The Roles of Body Size and Dominance in Division of Labor Among Workers of the Eusocial Wasp Polybia occidentalis (Olivier) (Hymenoptera: Vespidae)

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ABSTRACT: Dominance interactions among workers may influence division of labor within the worker caste of eusocial insect colonies. We examined the relationships between body size, dominance interactions, and age-based division of labor in the advanced eusocial (swarm-founding) wasp Polybia occidentalis (Olivier). Workers progressed through a series of task sets as they aged (age polyethism), but within task sets there was individual variability in the age of first task performance. Smaller-bodied workers passed through the age polyethism sequence more slowly: worker body size, as indicated by the length of the mesothoracic wing costa vein, bore a negative relationship with the age of first performance of tasks outside the nest. Larger-bodied workers therefore performed tasks that removed them from opportunities for direct reproduction in the nest interior at an earlier age. Smaller workers were also more likely to be dominant in observed social interactions, suggesting that patterns of social dominance are involved in structuring division of labor among P. occidentalis workers, with larger workers playing a subordinate role.

Workers of a minority of ant species and of most termites are divided into morphologically distinct castes (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). In these species, the allocation of duties in the worker force is based in large part on differences in body size. In contrast, workers of most ants and of all eusocial insects with flying workers (bees and wasps) are monomorphic; body size variation exists, but is distributed unimodally, and growth is isometric. Little is known about the role of body size in division of labor in species with monomorphic worker castes.

Waddington (1981) found that body size variation was low in bee species that use communication for recruitment to food sources relative to species that do not recruit to food, suggesting that selection can act on body size variation to promote effective division of labor in species with monomorphic workers. Furthermore, a pattern of younger age of first foraging and/or of increased probability of foraging in larger-bodied workers has been noted in honey bees (Kerr and Hebling, 1964; Waddington, 1988), bumble bees (Free, 1955), and yellowjacket wasps (Spradbery, 1972). Breed et al. (1978) noted the opposite pattern in sweat bees.

The relationships of body size to division of labor that have been recorded in monomorphic species are difficult to interpret because it is not known how body size differences translate into behavioral variation. One possibility is that dominance interactions among workers, which may be based on body size differences, play a role in shaping division of labor. If social dominance is interpreted broadly as occurring outside the context of direct reproductive competition (Jeanne, 1991),
then studies on vespine and polistine wasps suggest that social grooming and food solicitation represent dominance interactions among workers (Montagner, 1966; West Eberhard, 1969; Akre et al., 1976). These interactions among workers may influence task performance.

The aim of this study was to determine if there is a relationship between body size, the outcome of dominance interactions, and age-based division of labor in the advanced eusocial (swarm-founding) wasp *Polybia occidentalis* (Olivier). *Polybia occidentalis* workers exhibit age polyethism, but individuals vary in the rate of passage through the age sequence of tasks (Jeanne et al., 1988; O'Donnell and Jeanne, 1992).

We addressed two questions on division of labor among *P. occidentalis* workers: 1. Is worker body size correlated with rate of progression through the age-based task sequence? 2. Are outcomes of social dominance interactions dependent on worker body size such that dominance may play a role in structuring division of labor?

**Materials and Methods**

**WASP INTRODUCTIONS, BEHAVIORAL OBSERVATIONS, AND COLLECTIONS:** Field work was conducted from 28 August to 18 October 1991 at Centro Ecologico la Pacifica in Guanacaste Province, Republic of Costa Rica. Two *P. occidentalis* colonies of moderate size (Colony A: 4 layers of nest comb, 953 unmarked adults; Colony B: 4 layers of nest comb, 381 unmarked adults at the end of the study) were chosen as subjects for behavioral observations in the field.

*Polybia occidentalis* combs from three other colonies were maintained in the laboratory at ambient temperature. Every 24 hr, all newly-emerged adults were removed from these combs. A cohort of 15 of the young adults was anesthetized with diethyl ether, marked with paint pens for individual recognition, and introduced into one of the observation colonies. These adults are accepted when introduced into non-natal observation colonies (O'Donnell and Jeanne, 1992). Each observation colony received a cohort of introduced wasps every other day.

