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Behavioral interactions of the invasive Argentine ant with native ant species

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Summary. The Argentine ant, *Linepithema humile*, has invaded many areas of the world, displacing native ants. Its behavior may contribute to its competitive success. Staged and natural encounters were observed at food resources in the field, between Argentine ants and eight ant species native to northern California. There was no relation between the frequency of aggression by any ant species and the outcome of encounters, though Argentine ants were more likely than ants of native species to behave aggressively. When an ant of one species initiated an encounter of any kind with an ant of another species, the ant that did not initiate was likely to retreat. This was true of all species studied. Most encounters between ants were initiated by Argentine ants. Thus the native species tended to retreat more frequently than Argentine ants. Interactions between Argentine ants and native species at food resources, causing ants of native species to retreat, may help Argentine ants to displace native species from invaded areas.

Key words: Linepithema humile, aggression, behavior, resource competition, interference, invasion, Argentine ant.

There is considerable evidence that interspecific competition contributes to patterns of distribution and abundance in ant communities (Brian, 1966; Lynch et al., 1980; Davidson, 1985; Rosengren, 1986; Savolainen and Vepsäläinen, 1988; Vepsäläinen and Savolainen, 1990; Andersen, 1992; Andersen and Patel, 1994). Interference competition, in the form of aggressive behavior among worker ants, is often important in the displacement of one ant species by another (Savolainen and Vepsäläinen, 1988; Andersen and Patel, 1994). *Linepithema humile*, the invasive Argentine ant, is native to South America and has spread around the world. Argentine ants form diffuse colonies of loosely connected nest associations which reproduce by budding (Keller, 1991). Where it invades, the Argentine ant generally displaces native ant species and often other native arthropod species as well (Erickson, 1971; Slingsby and Bond, 1984; Medeiros et al., 1986; Holway, 1995; Human and Gordon, 1997). Behavioral interactions may contribute to the success of the Argentine ant as an invader (Way et al., 1997).

The few native ant species that persist in areas invaded by the Argentine ant may be those that forage in different habitats from the Argentine ants and are less likely to encounter them (Ward, 1987). Previous work (Human and Gordon, 1996) shows that ants of native species that share foraging habitats with Argentine ants avoid invaded areas and have lower foraging success there. Previous work also suggests that behavioral interactions of native and Argentine ants, which vary among species, are as important as the relative numbers present. Which species persisted at a bait did not depend on the number of native ants present before Argentine ants were introduced (Human and Gordon, 1996). Here we examine the effect of behavior on the outcome of encounters between Argentine ants and native species at food resources.

Methods

We conducted experiments and made observations between May 1993 and May 1995 at Jasper Ridge Biological Preserve, a 450-hectare reserve in San Mateo County, northern California. The Argentine ant has invaded approximately 30% of the Preserve. Over the last three years, it has moved into new areas at a rate of up to 300 m/year. Native ant species have disappeared from newly invaded areas.

Behavioral observations were made during encounters between groups of ants at food resources. Detailed methods for baiting experiments are described elsewhere (Human and Gordon, 1996). Two types of food baiting experiments were used. In the first, here called "baiting sessions", we did not manipulate the presence of *L. humile* or native species. Baits, consisting of some combination of cookie crumbs, tuna, and honey, were set in areas along the edges of the *L. humile* invasion and the recruitment of all species of ants was recorded. Baits were placed in a grid pattern at 10 m intervals in 75 sites which covered the edges of the *L. humile* range. Baits were set out between 5:00–6:00 or 18:00–19:00, to attract both diurnal and nocturnal species. Every 20 min for

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3 h, the behavior of ants was observed for 30 s. We recorded the number of ants of each species and all behavioral interactions among them.

In a second set of experiments, we introduced a *L. humile* colony to a bait near the nest of a colony of a native ant species, at a site at least 40 m and up to 300 m from any of the baits described in the previous paragraph. Laboratory colonies of *L. humile*, each containing 1–6 queens, 500–1500 workers, and brood of all stages, were taken to areas of the Jasper Ridge Preserve not infested with *L. humile*. The laboratory colonies were housed in boxes fitted with exit tubes through which *L. humile* workers, but not queens, could pass.

