



Polybia wasp biting interactions recruit foragers following experimental worker removals

SEAN O'DONNELL

Animal Behavior Program, University of Washington

(Received 12 May 2005; initial acceptance 14 June 2005;
final acceptance 22 July 2005; published online 7 February 2006; MS. number: A10160R)

Communicative interactions between colony members, or worker connectivity, can affect division of labour in insect societies. Nestmate workers of the eusocial paper wasp *Polybia occidentalis* engage in biting interactions, and correlational evidence suggests that biting promotes foraging by the workers that are bitten. I used experimental forager removals to test whether biting is a form of worker connectivity, inducing new recruits to enter the foraging force. I observed colonies with marked workers during a pretreatment (control) period, then removed all arriving foragers on the following day. Foraging ceased after several hours of forager removals, and remained depressed on the following morning. I grouped the remaining workers into four behavioural categories: nonforagers, individuals that stopped foraging after the manipulation, continuing foragers that were active before and after the manipulation and recruited foragers that began foraging after the manipulation. After the manipulation, the recruited foragers were bitten at similar rates to the continuing foragers and, most importantly, were the only ones that were bitten at significantly increased rates after the manipulation. Most recruits were observed being bitten before they began foraging. However, some recruits were not observed being bitten, and worker responses to biting were often gradual. These patterns suggest that the effect of biting is to modulate the probability of foraging in bitten workers. The experiments show that biting helps to induce foraging. Biting is a form of worker connectivity, serving as a mechanism of communication between *Polybia* workers that affects colony responses to changing conditions.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Division of labour between workers in eusocial insect colonies involves individual task specialization. Colonies are dynamic, so adaptive division of labour must also accommodate worker behavioural flexibility. Workers can show flexibility by switching between tasks or by adjusting their rates of performing a task. Summed across the worker population, the amount of worker effort allocated to different tasks is expected to track changes in colony needs. I suggest the term 'worker connectivity' to refer to communicative interactions between workers that regulate task performance and division of labour. Sharing information can effectively expand workers' sensory environment, allowing them to make more efficient task decisions than would be possible if they responded only to local cues that they encountered directly (Seeley et al. 1991). Mechanisms of worker connectivity range from simple encounters with nestmates (Gordon et al. 1993;

Pratt 2005) to specialized communicative displays (Sherman & Visscher 2002).

Swarm-founding eusocial paper wasps show some of the most complex forms of worker division of labour seen in insect societies (O'Donnell & Jeanne 1992). In species of *Polybia* and *Metapolybia*, workers show well-developed temporal polyethism and strong task specialization (Karsai & Balazsi 2002). Subsets of complex tasks are finely partitioned between cooperating teams of nestmates (Jeanne 1996; Karsai & Wenzel 2000). In one well-studied system, *P. occidentalis* workers respond to changes in colony conditions by entering and leaving the forager force. Foraging requires workers to fly from the nest, often spending much of their time away. Foraging is associated with reduced worker longevity in *P. occidentalis* (O'Donnell & Jeanne 1992). While on the nest, *Polybia* workers frequently engage in biting interactions (O'Donnell 2001a). Correlational and developmental data suggest that biting interactions affect foraging behaviour in the workers that are bitten. Biting appears both to induce and to maintain foraging behaviour in bitten workers. Evidence for induction of foraging includes the facts that on-nest workers

Correspondence: S. O'Donnell, Department of Psychology, Box 351525, University of Washington, Seattle, WA 98195, U.S.A. (email: sodonnell@u.washington.edu).

are more likely to depart the nest and forage immediately after being bitten, and that workers' age at first foraging covaries with their ages and rates of being bitten (O'Donnell 2003). Two pieces of evidence that biting maintains foraging are that active foragers are often bitten when they return to the nest, and that workers' foraging rates correspond to their rates of being bitten (O'Donnell 2001a). In this study, I used experimental manipulations of colony social structure (i.e. the removal of active foragers), to test more critically whether biting regulates the induction of foraging in *P. occidentalis*. I asked whether biting is directed specifically at those workers that are recruited into the forager force.

