

## **Territorial Marking in the Desert Ant *Cataglyphis niger*: Does It Pay to Play Bourgeois?**

**T. Wenseleers,<sup>1,2,4</sup> J. Billen,<sup>2</sup> and A. Hefetz<sup>3</sup>**

*Accepted August 1, 2001; revised October 23, 2001*

---

*Here we report on territorial behavior in the desert ant *Cataglyphis niger*. We show that, similar to the “bourgeois strategy,” contests are settled quickly through nonescalating fights, with the owner of the territory usually being placed in the winning role. The chemical cue that advertises ownership is shown to come from pheromones secreted by the cloacal gland. Differences in size did not influence the outcome of the experimental contests, but resource value did. The observed results fit in well with the biology of *Cataglyphis*, where, due to the harsh semidesert environment, fighting costs ( $C$ ) are expected to be high relative to the value of the contested resources ( $V$ ). A situation where  $V < C$  is exactly that in which bourgeois behavior is expected to be seen.*

---

**KEY WORDS:** territoriality; hawk–dove game; bourgeois behavior; cloacal gland; *Cataglyphis niger*.

### **INTRODUCTION**

Despite the presence of a large array of potential reproductive conflicts in social insect colonies, when it comes to foraging, nepotistic alliances are unlikely to be formed. Hence, cooperative worker behavior and division of labor are two key features of the social insects that enable them to exploit

<sup>1</sup>Department of Animal & Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

<sup>2</sup>Zoological Institute, University of Leuven, B-3000 Leuven, Belgium.

<sup>3</sup>Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel.

<sup>4</sup>To whom correspondence should be addressed at Department of Animal & Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK. Fax: +44 114 222 0002. E-mail: T.Wenseleers@sheffield.ac.uk.

and dominate most of the ecosystems they occupy. Such a coordinated effort requires a sophisticated communication system that in ants is based primarily on chemical signals (Hölldobler and Wilson, 1990), produced by an array of exocrine glands (Billen and Morgan, 1998).

Most research in chemical communication in ants has been directed toward elucidating signals that are broadcast between nestmates, e.g., alarm and trail pheromones (Jackson and Morgan, 1994). With respect to internidal interactions, most empirical work has focused on nestmate recognition. In general, workers seem to have a good ability to distinguish nestmates from non nestmates and to adjust their level of aggression accordingly (reviewed by Vander Meer and Morel, 1998; Lenoir *et al.*, 1999). Both innate [genetic, pheromonal cues derived from queen and/or workers (e.g., Provost, 1991; reviewed by Waldman *et al.*, 1988)] and environmental cues (e.g., Stuart, 1987; Obin and Vander Meer, 1988) have been shown to be involved, and in a few cases colony-specific cuticular hydrocarbons have been shown to play an important role (e.g., Hefetz *et al.*, 1996, Lahav *et al.*, 1999).

It is clear, therefore, that ants from different colonies can recognize each other as alien and attack each other if this is in their best interest [reviewed by Wilson (1971), Carroll and Janzen (1973), and Hölldobler and Wilson (1990); costs and benefits of territoriality are discussed by Hölldobler and Lumsden (1980), Lumsden and Hölldobler (1983), and Johnson *et al.* (1987)]. More controversial is whether territoriality may also involve pheromones. For instance, it has been proposed that pheromonal “signposts” that warn conspecifics away may be deposited (cf. Kaufmann, 1983). In ants, suggestive evidence for such territorial pheromones has been gathered for leafcutter ants (Jaffe *et al.*, 1979; Hölldobler and Wilson, 1986; Vilela and Howse, 1987; Whitehouse and Jaffe, 1996) and for *Camponotus rufipes* (Jaffe and Sanchez, 1984), *Cataglyphis cursor* (Mayade *et al.*, 1993), *Myrmica rubra* (Cammaerts *et al.*, 1977; Cammaerts and Cammaerts, 1987), *Oecophylla longinoda* (Hölldobler and Wilson, 1977), *Rhytidoponera metallica* (Haskins and Haskins, 1983), and *Solenopsis geminata* (Jaffe and Puche, 1984). However, the concept of “territorial pheromones” is used in different contexts in these studies, e.g., in *Myrmica* it refers to differences in walking speed on territorially marked versus unmarked substrate (Cammaerts and Cammaerts, 1987), and in *Atta laevigata* it refers to a territorial owner fighting advantage (Whitehouse and Jaffe, 1996). Furthermore, in all of these studies, the adaptive value of territorial pheromones is left unexplained. In particular, it remains unclear why an intruder should respect a signal of ownership if it could likely gain more resources by disrespecting it.

