Worker biting interactions and task performance in a swarm-founding eusocial wasp (*Polybia occidentalis*, Hymenoptera: Vespidae)

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Workers in many insect societies interact via body contact with their nest mates, and social biting and other forms of contact may play a general role in regulating task performance. Here I present evidence that social biting affects task performance without direct reproductive conflict in *Polybia occidentalis*, a swarm-founding eusocial wasp. *Polybia occidentalis* workers engaged in social biting with nest mates. Most workers that were active on the nest surface participated in biting interactions, but individuals differed significantly in their rates of biting and of being bitten. Rates of being bitten corresponded with nonproductive task performance: more biting was directed at foragers than nonforagers, and foraging rates were correlated with rates of being bitten. Furthermore, some on-nest workers initiated foraging activity immediately after they were bitten. Together these patterns suggest that social biting influences foraging rates by increasing workers’ probabilities of leaving the nest. Variation in biting rates did not correspond with differences in reproductive physiology: highly active biters and recipients did not differ in body size or in ovary development. In *P. occidentalis* and in other eusocial insects with large worker forces, biting and other types of social contact among workers may regulate task performance independently of direct reproductive competition. Key words: body size, foraging, ovary development, polyethism, reproductive conflict, social organization. [Behav Ecol 12:353–359 (2001)]

Division of nonreproductive tasks among workers, or polyethism, is a key adaptation promoting the evolutionary and ecological success of eusocial insects (Wilson, 1990). As insect colony sizes have increased over evolutionary time, new challenges have arisen for regulating the labor force. In small colonies of up to a few dozen members, polyethism can be effectively regulated via central, hierarchical control from the queen or other dominant individuals (O’Donnell, 1998a; Reeve and Gamboa, 1987). However, centralized task organization is not possible in larger insect societies, and instead the worker caste is self-organizing (Nicolis and Prigogine, 1977; Seeley, 1989; Wilson and Hölldobler, 1988). Self-organization requires that workers share information about task performance needs (Kaufman, 1991). Identifying the communicative interactions among workers that regulate polyethism remains as a central challenge to insect sociobiology (Jeanne, 1986a; Robinson et al., 1989; Seeley, 1986).

Dominance status and aggression among group members have been shown to affect division of labor in many animal societies (cooperatively breeding birds; Brown et al., 1997; primates, including humans; Drea and Wallen, 1999; Hawley, 1999; but see Jacobs and Jarvis, 1996 for a counter-example in naked mole rats). West-Eberhard (1981; see also Jeanne, 1991) hypothesized that worker-like behavior will be performed by the losers of fights over direct reproduction in animal societies. West-Eberhard’s model predicts that task performance decisions will correlate with variation in direct reproductive value; more fecund, dominant individuals should avoid risky or costly behavior such as foraging. This model is supported for some eusocial insects by two observations. First, social aggression often determines reproductive division of labor, and second, workers’ aggressive status often corresponds to their reproductive physiology (honey bees; Hillesheim et al., 1989; Ratnieks, 1993; bumblebees; van Doorn, 1987; ants; Cole, 1981; Heinz and Oberstad, 1999; Powell and Tschinkel, 1999).

Other studies suggest that worker contact interactions can regulate task performance independently of direct reproductive conflict. Biting and other types of body contact occur in advanced insect societies. Contact interactions have been noted in species where workers have reduced opportunities for direct reproduction (Gordon and Mehlisabadi, 1999; Gordon et al., 1993; Montagner, 1966). In these species, worker interactions may function in the regulation of division of labor and task performance (O’Donnell and Jeanne, 1995).

