

Forum

Reproductive potential and division of labor in wasps: are queen and worker behavior alternative strategies? *

Introduction

Recent models for the evolution of division of labor in insect societies suggest that queen and worker behavior are complementary alternative strategies (WEST-EBERHARD 1981, JEANNE 1991). These models posit that a negative correlation exists between the ability to reproduce under social competition (direct fitness; queen behavior) and the performance of non-reproductive tasks for the colony (indirect fitness; worker behavior). In some species of eusocial wasps (Vespidae), individuals performing worker tasks (e.g., foraging) are less likely to succeed in replacing queens or in reproducing directly (WEST-EBERHARD 1969, JEANNE 1972, GAMBOA et al. 1978, STRASSMANN 1981a, GADAGKAR 1987). However, this relationship is weak or reversed in other eusocial vespids.

Individuals engaging in tasks that remove them from opportunities for egg laying are most likely to replace or supersede the queen and reproduce in a number of species. These individuals are able to accrue both indirect and direct fitness by working for their colonies and, later, reproducing. Therefore, the costs to direct fitness of engaging in worker behavior are not consistent across species, even within the independent-founding eusocial wasps. In other words, queen and worker behavior do not necessarily represent alternative strategies. In this article I review studies that demonstrate the diversity of relationships between reproduction and worker behavior in wasps, and discuss selective factors that may influence the degree and nature of behavioral separation of queen and worker behavioral roles within species or populations.

Reproducing and helping as complementary alternatives

WEST-EBERHARD (1975, 1981) proposed that adult social insects of inferior fertility are selected to pursue secondary alternative reproductive strategies. Secondary strategies often involve maximizing indirect fitness via helping (worker-like behavior), which is assumed to both exclude personal direct reproduction (queen-like behavior) and to complement the role played by reproducing social partners. According to WEST-EBERHARD (1981), "...the opposite nature of queen and worker specializations must have facilitated their evolution".

JEANNE (1991) extended the idea of separation of queen-like and worker-like behavior to explain the typical pattern of age polyethism in highly eusocial insects: workers progress from tasks performed inside the nest (presumably near opportunities for egg laying, and entailing low risk of mortality) to tasks outside and away from the nest (away from cells in which to oviposit, and entailing a higher risk of mortality). Under this scenario younger workers may be considered hopeful reproductives, and individuals behave as if they are sensi-

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tive to changes in their direct reproductive value (chances of laying eggs) relative to indirect reproductive value (fitness achieved through helping behavior).

These models for the evolution of division of labor posit that worker behavior entails some cost to direct reproduction, that is, there is a tradeoff between worker-like and queen-like behavior. However, as shown below, the magnitude of the fitness costs of worker behavior (in terms of increased mortality or reduced fecundity) appears to depend on ecological factors. These species or population-specific factors in turn determine whether engaging in worker behavior precludes later engaging in queen behavior.

Species in which worker-like behavior does not preclude reproduction

Experimental queen removals and natural queen disappearance change the social structure of colonies. These changes allow examination of plasticity in social roles for the females (cofoundresses or offspring) remaining on the nest. As in many independent founding Vespidae, *Polistes exclamans* queens that are removed from colonies are quickly replaced after intensified dominance interactions among the remaining females. Successive removals of *P. exclamans* queens showed that queen successors were consistently the oldest individuals on the nest (STRASSMANN & MEYER 1983). Most of the replacement queens had been active foragers, and prior to takeover had foraged at higher rates on average than non-replacement females. Replacement queens in *Ropalidia marginata* colonies had foraged at intermediate rates relative to nestmates prior to queen removal (CHANDRASHEKARA & GADAGKAR 1992), and similar results were obtained from queen removal experiments on *Polistes instabilis* (HUGHES & STRASSMANN 1988).

