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Apparent Dear-enemy Phenomenon and Environment-based Recognition Cues in the Ant *Leptothorax nylanderi*

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Abstract

Inter- and intraspecific competition was investigated in ants of the myrmicine genus *Leptothorax* in a deciduous woodland near Würzburg, Germany. The most common species, *L. (Myrafant) nylanderi*, lives in rotting pine, oak, and elder sticks and may locally reach densities of 10 nests per m^2. In the studied sites, only a small fraction of colonies were polydomous, i.e. single colonies typically did not inhabit several nest sites. The home ranges of *L. nylanderi* colonies overlap the ranges of other conspecific colonies and colonies of other species, especially *L.* (s.str.) *gredleri*. Foragers from different colonies encountering one another in the field back off without exhibiting strong aggression, suggesting that colonies do not defend absolute foraging territories. In laboratory experiments, the frequency and severity of agonistic interactions among workers from different colonies, all living in pine sticks, increased significantly with the distance between their nests. Workers from colonies nesting in different types of wood exhibited significantly more aggression. Experiments in which we transferred colonies from pine sticks into artificial pine or oak nests corroborate the hypothesis that nesting material strongly influences colony odour in *L. nylanderi*. The evolutionary significance of this apparent dear-enemy phenomenon is discussed.

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Introduction

Ants play an important role, both as predator and as prey, in most terrestrial ecosystems, and much attention has been paid to the structure of ant communities (HÖLLDOBLER & WILSON 1990). Inter- and intraspecific competition has been investigated, particularly concerning the more conspicuous, dominant genera, such as wood ants, honeypot ants, weaver ants or harvester ants, territorial contests of which often involve thousands of individuals defending their nests and foraging areas (MCCOOK 1880; MABELIS 1979; HÖLLDOBLER 1976 a,b; HÖLLDOBLER & WILSON 1977; HÖLLDOBLER & LUMSDEN 1980). Comparatively little is known about the numerous

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species of inconspicuous, smaller ants which are less readily observed in the field but nevertheless may be of great ecological importance. *Leptothorax* colonies consist of only a few dozen individuals and nest in small cavities, such as cracks in rocks, under bark, in rotten twigs, or in acorns. Despite their small individual and colony size, *Leptothorax* are among the most abundant ants in boreal and temperate habitats due to high densities of five nests and more per m^2.

Leptothorax typically forage solitarily for food and thus probably do not compete with bigger, trail-recruiting ants for large prey items. In encounters with larger ants, such as *Formica* or *Myrmica*, foraging *Leptothorax* crouch submissively or feign death (DOBRZANSKI 1966; SEIFERT 1986; SAVOLAINEN & VEPSÄLÄINEN 1989). Indirect evidence indicates, however, that *Leptothorax* and other ants might compete for nest sites. Colonies of *L. congruus* apparently are forced to emigrate from their nests by *Monomorium* spp. (YAMAGUCHI 1992). In several Nearctic *Leptothorax*, colonies seasonally spread out over several individual nest sites in summer, but aggregate for hibernation (ALLOWAY et al. 1982; HERBERS 1986). Experimental seeding of an area with artificial nest sites increased the rate of colony fragmentation (HERBERS 1986), suggesting that the number of natural nest sites restricted colony moving. Studies on actual competition within and between *Leptothorax* species, however, gave contradictory results. DOBRZANSKI (1966) observed workers of European *L.* (s.str.) *acervorum* gently carrying conspecific intruders, which were experimentally placed near their nest, away from the nest without injuring them. In contrast, ALLOWAY (1980) and STUART & ALLOWAY (1982, 1983) concluded from laboratory experiments that colonies of Nearctic *Leptothorax* (s.str.) are highly territorial and engage in deadly contests with their neighbours, which – similar to territorial wars among the far larger colonies of honeypot ants (HÖLLDOBLER 1967b) – may result in one colony eliminating the other and pillaging its brood.