The goal of this study was to assess the relationships of contact interactions (biting among nest mate workers) with task performance and with reproductive physiology in the swarm-founding wasp *Polybia occidentalis*. *Polybia* wasps are important subjects in studies of the regulation of division of labor (Jeanne, 1986b; O’Donnell and Jeanne, 1992). *Polybia* workers have well-developed temporal polyethism and exhibit a high degree of task specialization (Jeanne, 1986b; O’Donnell, 1998b). *Polybia occidentalis* colonies build ovoid nests that are enclosed in a covering envelope with a single entrance hole. At approximately 1 week of adult age, most workers move from performing in-nest tasks to performing tasks outside the nest. The older workers spend much of their time on the exterior nest surface where they are visible to observers, and later they begin flying from the nest to forage. Foraging workers nearly always arrive and depart from the nest surface, and transfer the materials that they collect to workers on the nest (Hunt et al., 1987; O’Donnell and Jeanne, 1992). Workers frequently engage in biting interactions with nest mates (O’Donnell and Jeanne, 1995).
I quantified rates of giving and receiving social biting for individually marked *P. occidentalis* workers, and simultaneously quantified on- and off-nest task performance. I used these data to test for relationships between biting interactions and individual differences in task performance. I also measured variation in body size and ovary development to determine whether individuals’ rates of biting and task performance were associated with morphology or reproductive physiology. I discuss evidence that biting regulates polyethism in *P. occidentalis* and in other large-colony eusocial species, and I suggest experimental manipulations to further test this hypothesis.

**METHODS**

**Study site and observation colonies**

Fieldwork was conducted from 12 to 23 July 1999 near Centro Ecologico La Pacífica, Guanacaste Province, Costa Rica (10°25’ N, 85°07’ W). Local habitats include savanna-like pasture with scattered shrubs, rice fields, and gallery forest, and the area is artificially irrigated throughout the year. *Polybia occidentalis* is abundant at this location. I selected three subject colonies based on ease of access (i.e., nesting within 2 m of ground) and of intermediate size for the population at La Pacífica (nests were approximately 12 cm in height). The subject nests were moved to covered, open shelters, shielded from rain and direct sunlight, and wired to a supporting frame. I moved the colonies at night to ensure that foragers would be present, and to minimize loss of adults during transport. I mounted a mirror behind each nest to facilitate observation of the entire nest surface, and to encourage foragers to approach the nest by flying toward the entrance hole. The subject colonies were not disturbed for at least 24 h after moving to allow the wasps to acclimatize to the new location. All colonies foraged on the day after they were moved.

I collected a subset of the workers from each subject colony and marked them for individual identification on the day prior to starting behavioral observations. To collect workers for marking, I placed a plastic bag containing an ether-soaked cotton ball around each nest in predawn light at 0445 h, before foragers had begun to leave the nest. I mildly alarmed the colony by tapping the bag, and I collected the adults that responded by flying into the bag. Wasp workers were kept anesthetized with ether, and by cooling them in a refrigerator, while they were marked. Each wasp was uniquely marked on the dorsum of the thorax with paint pens (O’Donnell and Jeanne, 1992). After marking, wasps were returned to their nests and placed into the nest entrance. I marked 250 female wasps in colony A, 353 in colony B, and 179 in colony C. I noted when males were present (recognized by silvery pubescence on the front of the face), but I did not mark them.

**Behavioral data**

I collected behavioral data while seated 0.5 to 1 m from the nests, facing the entrance opening. For each colony, I conducted two daily continuous observation sessions of 3 h duration on two consecutive days (12 h observation total per colony). Morning sessions started between 0700 h and 0745 h local time, and afternoon sessions started between 1200 h and 1240 h. These observation times sampled the most active foraging period for *P. occidentalis* at La Pacífica (Jeanne et al., 1988; O’Donnell and Jeanne, 1992).

I defined biting interactions as contact involving one wasp’s mandibles (the biter) chewing on a nest mate’s body (the recipient), at any location other than the mouth parts. Mutual mouth part contact occurs during food exchange and solicitation (Hunt et al., 1987). I distinguished three levels of intensity of biting interactions. Mild biting was the lowest intensity of interaction, and involved the biter slowly chewing on the recipient, without visibly moving the recipient’s body parts. Moderate intensity biting involved more vigorous, rapid chewing, with part of the recipient’s body being displaced or vibrated. Severe biting was the highest intensity category, involving more rapid movement and frequent changes in position by the biter. Severe biting was often accompanied by the biter bending the tip of her gaster toward the recipient in stinging movements, and recipients of severe biting were lifted partly or totally off of the nest surface.

I recorded all occurrences of biting interactions on auditory cassette tape and later transcribed the tapes. For each interaction I noted the time to the nearest min, identity (including unmarked) of the biting wasp(s), identity of the recipient wasp, and whether the recipient flew from the nest within 3 s of the termination of the interaction. I simultaneously recorded all occurrences of arrivals of marked foragers at the nest onto a written data sheet, noting time to the nearest min, identity of the forager, and what material was carried by the forager. Every 15 min, I scanned the entire surface of the nest, noting the identity (including unmarked) of all individuals present.

