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Original article

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Dominance and polyethism in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae)

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Abstract Dominance interactions affected patterns of non-reproductive division of labor (polyethism) in the eusocial wasp *Mischocyttarus mastigophorus*. Socially dominant individuals foraged for food (nectar and insect prey) at lower rates than subordinate individuals. In contrast, dominant wasps performed most of the foraging for the wood pulp used in nest construction. Social dominance also affected partitioning of materials collected by foragers when they returned to the nest. Wood pulp loads were never shared with nest mates, while food loads, especially insect prey, were often partitioned with other wasps. Dominant individuals on the nest were more likely to take food from arriving foragers than subordinate individuals. The role of dominance interactions in regulating polyethism has evolved in the eusocial paper wasps (Polistinae). Both specialization by foragers and task partitioning have increased from basal genera (independent-founding wasps, including *Mischocyttarus* spp.) to more derived genera (swarm-founding Epiponini). Dominance interactions do not regulate forager specialization or task partitioning in epiponines. I hypothesize that these changes in polyethism were enabled by the evolution of increased colony size in the Epiponini.

Key words Division of labor · Foraging · Social insects · Task partitioning · Task specialization · Eusocial wasp

Introduction

Division of non-reproductive tasks among nestmates, or polyethism, is thought to have been a major evolutionary advantage promoting the ecological success of eusocial insects (Wilson 1990). Identifying the factors that regulate polyethism, and how they have evolved within social insect taxa, remain as central challenges in insect sociobiology (Oster and Wilson 1978; Jeanne 1986a; Page et al. 1989). It has long been recognized that reproductive status in eusocial paper wasps (Vespidae: Polistinae) is affected by dominance interactions (Pardi 1948; West-Eberhard 1969). Research on a number of polistine species has recently demonstrated that dominance interactions can also structure polyethism (Reeve and Gamboa 1987; Jeanne 1991; O'Donnell and Jeanne 1995a; O'Donnell 1995, 1998a). Dominant individuals may avoid performing particular tasks when those tasks remove individuals from opportunities for direct reproduction (West-Eberhard 1981).

Dominance interactions can also influence behavior within the worker force when many individuals have little or no chance of reproducing directly (O'Donnell 1998b). When workers compete for social resources, dominant individuals may obtain greater control of both task performance and resource utilization. Workers can conflict over whether to perform certain tasks, especially those involving high energetic costs or risks of mortality (O'Donnell and Jeanne 1992, 1995b). Subordinate workers are expected to perform risky or costly tasks at higher rates. Foraging behavior entails great risks to workers, given its high energetic costs, wear and tear on the body that decreases longevity, and increased exposure to predators (O'Donnell and Jeanne 1995b). If dominance affects task performance, foraging should be performed by subordinate individuals. The predicted relationship between dominance and foraging behavior is often manifest in groups of reproductive females that cooperate in founding new nests (Gamboa et al. 1978; Litte 1979, 1981; Pfennig and Klahn 1985), but has rarely been tested among offspring workers (O'Donnell 1998a).

In addition to individuals performing different sets of tasks (specialization), polyethism comprises task partitioning (Jeanne 1986a). Task partitioning involves the

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performance of component tasks in a linked series by different individuals. If there is no partitioning, individuals perform the entire task series themselves. For example, if foraging is partitioned, foragers fixate on collecting materials and pass their loads off to adult nestmates for processing. If foraging is not partitioned, workers keep and work with their loads after returning to the nest.

In an earlier study, I hypothesized that dominance interactions influence patterns of task partitioning (O'Donnell 1995). Nestmates can compete for access to foragers' food loads for personal consumption. Control of food materials influences individuals' own physiology (Hunt 1994), as well as that of developing brood (O'Donnell 1998b). Wasps may also compete to control the processing of building material loads. The ability to monopolize building materials allows individuals to regulate nest growth. I predicted that more dominant individuals would take and utilize the materials collected by less dominant foragers. Conversely, dominant individuals should rarely give up their loads when they return to the nest from foraging.

I studied the effects of dominance interactions on polyethism in the independent-founding wasp *Mischocyttarus mastigophorus* Richards. I quantified dominance interactions, task specialization, and task partitioning to address two questions. First, do dominance interactions influence task performance? If so, I predicted that less dominant individuals would perform risky tasks, such as foraging, at higher rates. Second, do dominance interactions influence how forager-collected materials are partitioned at the nest? If so, I predicted that dominant individuals would be more likely to take materials from incoming foragers. I conclude by comparing polyethism in *M. mastigophorus* with other species of eusocial paper wasps. The structure of polyethism has evolved within the Polistinae (O'Donnell 1995), and comparison of polyethism among polistine genera can yield insight into how these evolutionary transitions occurred.