We here report observations on intraspecific competition in monogynous *Leptothorax (Myrafant) nylanderi*, which give insight into the behavioural ecology of this species and demonstrate a surprising effect of nesting material on colony odor and intercolonial discrimination. In addition, we investigated interspecific competition among *L. nylanderi* and other sympatric *Leptothorax* species.

Methods

Field experiments were conducted in an open pine (*Pinus sylvestris*) and oak (*Quercus petraea*) forest with scattered rose (*Rosa canina*), elder (*Sambucus nigra*), and blackthorn thickets (*Prunus spinosus*) in Sommerhausen near Würzburg, and a similar forest near the Theodor-Boveri-Institut in Würzburg. For field observations, colonies were located by following foragers back to their nests. For aggression tests, colonies were aspirated from their nests in rotting sticks and transferred to the laboratory in glass tubes. Aggression tests were performed in a neutral arena with a diameter of 1 cm. Ants were gently placed with forceps into differently marked plastic vials by an experimenter who did not know the origin of the colonies in the glass tubes. A second experimenter placed the ants from two plastic vials into the neutral arena. Experiments thus were double-blind, i.e. neither the person observing the behaviour nor the person putting the ants together for the experiment knew whether they were from neighbouring colonies, colonies nesting in the same type of nesting material, etc. Double-blind experiments were obviously not possible when two different species were tested. Interactions were observed for 5 min directly after the ants were transferred into the arena, and the number of amicable, neutral or aggressive interactions during this period was noted. Five different categories of interactions of increasing aggression were observed: allogrooming, backing off, mutual antennation, violent antennation bouts, and biting. In comparisons of aggression in different tests, only biting was evaluated, as this behaviour did not grade into other types of behaviour and thus could most reliably be identified.

To analyse the influence of the nesting material on nestmate discrimination, colonies of *L. nylanderi* were transferred from their natural nests into artificial nests consisting of 7-cm-long pine or oak sticks of 1 cm diameter into which a 6-cm-long, 3-mm-wide hole was drilled. They were kept in the laboratory under artificial temperature and dark/light rhythms (BUSCHINGER 1973, 1974). Ants were fed ad libitum twice per week with diluted honey and pieces of crickets.

Workers were tested only once and killed after the experiment. Statistical analyses were performed using the program Statistica 4.5 (StatSoft 1993).

Results

Species Composition and Nest Density

In total, more than 500 nests of six *Leptothorax* species were collected in our study site in Sommerhausen. *L. (Myrafant) unifasciatus* and *L.* (s.str.) *acervorum* were quite rare and found living under bark at the base of pines; *L. unifasciatus* nested only in extremely sunny sites on the southern edge of the forest. *L. (M.) corticalis* and *L. (M.) affinis* were mostly collected in dead twigs on trees and only occasionally and temporarily occurred on the ground, presumably after their nests had been blown down by a storm. *L. (M.) nylanderi* and *L.* (s.str.) *gredleri* were the most abundant ants in sticks on the ground and under bark. Whereas *L. nylanderi* occurred both in partly shaded edges of the forest and in more shaded areas deeper in the forest, colonies of *L. gredleri* were exclusively found near the forest edge and especially in sun-exposed blackthorn thickets (mean distance of nests from forest edge, *L. nylanderi*: 293 nests, $\bar{X} = 7.0$ m; *L. gredleri*: 24 nests, $\bar{X} = 1.1$ m, Mann–Whitney U-test, $U = 2575.5$, $p < 0.05$). Of a total of 350 nests found on five 5×5 m^2 plots, 326 were *L. nylanderi*, 20 *L. gredleri*, 3 *L. affinis*, and 1 *L. unifasciatus*. Average nest densities of *L. nylanderi* ranged from 0.54 to 5.96 nests/m^2, those of *L. gredleri* from 0.0 to 0.4 nests/m^2.

Field observations indicated that colonies of *L. nylanderi* may occasionally be polydomous, i.e. simultaneously inhabit several nest sites: in three cases, workers were observed moving between two nesting sites less than 4 cm apart. Of the 326 mapped nests of *L. nylanderi*, only nine were closer to their nearest neighbour than 10 cm. In eight of these pairs, only one nest contained a queen, whereas the other contained workers and brood only, and workers from different nests did not interact aggressively (see below). We therefore suggest that polydomy occasionally occurs in *L. nylanderi*. In the following experiments, however, only workers from queenright nests were used, and as *L. nylanderi* is typically monogynous (BUSCHINGER 1968), workers from different queenright nests were considered to belong to different colonies.