**Colony collections, wing length measurements, and ovary dissections**

I collected the subject colonies after sunset on the final day of observations. Nests were placed in a plastic bag with ether and immediately transferred to a freezer. When the adults ceased moving, the nests were dissected and adult wasps were removed from the nest material. Marked adults were sorted out. I placed all adult wasps in fixative (Kahle’s solution, 18:1:1 volumes 70% ethanol:glacial acetic acid:formalin). I noted the number of brood combs and brood developmental stages.

After fixing in Kahle’s solution for at least 4 weeks, the marked adults were transferred into 70% ethanol. I dissected the gasters (distal abdominal section) of females that had given or received significantly high rates of biting under a binocular microscope at ×40. I recorded workers’ degree of ovary development relative to fully developed ovaries possessed by *P. occidentalis* queens from the subject colonies. Ovaries were assigned categorical scores from zero (no visible oocyte development, filamentous) to three (fully developed, queen-like ovaries). The dissections were performed blind to the behavior of the wasps. Unmarked wasps from the subject colonies that were preserved and dissected by the same methods showed the full range of ovary development from filamentous, undeveloped ovaries to ovaries with numerous large oocytes. There was no indication of distortion of oocyte shape or size relative to freshly collected wasps (personal observation).

I removed both of the mesothoracic wings from the bodies of the females that had given or received significantly high rates of biting. The wings were unfolded and mounted flat on microscope slides with transparent tape. I scanned the mounted wings into computer image files at 600 DPI resolution, and measured wing length using the ruler tool of Adobe Photoshop 5.0 software. I measured the length of the rigid anterior wing vein (the costa vein) from its proximal base to the proximal end of the pterostigma. I used a similar measure of wing length in an earlier study, and found that it was strongly correlated with dry body mass (O’Donnell and Jeanne, 1995). Wing length measurements were performed blind to workers’ behavior, and left wing measurements were performed blind to right wing values. Individuals’ left and right wing measurements were highly correlated ($r = .90, p < .0001$), so I used the mean of costa vein lengths as an index of body size.
RESULTS

Colony composition
Each subject nest contained four layers of brood comb upon collection. All stages of brood (eggs, larvae of various sizes, and pupae) were present in each colony. Adult males were present only in colony B. Total numbers of adult females present when the colonies were collected were: colony A, 321; colony B, 540; colony C, 348.

Colony-wide rates of biting behavior
On average, 14.3 to 18.7 wasps were visible on the nest surface during scans (range five to 38). Most of the wasps present on the nest surface were marked; unmarked wasps comprised 5.5% to 19.8% of individuals present during scans. Biting interactions occurred at overall rates of 16.2 to 27.8 per h. Averaging over the number of wasps present on the nest surface during scans yielded estimates of 1.0 to 1.5 biting interactions per wasp per h on the nest.

Intensity of biting behavior
Biting interactions typically lasted less than 30 s, but occasionally extended for as long as 10 min. Biting interactions of mild and moderate intensity occurred at a higher rates than those of severe intensity in all colonies (Table 1 and Figure 1). The intensity of biting occasionally increased during interactions (4.2% of mild and moderate interactions increased in intensity), but intensity was never observed to decrease. Most changes in intensity were from mild to moderate (n = 14), followed by changes from moderate to severe (n = 9). A transition from mild to severe biting was observed once.

Some interactions involved more than one individual simultaneously biting a single wasp (6% to 16% of interactions). In these instances, from one to five additional workers joined in biting a wasp after the first worker initiated contact. Furthermore, recipients were often bitten by several nest mates sequentially, being bitten by one or more new workers within 10 s after each interaction terminated. Recipients typically remained immobile while being bitten, then groomed themselves or walked over the nest surface in the 10 s immediately following an interaction (but see section on Nest departures following biting).

Individual variation in rates of biting and of being bitten
Marked wasps’ behavior was consistent across the 2 days of observation. The proportion of scans during which individuals were present on the nest was highly correlated between days (colony A: r = .72, p < .01; colony B: r = .75, p < .01; colony C: r = .64, p < .01). Individuals’ rates of biting other wasps were also correlated between days, although this relationship was weaker in colony B than in the other colonies (colony A: r = .98, p < .001; colony B: r = .93, p < .01; colony C: r = .95, p < .001).

