largely the costs
of polygyny. On the other hand, any factor which significantly re-
duced adult life-span (or life-expectancy of a monogynous nest) would
increase the selective value of association, even when members' coef-
ficients of relatedness were low. Even in the most northerly regions,
levels of monogynous colony failure during pre-emergence can be
very high, including that for strictly monogynous species (Yamane,
1969).

Preferential association is usually accounted for in terms of kin
recognition, itself implying that responses of individuals to others are
a function of degree of genetic relatedness (Byers & Bekoff, 1986).
There is evidence that genetically dependent chemical odours (in re-
lation to environmental factors) could mediate such recognition and
distinction in wasps (Gamboa, 1988). This has also been indicated for
other species (see Gadagkar, 1985b, for review). Nevertheless, Grafen
(1990), has pointed out that appreciable assortment of interacting in-
dividuals is not, by itself, a conclusive argument in favour of kin se-
lection.

At present, then, kin selection, based on West's model can ac-
count for Polistine polygyny. However, in several instances, it is nec-
essary to invoke supplementary hypotheses, however reasonable they
may be, for this to be so. In some ecological conditions, West's model
constitutes a reasonable hypothesis. Yet this does not contradict the
occurrence of other mechanisms. In Ito's (1986) words, " . . . mutual-
ism, manipulation and kin selection may all have contributed to the
evolution of eusociality in the Hymenoptera."

However, we believe that another question deserves as much at-
tention as the more detailed study of environmental conditions which
each species encounters. This concerns definition of the point at
which natural selection actually acts, i.e., the identity and nature of
the trait affected. When West asks "what is the selective advantage
to join a colony as an auxiliary?" the question implies a prerequisite:
the relevant selective process would have consisted of the change
from a wasp that founds for itself to an auxiliary. It seemed to us that
the first prerequisite was to ask "what is, in fact, the basic difference
between species which respectively do and do not found polygynous
societies?" To answer this question, we tried to analyse the behaviour
of females belonging to a species that practise polygynous foundation
and compare it to that of other species.

## EMERGENCE OF A POLYGYNOUS SOCIETY: THE EXAMPLE OF
*Polistes dominulus*

In laboratory conditions, we observed the successive steps that lead to the formation of a polygynous society after putting two found-resses in the same cage. A flow chart (Figure 1) summarises these events. Bifurcations show where alternative responses are possible, but only one leads directly to a polygynous society.

When two wasps meet, they may turn aside and separate, with no further development of contact, though they may meet again later. This can happen under natural conditions when two wasps encounter one another in a noncompetitive situation, or at a drinking point. Absence of any further interaction is seen only between two captive *Polistes dominulus* females which have never met before, if their activity level is low. If contacts develop further after meeting (first branch point), antennal displays, described in various previous studies (Pardi, 1946, 1948; Gervet, 1964a), follow. When two or more *P. dominulus* females are placed in the same observation cage, they invariably engage in this type of interaction. Each wasp beats the foreparts of the other with its antennae, with accelerating intensity. This process may be interrupted at any moment; the wasps then separate. In an experimental nest-box, no wasp can flee far away and soon, both females encounter each other again.

When interactions of this kind are prolonged, there are two possible outcomes (the second branch-point). If such individual display patterns are maintained by both individuals (i.e., the interaction remains symmetrical), they graduate to overt aggression. A violent combat ensues, which may result in death of one of the wasps. This progression may again be interrupted at any stage by separation, whether because one or the other takes flight, or due to a disturbance. Alternatively, differences in individual behaviour may appear. One of the wasps ceases antennal beating, lowers the head and antennae, and adopts a characteristic (acinetic) posture, while the other continues its antennal beating. The asymmetry is stable, persisting over any number of subsequent encounters between the same individuals. The intensity of the interaction may, however, wane with time. The antennal and associated movements may become scarcely perceptible, even though a fundamental asymmetry in the response persists.

