Myrmecologische Nachrichten	9	13 - 19	Wien, Dezember 2006

Attack of the invasive garden ant: aggression behaviour of *Lasius neglectus* (Hymenoptera: Formicidae) against native *Lasius* species in Spain[1]

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Abstract

Invasive species often dramatically change native species communities by directly and indirectly out-competing native species. We studied the direct interference abilities of the invasive garden ant, *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, by performing one-to-one aggression tests of *L. neglectus* workers towards three native *Lasius* ant species that occur at the edge of a *L. neglectus* supercolony in Seva, Spain. Our results show that *L. neglectus* is highly aggressive against all three native *Lasius* species tested (*L. grandis* FOREL, 1909, *L. emarginatus* (OLIVIER, 1792), and *L. cinereus* SEIFERT, 1992), expressed as a higher attack rate of *L. neglectus* and behavioural dominance throughout the aggressive encounters. Attacks of *L. neglectus* were performed fastest and most frequent against *L. grandis*, and also the highest antennation frequencies were observed in encounters between these two species. This could be due to the largest difference in body size, or due to a greater overlap in ecological niche between *L. neglectus* and *L. grandis* compared to the other two native species. There was only weak support for *L. neglectus* workers from the periphery of the supercolony to be more aggressive relative to workers from the centre, even though the former encounter native ant species on a daily basis at the edge of the supercolony.

Key words: *Lasius neglectus*, interference, interspecific competition, invasive ants, aggression behaviour, ecological dominance.

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Introduction

The introduction of exotic species outside their native distribution range adds to local species communities in the short run. In the long run, however, these same introductions can be destructive, leading to a massive decrease in the local biodiversity (WILCOVE & al. 1998, SAX & al. 2005). A small number of ant species are particularly good invaders (PASSERA 1994, TSUTSUI & SUAREZ 2003, LOWE & al. 2004), and can potentially have devastating effects on the ecosystems they invade (O'DOWD & al. 2003, SANDERS & al. 2003). It is characteristic for invasive ants that they, after a short time lag after their introduction, establish extremely dense populations consisting of a large network of cooperating nests (supercolonies) that become ecologically dominant replacing native ant species and even other arthropods (PASSERA 1994, HUMAN & GORDON 1997, OLIVERAS & al. 2005).

This high ecological success is caused by the extraordinary competitive abilities of the invasive ants regarding both direct interference competition, and indirect exploitation competition (reviewed in HOLWAY & al. 2002). Invasive ants, such as the Argentine ant *Linepithema humile* (MAYR, 1868), the red imported fire ant *Solenopsis invicta* BUREN, 1972, and the yellow crazy ant *Anoplolepis gracilipes* (SMITH, 1857), have been shown to be very aggressive towards native ants and perform very well in interference competition, through both physical aggression and the use of chemical defensive compounds by workers (HUMAN & GORDON 1996, HOLWAY 1999, HUMAN & GORDON 1999, MORRISON 2000). In addition to aggressive interactions taking place over domination of food, some invasive ants even perform nest raids of local ants (*L. humile* and *S. invicta*, in HOLWAY & al. 2002).

However, invasive ants can often be smaller in body size relative to the native ant species (MCGLYNN 1999), and thus, despite their high aggression levels towards local ants, they are not always dominant in one-to-one interactions (HOLWAY 1999). Direct competition is therefore only a partial explanation for the success of invasive ants in outrivaling the native species, and their success ultimately depends on the high densities they reach in their introduced range. This is because invasive ants use their resources to produce very large numbers of small workers (HUMAN & GORDON 1997, HOLWAY & al. 1998), instead of producing few larger ones. In addition, their unicolonial social structure (the existence of extensive supercolonies consisting of many mutually non-aggressive nests) allows for very high

[1] This study is dedicated to the memory of the late Stefan Schödl.

worker densities in the habitat, as no territorial borders exist between nests in the entire population. Native ant species, on the contrary, often produce larger workers but in lower numbers and have a multicolonial population structure with interspersed nests (BOURKE & FRANKS 1995, OLIVERAS & al. 2005).