Most marked workers bit, and/or were bitten by, other workers (58% to 64% of marked workers). Workers varied significantly in their rates of biting other workers, and in their rates of being bitten. For both biting and being bitten, workers that never performed the behavior, and workers that performed the behavior at exceptionally high rates, were more frequent than expected if biting rates were equal among workers (Figure 2; test of goodness-of-fit to Poisson distribution, G14,815 = 19.4 to 92.0, all p < .005). From three to seven individuals in each colony initiated or received social biting more often than expected under the assumption of equal colony-wide rates (Figure 2; binomial test, p < .05). Single individuals in colonies A and C were exceptionally active biters on both observation days, biting nest mates at rates of over nine interactions per h (Figure 2). These individuals were biters in 57% and 42% of their colony’s interactions, respectively. Adult males were present only in colony B. Males were bitten by their female nest mates (18.3% of biting interactions were directed toward males). Males were never observed to bite other wasps.

Active biters interacted with many nest mates, rather than directing their biting at a few targets. For all colonies, the number of recipients of an individuals’ biting correlated strongly with their total biting rates (only workers that bit nest mates more than once were included; colony A: r = .97, p < .0001, colony B: r = .82, p < .0001, colony C: r = .96, p < .0001). The maximum number of nest mates bitten by single workers ranged from 11 to 36. Frequent recipients were bitten by numerous nest mates, and the number of biters interacting with each wasp was strongly correlated with her rate of being bitten (only workers that were bitten more than once were included; colony A: r = .70, p < .001, colony B: r = .71, p < .001, colony C: r = .82, p < .0001).

Table 1
Colonies-wide frequencies (per-h rates in parentheses) of biting interactions of differing intensity in three Polybia occidentalis colonies

<table>
<thead>
<tr>
<th>Interaction intensity</th>
<th>Colony A</th>
<th>Colony B</th>
<th>Colony C</th>
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<tbody>
<tr>
<td>Mild</td>
<td>70 (11.7)</td>
<td>92 (15.3)</td>
<td>184 (30.5)</td>
</tr>
<tr>
<td>Moderate</td>
<td>93 (15.5)</td>
<td>47 (7.8)</td>
<td>89 (15.0)</td>
</tr>
<tr>
<td>Severe</td>
<td>64 (10.7)</td>
<td>36 (6.0)</td>
<td>21 (3.5)</td>
</tr>
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Figure 1
Drawing from a photograph of a P. occidentalis worker biting a nest mate with moderate intensity. Note that the left forewing of the recipient wasp (shaded) has been bent away from her body by the biter (indicated by the arrow). The recipient is engaging in mouth-to-mouth liquid exchange (trophallaxis) with another wasp.

Data analysis
All ranges presented are the range of values across the three subject colonies. I tested the distribution of individuals’ rates of biting and of being bitten against the Poisson distribution of expected rates using a G-test, pooling categories with expected frequency values less than three, and estimating degrees of freedom as recommended by Sokal and Rohlf (1981). Individuals that engaged in biting interactions at significantly high rates were identified for further analysis using a binomial test (p < .05); the null hypothesis of the binomial test was expected frequency values less than three, and estimating degrees of freedom as recommended by Sokal and Rohlf (1981).
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Figure 2

(A) Frequency distributions of rates at which workers bit nest mates in three Polystyra occidentalis colonies. Expected Poisson frequency distributions (null hypothesis) are indicated by the solid lines. Workers that bit nest mates at significantly higher than expected rates (binomial test) are indicated by black bars. (B) Frequency distributions of rates at which workers were bitten by nest mates in three Polystyra occidentalis colonies. Expected Poisson frequency distributions (null hypothesis) are indicated by the solid lines. Workers that were bitten at significantly higher rates than their nest mates (binomial test) are indicated by black bars.

Wing length and ovary development

Most of the highly interactive wasps survived until their colonies were collected (significantly active biters collected: colony A: 3/3; colony B: 5/6; colony C: 3/3. Significantly frequent recipients collected: colony A: 4/6; colony B: 3/3; colony C: 6/7). Mean wing lengths did not differ among colonies, and did not differ between active biters and recipients (two-way ANOVA, all \( p > .50 \)).

