

THE DEVELOPMENT OF BITING INTERACTIONS AND TASK PERFORMANCE IN A TROPICAL EUSOCIAL WASP

by

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Summary

Swarm-founding wasp workers (genus *Polybia*) exhibit developmental changes in task specialization known as temporal polyethism. Young workers typically remain inside the nest, followed by a period of working on the exterior nest surface, and later by foraging. *Polybia* workers on the nest exterior engage in biting interactions with their nest mates, and workers that are bitten are more likely to forage. To assess whether biting interactions influence the rate of temporal polyethism in *P. aequatorialis*, I tested for associations between on-nest workers' receiving biting and their ages at onset of foraging. As predicted, most workers were bitten several days before they began foraging. Workers that were bitten sooner after appearing on the nest surface also began foraging sooner. Furthermore, workers that were bitten at higher rates began foraging at younger ages. These patterns suggest that biting interactions play a role in initiating the onset of foraging. Most workers continued to receive biting after they began foraging, and workers were more likely to depart the nest immediately after being bitten. Therefore, biting apparently also functions to maintain foraging behaviour.

Introduction

Eusocial insects exhibit a range of mature colony sizes spanning more than five orders of magnitude (Hölldobler & Wilson, 1990; Jeanne, 1991; Kas-

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pari & Vargo, 1995). Decentralized control of task performance has accompanied the evolution of larger, more complex insect societies (O'Donnell, 1998a; Bourke, 1999; Anderson & McShea, 2001). Larger insect societies are self-organizing rather than hierarchical, meaning that the workers rely on cues from the environment and their nest, and on signals from other workers, when making decisions about which tasks to perform (Nicolis & Prigogine, 1977; Jeanne, 1986; Bonabeau *et al.*, 1997). Therefore, a full understanding of colony organization must include analyses of the communicative interactions among nest mates that affect task performance. Identifying the worker interactions that regulate polyethism is a central challenge to insect sociobiology (Robinson *et al.*, 1989; Seeley, 1998; Gordon & Mehdiabadi, 1999).

Worker aggression may represent an important means of regulating task performance in insect societies. Aggression among nest mate workers occurs in many species of eusocial insects, and aggressive interactions often affect task performance (bumble bees: Duchateau, 1989; paper wasps: Pardi, 1948; Gamboa *et al.*, 1990; O'Donnell, 1998b; ants: Heinze & Oberstadt, 1999). For example, subordinate individuals are more likely to perform risky tasks such as foraging and colony defense (West-Eberhard, 1981; Powell & Tschinkel, 1999; Markiewicz & O'Donnell, 2001).

Aggression is frequently associated with reproductive competition among workers. However, Wilson (1985) predicted that ritualized forms of aggression may persist in complex societies, even when reproductive competition among workers is reduced or absent. Aggressive interactions that are derived from competitive behaviour in ancestral species may function to organize workers' task performance, even in the absence of direct competition (Wilson, 1985; O'Donnell, 2001a). Swarm-founding wasp workers (genus *Polybia*) may provide an example. *Polybia occidentalis* workers engage in biting interactions with their nest mates (O'Donnell and Jeanne, 1995), and similar interactions have been observed in other swarm-founding wasps (Strassmann *et al.*, 1997; Strassmann *et al.*, 2002). *Polybia* workers differed in their rates of biting and of being bitten, but differences in biting rates were not associated with variation in body size or in ovary development, suggesting that biting was not associated with direct reproductive competition. Foraging behaviour was induced in bitten workers (O'Donnell, 2001a).

As in many eusocial insects, adult *Polybia* workers progress through a series of task specializations as they age. This pattern is referred to as temporal polyethism (Wilson, 1971; Calderone & Page, 1996). Tasks that are

performed away from the nest, such as foraging, follow in-nest and on-nest task performance in the developmental task sequence. *Polybia* workers vary widely in their rates of passage through the task sequence (Jeanne *et al.*, 1988; O'Donnell, 1998b), raising the possibility that biting interactions could contribute to variation in the rate of temporal polyethism.