On days alternating with worker introductions, behavioral data were collected by an observer at an observation colony during continuous sessions of 1.5 hr in the morning and 1 hr in the afternoon. Behavioral acts of all visible wasps were recorded in scan samples of the nest entrance and the entire nest surface every 10 min (see O'Donnell and Jeanne, 1993 for ethogram), and all occurrences of foraging behavior were recorded. Behavioral acts were categorized as occurring inside the nest, on the nest surface, and away from the nest (foraging). Social interactions—solicitation of crop contents and grooming—were analyzed as dominance interactions among workers (Jeanne, 1991). Wasps soliciting crop contents antennate and mandibulate the mouthparts and antennae of nestmates and extend their mouthparts toward the solicited wasp; grooming involves mandibulation of other parts of a nestmate’s body and varies in intensity from mild mouthing to violent biting. A worker was categorized as dominant when she was the active partner in a grooming or solicitation interaction, and as submissive when she was the recipient of grooming or solicitation. Only the relative status (dominant or submissive) of marked workers observed in social interactions was recorded during scan samples; intensity of interactions and identity of interacting partners were not noted.
After three weeks of observations the colonies were collected by enclosing the nest in a plastic bag with ether. Collections were made at night to ensure that all workers would be present. Marked wasps were sorted from unmarked wasps and stored frozen at -10°C. Upon collection we obtained 109 workers from each colony of differing ages (4 to 23 days) with known behavioral histories.

**COSTA VEIN LENGTH MEASUREMENTS:** Following oven drying, weighing, and lipid extraction (methods and results to be presented elsewhere), costa vein length on the mesothoracic wing was measured to the nearest 0.025 mm using an ocular micrometer at 25 x magnification. The costa was measured in lateral aspect, from the keel across the base of the costa and subcosta veins (beneath the tegula; Fig. 102 in Richards, 1978) to the distal end of the pterostigma. This measurement of the wing was chosen over total wing length because the costa is rigid, and was less often bent or damaged than the wing tips. The right mesothoracic wing costa was measured unless it was damaged, in which case the left wing was used. Survival analysis (SAS, 1985) was used to measure the effect of body size on age of first performance of behavioral acts outside the nest.

**Results**

Costa lengths were obtained from 108 individuals in colony A and from 109 individuals in colony B. Distributions of costa length and of body weight were unimodal (Fig. 1). In both colonies costa vein length was significantly positively correlated with dry body weight (Fig. 1; Colony A: $r = 0.46$, d.f. = 106, $P < 0.001$; Colony B: $r = 0.72$, d.f. = 107, $P < 0.001$). Costa length is therefore a good indicator of body size, although the relationship was weaker in Colony A than in Colony B. Some of the variance in dry body weight relative to costa length was due to differences in lipid content among workers (S.O'D., unpubl. data).

Distributions of first observed age of task performance differed among behavioral acts in the nest, on the nest, and away from the nest (Survival analysis, Colony A: Wilcoxon $\chi^2 = 13.12$, d.f. = 2, $P < 0.005$; Colony B: Wilcoxon $\chi^2 = 50.31$, d.f. = 2, $P < 0.001$). Within colonies there was variation in the age at which workers were first observed outside the nest, but distributions of ages of workers leaving the nest interior did not differ between colonies (Fig. 2; Wilcoxon test for equality of age distributions, $\chi^2 = 1.26$, d.f. = 1, $P > 0.25$). Smaller wasps spent more days working in the nest interior than larger wasps: costa length was negatively associated with age at first performing outside nest tasks (Survival analysis, Wilcoxon rank test statistic = -3.68, $\chi^2 = 8.01$, d.f. = 1, $P < 0.005$).

Twenty workers from Colony A and 19 from Colony B were observed to engage in grooming and solicitation interactions during the study (Table 1). The distributions of workers with small (<colony mean costa length) and large (>colony mean costa length) wings into dominance categories (those dominant in all observed interactions versus those submissive in some or all interactions) were similar in the two colonies (Table 1). When individuals from both colonies were pooled, workers with small wings were significantly more likely to be dominant in all observed social interactions than were workers with large wings (Likelihood ratio $\chi^2 = 7.49$, d.f. = 1, $P < 0.01$). This difference was not due to the subordinate workers having been observed more often; the number of records of social interactions did not differ among workers in the two dominance categories (Wilcoxon $Z = 1.74$, d.f. = 1, $P > 0.05$).
Fig. 1. Dry body weight in mg plotted against costa vein lengths in mm for *P. occidentalis* workers from two observation colonies. Mean (±SD; sample size) costa lengths were 4.38(±0.14; n = 108) for Colony A and 4.30(±0.18; n = 109) for Colony B.
Fig. 2. Distributions of the age of first performance of behavioral acts on the outside surface of the nest by *P. occidentalis* workers from two colonies. The cumulative proportion of workers added to each colony observed engaging in outside nest tasks is plotted on the Y-axis.