Methods

Study species

M. mastigophorus is relatively common at higher elevations (above 1475 m) at the study site in Monteverde, Costa Rica (10°18′ N, 84°49′ W) (O'Donnell and Joyce, in press). Nests are constructed on the eves of buildings, under leaves, and on rootlets in road banks. Male and female adults exist in two discrete color morphs, each of which mimics a different sympatric species of *Agelaia* (Vespidae: Epiponini). Colonies that have produced adult offspring usually comprise several dozen adults, including males and females (O'Donnell and Joyce, in press).

Collection of behavioral data

Field work was conducted between 25 July and 11 August 1997, during the rainy season in Monteverde. The six subject colony nests were located on the eves and rafters of a building at approximately 1500 m elevation. Adult wasps present on the colonies (labeled A–F) were marked for individual identification with paint pens. Because the subject colonies had already produced adult offspring when located, I could not determine whether worker females were foundresses or daughters that had emerged on the nests. Behavioral data were collected by an observer seated on scaffolding or standing on a ladder within 0.5 m of the face of the nest. Behavioral observations were conducted for 3 continuous hours in the morning (between 0800 hours and 1140 hours local time) and two continuous hours in the afternoon (between 1300 hours and 1630 hours local time) on two consecutive days per nest, for a total of 10 h observation time per colony (9 h total at colony E). All social interactions, forager departures and arrivals, and material transfers were recorded, noting the identity of interacting adults, and time to the nearest minute.

Behavioral acts coded as dominance interactions included biting, chasing, displacing (one individual fled another upon approach but was not followed) and darting (one individual leapt toward another but did not make physical contact). In all cases, a subordinate individual was clearly identified when it crouched, fled, or turned away from the aggressor. See Itô (1985) for descriptions of dominance interactions in primitively eusocial wasps, including *Mischocyttarus* spp.

Statistical analyses

Contingency table analyses (testing relationships between categorical variables) were performed with the likelihood ratio Chi-square test (Fienberg 1989). I tested whether foraging trips differed in duration among materials using the survival analysis Wilcoxon test (SAS 1985). Foraging trips that were initiated before the start of observations were included in the analysis as censored values (Pyke and Thompson 1986).

I calculated a dominance index for each individual (male and female) as follows: dominance index = (number of times individual was dominant–number of times individual was subordinate)/number of observation hours the individual spent on the nest.

This index (rather than relative dominance rank) was developed to assess the relationship between polyethism and dominance status for two reasons. First, position in a linear dominance order could not be determined for many individuals because relatively subordinate individuals rarely engaged in dominance interactions with each other. Second, this index includes information on the overall rate at which an individual gave and received aggressive behavior. I wanted to test the quantitative effects of dominance interactions on task performance and partitioning. Effects of individuals' dominance status, as indicated by the dominance index, on task performance (food foraging rates) and task partitioning (rates of taking food from foragers) were tested using linear regression (Sokal and Rohlf 1981; SAS 1985). For these analyses, dependent variables were nested within colonies in the regression models to control for inter-colony differences. Variables coded as proportions were arcsine transformed to normalize their distributions (Sokal and Rohlf 1981).

Results

Foraging and dominance interactions

All subject colonies had produced adult offspring and included female (f) and male (m) adults (colony A: 17 f, 8 m; B: 13 f, 13 m; C: 14 f, 29 m; D: 18 f, 11 m; E: 10 f, 9 m; F:20 f, 4 m). Males left their nests but were not observed returning with materials. Males dominated female nestmates (unpublished data) and took food from arriving foragers. Female foragers returned to nests with

liquids that were fed to adult nestmates and larvae (scored as nectar), masticated balls of insect flesh (prey), and wood pulp used in nest construction. Foragers specialized on different materials (marked foragers making three or more trips pooled among colonies; likelihood ratio $\chi^2 = 112.07$, $df = 44$, $P < 0.001$; numbers of foragers were too small to permit separate tests for each colony). In all colonies, a single female was dominant over all other females (i.e., only this female dominated all others more often than she was dominated by them). In two colonies where oviposition was observed, only the most dominant female laid eggs. The most dominant females were designated as the queens. Queens were rarely observed collecting food materials (only the queen from colony D made one nectar-foraging trip). Most other foragers devoted some of their effort to nectar collection (67% to 100% of foragers in each colony; 88% of all foragers). Relatively few foragers collected wood pulp (0% to 40% of foragers in each colony; 16% of all foragers), and these were often females of high dominance rank. In the three colonies that collected pulp, queens and the next-highest ranking (β) female made the largest numbers of pulp trips. Nectar and prey trips required similar amounts of time in the field (mean ± SE nectar trip duration = 47.3 ± 3.6 min; mean ± SE prey trip duration = 40.6 ± 6.8 min; survival analysis Wilcoxon $\chi^2 = 0.17$, $df = 1$, $P > 0.50$; because the longest nectar and prey trips were censored values, the estimates of mean trip times are biased toward low values). Pulp trips were of significantly shorter duration (mean ± SE pulp trip duration = 15.6 ± 6.2 min; survival analysis Wilcoxon $\chi^2 = 35.09$, $df = 1$, $P < 0.001$). Food foraging rates were negatively associated with dominance status (Fig. 1; $F_{6,65} = 8.97$, $r^2 = 0.45$, $P < 0.001$).