The goal of the study presented here was to assess whether the rate and age at which *Polybia* workers are bitten are related to variation in temporal polyethism. As subjects I employed *P. aequatorialis*, a species closely related to *P. occidentalis* and with similar patterns of division of labour (Richards, 1978; O'Donnell, 1998b). I collected long-term developmental data on biting and task performance from individually marked, known-age workers. I addressed two main questions. 1. Does the developmental timing of biting interactions affect the rate of temporal polyethism, particularly the age at initiation of foraging? If so, I expected workers to be bitten before starting foraging. I also predicted that individual variation in the onset of being bitten would be temporally associated with the start of foraging. 2. Are there long-term individual differences in rates of being bitten? Differences in rates of receiving biting could also affect the rate of temporal polyethism. If so, I expected that workers bitten at higher rates would forage at younger ages.

Methods

Study site and subject species

I collected behavioural data in the field in Monteverde, Puntarenas Province, Costa Rica (10°18'N and 84°9'W), during the rainy season (June-July) of 2000. *Polybia aequatorialis* colonies occur most densely at elevations from approximately 1300 to 1700 m in the Monteverde area (O'Donnell, 2000). Like other *Polybia* species, *P. aequatorialis* nests comprise several horizontal layers of comb which are enclosed by an outer envelope. The nest envelope has a single entrance/exit hole. *Polybia* workers' temporal polyethism is related to their nest architecture. Workers typically first perform tasks inside the nest. Later they shift to tasks performed on the exterior of the nest envelope, and finally they leave the nest to forage (Jeanne *et al.*, 1988; O'Donnell & Jeanne, 1993).

Observation colonies, marking and introduction of workers

I selected three *P. aequatorialis* colonies subject colonies that were estimated to contain several thousand adult workers based on their nest sizes and defensive responses (unpublished data). I moved the colonies on 1 to 5 June 2000 to observation shelters where they were protected from rain and direct sun. The colonies were moved at night to insure that foraging workers would be present in the nests, and to minimize the loss of workers in transit. I wired

each colony's nest to a wooden frame approximately 1m above the ground. Small mirrors were mounted behind the nests, opposite the nest entrance hole, to facilitate observation of the entire nest surface. The colonies were left undisturbed for at least four days prior to worker introductions.

I collected brood combs from three additional *P. aequatorialis* colonies between 7 and 13 June 2000 to serve as a source of subject workers, because newly-emerged workers cannot be collected from *Polybia* colonies without destroying their nests. Newly-emerged (≤ 24 h old) *Polybia* adults are accepted into foreign colonies, and their behaviour is similar to that of wasps marked on their natal nests (Jeanne *et al.*, 1988; O'Donnell & Jeanne, 1993; O'Donnell, 1998b). The cues used in nest mate recognition apparently develop later, as older adults are not accepted into foreign colonies (personal observation). Combs that contained mature, dark pupae were maintained at ambient temperature in plastic containers. I removed all adult wasps that emerged from the combs every 24 h, and arbitrarily chose a subset of the newly-emerged females as subjects. I anesthetized the wasps with ethyl ether until they were immobile, then marked them on the dorsal surface of the thorax with paint pens. Each wasp received a unique combination of paint spots in a numerical code. The subjects for each observation colony were marked in a continuous numerical series (*e.g.* 1-150), and each observation colony's number series was unique.

I introduced 25 marked, newly-emerged workers into the observation colonies every other day beginning 8 June (colonies A and B) or 9 June (colony C). I continued marking and introducing workers for 12 days until a total of 150 individuals had been introduced into each observation colony. I collected behavioural data from each observation colony on days alternating with worker introductions. Marked workers ranged from 15 to 25 days of adult age at the end of the study.

Behavioural observations

All behavioural data were recorded onto audio cassette tapes and later transcribed onto data sheets. I collected behavioural data while seated 0.5 m from the nests, facing the nest entrance hole. I observed each colony every other day over the course of 25 days. Observation sessions lasted 2 continuous hours in the morning (starting between 0645h and 0925h) and one continuous hour in the afternoon (starting between 1225h and 1505h; total observation time was 3 h/colony/day). Each colony was observed for 39 h total.