Excepting one female in colony C, no dissected females exhibited ovary development. No opaque or swollen oocytes were visible in the ovaries, and the ovaries were classified as filamentous. Wasp number 165 from colony C had well-developed ovaries with many enlarged, opaque oocytes. However, her ovaries appeared to be in decline (some distal oocytes were shrunk and misshapen), and she had a heavy load of unidentified parasites (possibly gregarines; Richards, 1978). This female did not forage, and was recorded on the nest surface only on the second day of observations, when she was bitten at a high rate.

Biting and foraging behavior

Workers foraged for two food materials, nectar and prey, and for two building materials, water and wood pulp. Most workers collected a single material (61% to 100% of marked foragers collected one material), and the remainder of foragers collected two materials.

Foragers were bitten at higher rates than nonforagers (Figure 3; Kruskal-Wallis test, colony A: \( X^2 = 13.1, df = 1, p < .001 \); colony B: \( X^2 = 4.7, df = 1, p < .05 \); colony C: \( X^2 = 16.0, p < .001 \)). Workers that were bitten at higher rates also foraged at higher rates (Figure 4; colony A: \( r = .68, p < .001 \); colony B: \( r = .50, p < .001 \); colony C: \( r = .30, p < .005 \)). High rates of biting were directed toward both food and nest material foragers. Both active biters and recipients foraged. Active biters were less likely to be foragers than recipients, although this difference was not significant (5/13 active biters foraged, 12/16 frequent recipients foraged; likelihood ratio \( X^2 = 3.23, df = 1, 0.10 > p > .05 \)). The two workers that bit nest mates at exceptionally high rates (colony A and colony C) were active as nectar and pulp foragers, respectively.

Nest departures following biting

Biting interactions were sometimes immediately (i.e., within 3 s) followed by departure of the recipient from the nest. More intense interactions were more likely to be followed by the immediate departure of the recipient (interactions followed by departure: \( n = 26, 21.5\% \) of severe biting, \( n = 14, 6.1\% \) of moderate biting, \( n = 6, 1.7\% \) of mild biting; logistic regression after accounting for colony and individual effects, \( X^2 \)
Workers varied in their rates of biting. Both significantly active biters and significantly frequent recipients were present in each colony. The fact that rates of giving and receiving biting were not distributed randomly indicates that workers differed in their relative social status. These patterns raise the question of what factor or factors determine variation in biting behavior. Highly active biters interacted with large numbers of nest mates. Conversely, several workers often bit a single nest mate simultaneously, and recipient wasps were often bitten by several nest mates sequentially.

There may be a mechanism for common recognition of targets of biting, in other words, an unknown factor that incites biting by nest mates. Some eusocial wasps respond aggressively to nest mates that have well-developed ovaries, possibly distinguishing them via chemical cues (Downing and Jeanne, 1985; West-Eberhard, 1977). Aggression toward more fecund nest mates suggests that it functions as a form of reproductive policing in some contexts (Ratnieks, 1988). *Polybia occidentalis* workers exhibit partial ovary development when young, up to approximately 7 days of adult age, but workers’ oocytes are typically resorbed around the age at which they begin performing outside-nest tasks (O’Donnell, in press). No effects of worker body size or ovary development on biting behavior were found in this study. Therefore, biting interactions among *P. occidentalis* workers on the nest surface were not related to direct reproductive conflict. Similarly, ovary development bore no relationship with biting interactions among yellow jacket wasp workers (*Vespula*; Montagner, 1966). In *P. occidentalis* and yellow jackets, worker social biting occurs outside the context of direct competition over reproduction.

Although *P. occidentalis* workers differed in social status, the proximate mechanisms for these differences remain unclear. One possibility is that propensity to give or receive biting changes predictably over the course of adult development. Long-term observations of marked, known-age wasps are needed to determine how biting behavior changes as workers age. Alternatively, genotypically different nest mates may consistently vary in biting rates, and biting may also be a form of genetic nepotism if it is directed at genetically dissimilar workers. *Polybia* colonies possess multiple queens and relatively high genetic diversity (Queller et al., 1988), and genetic effects on foraging and in-nest task performance have been demonstrated in *P. aequatorialis* (O’Donnell, 1996, 1998b). However, Strassmann et al. (1997) found no genetic evidence for nepotism in *Parachartergus colobopterus* biting interactions.