L. nylanderi colonies appeared to be randomly distributed. According to CLARK & EVANS (1954), the ratio $R = r_A/r_E$ gives an estimate of the randomness of nest distribution, where r_A is the mean distance between two neighbouring nests, r_E is $\frac{1}{2}p^{-1/2}$, and p is the average nest density. When nest distribution is perfectly random, R equals 1; when nests are overdispersed, as is the case in territorial species, $R > 1$, and when nests are aggregated, e.g. due to frequent polydomy, $R < 1$. For two plots we

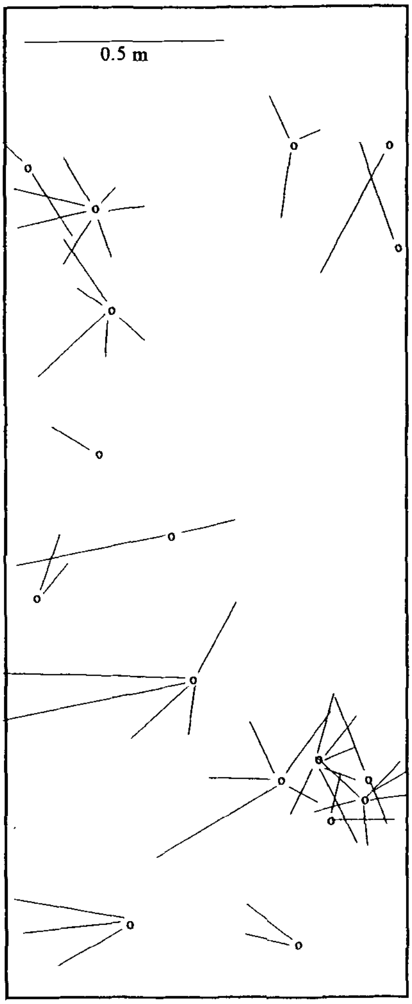

Fig. 1: Distribution of 17 queenright colonies of *L. nylanderi* and their foraging ranges. Foragers were followed back to their nests from the site where they were first encountered in the field. Foraging areas clearly overlap

calculated R-values of 1.11 and 1.21, which were not significantly different from 1 (two-tailed t-test, plot A: $df = 86$, $t = 0.234$, $p > 0.1$; plot B: $df = 147$, $t = 0.494$, $p > 0.1$).

In the second study site near the Theodor-Boveri-Institut in Würzburg, *L. nylanderi* was the only *Leptothorax* species, but occurred at similar densities as in Sommerhausen.

Home Range and Intercolonial Aggression

During approximately 70 h of field observation, 65 *L. nylanderi* foraging workers from 21 colonies and 6 *L. gredleri* from one colony were observed returning to their nests in the field. The foraging areas of different *L. nylanderi* colonies and of *L. gredleri* and *L. nylanderi* colonies greatly overlapped, suggesting that *L. nylanderi* does not defend absolute territories against foragers of the same or a related species (Fig. 1).

In seven cases, two foragers from different colonies were observed meeting in the field, which resulted in backing off of one or both workers. In one field experiment we placed the nest of one colony, A, immediately next to the nest of another, colony B. After about 1 h, two workers of the resident colony B walked into the nest entrance of A and immediately engaged in biting and stinging with A workers. Within 2 h, 28 of these mandible fights were observed, in all of which B workers entered nest A, pulled and carried A workers out of the nest and dropped them some 15 cm away. B workers began to emigrate from their nest 1.5 h after the commencement of the experiment and carried other workers, brood, and the queen to a site in the leaf-litter 20 cm from the colony. After about 2 h, colony A also began to move to a new site under bark, 10 cm from the old nesting site. One day after the experiment, most workers, the larvae, and the queens of the two colonies were found in their respective new nesting sites, and only a minority was present in the old nests.