At the start of each observation session, and every 15 min thereafter, I scanned the entire exterior surface of the nest and as much of the lower comb as was visible through the nest entrance. I noted the identity of all marked workers that were visible. I conducted 14 scan samples per colony per day. Throughout each observation session I also recorded all occurrences of tasks performed by marked workers and time of onset of task performance to the nearest minute. The on-nest tasks that I recorded included nest building and maintenance, handling of building materials, and taking food and building materials from arriving foragers. I recorded all occurrences of marked forager arrivals and departures, noting the material that was carried by the foragers whenever possible. See O'Donnell (2001b) for an ethogram of *P. occidentalis* worker behaviour, which is similar to *P. aequatorialis* behaviour.

I defined biting interactions as social contact involving one wasp (the biter) chewing on a nest mate's body (the recipient) at any location other than the mouth parts (O'Donnell, 2001a). Mutual mouth part contact occurs during food exchange and solicitation (Hunt *et al.*, 1987). I distinguished three levels of intensity of biting interactions (O'Donnell, 2001a). Mild

biting was the lowest intensity of interaction, and involved the biter gently 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 visibly displaced or vibrated. Severe biting was the highest intensity category, involving 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 were lifted partly or totally off of the nest surface. I recorded all occurrences of biting interactions that involved at least one marked wasp. For each biting interaction I recorded the identity of the participants and the intensity of the biting. I also noted whether the recipient departed the nest immediately after being bitten (within an arbitrarily chosen time window of 3 sec).

Data analysis

I used the binomial test (critical $p < 0.05$) to identify individuals that were bitten at significantly high rates, against the null hypothesis that all colony mates were bitten at equal rates (O'Donnell, 2001a). I estimated the amount of time that the workers spent on the nest from their appearance in scan samples, with presence during one scan representing 15 min of on-nest time. I used survival analysis to test for differences in the distributions of ages of first performance of tasks, and to test for associations of covariates with age of first performance of tasks. Survival analysis provides unbiased analysis of time distributions by including censored values (Pyke & Thompson, 1986). Censored values are data points for individuals that had not performed a given task by the end of the study. I used workers' ages when last observed as their censored age values if they had not performed a task by the end of the study.

Results

Workers that were never observed on the nest exterior were excluded from further analysis. Some of these workers were still performing in-nest tasks at the end of the study (pers. obs.). I collected behavioural data on tasks and biting interactions from 367 workers (Colony A: 116 workers, 77% of the total that were added; Colony B: 129 workers, 86%; Colony C: 122 workers, 81%).

Individual differences in biting behaviour

I observed a total of 1488 biting interactions, an average of 4.05 interactions/worker summed across colonies. Most workers participated in biting interactions (Colony A: 76%, Colony B: 84%, Colony C: 68%). Mild-intensity biting interactions were the most frequent, and severe interactions the least frequent, in each colony (Colony A: 56.5% of biting interactions were mild, 40.0% moderate, 3.5% severe; Colony B: 50.8% mild, 41.4%

moderate, 7.7% severe; Colony C: 52.8% mild, 43.5% moderate, 3.4% severe). Workers were bitten at mean rates of 0.54 to 0.99 interactions per hour on the nest (ranges among colonies). Rates of receiving biting varied among individuals. In each colony, a subset of the workers were bitten by nest mates significantly more often than expected if biting rates were equal among workers (Binomial test with critical value $p < 0.05$, Colony A: 20.5% of workers were bitten at significantly high rates, Colony B: 23.0%, Colony C: 17.9%). Wasps bitten at significantly high rates did not differ from their nest mates in overall rates of on-nest task performance (t -tests, all $p > 0.10$). Among all workers, those that were bitten at higher rates were younger when they initiated foraging (Survival analysis Wilcoxon test; Colony A: test statistic = -11.45 , $df = 1$, $p < 0.0001$, Colony B: test statistic = -20.47 , $df = 1$, $p < 0.0001$, Colony C: test statistic = -4.48 , $df = 1$, $p < 0.05$).