The high worker density gives invasive ants a clear advantage in, e.g., displacing native ants from food resources (e.g., HUMAN & GORDON 1996, HOLWAY 1999, MORRISON 2000, HOLWAY & CASE 2001 reviewed in TSUTSUI & SUAREZ 2003). First, the numerical advantage gives them a head start in exploitative abilities, since colonies with many workers can maintain larger numbers of scouts (leading to rapid discovery of food resources) and recruit larger numbers of workers (leading to dominance of the food resource) – thereby breaking the trade-off between discovery and dominance that normally exists in ant communities (FEENER 2000). Second, the unicolonial population structure also allows for a rapid local recruitment of workers because they do not have to recruit workers from their original nest, but from any nest of the interconnected network. Third, invasive ants tend to have a higher activity, both being active day and night and sometimes for a longer period in the year relative to the native ants (CLARK & al. 1982, HUMAN & GORDON 1996).

The above studies have been performed on several invasive ant species, all known for decades because of their pest status and ecological dominance in the introduced ranges. In this study, we focus on the invasive garden ant *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, which has received much less attention due to its very recent detection (the species was described only 16 years ago). Already now, however, it has been found to quickly spread across Europe and Western and Central Asia and to have devastating effects on the native species communities it invades (VAN LOON & al. 1990, TARTALLY 2000, ESPADALER & BERNAL 2004). Whereas approximately 30 populations were known in 2000, today, only six years later, populations have been reported from almost 100 localities, mostly representing parks and gardens in cities (http://www.creaf.uab.es/xeg/Lasius/index.htm).

Like the more well-known invasive ant species, *L. neglectus* is ecologically dominant in the introduced habitats (TARTALLY 2000, DEKONINCK & al. 2002, ESPADALER & BERNAL 2004). It forms enormous supercolonies occupying areas as large as 17 ha (in a population in Seva, Spain, X. Espadaler, pers. comm.), reaching higher numbers of workers relative to native ants (TARTALLY 2000). *Lasius neglectus* replaces native ant species, which might, among other factors be caused by its extremely high activity. Workers have been shown to be active 24 h / day from May to late October (ESPADALER & BERNAL 2004), whereas species native to Spain are probably more adapted to heat and could thus be restricted to warmer temperatures for activity than the introduced *L. neglectus.* Divergent thermal preferences of different ant species in the same community have been shown to significantly alter interspecific interference hierarchies (CERDA & al. 1997).

The above features show that *L. neglectus* is a strong competitor against native ants, and that it has strong indirect exploitative abilities. However, the competence of *L. neglectus* as a direct competitor in interspecific confrontations has not yet been investigated (X. Espadaler, pers. comm.). It is therefore not clear whether *L. neglectus* relies only on indirect competitive abilities when out-competing native ants, or if it is also highly aggressive against them. Aim of this study is to provide the first investigation, whether individual aggression behaviour of the invasive garden ant could be an additional mechanism for its expansion. Given the small body length of only 3 mm of *L. neglectus* workers, this invasive species is likely smaller than most native ants it encounters in its large distribution range. Still a high direct competitive ability is expected for this species, as it makes massive use of its chemical weapon (formic acid), at least compared to its non-invasive sister species *L. turcicus* SANTSCHI, 1921 (S.C. & L.V.U., own observation).