Apparent Dear-enemy Phenomenon

To analyse aggressive interactions between *Leptothorax* ants in detail, pairs of workers from the same colony, from two conspecific colonies, or from two heterospecific colonies were confined for 5 min in a neutral arena of 1 cm diameter in the laboratory, only a few h after collecting. All interactions were recorded. Whereas nestmates typically engaged in peaceful interactions, such as grooming or food exchange, alien ants were often violently antennated and bitten with the mandibles, or individuals backed off from each other. Allospecific ants were more strongly attacked than conspecific alien ants (62 intraspecific encounters among *L. nylanderi* from different colonies: $\bar{X} = 2.7 \pm$ SD 4.4 biting attacks in 5 min, $\tilde{X} = 1.0$; 14 encounters among *L. gredleri* from different colonies: $\bar{X} = 1.3 \pm$ SD 3.1, $\tilde{X} = 0$; 25 interspecific encounters: $\bar{X} = 11.2 \pm 9.7$, $\tilde{X} = 11$. Kruskal–Wallis H-test, $p < 0.0001$; unplanned comparisons tested with Tukey HSD-test: intraspecific encounters *L. gredleri* vs. *L. nylanderi* $p = 0.70$, intraspecific encounters *L. gredleri* vs. interspecific encounters $p < 0.001$, *L. nylanderi* vs. interspecific encounters $p < 0.001$).

In *L. nylanderi*, we observed a surprising effect of the distance between two nests on intercolonial aggression. Ants from neighbouring colonies, all living in rotting pine sticks, behaved much more gently in arena experiments than ants from more distant colonies (Fig. 2). Polydomy cannot explain this phenomenon, because all nests tested in these experiments contained a queen, and furthermore, ants from neighbouring nests interacted more aggressively than workers from the same nest or from different nests of a polydomous colony. An increase of aggression with nest distance was observed also in encounters between *L. nylanderi* and *L. gredleri*: two allospecific pairs of colonies were found nesting in the same stick, and in both cases, workers attacked individuals from the neighbouring colony less violently than they attacked workers from more distant colonies of *L. gredleri*. Workers of these neighbouring colonies of *L. nylanderi* and *L. gredleri* engaged in biting in a neutral arena significantly less frequently (first pair of test colonies, six replicates: $\bar{X} = 0.7$, $\tilde{X} = 1$; second pair: 11 replicates: $\bar{X} = 0.7$, $\tilde{X} = 0$)

