Foundress Associations in Polistine Wasps: Dominance Hierarchies and the Evolution of Social Behavior

Abstract. *Interactions among female paper wasps of newly founded colonies suggest that dominance relations assign social (reproductive) roles to siblings in a way advantageous to both dominants and subordinates. In various social animals dominance relations may have been an important prerequisite for the evolution of a division of labor between reproductive and nonreproductive (or less reproductive) adults.*

Social ("altruistic") behavior may be defined as activity of an individual benefiting the young of another of the same species. This includes a number of biological phenomena for which the classical Darwinian explanation in terms of advantage to the reproductive individual does not seem adequate. Consequently some biologists, for example, Wynne-Edwards (*1*), have postulated that selection for social characters operates on the group or population rather than on the individual. However Haldane (*2*), Hamilton (*3*), and Williams (*4*) have pointed out that most (if not all) social behavior can be explained in terms of advantage to the individual, either through benefit to the performer's offspring (with incidental benefit to those of another) or through increased replication of the performer's genotype due to enhanced reproduction by an aided relative (an individual having a similar genotype). This paper, based on observations of social paper wasps of the genus *Polistes*, shows how dominance hierarchies may contribute to the likelihood that social behavior will be advantageous to the individuals of a sibling group.

The single-comb, unenveloped nests of *Polistes* wasps are generally initiated by a single female, which in some species may be joined by from one to ten other "foundresses" (females on a nest prior to brood emergence) (*5*). Social colony foundation—cooperation of females in brood rearing before the emergence of offspring workers (*6*)— is common in *Polistes* despite the consequent sterility of large numbers of fertilized females. Twenty-eight (61 percent) of 46 *P. fuscatus* colonies examined just before brood emergence contained more than one adult female, as did 45 (97 percent) of 46 *P. canadensis* colonies examined at a comparable stage (*5*). Only one foundress of each colony ultimately becomes a queen (egg layer); the others become idle or, more commonly, sterile workers which care for the queen's brood but do not lay eggs

(*7*, *5*). Thus, 51 (53 percent) of the 97 fertilized, overwintered females associated with the 46 censused *P. fuscatus* nests were nonreproductives, as were 181 (79 percent) of the 227 foundresses observed in *P. canadensis*.

According to the reasoning of Hamilton (*3*), joining a foundress association would be advantageous to a consequently sterilized female if more replicates of genes like hers were produced as a result of the association than she could produce on her own. Specifically, association is beneficial to a worker if it meets the condition $k > 1/r$, in which k is the ratio of gain to loss in fitness, and r is an expression of the degree of genetic relationship between the associated females (*3*). Hamilton considers the sterility of daughter workers on a parental nest understandable in these terms since, assuming that the maternal queen mates only once, in insects (such as *Polistes*) with male haploidy, females have more genes "identical by descent" to those of their sisters ($r = \frac{3}{4}$) than to those of their own daughters ($r = \frac{1}{2}$). But Hamilton found it "difficult" to explain "the ready acceptance of nonreproductive roles by the auxiliaries" in *Polistes* foundress associations (*3*, p. 37) even among siblings since nonreproductive females are engaged in rearing the offspring of sisters (nieces), which are less closely related ($r = \frac{3}{8}$) to them than their own offspring would be.

However, the likelihood of association depends not only on the closeness of relationship among co-foundresses but also on the difference in independent reproductive capacity between associates and the degree to which the presence of the joiner augments the reproduction of the joined female—the k in Hamilton's expression $k > 1/r$. My hypothesis is that dominance relations during group formation may maximize k for each individual by enhancing the likelihood that relatively inferior reproductives—females likely to have few progeny on their own—become workers on nests of superior reproductives, which are thus free to specialize

in egg laying. Considerable indirect evidence indicates that associated foundresses are likely to be siblings (*3*, *5*); and observations of marked wasps indicate that females known to have emerged from the same parental nest associate in colony founding (*8*, *5*).

Pardi (*7*, *9*) demonstrated that a linear dominance hierarchy forms among the foundresses of a colony, and that there is a correlation between dominance order and ovary development: dominant individuals have larger ovaries than females ranking below them in a hierarchy do. I have observed dominance hierarchies among foundresses in *P. fuscatus, P. canadensis, P. flavus,* and *P. annularis*, as have Morimoto (*10*) in *P. chinensis* and Yoshikawa (*11*) in *P. fadwigae*. Yoshikawa noted that the most dominant worker becomes the primary egg layer following removal of the queen. Similarly, I have observed in *P. canadensis* that the most aggressive contender among females on a nest after removal of the queen begins laying eggs; and in *P. fuscatus* the highest ranking females in a hierarchy on a newly founded nest are the only egg layers (*5*). These observations indicate that Pardi's conclusions regarding dominance and ovary size in *P. gallicus* apply to other *Polistes* species. Thus, insofar as degree of dominance corresponds to degree of ovarian development (*12–13*), and relative ovary size is an indication of relative reproductive (egg-laying) capacity, dominance order is a measuring stick of relative reproductive capacity in *Polistes*.

Field observations show that foundresses initially move from nest to nest, and association requires differential dominance among the individuals of the group (*5*). In *P. canadensis* dominance conflict among sibling foundresses led in three cases to usurpation of the dominant queen's position by a newcomer. One of the ousted queens sat idle near her former nest, and two became queens of other colonies. In *P. fuscatus* five changes in residence led to two nest initiators' and egg layers' becoming nonovipositing subordinates (workers) on the nests of other females. Since relative dominance may act as a "measuring stick" of relative reproductive capacity, the formation of foundress associations may be a process by which siblings sort themselves into groups according to relative reproductive capacity, with inferior reproductives becoming sterile helpmates of reproductively superior siblings. The

dominance hierarchy in wasps, and perhaps other social animals, may thus play an important role in the assignment of different functions (roles) to closely related individuals having different reproductive capacities in such a way that both dominant and subordinate individuals derive reproductive benefit.