Observations of unmanipulated *P. instabilis* colonies in Costa Rica showed that dominant females were often among the most active foragers, including a female that copulated on the nest and may have been succeeding the queen (O'DONNELL 1994, 1995). *Polistes chinensis* workers on nests that had lost their queens formed dominance hierarchies. Dominance and probability of laying eggs correlated positively with age, and the most dominant individuals had previously foraged at high rates (MIYANO 1986). Some egg-laying workers continued foraging for water, nest construction material, and nectar, though they usually foraged at reduced rates. Several of the oldest workers in one *P. chinensis* colony foraged for approximately 30 days, then switched to egg laying at rates similar to their queen (MIYANO 1980). Workers in orphaned *Polistes snelleni* colonies were capable of mating and later producing female offspring (SUZUKI 1985). Finally, performance of foraging did not depend on dominance status or ovary development in *Polistes biglumus* foundress associations (MAKINO & AOKI 1982).

Workers of a number of species are capable of leaving their nests and founding new colonies, either if their original colony remains intact (satellite nests: STRASSMANN 1981b) or in response to nest destruction (DANI & CERVO 1992, MEAD et al. 1995). *Polistes exclamans* workers initiating satellite nests were more likely to have foraged for prey than non-initiators from the same colonies (STRASSMANN 1981b).

Reproductive division of labor has a strong age component in some primitively eusocial wasps. Younger females in polygynous colonies of *Ropalidia rufoplagiata* acted as foragers, while egg laying was performed by older females, suggesting an age-based separation of queen and worker behavior (SINHA et al. 1993). A similar pattern appears to hold for most species examined so far in the vespidae subfamily Stenogastrinae (TURILLAZZI 1989, 1991), the basal lineage in the clade containing all eusocial Vespidae (CARPENTER 1991).

As in all correlational studies of life history characters, it is unclear from the above examples whether a tradeoff between reproduction and worker behavior exists within individual females. For example, even if replacement queens are drawn from among foragers, engaging in worker behavior may reduce replacement queens' fecundity below what it would have been if they had avoided working. However, the existence of such an underlying tradeoff is irrelevant to the question of whether queen and worker behavior are exclusive alternative strategies that structure division of labor within societies. The fact that active workers can reproduce in some species, but do not reproduce in others, should lead us to examine in more

detail the factors that shape the diversity of queen and worker behavioral roles among species. Some authors have suggested that queen replacement by older foragers is characteristic of temperate species, while replacement by younger idle workers is a tropical phenomenon (STRASSMANN & MEYER 1983, CHANDRASHEKARA & GADAGKAR 1992), but tropical and subtropical populations of *Polistes instabilis* exhibit the so-called "temperate" pattern of replacement (HUGHES & STRASSMANN 1988; O'DONNELL 1994, 1995). A diversity of environmental factors may determine whether queen and worker behavior diverge in a given species or population.

The role of ecology in the evolution of queen and worker behavior

A lack of negative effects of engaging in worker behavior on direct reproduction seems paradoxical, given that workers spend much of their time away from the nest in presumably energy-expensive activities. However, little evidence exists to verify that worker behavior entails high fitness costs in terms of survival or future fecundity, particularly in independent founding species (O'DONNELL & JEANNE 1995). Foraging does appear to decrease the expected lifespan of *Polistes exclamans* adults (STRASSMANN 1981b, STRASSMANN et al. 1984). The risks and costs of worker behavior relative to queen behavior are likely to depend in part on a species' dominance structure, predation pressure, and seasonality. LITTE (1981) found that nests of *Mischocyttarus labiatus* suffered high rates of predation and parasitism, which suggests that time spent away from the nest may not always entail increased risk.

The costs of worker-like behavior must be considered relative to the benefits gained by helping (indirect fitness). An extreme case of overlap of queen and worker behavior is seen in queens of the Alpine wasp *Polistes biglumus bimaculatus*, which continue to forage at a high rate even after workers and gynes emerge from their nests (LORENZI & TURILLAZZI 1986). This high-elevation species is exposed to a truncated developmental season and relatively low predation pressure; queen foraging is presumably necessary under marginal abiotic conditions to maintain colony growth. *Polistes biglumus bimaculatus* demonstrates that social roles can be extremely divergent among species and are likely to be modified by ecology. Future research should focus on how ecological factors such as predation rates, prey availability, and seasonality act to favor or constrain the separation of queen and worker behavior.

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