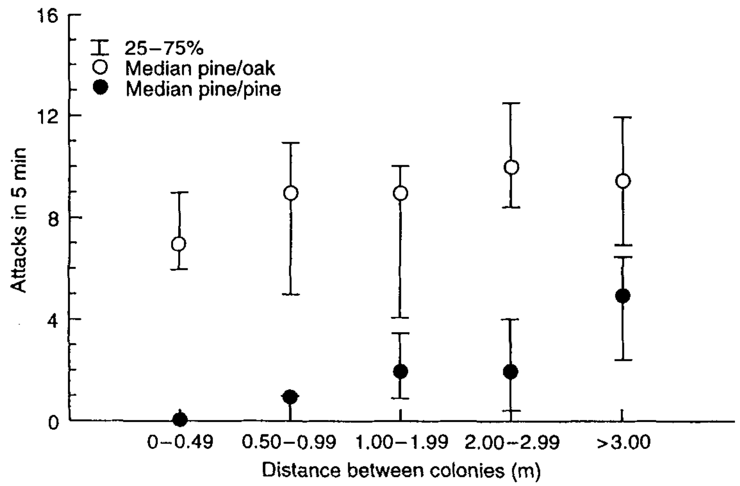

Fig. 2: Occurrence of aggressive interactions among workers of *L. nylanderi* from different colonies in relation to the distance between the test colonies. Ants from two colonies were confined in a neutral arena and all interactions were monitored for 5 min; the median and 25 % and 75 % quartiles of the frequencies of biting attacks in 5 min are shown (for details see text). In each distance category, at least nine different pairs of colonies were tested. When both test workers came from colonies that inhabited pine sticks (solid dots), ants from neighbouring colonies exhibited less aggression than ants from more distant colonies (69 colonies; Kruskal–Wallis H-test, $H = 29.28$, $p < 0.001$; Tukey HSD-test, 0–0.49 m vs. > 3.00 m: $p < 0.001$). Ants from colonies that inhabited different types of wood (open circles) were more aggressive towards each other and a distance effect was not apparent (75 colonies; $H = 3.75$, $p = 0.44$; Tukey HSD-test, 0–0.49 m vs. > 3.00 m: $p > 0.05$)

than workers from the same *L. nylanderi* colonies and workers from several other *L. gredleri* colonies collected at distances of more than 1 m (first *L. nylanderi* colony, 12 tests with different colonies of *L. gredleri*: $\bar{X} = 6.7$, $\tilde{X} = 3.5$; second colony, 16 tests: $\bar{X} = 9.9$, $\tilde{X} = 9$. Mann–Whitney U-test, first pair: $U = 9.5$, $p < 0.01$, second pair: $U = 28.5$, $p < 0.01$).

Influence of Nesting Material on Aggression

To analyse whether the correlation between aggression and colony distance is caused by spatial heterogeneities of colony odour, we investigated the influence of nesting material on intercolonial aggression. Workers from neighbouring colonies of *L. nylanderi* living in the same type of wood did not interact aggressively, whereas workers from similarly close colonies living in different types of wood (pine/elder, pine/oak, or pine/maple) attacked each other significantly more fiercely. Furthermore, aggression rate was not affected by the distance between nests (Fig. 2). In a second experiment, aggression between workers from 12 pairs of neighbouring colonies was tested. After that, one colony of each of six pairs was transferred into an artificial pine stick, the other into an oak nest. Both colonies of each of the remaining six pairs were transferred into different pine nests. Aggression between individual ants from the same pairs of colonies

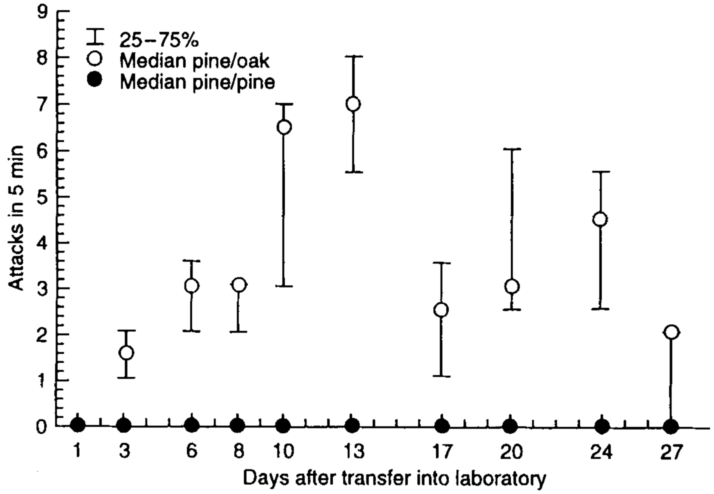

Fig. 3: Temporal changes in aggression between workers from *L. nylanderi* colonies inhabiting laboratory nests of different material. Aggression between 12 pairs of colonies from neighbouring, natural pine sticks was tested directly after collection. The pairs were then divided into two experimental groups. In the first group (six pairs), both colonies of each pair were transferred into two separate nests consisting of pine wood. In the second group (six pairs), one colony of each pair was transferred into a pine nest, the other into an oak nest. Aggression between the pairs was tested over 27 d of laboratory culture. The median and 25 % and 75 % quartiles of the frequencies of biting attacks in 5 min are shown. Whereas no aggression was observed between workers nesting in the same type of wood (solid dots), aggression increased between workers from colonies nesting in different nesting material (open circles)

were tested every 2 d or 3 d. Whereas aggression rate between six pairs of colonies both transferred into pine nests remained low, aggression rate increased between ants from six pairs of colonies transferred into different nest types. Aggression reached a maximum after 13 d, but decreased thereafter (Fig. 3).