To answer this question, I made use of a pattern that I noted during earlier studies of genotypic effects on forager specialization in *Polybia* (O'Donnell 1996). When I collected arriving foragers from *P. aequatorialis* colonies, foraging ceased after several hours of continuous forager removals (similar patterns have been observed in *Pogonomyrmex* harvester ants: Gordon 2002). Foraging rates apparently remained depressed for at least part of the day following the removals. *Polybia* workers are recruited into the foraging force following forager removals (Jeanne 1996), and in response to nest damage (O'Donnell & Jeanne 1990), but the behavioural mechanisms by which new foragers are recruited are unknown. The goal of this study was to test whether biting behaviour was associated with the recruitment of new foragers following experimental forager removals in *Polybia occidentalis*. If biting plays a role in inducing foraging, I predicted that recruited foragers would be bitten at higher rates than would their nestmates, and that receiving biting would precede foraging in the recruited workers.

METHODS

Study Site and Behaviour of Subject Species

Field research was conducted on private property near the town of Cañas in Guanacaste Province, Costa Rica (10°25'N, 85°07'W). The local habitat is disturbed pasture/savannah in the tropical dry forest lifezone (Holdridge 1967). *Polybia occidentalis* nests are abundant in low shrubs and hedges in the area.

Polybia nests are ovoid and comprise a series of circular, horizontal combs enclosed by a covering envelope. The envelope has a single entrance hole through which workers enter and exit. Workers show strong temporal polyethism, typically working inside the nest when younger, working on the nest surface at intermediate ages (e.g. building, taking loads from arriving foragers), and finally, leaving the nest to forage when older (O'Donnell & Jeanne 1992). *Polybia occidentalis* foragers nearly always land on the outside of the nest and transfer the materials that they are carrying to workers on the nest surface (Hunt et al. 1987). *Polybia* workers on the exterior nest surface frequently engage in biting interactions (O'Donnell 2001a, 2003). Biting involves workers chewing on nestmates' bodies. Several wasps sometimes participate in biting a single nestmate.

Preparing the Subject Colonies

I chose four subject colonies that were found nesting in accessible locations (here labelled colonies A, B, C and D; Colony D was labelled 'Colony I' in my field notes). The subject colonies occupied nests of four to six layers of comb. Nests of this size typically house several hundred adults at the study site (personal observation). Before data collection I moved the nests at night. I wired the nests to frames underneath observation shelters where they were protected from rain and direct sun. I mounted a small mirror behind each nest to provide a view of the entire exterior nest surface and to encourage foragers to land near the nest entrance hole. Foragers carrying food and building materials arrived at each nest on the morning after it was moved, suggesting that transporting the colonies caused minimal disruption. I left the nests undisturbed for at least 48 h after moving them.

Marking Wasp Workers for Individual Identification

I collected and marked workers from the subject colonies beginning before dawn (0450 hours local time) on the day preceding control observations. I mildly disturbed the nest by tapping on the envelope, inducing a few hundred wasps to run onto the exterior envelope but not to fly (London & Jeanne 2003). I then plugged the nest entrance with cotton. I enclosed the nest in a plastic bag containing a vial of ether-soaked cotton, thereby anaesthetizing and capturing several hundred workers. After 1–2 h I returned to the nest, plugged the entrance, and again captured workers from the nest exterior by bagging and anaesthetizing them. The bagged workers were held in a refrigerator and were re-anaesthetized with ether in small batches (approximately 30 individuals) while they were marked. I marked each worker's thoracic dorsum in a numerical code using paint pens. Marks were sequential and unique within colonies. Every 50–100 marked workers were returned to the nest as they recovered from anaesthetization and were dropped into the nest entrance hole. I marked 177–599 wasps per colony ($\bar{X} = 318$ marked workers). All workers were returned to their nests by 1400 hours of the day they were removed. Not all wasps in the colonies were marked, and some marked workers did not forage or perform on-nest tasks during observations.

Experimental Design

Experimental trials consisted of one day of premanipulation control observations, followed by a day of forager removals, then by one or more days of postremoval observations. The nests and all wasps were removed from the shelters after sunset on the last day of observations.

Starting in the early afternoon of the day after control observations, I collected all foragers that landed on the nest. I collected arriving foragers for at least 2 h, and until no more foragers arrived for at least 1 h of continuous observation. Removed foragers were immediately killed by

placing them in fixative. The postremoval observations were started on the following day.

