

## PARASITES, WORKER POLYMORPHISM, AND QUEEN NUMBER IN SOCIAL INSECTS

Social life not only provides various benefits but also entails costs such as increased vulnerability to pathogens and parasites with short life cycles. This is because physical proximity and contact rates are increased in groups, which thereby increases the chance that individuals will encounter parasites or pathogens introduced by other group members (Alexander 1974; Hoogland and Sherman 1976; Tooby 1982; Hamilton 1987). Here I suggest that pathogens and parasites might be important in shaping different components of the social structure of insect colonies. Specifically, I argue that pathogens might be one of the factors accounting for the association that Frumhoff and Ward (1992) found between queen number per colony and the presence/absence of polymorphic workers in ants.

Social insects exhibit the most extreme forms of social life, with colonies of some species having thousands or even millions of individuals (Wilson 1971). An additional characteristic of social insects that makes them particularly susceptible to parasites and pathogens is the potentially high genetic relatedness among nest mate individuals. Closely related hosts may be similar in their susceptibility characteristics, which would facilitate the spread of pathogens within a colony (Tooby 1982; Hamilton 1987; Seger and Hamilton 1988; Sherman et al. 1988; Hamilton et al. 1990). Hamilton (1987) and Sherman et al. (1988) suggest that multiple mating by hymenopteran queens may have evolved as a means to increase genetic variation within colonies, which would thereby reduce the likelihood that parasites or pathogens will diminish the worker/defense force to the point of jeopardizing the colony's survival and reproduction (see also Keller and Reeve 1994). The genetic diversity hypothesis receives some support from Shykoff and Schmid-Hempel's (1991) finding that parasite transmission in social groups of the bumble bee *Bombus terrestris* apparently correlates with the degree of relatedness among hosts.

An important factor affecting genetic variability within colonies is the number of queens per colony (see, e.g., Queller 1993; Ross 1993). Only in hymenopteran colonies with multiple fertile queens (polygyny) can the mean relatedness among workers decrease below 0.25. Indeed, there are many polygynous species in which relatedness among workers is very low (or even indistinguishable from zero) because many queens, not highly related to each other, reproduce in the same colony (Hölldobler and Wilson 1990; Herbers 1993; Rosengren et al. 1993; Ross 1993). Thus, one potential advantage of polygyny, at the colony level, is that it increases genetic variability and thereby decreases susceptibility to parasites. It

is unlikely that polygyny has evolved in social insects only in response to pathogens and parasites. Other ecological factors such as rates at which colonies lose their queen(s) and the dispersal risks experienced by female sexuals certainly influence the threshold over which colonies benefit from reaccepting secondary queens (Nonacs 1988, 1993; Herbers 1993; Rosengren et al. 1993; see also other chapters in Keller 1993). However, everything else being equal, the threshold for the evolution of polygyny should be lower in species more likely to suffer high parasitic or disease loads.

One factor that may affect the parasite load of a species is the presence/absence of polymorphic workers. Tooby (1982) pointed out that one possible strategy for hosts to resist pathogens is to "express different phenotypes, as the result of development noise or plasticity and this may interfere with parasitism in much the same way as tissue differentiation does" (p. 573). Social insects exhibit striking examples of phenotypic plasticity, with morphological castes having long been cited as a prime example of nongenetic polymorphism (Huxley 1932; Wheeler 1992; Keller and Ross 1993*a*, 1993*b*). Morphological differentiation between castes in the eusocial insects may thus act as an impediment to parasitism (Tooby 1982). Workers of different castes differ not only in their morphology but also in physiological attributes such as metabolic rate (Calabi and Porter 1989) and hormonal titers (Suzzoni et al. 1980), which may further influence susceptibility to specific parasites. Additionally, the existence of morphological castes is frequently associated with caste-related behavioral specialization (Oster and Wilson 1978), which greatly reduces the number of interactions and the probability of parasite transmission among members of different castes. Finally, the existence of individuals of different size and morphology may also provide an effective means of protection against parasitoids and parasites. For example, a recent study by Feener and Moss (1990) suggests a curious behavior of small minor workers evolved as a defense against phorid flies in leaf-cutting ants of the genus *Atta*. These authors showed that hitchhiking of minor workers on leaf fragments carried by large workers significantly reduces the probability that phorid flies will attack and successfully deposit eggs in the head capsule of the large workers.

If it is true that morphological differentiation between castes impedes parasite transmission, then one would predict a negative correlation between polygyny and the degree of polymorphism in ants. This is because the benefits from reaccepting additional queens (i.e., additional genetic variability reducing susceptibility to parasites) should be higher in species without distinct morphological worker castes.