In a third experiment, we split colonies from natural pine nests into two queenless fragments which were transferred in the laboratory, either both into pine sticks or one into a pine, the other into an oak stick. As expected, no aggression was observed when former nestmates were tested in an arena experiment on the day of colony fragmentation. In 10 tests during 4 wk following separation, no aggression could be observed among former nestmates which had been transferred into different pine nests. In contrast, nestmates transferred into different nest types exhibited aggression from the third day after separation on. Aggression reached a maximum on day 10 of the experiment and decreased thereafter (Fig. 4).

Discussion

Leptothorax (Myrafant) nylanderi is one of the most common ants in Central Europe (Kutter 1977) and locally reaches densities of more than one nest per m^2 (Seifert 1986, 1993). In one of our two study populations near Würzburg, *L. nylanderi* was the only species of this genus, whereas near Sommerhausen it co-occurred with two

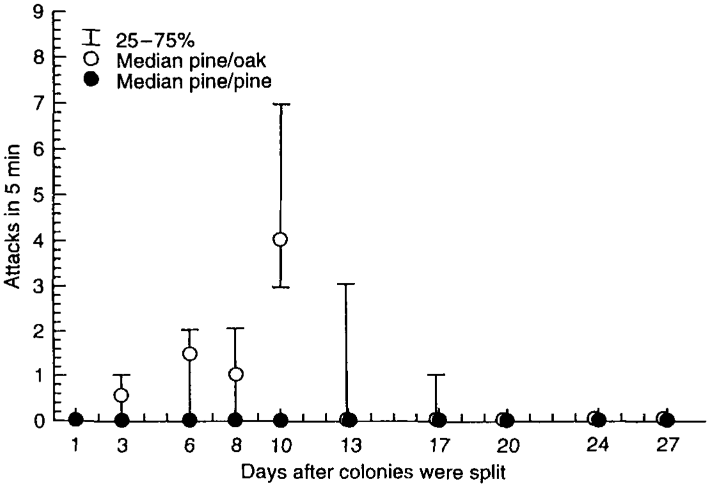

Fig. 4: Temporal changes in aggression between former nestmates of *L. nylanderi* which were transferred into different nest sites. Six colonies were split into two queenless groups of workers and brood which were both housed in pine sticks; 12 additional colonies were similarly split into two fragments each, one of which was housed in a pine stick and the other in an oak stick. Aggression between the pairs was tested over 27 d of laboratory culture. The median and 25 % and 75 % quartiles of the frequencies of biting attacks in 5 min are shown. Whereas no aggression was observed between former nestmates transferred into separate pine sticks (solid dots), the frequency of biting attacks between former nestmates living in different nesting material increased over the first 10 d and then declined (open circles)

Leptothorax (s.str.) and at least three other *Myrafant*. Nest densities were extraordinarily high, occasionally surpassing five nests per m^2. The presence of a queen in most nests of this monogynous species suggests that polydomy occasionally occurs but is a rare phenomenon and that despite the high density, the majority of nests are independent of each other. Random spacing of the nests and overlapping home ranges indicate that *L. nylanderi* does not defend absolute territories against foragers of the same species or other *Leptothorax*, though the nest itself is defended against intruders. In the field, workers backed off when meeting a forager from another colony, but violent fighting ensued when an alien nest was placed immediately next to a colony. During forced encounters in a neutral arena, the fierceness of aggression between individuals from different colonies was strongly influenced by the distance between their nests: workers from neighbouring queenright colonies were treated less aggressively than workers from colonies several metres away. Similar results were obtained when workers were not confined in a neutral arena, but when a worker from another colony was introduced into the nest of a test colony (C. BÜRGER and J. BURKHARDT, Univ. Tübingen, pers. comm.); aggression between resident ants and intruders was much stronger than in neutral arena encounters (A. HIPPERT, unpubl. data). The correlation between aggression and distance held also for interspecific encounters. *L. nylanderi* typically attacked workers of *L. gredleri* and other *Leptothorax* species much more fiercely than conspecific alien ants – in contrast to what one might expect from Gause's law, but as occasionally observed in other sympatric pairs of closely related ant species (DE VROEY