Material partitioning and dominance interactions

The degree to which materials collected by foragers were partitioned with nestmates differed significantly among nectar, prey, and pulp (Fig. 2; likelihood ratio $\chi^2 = 38.6$, $df = 4$, $P < 0.001$). Prey loads were most likely to be given up entirely to nestmates by incoming foragers, while pulp loads were never partitioned with nestmates. An individual's dominance status affected the probability that it would take food loads from arriving foragers. Dominant individuals were more likely to be fed by arriving nectar and prey foragers (Fig. 3; $F_{6,139} = 5.17$, $r^2 = 0.18$, $P < 0.001$).

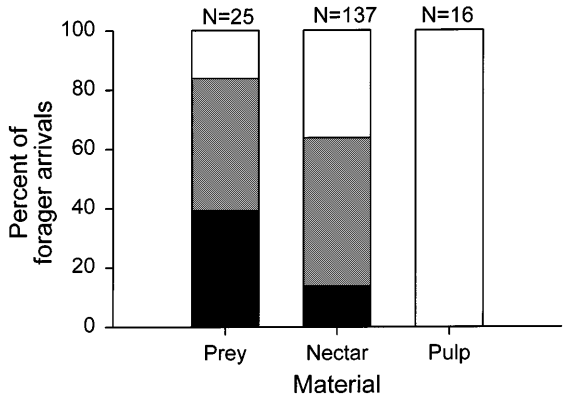

Fig. 2 Partitioning of loads of different materials collected by *M. mastigophorus* foragers from six colonies. Sample sizes (numbers of foraging trips) are given above the bars [*open bars* load was used by forager (not partitioned), *shaded bars* load was shared with nest mates (partial partitioning), *black bars* load was given up entirely to nest mates (complete partitioning)]

Discussion

Patterns of division of labor

Nearly all *M. mastigophorus* foragers devoted some effort to nectar collection, a pattern often observed in eusocial wasps (O'Donnell and Jeanne 1990; Giannotti et al. 1995; O'Donnell 1995). Wood pulp was collected

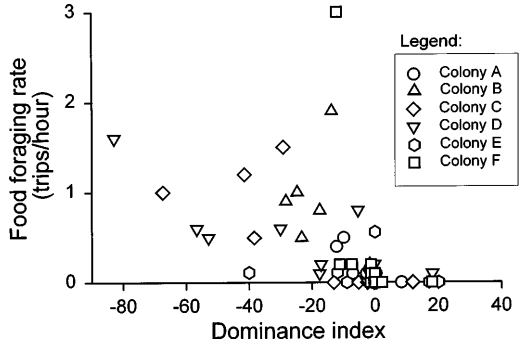

Fig. 1 Relationship of dominance behavior with rate of food foraging by *Mischocyttarus mastigophorus* wasps from six colonies. Since males did not forage, only individually marked females were included in this analysis

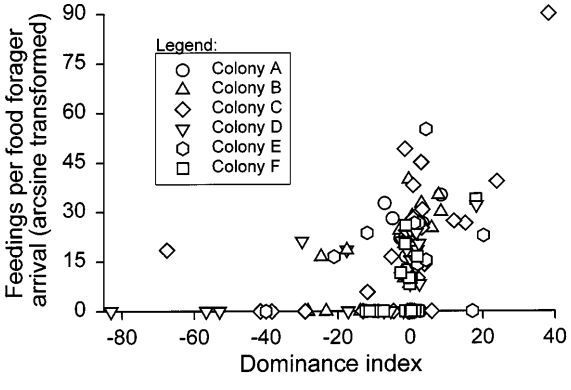

Fig. 3 Relationship of dominance behavior with rates of taking food from foragers for *M. mastigophorus* wasps from six colonies. Only those food forager arrivals during which each wasp was present on the nest were used in calculating rates of taking food. All marked wasps (males and females) were included in this analysis

by relatively few individuals to the exclusion or near exclusion of food materials. Collection of wood pulp was largely restricted to the most dominant individuals.

Materials collected by *M. mastigophorus* foragers differed in the degree to which they were partitioned, and material partitioning followed a common pattern in independent-founding species (Jeanne 1991): wood pulp was partitioned least often (not at all in *M. mastigophorus*) and prey loads were partitioned most often. The observed patterns of task partitioning are consistent with conflict over material handling at the nest, which was resolved based on differences in dominance status. Subordinate *M. mastigophorus* workers were more likely to collect food materials, while most wood pulp was collected by dominant females.