Some evidence suggests that polygyny is indeed more frequent in species lacking polymorphic workers. Frumhoff and Ward (1992) surveyed the relationship between the number of queens per colony and the degree of nest mate worker size variation in ants. They tested Oster and Wilson's (1978) hypothesis that polygyny should facilitate worker reproduction and therefore constrain the evolution of worker polymorphism. Worker polymorphism should be opposed by individual selection when there are reproductive opportunities because individuals of specialized worker castes generally have lower abilities or opportunities to reproduce (Oster and Wilson 1978; Frumhoff and Ward 1992). Workers in a sol-

dier or forager caste, for example, are at greater risk than castes specialized in brood tending. As predicted by Oster and Wilson (1978), a comparative study showed that polygyny is significantly rarer in taxa with strongly polymorphic workers than in those with monomorphic species (Frumhoff and Ward 1992). However, because queen number is a much more labile trait than is the degree of worker size variation, Frumhoff and Ward (1992) concluded that the link between queen number and worker polymorphism is inverted, with polygyny being less likely to arise in taxa with strongly polymorphic species. This causal association is consistent with a lower parasitic pressure in polymorphic species increasing the threshold for the evolution of polygyny.

Although various pathogens have been identified in ants (e.g., viruses, bacteria, unicellular fungi, microsporidia, neogregarines, nematodes: Jouvenaz 1986; Hölldobler and Wilson 1990, pp. 554–555), little is known about the incidence of these pathogens, their effect on colony productivity, and the mechanisms of defense in ants. In many ant species workers have a metapleural gland that produces antiseptic substances that are effective antibiotics against *Escherichia coli* (Maschwitz et al. 1970; Maschwitz 1974; Hölldobler and Wilson 1990). However, the spectrum of microorganisms against which these substances are effective is unknown, and it is unclear precisely how effective these substances are against such microorganisms. Jouvenaz (1986) pointed out that the study of diseases of fire ants is largely in an exploratory stage, yet this is the most extensively studied group of ants (particularly *Solenopsis invicta*) with respect to endoparasites. To date, most of the endoparasites identified in *S. invicta* have a low incidence or are not very pathogenic. However, this condition does not imply that parasites are unimportant because even a small effect of pathogens on colony efficiency and/or productivity may have dramatic effects in intra- and interspecific competition. For example, Feener (1981) showed that in the ant *Pheidole dentata*, phorid flies, although rare relative to their hosts, dramatically decrease the competitive ability of this species against its enemy *Atta texana*. Similarly, the foraging activity of *Pheidole titanis* is strongly affected by phorid flies, although the parasitism rate by flies is less than 2% (Feener 1988). This observation led Feener (1988) to conclude that results of these studies suggest that the present abundance of a parasite is not a good indicator of its ecological impact on hosts. Weak effects of parasites or pathogens on colony efficiency and/or productivity are also likely to have significant effects on intraspecific competition. Intraspecific competition is a critical component of the ecology of many ant species, and studies of contests between colonies of different sizes show that larger ones are more likely to win (see, e.g., Hölldobler 1981; Adams 1990). Thus, even if a parasite only slightly decreases the productivity of a given colony (thus its overall colony size), this effect may decrease the colony's ability to compete with neighboring colonies and ultimately significantly affect the lifetime reproductive success of its members.

Unfortunately, almost no studies consider the factors affecting the transmission of parasites among nest mates and differential susceptibility of castes to parasites and pathogens. In *Lasius flavus*, the mite *Antennophorus grandis* has been shown to occur preferentially on the smaller nurse workers (Franks et al. 1991). This host size specificity may be linked to the fact that the mite may be able to adhere

strongly enough only to the gula (chîn) of small workers to avoid being dislodged by the host insects. Similarly, differences among large and small workers in their susceptibility to two rhabditid nematodes have been reported in *Acromyrmex octospinosus* (Kermarrec et al. 1990). Large workers of this species have been shown to be less susceptible to the nematode *Neoapectana carpocapsae* than are small workers. In contrast, large workers are more susceptible to the other nematode, *Heterorhabditis bacteriphora*. These findings are consistent with an ability of morphological caste differentiation to affect susceptibility to parasites.

Definitive evidence for the parasite hypothesis proposed to account for the association between queen number and worker polymorphism will require experimental tests comparing parasite transmission between individuals of the same and different morphological castes, comparison of parasite load between closely related monomorphic and polymorphic species, and/or comparison of parasite load in species with intraspecific variation in levels of worker polymorphism. A problem with studies aimed at comparing parasite load between monomorphic and polymorphic species is that other colony characteristics such as colony size may be correlated with the presence/absence of morphological castes. Morphological castes are more common in species with large colony size (Oster and Wilson 1978), and large colonies are likely to attract more guests, including parasites, in both ecological and evolutionary time. Thus, colony size should be controlled for in interspecific, as well as intraspecific, comparisons when the degree of worker polymorphism is correlated with variation in colony size. Such studies may shed light on whether pathogens and parasites have been important in shaping social organization in insects and to what extents polygyny and morphological castes provide effective defense against parasites.

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