1979; STUART 1991). However, when a *L. gredleri* colony nested in close proximity to a *L. nylanderi* colony, interactions consisted only of short inspective antennation rather than biting. It thus appears unlikely that *L. nylanderi* defends absolute territories and engages in territorial wars or intraspecific slave raids, as reported from several Nearctic *Leptothorax* (ALLOWAY 1980; STUART & ALLOWAY 1982, 1983). In contrast, our study corroborates observations on *L. acervorum* (DOBRZANSKI 1966), which also reacted towards alien ants in a rather docile way.

In our experiments, *L. nylanderi* were apparently capable of distinguishing between ants from neighbouring and more distant colonies, exhibiting what has been referred to as a 'dear-enemy phenomenon' (TEMELES 1994). It was suggested that this behaviour is ultimately caused by strangers posing a greater threat than neighbours because strangers might have been forced to leave their own nests and might now be searching for a new site, whereas a well-known neighbour typically has its own nest. In ants, foragers of the harvester ant *Pogonomyrmex barbatus* (GORDON 1989) appear similarly to be capable of discriminating between neighbours and alien ants, but react more strongly to neighbours than to strangers. A distance effect on aggression in the same direction as in *L. nylanderi*, but on a different scale of distances, was reported from *Leptothorax curvispinosus* (STUART 1987a), *Acromyrmex octospinosus* (JUTSUM et al. 1979) and *Cataglyphis niger* (A. HEFETZ pers. comm.), where workers from alien colonies in the same subpopulation were less fiercely attacked than workers from subpopulations hundreds or thousands of metres away. In *Ephebomyrmex imberbiculus*, a North American harvester ant, the violence of attacks increased with distance over a range of 50 m (K. SCHILDER, J. HEINZE and B. HÖLLDOBLER, unpubl. data).

Proximately, in mammals or birds a dear-enemy phenomenon could result from learning. Though learning or imprinting are important in insect societies (HÖLLDOBLER & WILSON 1990; HAMMER & MENZEL 1995), it appears unlikely that they play a major role in the apparent dear-enemy phenomenon in *L. nylanderi.* As test workers in our experiment were randomly chosen from the colony and thus included both experienced foragers and inexperienced nurses, the results of our experiments could be explained by learning or imprinting only by assuming that workers not only learn the recognition labels of ants from neighbouring colonies by repeatedly encountering them during foraging but also transmit their knowledge to other nestmates. Alternatively, a correlation between aggression and distance could result from colony recognition cues covarying with microhabitat. It has been suggested that recognition cues in ants are complex mixtures of cuticular substances of low volatility, such as hydrocarbons and probably also fatty acids, esters etc. (BONAVITA-COUGOURDAN et al. 1987; MOREL et al. 1988; KAIB et al. 1993). The origin of these recognition cues is still unclear, but the components could originate from each individual ant, from the queen, or from the environment (HÖLLDOBLER & CARLIN 1987), and they are probably transferred between individuals by trophallaxis or allogrooming to form a colony odour 'gestalt' which is more or less homogeneous throughout the colony (CROZIER & DIX 1979). In different species of formicoxenine ants, experiments indicate both a 'gestalt' odour (STUART 1987b, 1988; KAIB et al. 1993; HEINZE et al. 1994) and a queen-dominated colony odour (PROVOST 1989), with environmental cues playing a role when genetical odour cues lack diversity (STUART 1987a).

The covariance of the similarity of colony odours and the distance between colonies, as observed in *L. nylanderi*, might result either from high genetic viscosity of the population or from environmental factors contributing considerably to the composition of recognition cues. In the first case, due to budding or short dispersal by young queens, neighbouring colonies could be related and genetical odour cues would thus be more similar than between more distant colonies. In the second case, odour cues would be more similar between neighbouring colonies as they are exposed to the same microhabitat.