Such stable differences between individuals at the outcome of a fight, which may have involved no more than a slight preliminary interaction, come under the classical definition of social dominance. The fight that results can be described as a differentiation contest (Yoshikawa, 1956).

Emergence of a dominance relationship between two foundresses in reproductive condition, and ultimately the decrease in aggressive
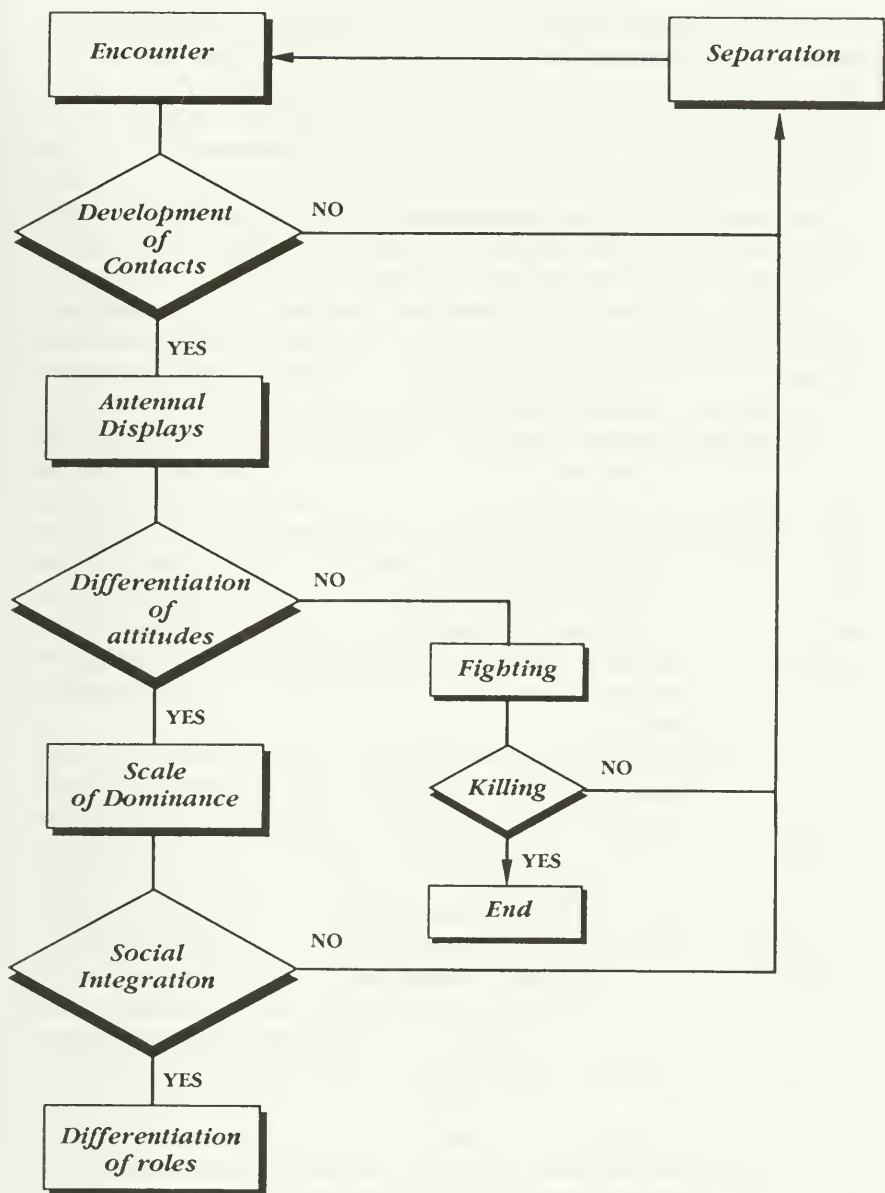
**FIGURE 1.** Succession of events during the formation of a poly-gynous society.

interactions which results are alone not enough to ensure their integration in a digynous society. Two alternatives may then be open (the third branch-point):

In species where polygynous foundation does not exist, the subordinate is attacked or moves away whenever it attempts to return to the nest, even if it adopts subordinate behaviour. If it is the original foundress which assumes subordinance, this is called usurpation (Yoshikawa, 1955). Such species are said to be strictly monogynous.