Behavioural Observations

Behavioural data were collected by an observer seated facing the entrance hole of the nest at a distance of 1 m. A single observer collected all behavioural data for each subject colony. Behavioural data were recorded on audiocassettes and transcribed later the same day. Each colony was observed for two continuous observation sessions of 2 h each per day (three sessions were terminated early during periods of heavy rainfall). Morning sessions began at 0700–0800 hours local time, and afternoon sessions began at 1300–1330 hours local time, for a total of 3–4 h of observation per day. During observation sessions, the observer recorded all occurrences of forager arrivals, noting the forager's identity (including unmarked). Observers also recorded all occurrences of biting interactions, noting the identity of the recipient and all biters (including unmarked). Finally, the observers scanned the nest surface every 15 min, noting the identity of all marked wasps present on the nest surface.

Data Analysis

I included all behavioural records, including unmarked workers, to calculate colonywide rates of biting and foraging. Other analyses were performed only on the marked workers. For Colony B, I pooled the data from the three postremoval observation days when estimating workers' rates of task performance after removals. I categorized workers into four behavioural classes based on how they responded to the manipulations: workers that did not forage before or after the manipulation (nonforagers), workers that foraged only before the manipulation (stopped foragers), workers that foraged both before and after the manipulation (continuing foragers) and workers that foraged only after the manipulation (recruited foragers). I used ANOVA (GLM, implemented in SAS 9.1, Cary North, Carolina, U.S.A.) to test for effects of categorical covariates (subject colony, worker behavioural class) on continuous response variables (foraging rate, biting rates). For all statistical tests I treated colonies as replicates, and I included colony identity as a variable in all statistical models. I used Tukey HSD post hoc tests, critical $\alpha = 0.05$, to make all pairwise comparisons between means (Sokal & Rohlf 1981).

RESULTS

Effects of Forager Removals

The numbers of marked and unmarked foragers removed, and summaries of individual worker behaviour before and after manipulations, are presented in Table 1. In all colonies, foraging ceased (no arrivals in at least 1 h) after several hours of forager removals on the second day of the trial. In general, both foraging and biting rates

Table 1. Numbers of *Polybia occidentalis* workers from four colonies, categorized by their behaviour before and after experimental worker removals

	Colony			
	A	B	C	D
Number of marked foragers active before manipulation	23	66	49	49
Number of foragers removed (marked foragers in parentheses)	24 (7)	17 (10)	32 (18)	21 (8)
Number of marked workers that stopped foraging	15	50	17	29
Number of marked workers that continued foraging	1	6	14	12
Number of marked foragers that were recruited	10	16	8	19

were lower at the start of the postremoval observation (Fig. 1). Total foraging rates (arrivals/15 min) were significantly lower during the postmanipulation morning observations than during the control morning observations for all colonies except Colony D (Fig. 1). Foraging rates increased during postremoval afternoon observations except in colony B, which was observed for two additional days until foraging rates recovered to preremoval rates. Mean colonywide rates of biting were lower on the morning after forager removals than on the preremoval morning, except in Colony C (Fig. 1).

Biting and Worker Responses Following Forager Removal

Most of the recruited foragers were observed being bitten, and many of them (range 26–75%) were observed being bitten before they began foraging (Table 2). Several of the recruited foragers were bitten during the first morning postremoval observation period, and they began foraging in the afternoon of the same day (Table 2).

Continuing foragers and recruits arrived at similar rates during postremoval observations (ANOVA: $F_{1, 82} = 0.15$, $P = 0.70$). The worker behavioural classes differed significantly in the rates at which they were bitten during the postremoval observations (ANOVA: $F_{3, 565} = 58.0$, $P < 0.0001$; Fig. 2). Post hoc comparisons of group means showed that the recruited foragers were bitten at higher rates than were nonforagers and stopped foragers, and at similar rates to the continuing foragers (Fig. 2). The worker behavioural classes also differed significantly in the direction and magnitude of change in their rates of receiving biting from control to postremoval observations (ANOVA: $F_{3, 565} = 14.8$, $P < 0.0001$; Fig. 3). Post hoc comparisons showed that recruited foragers experienced the largest positive change in biting rates (Fig. 3).