We studied the behavioural interactions of the invasive garden ant, *L. neglectus,* with three native *Lasius* ant species, *L. grandis* FOREL, 1909, *L. emarginatus* (OLIVIER, 1792), and *L. cinereus* SEIFERT, 1992, that occurred on the edge (but were absent in the centre) of the above mentioned large supercolony of *L. neglectus* in Seva, Spain. All three native *Lasius* species are larger in body size than *L. neglectus* (estimates based on worker head size (mean of head width and length): *L. grandis* being approximately 35 % larger than *L. neglectus*, *L. emarginatus* 30 % and *L. cinereus* 20 %; size data from B. Seifert, pers. comm., SEIFERT 1992). We studied the direct interference abilities of *L. neglectus* against its native competitors by observing the aggressive behaviour occurring in one-to-one interactions between a single *L. neglectus* worker and a single worker of any of the other three species. Furthermore, we were interested in whether we could observe any difference in behaviour between *L. neglectus* workers from the centre of the colony relative to the periphery of the colony. Differences might be expected because workers in the centre mostly encounter other *L. neglectus* ants, as other ant species can hardly coexist in the centre of this large supercolony (X. Espadaler, pers. comm.). On the contrary, workers in the periphery daily encounter and might fight against other species in the process of range expansion of the colony, which is still in rapid growth (X. Espadaler, pers. comm.). One could therefore expect that the direct competitive abilities of *L. neglectus* workers at the edge of the colony could be higher than in the centre. Alternatively, decreased aggression could also occur as a result of the "dear enemy phenomenon", as can take place in some ants (HEINZE & al. 1996).

Methods

Samples: Samples of *L. neglectus, L. grandis, L. emarginatus*, and *L. cinereus* were collected in April / May 2003 in Seva close to Barcelona, Spain. A total of twelve nests were sampled for *L. neglectus*, six of which were from the centre and six from the edge (periphery) of the supercolony. Two to three nests of each of the species *L. grandis, L. emarginatus* and *L. cinereus* were collected directly at the edge of the *L. neglectus* supercolony.

Aggression tests: After the ants (workers and brood) had been transferred from the field to the laboratory, they were kept in small plastic boxes (7.5 × 5.5 × 5.0 cm) at a 25 / 20 °C day / night temperature cycle. One to two weeks after transfer into the laboratory, "aggression tests" were performed between individual workers of *L. neglectus* and individual workers of each of the three other species. Each of the twelve nests of *L. neglectus* were tested against the three other *Lasius* species, in 5 replicates per combination (using all nests of the other species against each *L. neglectus* nest), leading to a total of 60 aggression tests per species and 180 aggression tests in total.

Five minutes before the test, individual ants were removed from their colonies and placed in separate plastic vials (diameter 2 cm, height 5 cm; fluon coated sides). The two individual ants were then placed together into the "fighting arena" (petri dish, 5.5 cm diameter; preliminary tests revealed that the outcome of the fight was independent of the order of putting the ants into the dish), and observed for ten minutes at an ambient temperature of 22.5 ± 2 °C. Five behaviours – antennation, avoidance behaviour, gaster raising (i.e., spraying with formic acid), biting and fighting – occurred in the interactions. The frequency of each behaviour, i.e., the number of times a given behaviour was displayed (but not its duration), was recorded after a standard protocol (GIRAUD & al. 2002), separately for each minute. Encounters were classified as "aggressive" when gaster raising, biting or fighting occurred.

Direction of attacks: In 50 % of the aggression tests (n = 60), in which aggression took place (n = 121), the ant starting the attack could be determined. It was analysed, whether *L. neglectus* or the native *Lasius* species started the aggression more frequently, and whether the "direction of attack" deviated from 50 : 50 (Fisher's exact test). It was further tested whether workers of *L. neglectus* collected from the centre versus the periphery of the supercolony differed in the proportion of initiating an attack against the other species (t-tests; as aggression did not occur in all encounters, statistical comparison could not always be made for all 12 nests).

Timing of attacks: For each encounter it was determined, in which minute after putting the ants together aggression occurred. In non-aggressive encounters, the value of 10.1 minutes was assigned, as it could not be excluded that aggressive interactions might have occurred after the 10 min observation period. A General Linear Model (GLM) was performed with the "minute of first attack" as dependent variable and the following three factors: 1) native species (*L. grandis*, *L. emarginatus*, or *L. cinereus*), 2) collection site of *L. neglectus* workers (centre or periphery of the supercolony), and 3) the nest of *L. neglectus* workers. Mean values of the five replicates per nest were calculated and used in the statistical analysis.