The aim of this study is to investigate territorial behavior in the desert and *Cataglyphis niger*. Territorial behavior in the genus *Cataglyphis* has been documented by both direct [(Pickles, 1944; Mayade *et al.*, 1993); *C. niger*

(Hefetz, unpublished)] and indirect [overdispersion of nests in *C. albicans* (Schmid-Hempel, 1982)] means. Some authors regard this as paradoxical, given that *Cataglyphis* lacks recruitment and exploits highly ephemeral and unpredictable food sources, such as insect carcasses (Wehner *et al.*, 1983; Schmid-Hempel, 1984; Wehner, 1987; Müller and Wehner, 1988). With such biology, it would appear that territorial monopolization of food resources could never be beneficial (Hölldobler and Lumsden, 1980; Harkness and Isham 1983; Wehner *et al.*, 1983; Schmid-Hempel, 1984). Here we present a resolution to this puzzle, by showing that while *C. niger* ants do indeed defend their feeding ground, escalating fights generally do not occur because contests are settled according to an arbitrary bourgeois settlement (Maynard Smith, 1976, 1982) in which the owner generally wins. Ownership is shown to be signaled by pheromones secreted by the cloacal gland, an exocrine gland located near the hind gut (for the morphology of this gland see Wenseleers *et al.*, 1998). The adaptive benefits of such a strategy are discussed in the light of the specific biology of *Cataglyphis*.

## MATERIALS AND METHODS

### Collection and Culturing of Colonies

Two colonies of *C. niger* were collected near Tel Aviv, Israel, and were subsequently maintained in the laboratory in artificial nests consisting of interconnected humidity controlled plaster nest chambers. To mimic natural conditions as closely as possible, they were placed on a temperature gradient (22–30°C during the day, 18°C at night) and were connected to a floor-heated foraging arena (85 × 60 cm; 30°C during daytime, 18°C at night). The arena was exposed to a 500-W halogen light source under a 12:12 photoperiod regime and was supplied with a Whatman No. 2 filter-paper substrate.

### Experimental Contests

All experimental contests were carried out by placing two ants in a 6 × 6-cm plexiglass enclosure on either neutral or territorially marked substrate (marked for 2 weeks). The level of aggression was quantified using a cumulative index. Antennation, opening the mandibles, raising the abdomen, opening the mandibles + raising the abdomen, and spraying of formic acid were given increasing weight from 1 to 5. Subsequently, the most aggressive behavior exhibited by both parties was recorded every 10 s, weighted by this factor, and summed over a 5-min period to yield a cumulative “aggression index.” All dyadic contests were replicated 10 times for each colony. The

effect of pheromonal ownership was tested by using the same pair of ants two times, once on a substrate marked by the colony of the first ant and a second time on a substrate marked by the colony of the other ant (in randomized order). In this way we could accurately test whether a change in pheromonal ownership caused a corresponding flip in contest outcome. To avoid previous experience effects, we allowed both ants to recover for at least 2 days before using them a second time. Even if 2 days would not have been completely effective in clearing previous experience effects, however, it would not have affected our statistical conclusions, since the order in which any ant was observed on either own or opponent territory was effectively random. An owner advantage was tested for using a two-way repeated-measures ANOVA, with “colony” and “pheromonal ownership” as within-subjects factors. This statistical design was used to take into account properly the dependency that results from using the same ant pair twice. Effects of size and resource value asymmetries, on the other hand, were tested separately on neutral (unmarked) and marked terrain using an independent design and analyzed using a two-way ANOVA, with “colony” and “asymmetry” as between-groups factors.