In 1993, workers of native species, *Camponotus semitestaceus*, *Pheidole californica* or *Messor andrei*, were allowed to recruit to baits, placed approximately 50 cm, 5 cm, and 50 cm, respectively, from their nest entrances. Then *L. humile* workers were introduced to the baits. In 1993, experiments with three colonies of each of the above species were replicated three times with at least 48 h between replicates using a given colony. There were no control baits in 1993.

In 1994 and 1995, *L. humile* workers were introduced to one experimental bait, and there was a second, control bait 10 to 20 cm away to which no *L. humile* workers were introduced. We then recorded recruitment to both baits by *L. humile* and native species. These experiments used some of the same native ant colonies used in 1993. Each experiment consisted of two replicates for each colony, with three colonies of *P. californica* and *M. andrei*, and two colonies of *C. semitestaceus* in the summer of 1994, and three replicates each for three colonies of *Prenolepis imparis* in early spring of 1995. Experiments for each native species were conducted during the season and at the time that species appeared to be most active, night for *C. semitestaceus*, morning or late afternoon for *M. andrei*, morning for *P. imparis* and dawn or dusk for *Pheidole californica*.

We observed baits for 30 s intervals every 5 min in 1993, and every 2 min in 1994 and 1995, recording the number of ants of each species and all behavioral interactions between ants of different species. An experiment ended when one species left the bait and the other foraged alone for over 15 min, in which case the remaining species was considered to persist, or after 1.5 hrs if ants of both species continued to forage at the bait. The outcomes of introduction experiments were classified as 1) native ant species persisted, 2) Argentine ants persisted, or 3) both persisted.

For all interactions observed during both baiting sessions and introduction experiments, behavior was recorded as shown in Table 1, classified as aggressive, retreat, or neutral.

Data analyses

For the baiting sessions, we used a G-test to compare the proportion of native species' behavior and the proportion of *L. humile* behavior that was aggressive. Because there were few interactions during baiting sessions, there were not sufficient data to compare each native species with *L. humile*, and so we pooled the data for all native species.

To compare the behavior of *L. humile* and native species in the introduction experiments, we calculated for each species in each experiment the proportion of acts, out of all behavioral acts recorded, that were aggressive (as defined in Table 1). Ten of the 52 introduction experiments were omitted because, although both *L. humile* and ants of native species were present, there were fewer than three interactions of any type, and thus the calculation of a proportion might not be representative. We used Fisher's exact tests to compare, for each native ant species, the number of experiments in which *L. humile* performed more aggressive acts than the native species did, to the number of experiments in which the native species performed more aggressive acts than *L. humile* did.

We then tested whether aggression affected the outcome of introduction experiments. We used Mann-Whitney U-tests to compare, for each native ant species-*L. humile* pair, the proportion of acts, out of all behavior recorded, that was aggressive in experiments of the two outcomes, either *L. humile* or a native ant species persisted.

To determine if native species or Argentine ants initiated most interactions, we compared the proportions of all interactions that were initiated by each species, using Chi-squared tests. This analysis included interactions during both baiting sessions and introduction experiments. For ants of four native species, interactions with Argentine ants were rare and were observed only during baiting sessions. The data for these four species were pooled for analysis (Table 2).

We compared the behavior used to initiate interactions, and the response to such behavior, in *L. humile* and native species. The first behavioral act recorded in an interaction between an ant of *L. humile* and an ant of a native species was classified as aggressive or neutral (Table 1). The behavioral response to that initiating act was classified as retreat, fight, or neutral, (Table 1). Neutral response behaviors were rarely observed. For each *L. humile*-native species pair, we used a G-test to compare the numbers of interactions initiated by each species that were

Table 1. Categories of ant behavior during encounters

Aggressive	
Lunge/chase:	moving quickly with open mandibles toward an ant of another species
Bite:	biting any part of another ant's body
Gaster tilt:	tilting the gaster upwards while facing another ant, or directing the gaster towards another ant
Block tube:	standing in the exit tube of the *L. humile* colony with open mandibles, preventing the exit of *L. humile* ants.
Retreat	
Run:	changing direction and moving quickly away after encountering an ant of another species
Spasm:	curling up and cleaning antennae or legs after encountering an ant, or moving legs or body spasmodically after encountering an ant
Neutral	
Antennate:	antennating an ant of another species, not followed by aggressive or retreat behavior

Table 2. Tendency of native ant species and Argentine ants to initiate encounters