Discussion

*Polybia occidentalis* worker body size was negatively related to age of first performance of out-of-nest tasks. Faster passage through age polyethism or performance of risky tasks by larger bodied workers appears to be a common pattern, documented in diverse eusocial insect lineages. Kerr and Hebling (1964) presented data suggesting that among Africanized honey bee (*Apis mellifera adansonii*) workers, earlier performance of age-based tasks was associated with greater body size. Nowogrodzki (1984) reported not finding this pattern in honey bees, but presented no data. Cidecyan (1984; cited in Waddington, 1988) found that larger bodied honey bees foraged more frequently and differed from smaller bees in rates of performance of in-hive tasks (the nature of these differences was not determined). Studies on bumble bees (*Bombus agrorum, B. sylvarum, and B. lucorum*) showed that larger bodied workers were both more likely to forage and began foraging at a younger age than smaller workers (Brian, 1952; Free, 1955). Spradbery (1972) found that foragers of the yellowjacket *Vespula germanica* were larger than nest wasps during the growth phase of colony development. Why large body size might be associated with more rapid age polyethism is unknown, both with respect to adaptive value to the colony (if any; Waddington, 1988) and to the mechanisms that underlie the association.

One possible mechanism linking body size with division of labor is dominance interactions among workers, which appear to influence division of labor in diverse insect societies (Jeanne, 1991). Experimentally assembled honey bee colonies with
Table 1. Numbers of large winged (individuals with > colony mean costa length) and small winged (individuals with < colony mean costa length) workers observed engaging in grooming and solicitation interactions. Only dominant: worker was the active participant in every grooming or solicitation interaction observed. Some submissive: worker was passive in at least some of the interactions in which she engaged.

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<td>Only dominant</td>
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varying proportions of workers selected for dominant and subordinate behavior exhibited decreased brood production, comb building, and food hoarding with increasing representation of dominant bees (Hillesheim et al., 1989). Studies on Polistes paper wasps (reviewed in Reeve, 1991) and bumble bees (Honk et al., 1981; Doorn and Heringa, 1986) suggest a link between low social dominance rank and increased probability of foraging; in some Polistes spp. older workers, which are often smaller, tend to be dominant (Strassmann and Meyer, 1983; Hughes and Strassmann, 1988; S.O'D., pers. obs.). Yellowjacket workers (Vespula spp.) engage in aggressive mauling and more subtle food solicitation interactions, which may incite subordinate individuals to perform tasks outside the nest (Montagner, 1966; Akre et al., 1976). The studies on Vespula did not examine the relationship of body size with dominance, but Montagner (1966) noted that dominance status did not correlate well with age or ovarian development.

We found that smaller P. occidentalis workers were more likely to be dominant in social interactions. Our observations are consistent with the pattern expected if dominance interactions based on body size influence the rate of age polyethism, such that subordinate workers move out of the nest at an earlier age. Larger-bodied wasps apparently move away from opportunities for direct reproduction into more "worker-like" behavioral roles (West Eberhard, 1981) at an earlier age. These results should be considered as preliminary, since the intensity of interactions, and the identity and size of both interacting partners, were not recorded. The pattern of dominant smaller-bodied workers has also been noted in several Polistes species, but in most of these cases body size was confounded with order of emergence and worker age (reviewed in Reeve, 1991). More data on social interactions among workers and their relation to body size are needed to assess the importance of these factors in regulating division of labor in monomorphic eusocial insects. Our data suggest that dominance interactions among workers play a wider role in polyethism than previously recognized.

Acknowledgments

Thanks to Keith Waddington and two anonymous reviewers for helpful comments on an earlier version of the manuscript. Research was supported by a
tropical fellowship (to S.O'D.) from the Organization for Tropical Studies/Pew Charitable Trust, USDA Hatch Grant 3544 (to R.L.J.), and a postdoctoral fellowship from the NSF funded University of California at Davis Animal Behavior Research Training Grant (to S.O'D.).

Literature Cited