Developmental timing of biting interactions and foraging

Workers usually first received biting several days after they become active on the nest surface (Fig. 1; difference in mean ages of first working outside the nest and first receiving biting, Colony A: 5.0 days, Colony B: 3.1 days, Colony C: 4.2 days). Most foragers were observed being bitten by their nest mates before their first foraging trip (Colony A: 84.8% were bitten before foraging; Colony B: 79.2%; Colony C: 59.2%; overall test of bias toward occurrence of biting before foraging $\chi^2 = 7.0$, $df = 1$, $p < 0.01$). Within colonies, workers' ages when first bitten were significantly younger than their ages at first foraging (Fig. 1; Difference in mean ages of first receiving biting and first foraging, Colony A: 5.4 days, Colony B: 1.8 days, Colony C: 3.4 days. Survival analysis Wilcoxon tests for differences in distributions of ages of first receiving biting and first foraging, Colony A: test statistic = 33.5, $df = 1$, $p < 0.0001$, Colony B: test statistic = 62.3, $df = 1$, $p < 0.0001$, Colony C: test statistic = 20.5, $df = 1$, $p < 0.001$). In each colony, workers that were bitten sooner after appearing on the nest surface began foraging sooner (Survival analysis Wilcoxon test; Colony A: $N = 33$ foragers, test statistic = 49.2, $df = 1$, $p < 0.01$; Colony B: $N = 48$ foragers, test statistic = 36.0, $df = 1$, $p < 0.05$; Colony C: $N = 49$ foragers, test statistic = 53.9, $df = 1$, $p < 0.05$).

Many workers continued to be bitten after they had initiated foraging (range among colonies: 63.6% to 76.5% of workers were bitten after the