Ant species	N encounters	Species initiating behavior		P
		Argentine ants	Native spp.	
Introduction experiments				
C.s.	102	86	16	**
M.a.	67	54	13	**
P.c.	82	67	15	**
P.i.	68	53	15	**
Baiting experiments				
Four species	12	9	3	*
Total encounters	332	269	62	

** $P < 0.01$, * $P < 0.05$, chi-squared tests adjusted for multiple tests with the sequential Bonferroni correction. Species abbreviations are as in Table 3. Data for the first four species listed, Cs, Ma, Pc, and Pi, include interactions from both introduction experiments and baiting sessions. The value for baiting experiments is the sum of the results for four species: Cc, Fm, Sm, and Ts.

aggressive or neutral, and to determine whether an aggressive initiation affected the probability of retreat by the other species. Data from both baiting sessions and introduction experiments were included.

Results

In 30 of 750 baiting sessions in 1993 and 1994, ants of both *L. humile* and native species recruited simultaneously to baits and encountered each other. In all introduction experiments performed in 1993, 1994 and 1995, interactions were observed between *L. humile* and native species. The maximum numbers of ants involved in interactions in an introduction experiment ranged from 3–24 *L. humile* with 3–21 *C. semitestaceus*, 7–40 *L. humile* with 2–52 *M. andrei*, 8–35 *L. humile* with 1–19 *P. californica*, and 4–45 *L. humile* and 2–24 *P. imparis*. Comparing maximum numbers, *L. humile* outnumbered *C. semitestaceus* in 4 out of 13 experiments, *M. andrei* in 3 out of 15, *P. californica* in 14 out of 15, and *P. imparis* in 8 out of 9.

Frequency of aggression

Species differed in the frequency of aggressive behavior (Table 3). For example, 67% and 56%, respectively, of the behavior of *L. humile* and *P. imparis* during introduction experiments was aggressive. By contrast, *Formica moki, Solenopsis molesta,* and *Tapinoma sessile* were never observed to be aggressive. Only *L. humile* and *P. imparis* tilted their gasters, possibly emitting defensive chemicals, in observations made during baiting sessions and introduction experiments. In other observations, *C. coarctata* and *T. sessile* occasionally tilted their gasters when interacting with ants of other species. On the rare occasions that Argentine ants tilted their gasters at other ants, the other ants sometimes responded with vigorous grooming or spasms, but sometimes did not respond at all.

During baiting sessions, ants of *L. humile* behaved aggressively more frequently than ants of native species (*L. humile* behaved aggressively in 21 of 42 encounters; native ants behaved aggressively in only 5; $P < 0.001$, G-test with William's correction).

During introduction experiments as well, ants of *L. humile* were more likely to behave aggressively than were ants of native species (Fig. 1). In both years, *L. humile* was significantly more likely to behave aggressively than were *C. semitestaceus, M. andrei, Pheidole californica,* and *Prenolepis imparis* ($P = 0.005$, $P = 0.03$, $P = 0.0001$, $P = 0.01$, respectively, Fisher's exact tests, sequential Bonferroni correction for multiple tests).

Persistence at baits

During introduction experiments, persistence at baits by Argentine ants was somewhat, though not significantly, associated with aggressive behavior. When *L. humile* persisted, 77% ± 3% (mean ± standard error) of its behavior was aggressive; when it was displaced, 61% ± 10% was aggressive ($P = 0.086$, Mann-Whitney U-test). There was also no significant association between aggressive behavior and persistence at baits for native ant species (native ants persisted 0.37 ± 0.10, displaced 0.29 ± 0.05, $P = 0.424$, Mann-Whitney U-test).

When we compared native ant species individually with *L. humile*, we found no relation between the outcome of an interaction and the amount of aggressive behavior. When *C. semitestaceus* or *M. andrei* persisted against *L. humile*, the native species were no more aggressive than when they were

Table 3. Behavior of ants of native species and *L. humile* during baiting sessions and introduction experiments. Behavior categories are described in Table 1. "Kill ant" indicates that one ant killed an ant of another species by biting it, and "die" indicates that the bitten ant died. Listed are the proportions of all behavior observed during introduction or baiting experiments in which ants behaved as noted. The last row, N, indicates the total number of encounters between ants of *L. humile* and the indicated native species. Species abbreviations: Cc = *Crematogaster coarcata,* Cs = *Camponotus* spp., Fm = *Formica moki,* Lh = *Linepithema humile*, Ma = *Messor andrei*, Pc = *Pheidole californica*, Pi = *Prenolepis imparis*, Sm = *Solenopsis molesta*, and Ts = *Tapinoma sessile*