In species which do polygynous foundation, like *P. dominulus*, the two wasps can continue to cohabit. They adopt their complementary behavioural attitudes with progressively decreasing intensity in later encounters. Then, but only then, can social integration be said to exist. Such species are said to be potentially polygynous.

In this last instance, hierarchical differentiation is followed by a difference in reproductive activity, and in the expression of other activities. The polygynous society is then said to be functionally monogynous. The same kind of differentiation seems to occur in all Polistine species during polygynous foundation which have been studied so far, concerning laying, differential oophagy and contribution to social tasks. Thus, the difference between the two kinds of species does not concern the existence of a differentiation fight nor the subsequent existence of a stable differentiation of attitudes but the consequences of such a differentiation.

In a strictly monogynous species, fights of this kind occur particularly when a foundress regains a nest already occupied by another foundress. At the end of such a fight (of variable degree of violence) protagonists may adopt complementary dominant and subordinate postures, unless one individual previously abandons the nest (Yoshikawa, 1955; Kasuya, 1981; Makino & Aoki, 1982). Departure of the wasp which has "lost" the fight (and which has adopted a submissive or acinetic posture) is the most evident outcome. The behavioural difference resulting from combat supresses attraction of one individual to the nest occupied by the other. The latter continues to harrass, if not aggress, any foundress that comes to the nest, even if it adopts a submissive posture.

Potentially polygynous species do not differ fundamentally from strictly monogynous species, either in intrinsic tendency to join an already occupied nest, or engaging in a combat at the nest, which will lead to differentiation. Two traits which involve a certain ritualization of social contacts do, however, allow the two categories to be distinguished:

When a wasp of a polygynous species becomes subordinate, its attraction to the nest does not disappear, and it remains on the comb, adopting a submissive posture at any encounter with the dominant companion. A more detailed study has shown lower nest presence, but

more particularly, that the behaviour of the subordinate is different (Pratte, 1990a, b). Response to social stimulation is modified after establishment of a hierarchy, with increased responsiveness to larvae and reduced egg-laying (Röseler et al. 1984, 1986), and differential oophagy (Gervet, 1964b).

A wasp which becomes dominant usually ceases to aggress its protagonist as soon as the latter adopts a submissive (acinetic) posture. Its dominance is then expressed in a calmer, more ritualized expression of its initial aggressiveness. Correlated behavioural modifications (increased laying, prolonged nest occupation) also indicate that there are other differences in the behavioural responses related to the nest comb. The events shown in Figure 2 outline the interactions and the assumption of different behavioural roles by the individuals concerned, for strictly monogynous and potentially polygynous species respectively.

We stress here that the difference between the two kinds of species simultaneously involves the wasp that has won a fight, and the one that has lost it. If a wasp of a strictly monogynous species loses a combat, if only through brief submission, it abandons the nest. If it is from a polygynous species, it remains at the nest, and becomes an auxiliary. When a wasp from a strictly monogynous species wins a combat, it maintains essentially the same behaviour towards other females. Its attacks are not stopped by the submissive posture of the other wasp. A wasp from a potentially polygynous species, on the other hand, assumes queen behaviour. It then adopts dominant behaviour towards other individuals, which replaces its initial aggressiveness.

We suggest that all these traits of behaviour express, according to the social situation, various consequences of only two "norms of reaction:" a strictly monogynous and a potentially polygynous norm of reaction. So the question of the selective origin of polygynous foundation becomes "what is the selective advantage of becoming a potentially polygynous female?"