Our observation that neighbouring colonies living in different types of wood interact significantly more aggressively than neighbouring colonies that inhabit the same type of wood strongly supports the importance of environmental cues in determining colony odour. However, this result cannot completely rule out that ants with genetically similar odour cues live in similar nesting sites, because young queens might found their own nests preferentially in the same nesting material as the maternal colony. Experimental manipulations, in which colonies were split and housed in two different types of nests, however, clearly show that odour cues derived from the nesting material may lead to aggression between former nestmates and suggest that environment-based odour cues are used to distinguish between ants from different colonies. Furthermore, the finding that *L. nylanderi* treated workers from neighbouring *L. gredleri* colonies, which inhabited the same decaying trunk as the *L. nylanderi*, less aggressively than *L. gredleri* or *L. nylanderi* workers from more distant colonies, also suggests that environmental odour cues are more important to distinguish between neighbours and ants from more distant colonies than genetical cues, at least in our experimental context, i.e. in encounters in a neutral arena or probably in the foraging area surrounding the nest. Similarly, colony odour of the leaf-cutter *Acromyrmex octospinosus* appears to be strongly affected by the plant material carried in by foragers (JUTSUM et al. 1979).

Whereas in a neutral arena *L. nylanderi* did not exhibit strong aggression towards workers from neighbouring colonies, the latter were attacked when introduced into the nest itself. In a different context, other odour cues, such as genetical cues, may be important, or discrimination based on environment-based cues is more fine-grained than in experiments in a neutral arena. Furthermore, aggression among workers from different colonies ceased after prolonged laboratory culture, even when the ants were kept in different nesting material. The ants used in the latter experiment, however, were from queenless colony fragments and orphaning might well lead to the loss of discriminatory capability or motivation in workers: queenless colony fragments of different origin can occasionally be merged without aggression among the alien ants.

What could be the ecological significance of the strong reliance on environmental odour cues? According to STUART (1987a), in *L. curvispinosus*, environmental cues function as a mechanism to permit the segregation of colonies that are genetically closely related, i.e. due to the separation of colony fragments of a previously polydomous colony or related founding queens nesting in close proximity to each other. A dear-enemy phenomenon as observed in *L. nylanderi* might then be an unselected epiphenomenon caused by the loss of genetic variation together with the microhabitat uniformity. Though the genetical composition of *L. nylanderi* populations is not yet known, it appears unlikely that genetical odour cues are too homogeneous for nestmate discrimination. This is especially the case in the relation between *L. nylanderi* and *L. gredleri*.

A second explanation, still to be tested, appears to be more appropriate: *L. nylanderi* might indeed use environmental odour cues to distinguish between foragers from neighbouring and distant colonies. *Leptothorax* colonies typically nest in preformed cavities, and there is evidence that these are limited in most habitats and that competition for nest sites is high (HERBERS 1986, 1989). In *L. nylanderi*, a strong, positive correlation of colony size and the size of the nest site as well as field observations suggest that colonies frequently move, because their old nest sites are too small, were destroyed or decomposed (S. FOITZIK, unpubl. data). Thus, *L. nylanderi* are constantly searching for suitable nest sites. Whereas workers typically forage for less than 1 m, we observed a colony moving over a distance of several m. When workers bearing the label of a different microhabitat are encountered, they are probably scouting for a new nest site and might pose a threat to a resident colony.

Aggression against strangers rather than the defence of absolute territories might probably also better explain the results of STUART & ALLOWAY (1982, 1983), according to which Nearctic *Leptothorax 'muscorum'* (*L.* cf. *canadensis, L.* sp. A and perhaps other species, HEINZE 1989, 1993) fought fiercely in laboratory experiments. In their experimental set-up, two colonies were simultaneously placed into an arena – alien workers encountered thus were non-neighbours. Our observations, but also the high density and the small size of colonies, suggest that formicoxenine ants generally do not defend foraging territories or engage in territorial contests. Most territorial ants have a much higher average worker number (LEVINGS & TRANIELLO 1981). Instead, fierce competition for nesting sites might occasionally lead one colony to attempt to expel another from a nest site.

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