	Behavior during baiting sessions								during introduction experiments				
	Lh	Cc	Cs	Fm	Ma	Pc	Sm	Ts	**Lh**	Cs	Ma	Pc	Pi
Lunge/chase	0.31	0.14	0.04	0	0	0	0	0	0.22	0.09	0.07	0.05	0.06
Bite	0.17	0	0.08	0	0	0	0	0	0.40	0.06	0.12	0.14	0.27
Gaster tilt	0.06	0	0	0	0	0	0	0	0.05	0	0	0	0.22
Kill ant	0.03	0	0.04	0	0	0	0	0	0	0.22	0.07	0.01	0.01
Block tube	0	0	0	0	0	0	0	0	0	0.02	0.05	0	0
Any aggressive behavior	0.56	0.14	0.17	0	0	0	0	0	0.67	0.40	0.30	0.20	0.56
Antennate	0.31	0	0	0	0	0.50	1.00	0	0.11	0.01	0.13	0.05	0.01
Run	0.11	0.86	0.50	1.00	0.67	0	0	1.00	0.09	0.42	0.42	0.64	0.35
Spasm	0	0	0.29	0	0.33	0.25	0	0	0.05	0.17	0.15	0.10	0.08
Die	0.03	0	0.04	0	0	0.25	0	0	0.08	0	0	0.01	0
N	36	7	24	3	3	4	2	2	293	81	60	81	78

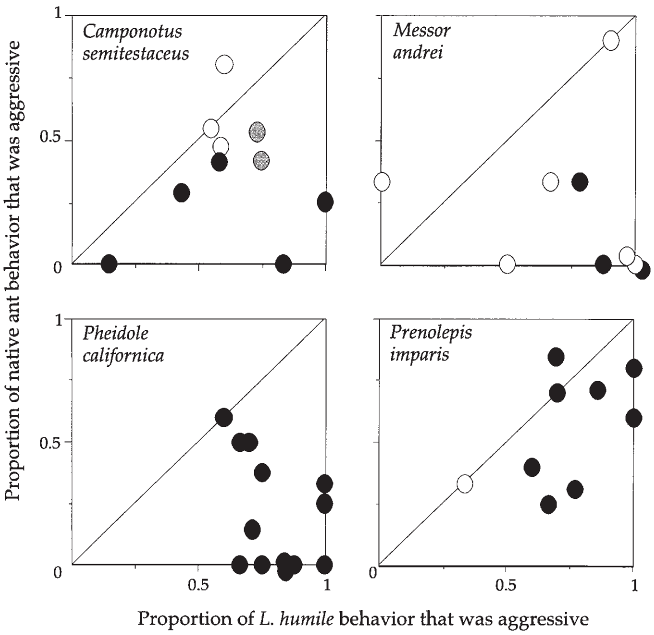

Figure 1. Results of introduction experiments. Each circle represents a single experiment and shows the proportion of *L. humile* and native ant behavior that was aggressive. On the diagonal line, the frequency of aggression by *L. humile* is equal to that of the native ant species. Circles located below the dotted line represent experiments in which ants of *L. humile* behaved aggressively more often than ants of native species. The shading of each circle indicates the outcome of the introduction experiment: black circles represent experiments in which only *L. humile* persisted at baits, shaded circles indicate that both species persisted, and open circles indicate that only native ants persisted

displaced (proportion of *C. semitestaceus* behavior when it persisted 0.6 ± 0.03, when displaced 0.19 ± 0.03; for *M. andrei* when it persisted 0.26 ± 0.13, when displaced 0.11 ± 0.04). The same was true for *L. humile* against either of the two native species (against *C. semitestaceus*, aggressive behavior by *L. humile* when it persisted 0.6 ± 0.11, when displaced 0.58 ± 0.001; against *M. andrei*, *L. humile* behavior when it persisted 0.88 ± 0.01, displaced 0.68 ± 0.15). For all comparisons, Mann-Whitney U-tests P's > 0.1.

Effect of behavior used to initiate interactions

Argentine ants initiated the majority of interactions (272 of 363, 75%) between ants during both introduction experiments and baiting sessions (Table 2). Argentine ants constantly patrolled the areas around baits, frequently approaching nearby ants. Ants of all native species rarely approached Argentine ants even when close to them.