Dominance interactions and division of labor

Polyethism in *M. mastigophorus* was affected by queen-worker and worker-worker interactions. Reeve and Gamboa (1987; see also Gamboa et al. 1990) posited that independent-founding wasp queens act as central pacemakers, behaviorally regulating workers' task performance. However, in some species, dominance interactions among workers apparently induced foraging by workers (Premnath et al. 1995; O'Donnell 1998a; R.L. Jeanne, personal communication). Worker dominance can play a role in structuring polyethism, even though interactions among workers may have relatively little effect on reproductive competition within colonies.

Few studies have directly measured the relationship between dominance interactions and worker polyethism. However, several consistent patterns in independent-founding wasps suggest that worker dominance status affects both task performance and task partitioning. First, dominance interactions appear to play a role in inducing workers to collect food (nectar and prey). In both foundress associations and in post-emergence colonies, subordinate wasps are most likely to forage for food (*Mischocyttarus* spp.: this study; Litte 1977; Itô 1984; *Polistes* spp.: Reeve and Gamboa 1987; Gamboa et al. 1990; Giannotti and Machado 1994; *Ropalidia* spp.: Chandrashekara and Gadagkar 1991; Premnath et al. 1995). In contrast, building materials (wood pulp) are often collected by the most dominant females (*Mischocyttarus* spp.: this study; Litte 1977, 1979, 1981; *Polistes* spp.: Gamboa et al. 1978). Foraging is among the riskiest tasks, and is often associated with decreases in worker longevity (reviewed in O'Donnell and Jeanne 1995b). However, wood pulp foraging trips are of shorter duration than food material trips (Litte 1977; Post et al. 1988; Giannotti et al. 1995; O'Donnell 1995). Therefore, building material collection may entail fewer risks and lower physiological costs to foragers (O'Donnell and Jeanne 1992, 1995b). O'Donnell and Jeanne (1992) found that *Polybia occidentalis* foragers that devoted more effort to building materials had longer lifespans than foragers specializing on food materials. Lower costs may partially explain why dominant wasps are more likely to collect wood pulp.

Dominance interactions can affect the degree and kinds of partitioning of materials within colonies. Dominant wasps were more likely to take loads from foragers, and conversely less likely to give up portions of loads they had collected (this study; Litte 1979, 1981; Itô 1984; Chandrashekara and Gadagkar 1991). The common observation that pulp loads are partitioned less often than food (especially prey) loads may be due to the fact that, in independent-founding polistines, dominant females (including queens) often collect wood pulp.

Implications for the evolution of polyethism

Compared to more derived taxa (Neotropical swarm-founding Epiponini; Carpenter 1991), independent-founding Polistinae such as *M. mastigophorus* typically exhibit less individual task specialization and weaker task partitioning (reviewed in Jeanne 1991; O'Donnell 1995). Increased task specialization and task partitioning may have evolved in concert with increased colony size in the Epiponini. Species with larger colonies are more likely to support inactive reserves of workers. By calling up workers from inactive reserves, discrepancies between forager arrival rates and rates of unloading by nest wasps can be minimized. Swarm-founding *Polybia* spp. foragers are often highly specialized on collecting a single material, and foragers' loads are nearly always passed off to nest wasps regardless of material (Jeanne 1986b; Hunt et al. 1987; O'Donnell and Jeanne 1990; O'Donnell 1996; personal observations). However, Jeanne (1986b) showed that *P. occidentalis* foragers were more likely to switch among tasks, and less likely to partition their loads, in small colonies (< 50 adults) than in large colonies (>350 adults).

The relationship between dominance interactions and polyethism has also apparently evolved in the transition from independent-founding to swarm-founding social structures. Dominance interactions do not influence material partitioning in the Epiponini, because all materials are partitioned at high rates. Furthermore, dominance may play little or no role in epiponine forager specialization on materials. Workers performing the same tasks within *P. aequatorialis* colonies were more genotypically similar to each other than to nestmates performing other tasks, suggesting that there are genotypic effects on task specialization in polygynous epiponine wasps (O'Donnell 1996, 1998c). Dominance interactions may play a role in induction of foraging, however. Larger-bodied *P. occidentalis* workers moved from in-nest to on-nest tasks at an earlier age than smaller nestmates, and were also more likely to be subordinate in dominance interactions with smaller workers (O'Donnell and Jeanne 1995a). *Polybia* is a relatively derived genus within the Epiponini; studies of more basal genera of Epiponine wasps, such as *Apoica* and *Agelaia* (Carpenter 1991), may yield further insights into

how the role of dominance interactions in structuring worker polyethism has evolved.

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