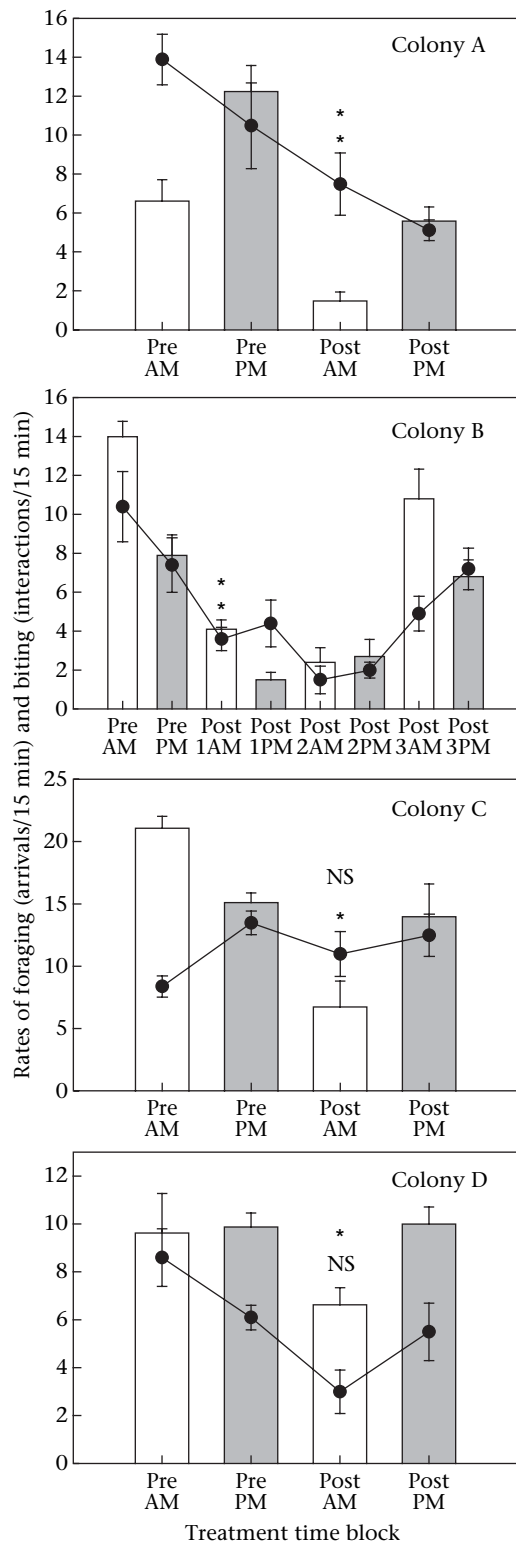


Figure 1. Total colony mean \pm SE foraging rates (arrivals/15 min), and line-scatterplot showing mean \pm SE total rate of biting interactions (number of workers bitten/15 min) for four *Polybia occidentalis* colonies. Each bar represents an observation period (\square : morning; \blacksquare : afternoon). Symbols above the first postremoval morning observation period (Post AM) are results of post hoc tests (Tukey HSD) comparing that period with the morning control observation period (Pre AM). The upper symbol is the test for changes in biting rates, the lower symbol is the test for changes in foraging rates. * $P < 0.05$.

Table 2. Summary of the relative timing of observed biting and foraging, following experimental forager removals, for marked recruited foragers from four *Polybia occidentalis* colonies

	Colony			
	A	B	C	D
Not bitten	1	6	1	10
Foraged first	2	4	1	5
Bitten first	7	6	6	4
Bitten in AM, foraged in PM	4	1	3	2

AM: morning observation period; PM: afternoon observation period.

Behaviour of Wasps that Bit Nestmates

Workers' rates of biting nestmates before and after removals were positively correlated (Pearson correlation: Colony A: $r_{180} = 0.50$, $P < 0.0001$; Colony B: $r_{147} = 0.41$, $P < 0.0001$; Colony C: $r_{92} = 0.44$, $P < 0.0001$; Colony D: $r_{114} = 0.51$, $P < 0.0001$). The worker behavioural categories did not differ significantly in rates of biting nestmates following worker removals (ANOVA: $F_{4, 587} = 1.29$, $P = 0.27$). In each colony, most workers never or rarely bit nestmates, but a few individuals bit nestmates at high rates (Fig. 4). The most active biters came from a number of behavioural categories, including some recruited foragers (Fig. 4).