Such a change from the question asked by West to ours can be said to be a postulate. But we state that:

This postulate leads to clearly different conditions for selection. It seems to be reasonable or even, more likely, than the alternative one.

## AN EVOLUTIONARY MODEL

If, in a population, only some individuals possess the "potentially polygynous" norm of reaction, the achievement of a polygynous foun-
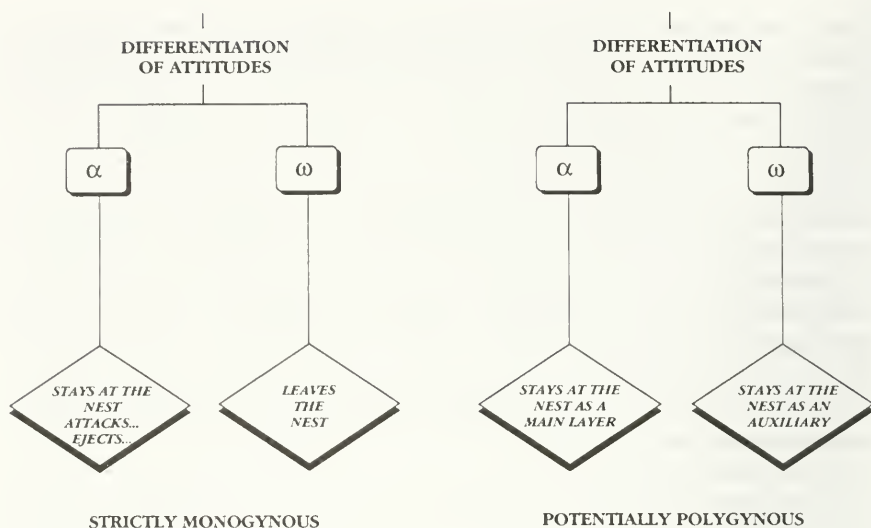
**FIGURE 2.** Differential forms of behaviour for both kinds of species after differentiation of attitudes.

dation does not, obviously, occur at random. It necessarily results from a behavioural screening: only females that possess this norm will actually be able to associate. This assumption leads to a model which has been called selection through affinity (or "pal selection").

Restricting the argument to digynous societies, it can be shown that the "potentially polygynous" norm will be selected if the following condition is fulfilled

$$P_{(f+j)} > P_{(f)} + P_{(j)}$$

with the same parameters as in West's formula.

Or, if one supposes that there is no difference in productivities of joiner and founder:

$$P_{(f+j)} > 2P_{(f)}$$

The main difference between this condition and that of West's model is the disappearance of parameter $r$ expressing the degree of kinship. In fact, we can obtain this formula by making $r$ equal to one in West's formula.

That is not surprising: parameter $r$ expresses (according to Sewall Wright) the probability for two individuals to have a gene in common. The active assortment, in a model through affinity, ensures its value to be equal to one, concerning the gene responsible for associa-

tion, and this one only. Then, this model is a model of genetic related-ness: it is not a model of kin selection.

Consider a population (N) with a proportion (n) of potentially poly-gynous wasps and (1-n) strictly monogynous wasps. For simplicity sup-pose that:

- Each wasp has one encounter with another wasp, at the end of which it either founds alone, or enters a digynous society.
- The various possible encounters are a function of the proportions of the two types of females present in the parent population.
- Each wasp transmits its behavioural characteristic to its descendants. We are therefore referring here, metaphorically, to a "gene" for "poly-gynous potential." Genetic dominance and recombinations, which are symmetrical for the two opposing traits, can be ignored, as far as transmission of the character is concerned, and would merely delay the selective process without changing its character.

Admitting these assumptions, any encounter between a potentially polygynous wasp and one which is not, will have no genetic conse-quences in the following generation, in terms of the "polygynous trait" considered here. Association will not occur, and each wasp will found its own colony, producing its own genetically similar offspring.