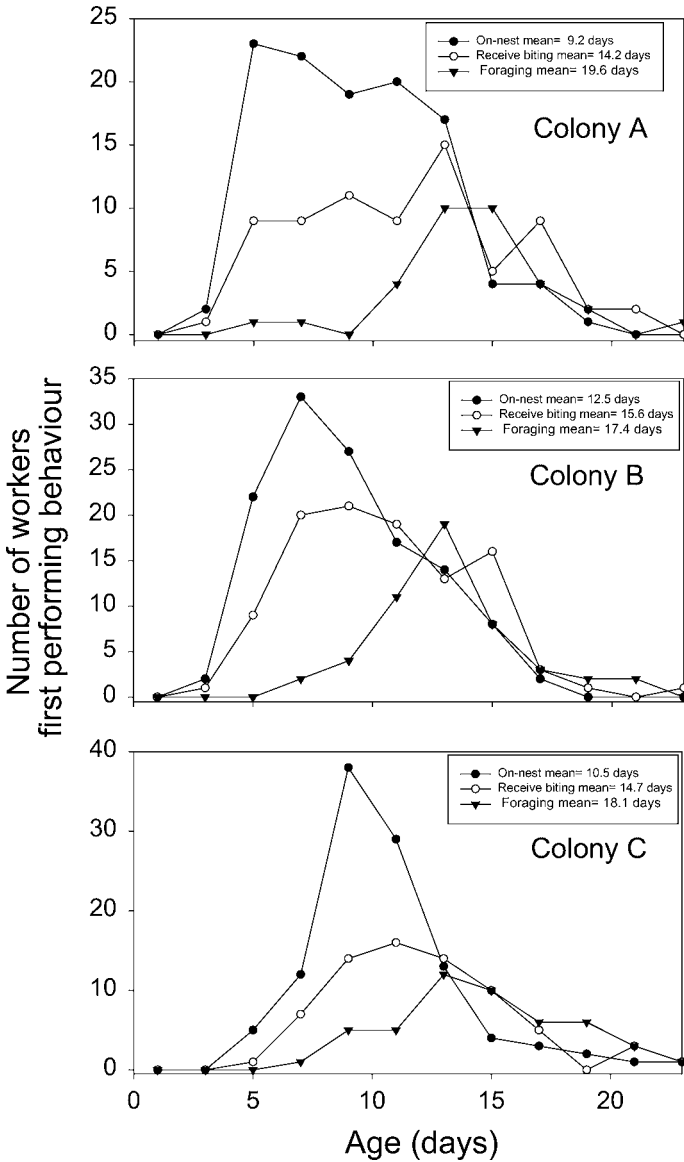


Fig. 1. Distributions of the age of first performance of behavioral acts by *Polybia aequatorialis* workers from three colonies. Numbers of workers first observed performing each task set (on-nest tasks, receiving biting, and foraging) are plotted against worker age. Mean ages of first performance for each task set were calculated using survival analysis, including censored values. Age at first receiving biting generally followed first performance of on-nest tasks, and preceded initiation of foraging.

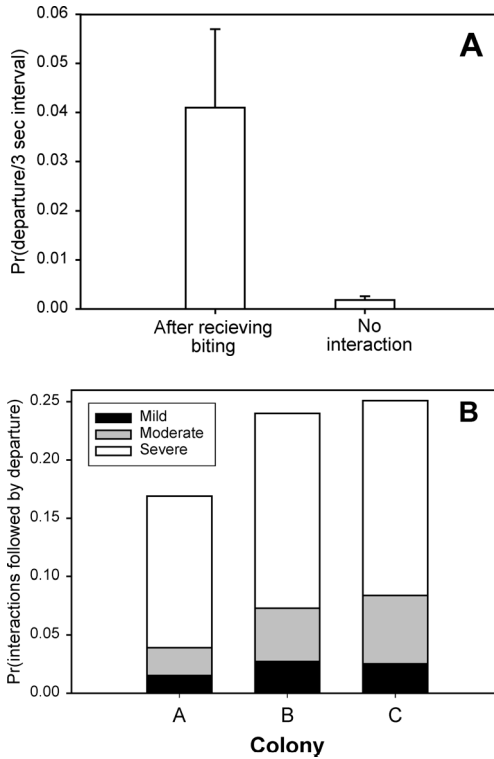


Fig. 2. A: Probabilities of nest departure by *Polybia aequatorialis* workers in 3 sec intervals immediately following biting interactions and at other times. Bars show mean and SD among three colonies. B: Proportions of biting interactions of different intensities (mild, moderate, and severe) that were immediately followed by the recipient's nest departure in three colonies of *Polybia aequatorialis*.

onset of foraging). Foragers were sometimes bitten by nest mates soon after they returned to the nest (pooled across workers; Colony A: 10% of forager arrivals were followed within 30 sec by biting; Colony B: 29%; Colony C: 19%). In many of these cases the foragers were bitten while they transferred their loads of materials to nest workers. Biting was directed to both food material foragers (*i.e.* those carrying nectar or prey) and building material foragers (*i.e.* those carrying wood pulp or water). Workers' probabilities of departing the nest within 3 sec of being bitten were 19 to 28 times higher than background departure rates (Fig. 2A; Fisher's exact test $p < 0.0001$ in all colonies). More intense interactions were more likely to be followed immediately (*i.e.* within 3 sec) by the recipient's departure from the nest

(Fig. 2B; Fisher' exact test, Colony A: $p < 0.05$, Colony B: $p < 0.001$, Colony C: $P < 0.01$).

Discussion

Biting interactions among *P. aequatorialis* workers were associated with the performance of foraging behaviour. The developmental data presented here are consistent with the hypothesis that biting interactions influence temporal polyethism. Biting appears to induce the onset of foraging in recipients. As predicted, both workers' age and rates of being bitten were associated with earlier onset of foraging. Workers were typically first bitten several days after making the transition from in-nest to on-nest task performance, and several days before they began foraging. Workers that were bitten sooner after becoming active outside the nest tended to forage earlier. Workers also differed significantly in their rates of receiving biting, and workers that were bitten at higher rates began foraging at younger ages.