DISCUSSION

The forager removals effectively shut down foraging on the day they were performed, and the decreased rates of foraging persisted into the following day. Reduced foraging presumably caused shortages in food and building

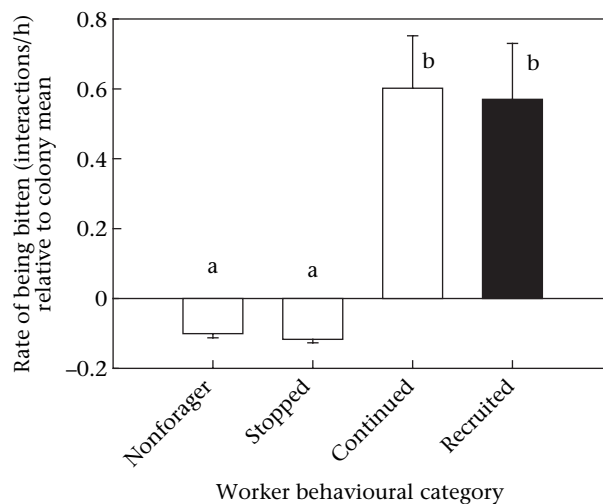


Figure 2. Mean \pm SE of *Polybia occidentalis* workers' rates of being bitten by nestmates following forager removals. Each workers' value is relative to her colony's mean rate of receiving biting. Letters above bars indicate results of Tukey's HSD post hoc means comparisons; bars with different letters were significantly different ($P < 0.05$). \blacksquare : recruited foragers.

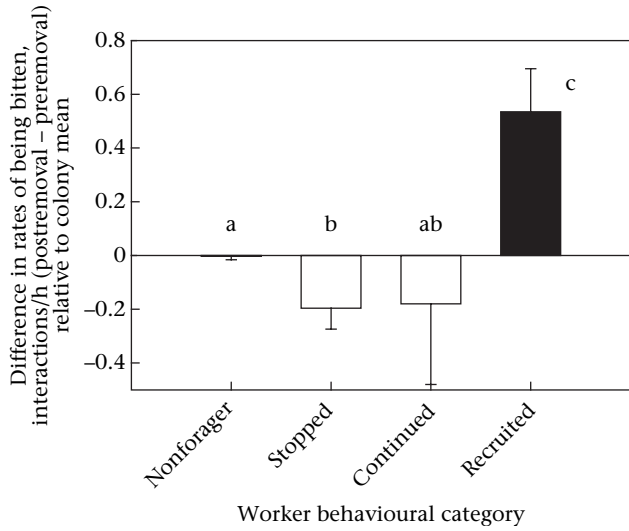


Figure 3. Mean + SE changes in *Polybia occidentalis* workers' rates of being bitten by nestmates from before to after forager removals. Each workers' value is relative to her colony's mean difference in rate of receiving biting. Letters above bars indicate results of Tukey's HSD post hoc means comparisons; bars with different letters were significantly different ($P < 0.05$). ■: recruited foragers.

materials, to which some workers responded by joining the forager force (O'Donnell & Jeanne 1990; Jeanne 1996).

As I noted in previous studies (O'Donnell 2001a, 2003), biting was directed most often at foragers. Continuing and recruited foragers were bitten at similar rates, and at higher rates relative to nonforagers and stopped foragers,

following the forager removals. Two lines of evidence suggest that foragers were recruited in response to being bitten. First, and a key finding of this study, the rate at which the recruited workers were bitten increased following forager removals. This increase occurred against a background of generally lower biting rates, and no other class of workers experienced an average increase in rates of being bitten. Second, receiving biting often preceded foraging in the recruits, in some cases by several hours. However, some recruits were first bitten after they began to forage, and a few recruits were not observed being bitten. Furthermore, some workers that were bitten did not forage. These observations are consistent with a modulatory effect of biting on foraging, in other words, being bitten increases a workers' probability of foraging. The finding that some recruited workers were bitten repeatedly over the course of several hours before foraging shows that biting does not elicit an immediate, deterministic response.