The only events which will cause a change in trait frequencies are encounters between two potentially polygynous females: each such en-counter leads to a digynous society producing $P_{(f+j)}$ potentially poly-gynous females, and encounters between two nonpotentially polygynous females which will be followed by the foundation of two monogynous societies producing $2P_{(f)}$ nonpotentially polygynous descendants.

Thus we can observe $n^2$ encounters between two potentially poly-gynous females which produce $n^2 \times P_{(f+j)}$ potentially polygynous fe-males in the next generation. In the same way, $(1-n)^2$ encounters be-tween two strictly monogynous females produce $2P_{(f)} (1-n)^2$ strictly monogynous females in the next generation. Finally, $2n(1-n)$ encoun-ters between one potentially polygynous and one strictly monogynous female, result in $2n(1-n) P_{(f)}$ potentially polygynous and $2n(1-n) P_{(f)}$ strictly monogynous females. If frequencies in the following generation, of potentially polygynous and strictly monogynous wasps are, respec-tively, $n'$ and $n''$ we have:

$$n' = n^2 P_{(f+j)} + 2 n (1-n) P_{(f)}$$

$$n'' = 2 (1-n)^2 P_{(f)} + 2n (1-n) P_{(f)}$$

The potentially polygynous trait will be selected for if:

$$n' > n$$

$$n'' < (1-n)$$

These conditions can be written as:

$$n^2 \times P_{(f+j)} + 2\,n\,(1-n)\,P_{(f)} > n$$

$$2\,(1-n)^2 \times P_{(f)} + 2n\,(1-n)\,P_{(f)} < 1-n$$

Simplifying the two inequalities by n and $(1-n)$ respectively:

$$n \times P_{(f+j)} + 2\,(1-n)\,P_{(f)} > 1$$

$$2\,(1-n) \times P_{(f)} + 2n\,P_{(f)} < 1$$

Which stresses that:

$$n \times P_{(f+j)} + 2\,(1-n)\,P_{(f)} > 2\,(1-n)\,P_{(f)} + 2n\,P_{(f)}$$

or, simplifying again:

$$P_{(f+j)} > 2\,P_{(f)}$$

## THE SELECTED TRAIT AND ITS BIOLOGICAL CHARACTERISTICS

The likelihood of the proposed model is bound to the relevance of a basic postulate; it concerns the functional unity of the norm of reaction that we consider as the target for selective processes. For that reason, we considered the behaviour of the females in both categories of species. According to our observations, several traits of behaviour do not differ from one category to the other one.

During winter, females can gather in overwintering groups. Dominance relationships seem to exist in these groups. Differentiation in individual behaviour during interactions is a part of species contact ritual. Individual wasps involved in confrontation during ovarian diapause show such behavioural differentiation as soon as they interact. Because of this, all members of hibernating groups are members of a hierarchy. It is true that overt dominance interactions are then rare, reflecting a low activity level. When seen, they indicate a typical linear hierarchy, with no associated differences in individual space use. Strong mutual attraction does, in fact, lead wintering individuals of several strictly monogynous Polistine species (*P. omissus, P. foederatus*) to associate in winter clusters, in a common shelter.

Two noteworthy events follow the resumption of reproductive activity. First, the pre-existing hierarchical relationships change and the newly established ones relate to individual endocrine conditions. Second, each wasp establishes an individual nesting area. Within it there is a restricted site, of specific functional significance (the "tache" = spot, *sensu* Deleurance, 1956) where activity is concentrated and nest construction begins.

The presence of the first structural nest components, and even more so of an incipient nest with several cells, has two effects. The nest is both attractive to and stimulating for any actively founding wasp. Indeed, a wasp which is in the prefoundation phase (*sensu* Deleurance, 1956) and which adopts a nest may immediately take up paper collection. The focal point (*tache*), and later the nest, becomes the site at which any reproductively active wasp tends to aggress others.