When *L. humile* interacted with *P. imparis*, ants of both species were equally likely to initiate interactions with aggressive rather than neutral behavior (proportion of initial behaviors that were aggressive: 89% *P. imparis*, 88% *L. humile*, P > 0.05). When *L. humile* interacted with *C. semitestaceus, M. andrei* and *Pheidole californica, L. humile* was more likely than the native species to initiate interactions aggressively (proportion of initial behavior that was aggressive: 79% for *C. semitestaceus*, 96% for *L. humile*, P = 0.05; 47% *M. andrei*, 90% *L. humile*, P = 0.02; 50% *P. californica*, 90% *L. humile*, P = 0.004; G-tests with William's correction, sequential Bonferroni correction, numbers of encounters shown in Table 2).

Behavioral responses depended upon the behavior of the ants that initiated the interaction. Ants responded aggressively only when the ant that initiated an encounter did so aggressively. But ants usually retreated, even when the initiator was aggressive (Fig. 2). Ants of all species were more likely to retreat when approached neutrally than when approached aggressively (P < 0.01 for native species responses to 269 encounters intiated by *L. humile*, P < 0.03 for *L. humile* responses to 62 encounters initiated by native species, G-test with William's correction). Overall, the most likely response by an ant of any species, to any other ant that initiated an interaction, either aggressively or neutrally, was to retreat. Ants of *L. humile* were as likely to retreat from all native ants as all native ants were to retreat from *L. humile* (Fig. 2, all P's > 0.2, G-test, sequential Bonferroni correction for multiple tests; numbers of encounters shown in Table 2). Ants of *L. humile* were slightly, but not significantly, more likely to retreat from ants of certain species, such as *C. semitestaceus*, than others, such as *Prenolepis imparis* (Fig. 2).

Discussion

We found no relation between the frequency of aggressive behavior and the outcome of interactions between species at food sources. No single behavior, such as the use of defensive chemicals, guarantees the Argentine ant success during conflicts over food or space. In fact, ants of *L. humile* and native species respond similarly to approaches by other ants: when one ant initiates an encounter, the ant that was approached tends to run away. Thus, an approach by an ant of a native species causes an Argentine ant to retreat. However, Argentine

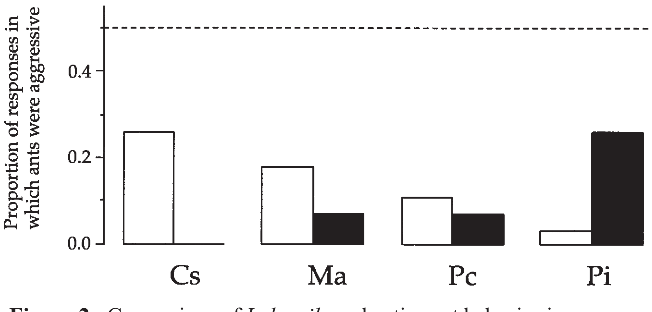

Figure 2. Comparison of *L. humile* and native ant behavior in response to encounters initiated by other ants. Each pair of bars represents the interactions of *L. humile* and the indicated species. Black bars show *L. humile*'s response to encounters initiated by ants of the native species; white bars show response of the native species to encounters initiated by ants of *L. humile*. The height of each bar shows the proportion of responses in which ants behaved aggressively; in the remaining encounters, ants retreated. Ants of all species were more likely to retreat than to fight back

ants initiate far more interactions than do ants of native species (Table 2), so conflict between individuals usually results in the retreat of ants of native species.

Although Argentine ants are aggressive more frequently than are native ant species, this does not necessarily cause native ants to retreat. Ants of all species were somewhat more likely to retreat in response to neutral behavior than to aggressive behavior. During introduction experiments, aggressive behavior made *L. humile* slightly, though not significantly, more likely to displace native species. Aggressive behavior by native ants toward *L. humile* had no significant effect on which species persisted at baits.

It is clear that Argentine ants are numerically dominant in the area studied. In a survey of this area using pitfall traps, *L. humile* outnumbered the most numerous native ant, *P. imparis*, by a factor of 14 (Human and Gordon, 1997). In many ant species, aggression is related to colony size (e.g., Gordon, 1992). *L. humile* nests are joined in a loose, supercolonial structure, without inter-colony aggression (e.g., Keller and Passera, 1989). This makes it difficult to specify the boundaries of a colony, or to measure the size of a colony. Moreover, there may be little evolutionary pressure for Argentine ants to calibrate aggressive behavior to colony size, since ants apparently move rather freely from one nest association to another.