**DISCUSSION**

Social biting was a common and conspicuous feature of *P. occidentalis* worker behavior, and is apparently widespread among Epiponini. My observations of *P. aequatorialis* (O’Donnell, 1998b), *P. enacia*, and *P. sericoa* (unpublished data) demonstrate that biting interactions among workers occur in other *Polybia* species, and similar behavior has been noted in the swarm-founding wasp *Parachartergus colobopterus* (Strassmann et al., 1997). Most *P. occidentalis* nest workers and foragers engaged in biting interactions. Biting interactions varied in intensity, and in the responses they elicited from the recipient wasp. Three facts suggest that biting interactions of different intensity are functionally similar. First, behavioral transitions occurred from milder to more intense biting. Second, workers that engaged in biting interactions at significantly high rates, either as biters or recipients, exhibited a range of interaction intensities. Finally, bitten workers departed the nest and began foraging immediately after interactions of all intensities, although they were more likely to do so after more intense interactions.

**Individual differences in biting rates**

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**The function of biting interactions and effects on task performance**

If *P. occidentalis* outside-nest workers were not competing for access to direct reproduction, what evolutionary forces maintain biting interactions? I propose that biting interactions play a role in regulating *P. occidentalis* workers’ task performance. Wilson (1985; also see Cole, 1981) predicted that aggressive interactions could persist among workers of derived eusocial species, even in contexts where the workers are sterile or nearly so. The data in this study suggest that this was the case in *P. occidentalis*. Biting was independent of ovary development, but was linked to foraging behavior. Workers departed their nests after being bitten, and in nearly all cases the departing workers began foraging. Recipient workers were more likely to forage, and rates of being bitten were correlated with foraging rates. Therefore, biting appeared both to initiate and to maintain foraging activity.

Adult *P. occidentalis* workers exhibit strong temporal polyethism, shifting from in-nest to on-nest, and finally to off-nest tasks as they age (Jeanne et al., 1988; O’Donnell and Jeanne, 1993). The developmental onset of foraging may be stimulated in workers that receive biting. Montagner (1966) proposed a similar function for intense biting interactions (mauling) among yellow jacket wasp workers (*Vespula*).

At the colony level, biting interactions could function both to maintain *P. occidentalis* forager activity, and to adjust overall foraging rates in response to changes in colony needs. If this is the case, then experimentally decreasing the rate of biting
interactions (e.g., by removing the most active biters; O’Donnell, 1998a) would lead to a decrease in the rate of foraging. Conversely, if biting interactions communicate information about colony needs for task performance, then biting rates should change in response to contingencies imposed on the colony. Experimental alterations of colony needs for certain tasks, such as nest damage manipulations (Jeanne, 1996; O’Donnell and Jeanne, 1996), should elicit effects on biting interactions.

The evolution of worker interactions and task performance

As eusocial insects evolve larger colony sizes, individual workers’ opportunities for direct reproduction decrease (Bourke, 1999), yet division of labor must still be achieved. As average colony size increases over evolutionary time, worker interactions may become increasingly independent of reproductive competition. The recent discovery of anarchistic honeybee workers, which lay eggs in the presence of the queen but do not elicit aggression, illustrates that worker interactions and reproduction can be decoupled (Oldroyd et al., 1999). Worker contact interactions in derived, large colony species are likely to evolve from dominance interactions over egg-laying rights in ancestral species. These interactions can become increasingly ritualized over evolutionary time (Wilson, 1985).

In highly derived eusocial taxa, worker contact interactions may give little indication of aggression or conflict, but retain the function of affecting division of labor. The dorsoventral abdominal vibration or shaking dance of honey bees (Apis mellifera) induces foraging behavior in recipient workers (Schneider et al., 1986; Seeley et al., 1998). The shaking dance may represent ritualized aggressive behavior, derived from dominance interactions that were ancestrally similar to those of worker bumblebees (van Doorn, 1987). In some ants, brief contacts with nest mates have been shown influence workers’ task performance (Gordon and Mehdiabadi, 1999; Gordon et al., 1993). I propose that ritualized contact interactions will continue to function in organizing labor as larger, more complex societies evolve from smaller, simpler ones. Support for this hypothesis requires demonstrating that worker contact interactions influence task performance, but that they depend less on variation in workers’ capacity for direct reproduction in more derived eusocial species. Within a eusocial clade, worker interactions will become less associated with direct competition as colony size, social complexity, and reproductive caste separation increase.

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REFERENCES