Some important aspects of the social mechanisms linking biting to forager recruitment remain unresolved. How were the recruits selected? What cues or signals elicit biting by nestmates? There may be a developmental component to workers being targeted for biting. In *P. aequatorialis*, known-age workers were typically bitten several days after beginning work on the outer nest surface, and several days before they began foraging (O'Donnell 2003). In *P. occidentalis*, variation in rates of giving and receiving biting did not correspond to ovary development or body size (O'Donnell 2001a, b). In contrast, *Parachartergus colobopterus* workers inside the nest directed more biting at relatively young females with partial ovary development, suggesting that reproductive

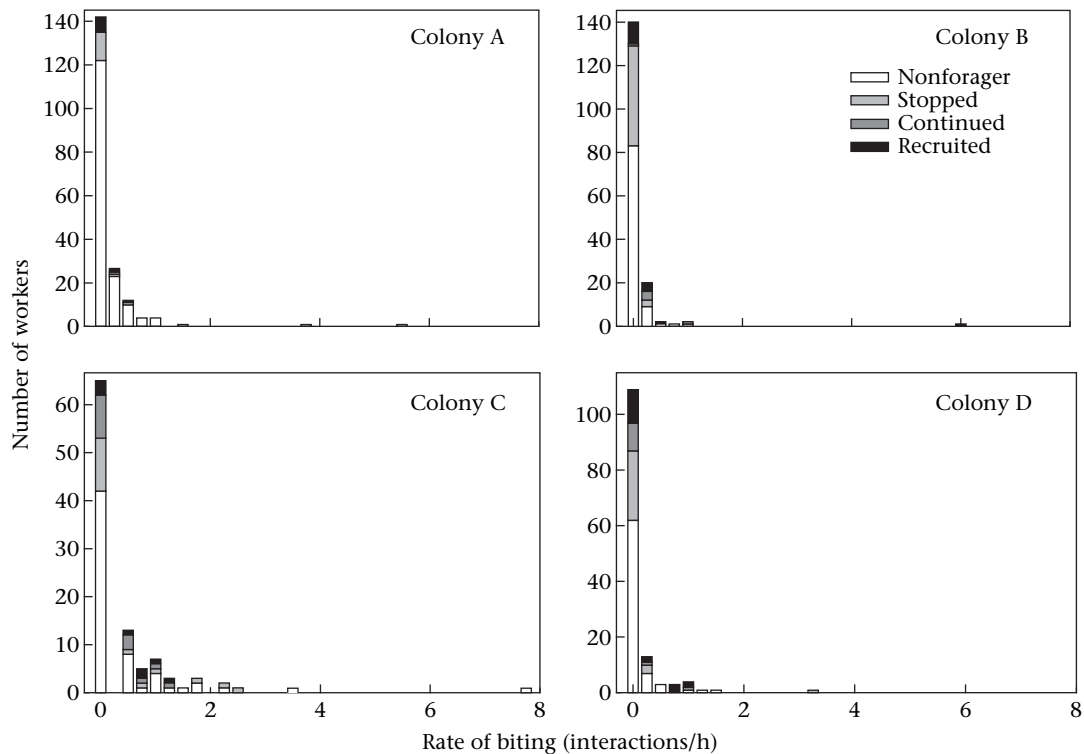


Figure 4. Distributions of rates of biting nestmates by *Polybia occidentalis* workers from four colonies.

competition can affect biting interactions (Platt et al. 2004). *Parachartergus* workers do not show evidence of genetic nepotism when biting nestmates (Strassmann et al. 1997).

A similar set of questions relates to the biters. What factors determine workers' probabilities of becoming active biters? In this study, as in an earlier, developmental study (O'Donnell 2003), I found evidence for consistency of workers' rates of biting nestmates before and after the forager removals. This result suggests the possibility of physiological or genetic differences in biting propensity, but the nature of these differences is unknown. An untested possibility is that high-rate biters have information about colony levels of need for foraging, possibly as a result of patrolling the nest surface.