### **Exocrine Gland Bioassays**

To investigate the source of the territorial pheromone, workers of each of the two colonies were killed by immersion in liquid nitrogen, and various glands (cloacal, Dufour’s, poison, and pretarsal glands and rectal sac) were dissected out in sterile insect Ringer solution (Table II). Using a Pasteur pipette, 1 ml of acetone extract at a concentration of one ant equivalent in 100  $\mu$ l acetone was then homogeneously applied to a 6  $\times$  6-cm Whatman No. 2 filter paper. On these substrates, we repeated the staged encounters as described above, but using a total of 14 replications instead of 20. “Pheromonal ownership” was tested in the same way as described above, using a two-way repeated-measures ANOVA.

## **RESULTS**

### **Effects of Ownership, Size, and Resource Value on the Outcome of Staged Encounters**

Although worker size may be assumed to be a good measure of strength or “resource holding potential” (RHP), our observations illustrate that it has no influence on the outcome of agonistic interactions, neither on marked nor on neutral territory (Table I). On the other hand, when strong feeding stress was induced in one of the opponents, escalated fights occurred in both neutral

**Table I.** Effects of Worker Size, Feeding Stress (All Correlated Asymmetries; Two-Way ANOVA), and “Pheromonal Ownership” (an Uncorrelated Asymmetry; Two-Way Repeated-Measures ANOVA) on the Level of Aggression and Outcome of Intercolonial Contests

Cumulative aggression index ( $\bar{X} \pm SD$ )				
Correlated asymmetries				
Resource holding potential				
Asymmetry				
Size	Larger <sup>a</sup>	Smaller	$F_{1,16}$	$P$
Marked terrain <sup>b</sup>	31.5 ± 7.7	31.7 ± 8.6	0.002	NS
Neutral terrain	21.9 ± 7.1	25.1 ± 7.3	0.93	NS
Resource value asymmetry				
Feeding stress <sup>c</sup>	High	Low		
Marked terrain <sup>b</sup>	35.6 ± 6.7	32.5 ± 6.4	6.78	<0.01
Neutral terrain	36.0 ± 5.3	20.3 ± 4.4	13.83	<0.05
Uncorrelated asymmetry				
Pheromonal ownership	Resident	Intruder	$F_{1,9}$	$P$
No size asymmetry <sup>d</sup>	36.5 ± 6.5	31.5 ± 5.1	7.47	<0.05
Randomized size asymmetry	35.0 ± 7.4	29.4 ± 4.3	12.97	<0.01

<sup>a</sup>Difference in interocular distance >20%.

<sup>b</sup>With randomized pheromonal ownership.

<sup>c</sup>High feeding stress, 3 weeks unfed; low feeding stress, fed every 2 days.

<sup>d</sup>Difference in interocular distance <20%.

and territorially marked arenas, and the intruder was sometimes observed to be seriously injured (Table I). In the absence of such strong resource value asymmetries, and irrespective of a size disadvantage, the chance for a worker to win a fight was much higher on its “own” vs an “alien” territory. On neutral terrain, the ants generally avoided any encounter (Table I).

### Exocrine Source of the Territorial Pheromone

When the same bioassay was carried out using a substrate that was artificially marked with glandular extracts, it turned out that only the cloacal gland elicited the pheromonal ownership effect described above (Table II). The poison gland induced agitation [which supports its alarm function in *Cataglyphis* (Hefetz and Orion, 1982)] but did not modulate aggression in favor of territorial owners.

## DISCUSSION

The characteristic individual foraging system of *Cataglyphis*, combined with its large worker size polymorphism, typically leads to simple dyadic

**Table II.** The Effect of Substrates Marked with Various Glandular Extracts on the Outcome of Dyadic Encounters Between Two Alien Ants (Two-Way Repeated-Measures ANOVA)

Substrate impregnated with acetone extract of	Cumulative aggression index ( $\bar{X} \pm SD$ )		$F_{1,6}$	$P$
	Owners	Intruders		
Cloacal gland	33.1 $\pm$ 6.2	27.8 $\pm$ 3.9	7.5	<0.05
Dufour's gland	24.4 $\pm$ 5.9	27.7 $\pm$ 6.9	3.32	NS
Poison gland	31.2 $\pm$ 6.3	29.7 $\pm$ 6.3	0.86	NS
Pretarsal gland	27.7 $\pm$ 6.0	28.1 $\pm$ 4.6	0.43	NS
Rectal sac	30.0 $\pm$ 7.4	27.4 $\pm$ 5.5	0.67	NS