Aggressive interactions at this stage occur mainly between wasps of which one at least is effectively engaged in founding. The small nest is, at this stage, an attractive object which is actively defended against other females. Fights occur when two females direct their activities towards the same nest, and the individual that loses this fight becomes a subordinate. The differences shown in Figure 2 can explain for both kinds of species, the observations described by several authors.

In a strictly monogynous species, this common attraction by the nest leads to an usurpation (Yoshikawa, 1955) when the fight is won by the newcomer. The first occupant, then, leaves the nest and is attacked as soon as it comes back. As Makino and Aoki (1982) said "the dominant appears not to accept the subordinate rather than to manipulate her." According to concepts used by Schneirla (1965 a, b), a common approach to the nest is replaced, in the subordinate, by a withdrawal out of this territory.

In some species having a low aggressiveness, peculiar conditions can allow several females to cohabit, at least temporarily, at the same nest (pseudopolygyny). This has been recorded, although rarely, under natural conditions in normally monogynous species: *P. Jadwigae* (Yoshikawa, 1962; Kasuya, 1981); *P. chinensis antennalis* (Yamane, 1973); *P. biglumis* (Makino, 1982). The condition has also been induced experimentally: *P. jadwigae* (Yoshikawa, 1956); *P. foederatus* (Perna, Marino Piccioli, & Turillazi, 1978).

The common feature in these observations is the absence of behavioural differentiation of the kind classically observed in species which are more frequently polygynous. We attribute such pseudopolygyny to simple habituation, rare under natural conditions, induced by manipulations which favour the establishment of compound nests or which forcibly impose cohabitation in small cages under experimental conditions. A relatively low level of aggressiveness in the species concerned would favour such habituation. It is well known (Itô, 1985) that the degree of inter-individual agressiveness varies according to species.

In this view, each wasp would actually behave as a solitary, despite the effective cohabitation, ignoring other wasps as factors liable to affect its own reproductive behaviour. This has been emphasised by

Perna et al (1978). Here, female cohabitation would then be polygyny only from the observer's point of view.

Absence of behavioural differentiation would then mean that if a wasp is to express nesting behaviour, it has only two possibilities. The first would be to approach and occupy any nest territory it encounters. The second would be to avoid them and go away, even if a female is led to cohabit with its dominant, it seems to be unable to display an auxiliary behaviour. Reciprocally to the previously quoted sentence of Makino and Aoki, the subordinate tends to leave the nest rather than to become an auxiliary.

In a potentially polygynous species a departure of the subordinate may occur occasionally. More commonly, it is followed by division of labour which leads the subordinate to become an auxiliary. To understand the change involved, we must ask what this behaviour implies.

Pratte (1990b) has found that the members of a hierarchy in a trigynous *P. dominulus* society do not all have the same preferences for, or responses to attractive stimuli. Similar observations have been made for a postemergent monogynous society (Theraulaz, Pratte, & Gervet, 1990; Theraulaz, Gervet, Thon, & Pratte, 1991a; Theraulaz, Gervet, & Semenoff, b). Nests are particularly attractive to subordinate wasps when they contain larvae. These release a regurgitation reaction, and/or elicit food collection, but those wasps are less reactive to stimulations releasing egg laying or differential oophagy. On the other hand, the response of the dominant to young larvae is weaker, while its orientation towards empty cells (available for egg laying) and eggs is stronger. We summarise these facts by saying that dominance relationships affect a process of approach-withdrawal within the framework of reproductive behaviour.

Expressing a ritualised fight, they lead the winner ( = dominant) to strengthen its attraction towards stimulations bound to the reproductive behaviour and the loser ( = subordinate) to reduce its responsiveness to these stimulations.

The transition from strictly monogynous to potentially polygynous norms of reaction would concern how to manage these opposite trends. In the first case, approach and withdrawal take a geometrical meaning: stay at the nest (and expel other females) or leave it (and avoid the winner female). In the second case, they concern specific modes of investment of social space: turn to a layer behaviour (and only fight opponent females) or to a behaviour of auxiliary as previously described.