Dominance throughout the fight: The direction of each behaviour was determined if possible, except for fighting, in which both ants equally perform biting and sometimes spraying. For each of the two ant species and each combination of nests, the frequency of each behaviour was calculated as the mean of the five replicates of ten minute encounters.

For the four behavioural types, for which the active species could be observed (antennation, avoidance, gaster raising and biting), GLMs were carried out for each of the three native *Lasius* species, testing whether the different behaviours were performed at different frequencies by *L. neglectus* and *L. grandis*, *L. emarginatus*, and *L. cinereus*, respectively. Collection site of the *L. neglectus* workers (centre or periphery) was included as a factor in the analysis.

We further tested, whether the total frequencies of behaviours (sum of *L. neglectus* and the respective other *Lasius* species) differed when *L. neglectus* was tested against *L. grandis*, *L. emarginatus*, and *L. cinereus*. As the same twelve nests of *L. neglectus* were used against all three species, Repeated Measure ANOVAs were performed for each of the three species and five behavioural types.

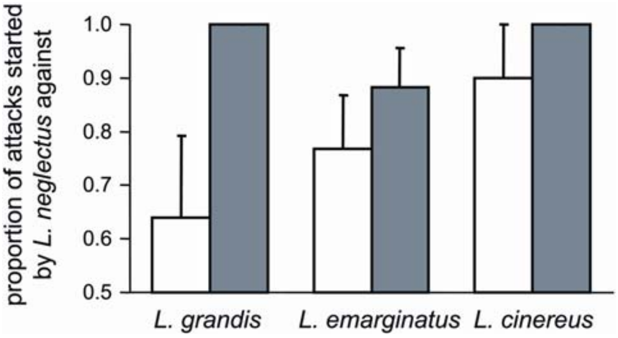

Fig. 1: Proportion of attacks (mean ± s.e.m.) performed by *Lasius neglectus* and directed against the native *Lasius* species *L. grandis*, *L. emarginatus*, and *L. cinereus*. *Lasius neglectus* workers from the edge of the supercolony (grey bars) showed non-significant tendencies for higher attack rates than workers collected in the centre (open bars).

General statistics: Data were tested for normality and equal variance before performing parametric tests. All given *P* values are two tailed. Statistics were performed with SPSS 13.0 and Sigma Stat 3.1.

Results

Aggression occurred frequently, in 63 - 75 % of the cases depending on the species of *Lasius* with which *L. neglectus* workers were paired in the aggression test (*L. neglectus* against *L. grandis*: aggression in 45 out of 60 cases and in 38 of 60 encounters against both *L. emarginatus* and *L. cinereus*). Only 3 of the 180 encounters were lethal to one of the competitor ants.

Direction of attacks: In approximately 50 % of the aggressive interactions, the ant starting the attack could be determined (52 % (24 / 45) of the aggressive interactions between *L. neglectus* and *L. grandis*, 55 % (21 / 38) of the aggressive encounters with *L. emarginatus* and 39 % (15 / 38) of the fights with *L. cinereus*). *Lasius neglectus* started the attacks in the majority of the cases: in 79 % (19 / 24) of the fights against *L. grandis*, in 76 % (16 / 21) against *L. emarginatus*, and in 93 % (14 / 15) against *L. cinereus*. Even though this was always more than 50 % of the encounters, the deviation from 50 : 50 was only significant for *L. cinereus* (Fisher's exact tests, 1 df; *L. neglectus* - *L. grandis*: $P = 0.069$; *L. neglectus* - *L. emarginatus*: $P = 0.197$; *L. neglectus* - *L. cinereus* $P = 0.035$).

Lasius neglectus workers from the periphery of the supercolony showed a tendency to attack the native ant species more frequently than workers collected from the colony centre (Fig. 1), however the differences were not significant (t-test: *L. grandis*: t = -1.899, 8 df, $P = 0.09$; *L. emarginatus*: t = -0.94, 8 df, $P = 0.37$; *L. cinereus* t = -0.882, 7 df, $P = 0.41$).