In insect societies, workers that are recruited to perform new tasks may perceive the increased colony need for those tasks directly (Jeanne 1996; Pratt 2004). For example, in this study, some of the workers may have responded to their own increased hunger levels by leaving to collect food. Alternatively, communication between workers can transmit information about colony needs for tasks. I propose the term 'worker connectivity' to refer to communicative interactions that affect task performance. Worker connectivity allows workers to change each other's thresholds of response to tasks. Connectivity potentially allows sharing of information among more workers, and across greater distances, such that direct worker contact or experience with a task stimulus is not necessary to elicit task performance. Connectivity may be especially valuable if there is task partitioning (Anderson & Ratnieks 1999), and/or when some tasks (for example, foraging away from the nest) remove workers from some kinds of task stimuli. The experimental results presented here suggest that biting interactions function as a mechanism of worker connectivity in *P. occidentalis*.

After modelling worker behaviour using a network approach, Page & Mitchell (1998; see also Fewell & Page 1999) suggested that division of labour can be an automatic outcome of social grouping. However, the widespread occurrence of worker communicative displays that affect task performance suggests that connectivity is under selection, often at the colony level, as a mechanism for regulating worker task performance (Beshers & Fewell 2001; Biesmeijer & Slaa 2004; Dornhaus & Chittka 2004). The communicative mechanisms that constitute worker connectivity differ between species. A wide array of sensory modalities is used, including touch/mechanical stimulation (this study; Schneider et al. 2004), chemical signals (Pankiw 2004) and substrate-borne vibratory signals (Connetable et al. 1999; a similar system may exist in eusocial rodents: Narins et al. 1997). Even within functionally similar task classes, species can differ in the mechanisms of worker connectivity. Foraging is an excellent and well-studied example. In some cases, simple contact with other workers can apparently influence workers' foraging decisions (Gordon 2002). In others, ritualized worker interactions affect the probability of foraging in recipients (Sherman & Visscher 2002; Schneider et al. 2004). Foraging ecology, including the costs and benefits of the resources that are collected, and social factors

such as colony size and nest architecture, may interact to affect the communicative mechanisms used in worker connectivity.

Acknowledgments

Douglas Wacker assisted with field research and data collection, and Adam Smith helped with data entry. Thanks to Jorge Hagnauer and his family for their continuing support of my field research in Guanacaste. Financial support was provided by U.S. National Science Foundation grants IBN-9904885 and IBN-0347315. Field research was conducted under permits from the Ministry of Energy and the Environment, Republic of Costa Rica.

References

- Anderson, C. & Ratnieks, F. L. W. 1999. Worker allocation in insect societies: coordination of nectar foragers and nectar receivers in honey bee (*Apis mellifera*) colonies. *Behavioral Ecology and Sociobiology*, **46**, 73–81.
- Beshers, S. N. & Fewell, J. H. 2001. Models of division of labor in social insects. *Annual Review of Entomology*, **46**, 413–440.
- Biesmeijer, J. C. & Slaa, E. J. 2004. Information flow and organization of stingless bee foraging. *Apidologie*, **35**, 143–157.
- Connetable, S., Robert, A., Bouffault, F. & Bordereau, C. 1999. Vibratory alarm signals in two sympatric higher termite species: *Pseudacanthotermes spiniger* and *P. militaris* (Termitidae, Macrotermitinae). *Journal of Insect Behavior*, **12**, 329–342.
- Dornhaus, A. & Chittka, L. 2004. Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). *Apidologie*, **35**, 183–192.
- Fewell, J. H. & Page, R. E., Jr. 1999. The emergence of division of labour in forced associations of normally solitary ant queens. *Evolutionary Ecology Research*, **1**, 537–548.
- Gordon, D. M. 2002. The regulation of foraging activity in red harvester ant colonies. *American Naturalist*, **159**, 509–518.
- Gordon, D. M., Paul, R. E. & Thorpe, K. 1993. What is the function of encounter patterns in ant colonies? *Animal Behaviour*, **45**, 1083–1100.
- Holdridge, L. R. 1967. *Life Zone Ecology*. San Jose, Costa Rica: Tropical Science Center.
- Hunt, J. H., Jeanne, R. L., Baker, I. & Grogan, D. 1987. Nutrient dynamics of a swarm-founding social wasp species, *Polybia occidentalis* (Hymenoptera: Vespidae). *Ethology*, **75**, 291–305.
- Jeanne, R. L. 1996. Regulation of nest construction behaviour in *Polybia occidentalis*. *Animal Behaviour*, **52**, 473–488.
- Karsai, I. & Balazsi, G. 2002. Organization of work via a natural substance: regulation of nest construction in social wasps. *Journal of Theoretical Biology*, **218**, 549–565.
- Karsai, I. & Wenzel, J. W. 2000. Organization and regulation of nest construction behavior in *Metapolybia* wasps. *Journal of Insect Behavior*, **13**, 111–140.
- London, K. B. & Jeanne, R. L. 2003. Effects of colony size and stage of development on defense response by the swarm-founding wasp *Polybia occidentalis*. *Behavioral Ecology and Sociobiology*, **54**, 539–546.
- Narins, P. M., Lewis, E. R., Jarvis, J. J. U. M. & O'Riain, J. 1997. The use of seismic signals by fossorial southern African mammals: a neuro-ethological gold mine. *Brain Research Bulletin*, **44**, 641–646.
- O'Donnell, S. 1996. RAPD markers suggest genotypic effects on forager specialization in a eusocial wasp. *Behavioral Ecology and Sociobiology*, **38**, 83–88.