Such a change reminds us of the case, rather frequent, of transition from territorial to hierarchical behaviour. By the way, *P. canadensis* (West-Eberhard, 1986) is, to some extent, intermediate between strictly monogynous and potentially polygynous species: A

form of territory related dominance was described, in which a territorial queen actively suppresses aggressive behaviour of nestmates via physical approach and attack. This condition would support the proposed link between dominance and territoriality or, in other words, the effect of social rank on the use of social space in the nest.

## Selection Through Affinity and Evolutionary Problems

At a theoretical level, a model of selection through affinity (or "pal selection") is more economical than the classical model of kin selection, but two remarks can be made:

We must show that a "pal directed" process is robust and can represent an evolutionarily stable strategy. In particular, any evolutionary trend is concerned with the problem of cheating, and we must ask if such a mechanism of active assortment can resist the income of a cheater.

It seems, according to several authors (Post & Jeanne, 1982; Gadagkar, 1985b; Gamboa, 1988; Gamboa, Reeve, & Pfennig, 1985), that some kin preference frequently exists for common association. This suggests that it led to some selective advantage, and thus, that some degree of kin selection did exist.

*False-pals and cheaters.*

Consider a population of "pals" accepting to become auxiliaries when they lose the fight of differentiation and becoming main layers when they win this fight. Suppose that a mutant "false pal" arises, which accepts help (that is, cooperates when dominant) but never gives it (defects when subordinate, and founds alone). In an environment of pals, "false-pals" will take the advantage and, thereby, eliminate all the "true pals" genes from the population. Then how can a "true pal" norm of reaction have been retained? We see only two possible answers to this question.

The first would argue that some structural constraint could have prevented the incoming of such a "false pal" behaviour. It may be that changes when dominant and subordinate would have consisted in the same ethological transition. Only a more accurate analysis of these norms of reaction will clarify this point.

The second one states that "false pal" behaviour is not an evolutionarily stable strategy. Since no mechanism can lead to an equilibrium between strains of "true pals" and "false pals," indeed the advantage of the "false pal" exists whatever the density of the "true pal." If the latter is eliminated, only monogynous foundation can occur and the "false pal" strategy no longer has any selective advantage, or can even be counterselected.

A "false pal" strategy can be stable only if a mechanism exists that leads to an equilibrium between "true pal" and "false pal" genes.

That is possible if "false pals" are, at the same time, "lazy," i.e., unable to found a new colony when alone. Then the scarcity of "true pals" leads to a rather drastic situation for false pals, while the few remaining "true pals" are able to found new colonies.

Such a regulatory mechanism is more easily involved if a genetic isolation between the two strains allows a "true pal" colony to lay only "true pal" offspring. Then an equilibrium can be established at a level that depends on the ability of each strain to promote its own strategy. In fact, such a "lazy false pal" behaviour exists; it is the one of the social parasites belonging to the Sulcopolistes genus. Thus, such a scenario would explain the origin of social parasitism among paper wasps.

### Pal Selection and Kin Selection

A process of kin selection for polygynous foundation can only occur if two (or even three) factors are involved: kin preference for association, ability for the subordinate to become an auxiliary, and ability for the dominant to accept its subordinate in the nest. A "pal selection" process involves only one change, which is the previously quoted change of norm of reaction. It is apparently more economical; but, at the same time, it involves one constraint: the existence of norms of reaction as described. Similarly, it suggests a grid for study of social reactions to polygyny. On the other hand, two differences between the models are relevant for evolution:

First, a "pal" directed process is faster than a "kin" directed process, since it can be considered (for evolution) as a "kin" process in which $r$ is equal to 1.

Second, its genetic effects are not the same: only the gene of the auxiliary which is responsible for association is replicated in the next generation, while the other ones are counterselected. This second difference leads to several consequences.