Field data indicate that k for two-foundress associations is large enough to admit the possibility of advantage to a subordinate joiner. The condition $k > 1/r$ can be rephrased as follows:

$$P_c > P_q + (1/r_1) P_1 + (1/r_2) P_2 \ldots$$
$$(1/r_n)P_n$$

in which P_c equals production of colony; P_q equals reproductive capacity of unaided queen; P_n equals reproductive capacity of nth subordinate; and r_n equals fraction of nth subordinate's genes identical by descent to those of queen.

P is best expressed as numbers of reproductive males and females produced, but, because of the difficulty of obtaining such data for many colonies having a known number of foundresses, I have estimated P in terms of the number of cells produced by foundresses during the period between nest founding and brood emergence. Values of P_c for nine single-foundress colonies (unaided queens) ranged from 12 to 31 cells in *P. fuscatus* (mean = 22.9 cells) (14). If, for example, the least productive of these queens became a nonlaying subordinate on the nest of an average female ($P = 22.9$ cells), and if both were offspring of a single female inseminated by only one male (r for siblings = ¾), P_c would have to be greater than 38.9 $[P_q + (1/r_1) P_1]$ for joining to be advantageous to the subordinate. Seven of eleven two-foundress colonies observed satisfied this condition, having P_c values of 47 to 67 cells.

As foundress number increases the number of cells produced per foundress decreases (5). That is, the more foundresses present the less the addition of one more augments P_c. If it is assumed that associated foundresses are siblings (and, hence, that their r values are similar), and if joining remains advantageous, the reproductive capacities (P) of successive joiners must generally decrease with order of joining ($P_1 > P_2 > P_3 \ldots P_n$). If relative dominance reflects relative reproductive capacity as suggested above, dominance rank would also be expected to decrease with order of joining. This was

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the case in a large (seven-foundress) association whose history was followed for 5 weeks: a linear hierarchy formed in which the nest initiator was the top-ranking female, and subordinates ranked two to seven in the order of their joining the association (5).

It appears likely that dominance-subordinance relations become established whenever differentially aggressive individuals repeatedly interact. In farm animals and caged zoo and laboratory animals hierarchies are probably often artifacts of confinement (16). Williams points out that even in animals naturally living in groups a dominance hierarchy is usually not a "functional" (directly selected for) organization, but is "the statistical consequence of a compromise made by each individual in its competition for food, mates, and other resources. Each compromise is adaptive but not the statistical summation" (4, p. 218). However, a hierarchy could become adaptive in sibling associations like those of *Polistes*, where selection might set the amount of dominance differential sufficient to cause advantageous subordination in place of continued conflict or flight. In *Polistes* the sufficient difference would be expected to vary with (i) availability of suitable nest sites and, hence, population density, since a poor nest site would reduce a subordinate's chances of independent success, and (ii) the required value of P_c compared to the highest possible reproductive capacity of the aided queen, whose egg production might approach a limit in a nonlinear fashion, necessitating a "graduated" sufficient difference in dominance. Selection would also favor individuals able to distinguish closeness of their genetic relationship with potential associates (even among siblings r varies from 0 to 1).

Dominance could function as suggested here in any social species having groups composed of genetically similar (related) individuals, and dominance hierarchies in which (i) dominance reflects reproductive capacity, (ii) dominant individuals are the primary reproductives, and (iii) the presence or activity of a subordinate augments the reproduction of the dominant. These conditions may exist in some primate societies. Dominance behavior is a fundamental determinant of primate social organization and is associated with (i) age and sexual aggressiveness and (ii) breeding success (17). Although there is little direct information on this point, it seems likely from descriptions of primate group co-

herence and composition given by Carpenter (18) that adult offspring tend to remain with or near the parental group, which should therefore contain a large proportion of more-or-less related individuals. In societies of some monkeys and apes, subordinate males participate in group defense and food-seeking (18) and must therefore aid in rearing offspring of more dominant (more frequently mating) males.

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References and Notes

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12. Pardi did not investigate the relationship of ovary size and dominance order before association. It could therefore be argued that small ovary size is an effect, not a consistent correlate, of subordinance. Even if further investigation proves this to be the case, I would maintain the hypothesis that dominance order reflects characteristics (perhaps hormonal) likely to influence reproductive capacity. Dissections of 11 *P. fuscatus* females collected on 27 Apr. 1964, about 2 weeks before onset of nest building, showed differences of a sort possibly associated with observed differences in dominance before nesting; ovaries ranged in size from 15 to 24 oocytes. Six females having 20 or more oocytes contained mature eggs, and five did not.
13. Number of oocytes present in the ovary was estimated by counting the number of bulges visible in the ovarioles at a magnification of 19× and dividing 2, every other bulge being a group of nurse cells.
14. This assumes that the sample of lone queens represents the entire range of individual independent reproductive capacities. This range is probably wider in both directions.
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16. For examples, see R. G. Beilharz and D. F. Cox, *Anim. Behav.* **15**, 117 (1967); H. Hediger, *Studies of the Psychology and Behavior of Captive Animals in Zoos and Circuses* (Criterion, New York, 1955); R. D. Alexander, *Behavior* **17**, 130 (1961).
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