- O'Donnell, S. 2001a. Worker biting interactions and task performance in a swarm-founding eusocial wasp (*Polybia occidentalis*, Hymenoptera: Vespidae). *Behavioral Ecology*, **12**, 353–359.
- O'Donnell, S. 2001b. Worker age, ovary development, and temporal polyethism in the swarm-founding wasp *Polybia occidentalis* (Hymenoptera: Vespidae). *Journal of Insect Behavior*, **14**, 201–213.
- O'Donnell, S. 2003. The development of biting interactions and task performance in a tropical eusocial wasp. *Behaviour*, **140**, 255–267.
- O'Donnell, S. & Jeanne, R. L. 1990. Forager specialization and the control of nest repair in *Polybia occidentalis* Olivier (Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, **27**, 359–364.
- O'Donnell, S. & Jeanne, R. L. 1992. Life-long patterns of forager behaviour in a tropical swarm-founding wasp: effects of specialization and activity level on longevity. *Animal Behaviour*, **44**, 1021–1027.
- Page, R. E., Jr & Mitchell, S. D. 1998. Self-organization and the evolution of division of labor. *Apidologie*, **29**, 171–190.
- Pankiw, T. 2004. Brood pheromone regulates foraging activity of honey bees (Hymenoptera: Apidae). *Journal of Economic Entomology*, **97**, 748–751.
- Platt, T. G., Queller, D. C. & Strassmann, J. E. 2004. Aggression and worker control of caste fate in a multiple-queen wasp, *Parachartergus colobopterus*. *Animal Behaviour*, **67**, 1–10.
- Pratt, S. C. 2004. Collective control of the timing and type of comb construction by honey bees (*Apis mellifera*). *Apidologie*, **35**, 193–205.
- Pratt, S. C. 2005. Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behavioral Ecology*, **16**, 488–496.
- Schneider, S. S., Lewis, L. A. & Huang, Z. Y. 2004. The vibration signal and juvenile hormone titers in worker honeybees, *Apis mellifera*. *Ethology*, **110**, 977–985.
- Seeley, T. D., Camazine, S. & Sneyd, J. 1991. Collective decision making in honey bees: how colonies choose among nectar sources. *Behavioral Ecology and Sociobiology*, **28**, 277–290.
- Sherman, G. & Visscher, P. K. 2002. Honeybee colonies achieve fitness through dancing. *Nature*, **419**, 920–922.
- Sokal, R. F. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W.H. Freeman.
- Strassmann, J. E., Klingler, C. J., Arevalo, E., Zacchi, F., Husain, A., Williams, J., Seppa, P. & Queller, D. C. 1997. Absence of within-colony kin discrimination in behavioural interactions of swarm-founding wasps. *Proceedings of the Royal Society of London, Series B*, **264**, 1565–1570.