encounters where the relative importance of both size and pheromonal ownership asymmetries can easily be evaluated. In animal contests, three kinds of asymmetries may be important (reviewed by Riechert, 1998): (1) asymmetries in fighting ability or "resource holding potential" (RHP) (e.g., due to size, strength, or site familiarity), (2) asymmetries in resource value (e.g., winning individual gains most), and (3) uncorrelated asymmetries (i.e., asymmetries uncorrelated with RHP or resource value that can control outcome, e.g., ownership). By organizing carefully selected dyadic encounters, we examined which types of asymmetries are important in settling territorial conflicts in the desert ant *Cataglyphis niger*.

Our experiments show that at low feeding stress, the bourgeois principle, "fight if owner, retreat if intruder" (Maynard Smith, 1976, 1982; for a classical study see Davies, 1978), was used as an arbitrary rule to settle conflict. The necessary cues for ownership were shown to come from pheromones secreted by the cloacal gland. Given that this gland is located near the distal opening of the hind gut (Wenseleers *et al.*, 1998), it seems likely that the cloacal gland ownership pheromones are deposited on the substrate using faeces as a carrier. If so, it would resemble the way in which mammals deposit territorial signposts, with urine acting as a carrier of accessory gland pheromones. In fact, our observations also resemble mammalian scent mark advertisement (e.g., Gosling, 1986) in that there, too, resource holders tend to have an "owner advantage" (Parker, 1974). In ants, comparable evidence for a pheromonally mediated territorial owner advantage has been collected in the leafcutter ant *Atta laevigata* (Whitehouse and Jaffe, 1996) and in *Oecophylla longinoda* (Hölldobler and Wilson, 1977).

Why does *Cataglyphis* adopt a bourgeois strategy and why is such a system not vulnerable to invasion by ants that do not respect ownership (Grafen, 1987)? Theory predicts bourgeois to be an evolutionary stable strategy when the costs of injury ( $C$ ) exceed the potential benefits of winning a fight ( $V$ ) [the payoffs in our case being calculated in terms of inclusive fitness (Maynard

Smith, 1976, 1982)]. In *Cataglyphis niger*, the harsh semidesert environment with unpredictable prey availability is expected to lead to such high costs and low potential benefits (Harkness and Isham, 1983; Wehner *et al.*, 1983; Schmid-Hempel, 1984).

Nevertheless, ownership was not the only asymmetry that settles conflicts in *Cataglyphis*. When the value of the contested resource (V) was artificially inflated by inducing feeding stress in one of the opponents, the level of aggression increased. This parallels observations in other species (Riechert, 1998). Size asymmetries, on the other hand, did not seem to have a major effect on contest outcome, apparently contradicting Nowbahari *et al.* (1999), who did find such an effect in *C. niger*. Perhaps this is due to our smaller sample size, where a small effect of size could have gone undetected. It needs to be stressed, however, that using the same experimental design, pheromonal ownership did have an influence on contest outcome, illustrating its relatively greater importance. Future work might try to transfer the rationale of our laboratory-based experiments to a field setting. Although this will not be easy (territorial ownership is nearly impossible to manipulate in the field), it would have the advantage of allowing better measures of winning and losing. For example, one could determine more easily which ant flees and which fights to victory. In a laboratory setting, we could merely measure which ant fought harder. Given the clear rationale for bourgeois behavior in *Cataglyphis*, field experiments might therefore be rewarding.

### ACKNOWLEDGMENTS

This research was funded by a collaboration program between the Ministry of Education of the Flemish Community and the Israeli Ministry of Science and Technology.

### REFERENCES

- Billen, J., and Morgan, E. D. (1998). Pheromone communication in social insects—Sources and secretions. In Vander Meer, R. K., Breed, M. D., Espelie, K. E., and Winston, M. L. (eds.), *Pheromone Communication in Social Insects: Ants, Wasps, Bees, and Termites*, Westview Press, Boulder, CO, pp. 3–33.
- Cammaerts, R., and Cammaerts, M. C. (1987). Nest topology, nestmate recognition, territorial marking and homing in the ant *Manica rubida* (Hymenoptera, Formicidae). *Biol. Behav.* **12**: 65–81.
- Cammaerts, M.-C., Morgan, E. D., and Tyler, R. (1977). Territorial marking in the ant *Myrmica rubra* L. (Formicidae). *Biol. Behav.* **2**: 263–272.
- Caroll, C. R., and Janzen, D. H. (1973). Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* **4**: 231–257.
- Davies, N. B. (1978). Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The resident always wins. *Anim. Behav.* **26**: 138–147.