Within the genome of the auxiliary, this fact gives a selective advantage to every mutation which, at other loci, could weaken the effects of the "pal" allele. But, this is true only if ecological conditions allow a monogynic foundation to give offspring.

A polygynous foundation obtained by a "pal" directed evolutionary process gives the best conditions for a subsequent selection of any "kin preference" gene which would have arisen at another locus in the genome of the joiner that becomes subordinate.

Thus, we can suppose that the evolutive appearance of polygyny in paper-wasps—or, more generally, in a semi-social group implying kin preference—would have involved two successive steps.

A process of pal selection, leading to groups of females possessing the main characteristics of polygynous societies, as described. In par-

ticular, this is compatible with Carpenter's (1989) scenario stating that a stage of casteless nest sharing may not have occurred.

The incoming of a kin preference bound to a new selective process having occurred after the appearance of the polygynous group.

Possible existence of these two steps suggest that the different hypotheses (parasocial group: Lin & Michener, 1972; polygynous family: West-Eberhard, 1978) point to possible scenarios but not to necessary prerequisites for a subsequent evolutionary trend to eusociality in insects.

## CONCLUSION

Even, if, by nature, an evolutionary model is to remain rather conjectural, we believe that the postulated selective process, discussed here under the term affinity selection or pal selection is plausible, given details of behaviour we have actually observed in Polistines. We would also stress that it is quite compatible with Hamilton's model (1964). We further note that it does not conflict with the kin selection model, but does appeal to some additional considerations, as illustrated by three points:

It is more parsimonious in its requirements than kin selection. However, it is clear that if wasps associate because they carry a same allele, the probability of affinity is greater for related wasps. This the more so where the frequency of the trait is still low in a population as a whole.

It is not open to Maynard Smith's (1976) objection (previously quoted), because expression of a potentially polygynous behaviour and choice of individual helped are not different traits of behaviour but simply different consequences of the same trait. The expression of the behaviour will itself automatically lead to assortment in a population of wasps possessing the trait. Here the model avoids the previously quoted difficulty in the Green Beard Model.

It leads to selection for genes associated with polygynous behaviour, without directly affecting other genome components, whereas a model involving kin relationships would tend, at least in the short-term, to facilitate transmission of genes frequent in the parent strain as well.

The implications of this fact for genetic diversity remain obscure in the case of a polygynous society, but these implications could become appreciable for an analogous model which considers assortive mating. Rushton et al. (1984, 1988) referring to a very different biological material (*Homo sapiens*), considered that selection based on genetic affinity could offer protection against excessive inbreeding. Optimal fitness, they write, ". . . consists in selecting a mate who is genetically similar but not actually a relative."

Beyond the problem treated here at the level of the Polistines, we would raise a problem central to the study of evolution, and more particularly relating to the evolution of behaviour. This is identification of the units of selection.

Gayon (1989) and Gliddon and Gouyon (1989) commented on confusion between two distinct problems. The first concerns the biological units between which selection operates (units of selection) and the second the nature of the unitary traits retained in a population by selection (units for selection).

The first has often been treated by ethologists and evolutionary theoreticians. The concepts of individual selection, group selection, kin selection, and interdemic selection have generated detailed mathematical models. It is now possible to consider both the ecological conditions and the behaviour which are required if they are to be valid.

In contrast, we have stressed the second of these problems, the definition of the selected trait. We believe that the question is essential to ethology: the most conspicuous feature of a behavioural trait, for the observer is not necessarily the most pertinent in terms of selection. We claim that one cannot state a selective process without having previously said what has been selected. Only by this manner will ethological analysis and selective models be able to enlighten each other. Then, it will be possible both to more accurately describe the selective origin of actual behavioural traits and to find how the behaviour can organize the network of interactions within a population and, thereby, direct its own evolution.

## ACKNOWLEDGMENTS

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