The results of this study show how the numerical dominance of *L. humile* may contribute behaviorally to its success as an invader. Because numbers of *L. humile* ants are high, and because *L. humile* recruits to food sources more quickly and explores space more effectively (Holway, 1999; Gordon, 1995; Human and Gordon, 1996), it may often encounter and displace ants of native species at food sources. Colonies of native species may interact with Argentine ants more frequently than they do with neighbors of native species. Encounters between ants of different native species are rare: during more than 750 baiting sessions, ants of different native species met only 17 times. During most summer days, whenever colonies of native ant species are active, so are colonies of *L. humile* (Human et al., 1998). Native species may suffer decreased foraging success in invaded areas because they retreat from encounters initiated by Argentine ants at food sources. Such decreased foraging success may lead to displacement by Argentine ants if it increases native species mortality or if it induces native species to emigrate from areas in which they encounter Argentine ants.

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References

Andersen, A.N., 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *Am. Nat. 140*: 401–420.

Andersen, A.N. and A.D. Patel, 1994. Meat ants as dominant members of Australian ant communities: An experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia 98*: 15–24.

Brian, M.V., J. Hibble and A.F. Kelly, 1966. The dispersion of ant species in a southern English heathland. *J. Anim. Ecol. 35*: 281–290.

Davidson, D.W., 1985. An experimental study of diffuse competition in harvester ants. *Am. Nat. 125*: 500–506.

Erickson, J.M., 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche 78*: 257–266.

Gordon, D.M., 1992. How colony growth affects forager intrusion in neighboring harvester ant colonies. *Behav. Ecol. Sociobiol. 31*: 417–427.

Gordon, D.M., 1995. The expandable network of ant exploration. *Anim. Behav. 50*: 995–1007.

Gordon, D.M. and A.W. Kulig, 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecol. 77*: 2393–2409.

Holway, D.A., 1995. Distribution of the Argentine ant (*Linepithema humile*) in northern California. *Cons. Biol. 9*: 1634–1637.

Holway, D.A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecol.* (in press).

Human, K.G.and D.M. Gordon, 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia 105*: 405–412.

Human, K.G. and D.M. Gordon, 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. *Cons. Biol. 11*: 1242–1248.

Human, K.G., S. Weiss, A. Weiss, B. Sandler and D.M. Gordon, 1998. The effect of abiotic factors on the local distribution of the invasive Argentine ant (*Linepithema humile*) and native ant species. *Environ. Entomol. 127*: 822–833.

Keller, L., 1991. Queen number, mode of colony founding, and queen reproductive success in ants (Hymenoptera Formicidae). *Ethol. Ecol. Evol. 3*: 307–316.

Keller, L. and L. Passera, 1989. Influence of the number of queens onnestmate recognition and attractiveness of queens to workers in the Argentine ant *Iridomyrmex humilis* (Mayr). *Anim. Behav. 37*: 733–740.

Lynch, J.F., E.C. Balinsky and S.G. Vail, 1980. Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*, *Paratrechina melanderi*, and *Aphaenogaster rudis* (Hymenoptera: Formicidae). *Ecol. Entomol. 5*: 353–371.

Rosengren, R., 1986. Competition and coexistence in an insular ant community – a manipulation experiment (Hymenoptera: Formicidae). *Annl Zool. Fenn. 23*: 287–302.

Savolainen, R. and K. Vepsäläinen, 1988. A competition hierarchy among boreal ants: Impact on resource partitioning and community structure. *Oikos 51*: 135–155.

Slingsby, and W.J. Bond, 1985. The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L.) Buek (Proteaceae). *S Afric. J. Bot. 51*: 30–34.

Vepsäläinen, K. and R. Savolainen, 1990. The effect of interference by formicine ants on the foraging of *Myrmica. J. Anim. Ecol. 59*: 643–654.

Ward, P.S., 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia 55*: 1–16.

Way, M.J., M.E. Cammell, M.R. Paiva and C.A. Collingwood, 1997. Distribution and dynamics of the Argentine ant *Linepithema (Iridomyrmex) humile* (Mayr) in relation to vegetation, soil conditions, topography and native competitior ants in Portugal. *Insectes soc. 44*: 415–433.