- Gosling, L. M. (1986). Economic consequences of scent marking in mammalian territoriality. In Duvall, D., Muller-Schwarze, D., and Silverstein, R. M. (eds.), *Chemical Signals in Vertebrates 4*, Plenum Press, New York, pp. 385–395.
- Grafen, A. (1987). The logic of divisively asymmetric contests: Respect for ownership and the desperado effect. *Anim. Behav.* **35**: 462–467.
- Harkness, R. D., and Isham, V. (1983). A bivariate spatial point pattern of ants nests. *Appl. Stat. J. Roy. Stat. Soc. C* **32**: 293–303.
- Harkness, R. D., and Maroudas, N. G. (1985). Central place foraging by an ant (*Cataglyphis bicolor* Fab.): A model of searching. *Anim. Behav.* **33**: 916–928.
- Haskins, C. P., and Haskins, E. F. (1983). Situation and location-specific factors in the compatibility response in *Rhytidoponera metallica* (Hymenoptera: Formicidae: Ponerinae). *Psyche* **90**: 163–174.
- Hefetz, A., and Orion, T. (1982). Pheromones of ants of Israel: I. The alarm-defence system of some larger Formicinae. *Isr. J. Entomol.* **16**: 87–97.
- Hefetz, A., Errard, C., Chambris, A., and Le Négrate, A. (1996). Postpharyngeal gland secretion as a modifier of aggressive behavior in the myrmicine ant *Manica rubida*. *J. Insect Behav.* **9**: 709–717.
- Hölldobler, B., and Lumsden, C. J. (1980). Territorial strategies in ants. *Science* **210**: 732–739.
- Hölldobler, B., and Wilson, E. O. (1977). Colony-specific territorial pheromone in the African weaver ant *Oecophylla longinoda* (Latreille). *Proc. Natl. Acad. Sci. USA* **74**: 2072–2075.
- Hölldobler, B., and Wilson, E. O. (1986). Nest area exploration and recognition in leafcutter ants (*Atta cephalotes*). *J. Insect Physiol.* **32**: 143–150.
- Hölldobler, B., and Wilson, E. O. (1990). *The Ants*, Harvard University Press, Cambridge, MA.
- Jackson, B. D., and Morgan, E. D. (1994). Insect chemical communication: Pheromones and exocrine glands of ants. *Chemoecology* **4**: 125–144.
- Jaffe, K., and Puche, H. (1984). Colony-specific territorial marking with the metapleural gland secretion in the ant *Solenopsis geminata* (Fabr.). *J. Insect Physiol.* **30**: 265–270.
- Jaffe, K., and Sanchez, C. (1984). On the nestmate-recognition system and territorial marking behavior in the ant *Camponotus rufipes*. *Insectes Soc.* **31**: 302–315.
- Jaffe, K., Bazire-Benazet, M., and Howse, P. E. (1979). An integumentary pheromone-secreting gland in *Atta* sp.: Territorial marking with a colony-specific pheromone in *Atta cephalotes*. *J. Insect Physiol.* **25**: 833–839.
- Johnson, L. K., Hubbell, S. P., and Feener, D. H., Jr. (1987). Defense of food supply by eusocial colonies. *Am. Zool.* **27**: 347–358.
- Kaufmann, J. H. (1983). On the definitions and functions of dominance and territoriality. *Biol. Rev.* **58**: 1–20.
- Lahav, S., Soroker, V., Hefetz, A., and Vander Meer, R. K. (1999). Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften* **86**: 246–249.
- Lenoir, A., Fresneau, D., Errard, C., and Hefetz, A. (1999). Individuality and colonial identity in ants: The emergence of the social representation concept. In Detrain, C., Deneubourg, J.-L., and Pasteels, J.-M. (eds.), *Information Processing in Social Insects*, Birkhäuser Verlag, Berlin, pp. 219–237.
- Lumsden, C. J., and Hölldobler, B. (1983). Ritualized combat and intercolony communication in ants. *J. Theor. Biol.* **100**: 81–98.
- Mayade, S., Cammaerts, M.-C., and Suzzoni, J. P. (1993). Home-range marking and territorial marking in *Cataglyphis cursor* (Hymenoptera, Formicidae). *Behav. Proc.* **30**: 131–142.
- Maynard Smith, J. (1976). Evolution and the theory of games. *Am. Sci.* **64**: 41–45.
- Maynard Smith, J. (1982). *Evolution and the Theory of Games*, Cambridge University Press, New York.
- Müller, M., and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**: 5287–5290.
- Nowbahari, E., Feneron, R., and Malherbe, M. C. (1999). Effect of body size on aggression in the ant, *Cataglyphis niger* (Hymenoptera; Formicidae). *Aggr. Behav.* **25**: 369–379.
- Obin, M. S., and Vander Meer, R. K. (1988). Sources of nestmate recognition cues in the imported fire ant *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Anim. Behav.* **36**: 1361–1370.

- Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47**: 223–243.
- Pickles, W. (1944). The territory and activities of the Algerian ant *Cataglyphis bicolor* F. s.-sp. *megalocola* Först. *Entomol. Month. Mag.* **80**: 61–63.
- Provost, E. (1991). Non-nestmate kin recognition in the ant *Leptothorax lichtensteini*, evidence that genetic factors regulate colony recognition. *Behav. Genet.* **21**: 151–167.
- Riechert, S. E. (1998). Game theory and animal contests. In Dugatkin, L. A., and Reeve, H. K. (eds.), *Game Theory and Animal Behavior*, Oxford University Press, Oxford, pp. 64–93.
- Schmid-Hempel, P. (1982). *Foraging Ecology and Colony Structure of Two Sympatric Species of Desert Ants—Cataglyphis bicolor and Cataglyphis albicans*, Ph.D. thesis, University of Zürich, Zürich.
- Schmid-Hempel, P. (1984). Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behav. Ecol. Sociobiol.* **14**: 263–271.
- Schmid-Hempel, P., and Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Soc.* **31**: 345–360.
- Stuart, R. J. (1987). Transient nestmate recognition cues contribute to a multicolonial population structure in the ant, *Leptothorax curvispinosus*. *Behav. Ecol. Sociobiol.* **21**: 229–235.
- Vander Meer, R. K., and Morel, L. (1998). Nestmate recognition in ants. In Vander Meer, R., Breed, M., Winston, M., and Espelie, K. (eds.), *Pheromone Communication in Social Insects*, Westview Press, Boulder, CO, pp. 79–103.
- Vilela, E. F., and Howse, P. E. (1987). Territorial marking with chemicals in *Atta sexdens rubropilosa*. In Eder, J., and Rembold, H. (eds.), *Chemistry and Biology of Social Insects*, Peperny Verlag, München, p. 451.
- Waldman, B., Frumhoff, P. C., and Sherman, P. W. (1988). Problems of kin recognition. *Trends Ecol. Evol.* **3**: 8–13.
- Wehner, R. (1987). Spatial organisation of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). In Pasteels, J. M., and Deneubourg, J. L. (eds.), *From Individual to Collective Behavior in Social Insects: les Treilles Workshop*, Birkhauser, Basel, pp. 15–42.
- Wehner, R., Harkness, R. D., and Schmid-Hempel, P. (1983). Foraging strategies in interindividually searching ants *Cataglyphis bicolor* (Hymenoptera: Formicidae). In *Information Processing in Animals, Vol. 1*, Gustav Fischer Verlag, Stuttgart, pp. 1–79.
- Wenseleers, T., Schoeters, E., Billen, J., and Wehner, R. (1998). Distribution and comparative morphology of the cloacal gland in ants (Hymenoptera: Formicidae). *Int. J. Insect Morphol. Embryol.* **27**: 121–128.
- Whitehouse, M. E. A., and Jaffe, K. (1996). Ant wars: Combat strategies, territory and nest defence in the leaf-cutting ant *Atta laevigata*. *Anim. Behav.* **51**: 1207–1217.
- Wilson, E. O. (1971). *The Insect Societies*, Belknap Press, Cambridge, MA.