Biting may have the additional effect of maintaining foraging behaviour in recipients. Active foragers were sometimes bitten by nest mates when they returned to the nest. Biting was directed at foragers carrying both food materials and nest-construction materials, indicating that biting was not driven solely by competition for food. Workers on the nest were more likely to depart immediately after being bitten, and the probability of departure increased with the intensity of the biting interaction. These patterns are similar to those noted in *P. occidentalis* (O'Donnell, 2001a).

The data presented here suggest that worker age influenced the probability of being bitten, but some individuals were bitten at higher rates independently of age. The chemical or other cues that elicit biting by nestmates are unknown. The similarities in task performance and biting behaviour of the introduced workers in this study to *Polybia* workers on their natal nests indicate that the patterns observed were not an artifact of foreign worker introductions (O'Donnell & Jeanne, 1995; O'Donnell, 1998b, 2001a). In the leafcutting ant *Atta cephalotes*, workers on the colony's garbage heap receive aggression from nest mates, possibly in response to chemical cues resulting from heap workers' contact with refuse (Hart & Ratnieks, 2001). Although biting was directed at some active *Polybia* foragers, most workers were bitten for several days before they began foraging. Therefore, biting interactions

were not responses to changes induced by foraging. Genetic diversity tends to be high among *Polybia* nest mate workers, in part because their colonies often include multiple laying queens (Richards, 1978; Queller *et al.*, 1988). The possibility that patterns of biting interactions are influenced by genetic differences among *Polybia* workers has not been tested. Strassmann *et al.* (1997) did not find evidence for genetic effects on patterns of social biting in the swarm-founding wasp *Parachartergus colobopterus*.

I could not determine whether biting interactions occurred inside the nests, nor whether biting earlier in life influenced workers' age at transition from in-nest to on-nest task performance. In the epiponine wasp *Parachartergus colobopterus*, workers engage in biting interactions inside the nest. Worker aggression in *P. colobopterus* may play a role in suppression of ovary development in young females (Strassmann *et al.*, 2002). In some swarm-founding wasp species, including *Polybia* species, workers exhibit at least partial ovary development when they are young (Richards, 1978; O'Donnell, 2001b). However, individual variation in giving and receiving biting was not associated with ovary development in *P. occidentalis* workers (O'Donnell, 2001a), suggesting that biting interactions on the nest surface were not associated with direct reproductive competition or with worker policing (Ratnieks, 1993; Visscher, 1996). Wilson (1985; also see Cole, 1981) suggested that dominance interactions can persist in ritualized forms in advanced eusocial species as a means of communication among workers about colony status and colony needs. If this hypothesis is correct, then ritualized derivatives of aggressive interactions may be maintained by colony-level selection, even in the absence of worker conflict over direct reproduction. Aggression, and ritualized interactions derived from aggression, can serve as an efficient means of dividing labour among workers.

Although *Polybia* biting interactions corresponded to short-term and long-term (*i.e.* developmental) changes in the probability of foraging behaviour, responses to biting were probabilistic. Not all bitten workers foraged, and many workers were bitten for several days before the onset of foraging. These patterns suggest that biting interactions are a modulatory form of communication, altering recipients' probability of responding to task stimuli. A similar form of modulatory communication is found in honey bees (*Apis mellifera*). Honey bee workers engage in a vibratory dance, which involves one working climbing onto the back of another (Schneider *et al.*, 1986; Seeley *et al.*, 1998). Like bitten *Polybia* workers, vibratory dance recipients do not

exhibit consistent or immediate changes in behaviour. The vibratory dance is performed at higher rates during periods of increased colony need for foraging, and is associated with increased activity and an increased probability of foraging in recipients (Schneider *et al.*, 1986; Nieh, 1998; Lewis *et al.*, 2002). In *Polybia*, cognitive summation of biting and other stimuli may be necessary for workers to determine whether their colony's need for labour surpasses their thresholds of response for performing a given task. Workers that bite nestmates at high rates may play an important role in regulating task performance, although the factors that elicit biting activity are unknown (O'Donnell, 2001a). Experimental manipulations of colony need for foraging or social structure (O'Donnell & Jeanne, 1990) will be useful in further testing the role of biting interactions in regulating task performance.

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