Timing of attacks: In the encounters where aggression occurred, it often started already in the first minute (87 % of the aggressive interactions with *L. grandis*, 56 % with *L. emarginatus* and 67% with *L. cinereus*). However, aggression was also observed to start later during the 10 min

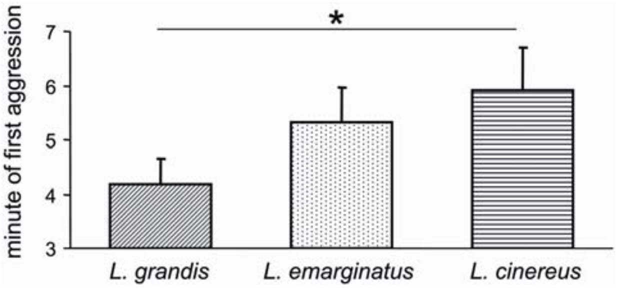

Fig. 2: Minute of first aggression (mean ± s.e.m.) occurring in encounters of *Lasius neglectus* against the three native *Lasius* species (*L. grandis*: hatched, *L. emarginatus*: stippled, and *L. cinereus*: striped). Aggression occurred earliest in interactions of *L. neglectus* and *L. grandis*. Significant differences are indicated (*: $P < 0.05$).

encounters, or not at all. The minute of the first aggression between the two ants differed between the three native ant species, but was independent of whether *L. neglectus* workers were collected at the edge or in the centre of the supercolony, and from which nest they originated (GLM, 36 df: species effect: $P = 0.02$; centre-periphery effect: $P = 0.47$; nest effect: $P = 0.23$). The average time until the first aggressive interaction occurred was shortest in encounters with *L. grandis*, intermediate against *L. emarginatus* and longest against *L. cinereus* (Fig. 2; Post-Hoc Tukey Tests all pairwise comparisons: *L. grandis* - *L. cinereus*: $P < 0.05$; *L. grandis* - *L. emarginatus* and *L. emarginatus* - *L. cinereus*: $P > 0.05$). This result reflects that aggression occurred both quickest and most frequently against *L. grandis* relative to the other two species.

Dominance throughout the fight: It was tested whether *L. neglectus* performed the observed behaviours (i.e., antennation, avoidance behaviour, gaster raising and biting) at different frequencies than the respective competitor ant, and whether *L. neglectus* workers collected from the centre of the supercolony might differ in their behaviour from workers collected at the colony edge. There was no significant effect of centre versus periphery in any of the analyses (GLMs, centre-periphery effect for each of the three species and the four behavioural types: $P > 0.05$), however the results clearly show that *L. neglectus* dominated in the aggressive encounters with all three native *Lasius* species (Fig. 3), as detailed below for the different behavioural types.

Lasius neglectus showed higher aggression, both in chemical defence (GLMs, 24 df; gaster raising: *L. neglectus* - *L. grandis*: $P < 0.001$; *L. neglectus* - *L. emarginatus*: $P = 0.01$; *L. neglectus* - *L. cinereus*: $P = 0.07$) and in physical defence (biting: *L. neglectus* - *L. grandis*: $P = 0.02$; *L. neglectus* - *L. emarginatus*: $P = 0.002$; *L. neglectus* - *L. cinereus*: $P = 0.01$) against all three species. Avoidance behaviour, on the contrary, was more frequent in the three native species of *Lasius* relative to *L. neglectus*, although significant only in *L. emarginatus* (*L. neglectus* - *L. grandis*: $P = 0.07$; *L. neglectus* - *L. emarginatus*: $P < 0.001$; *L. neglectus* - *L. cinereus*: $P = 0.07$).

The only behaviour not being linked to aggression or dominance is antennation, which is the behaviour preceding recognition and discrimination in ants and also frequently occurring between nest members (WILSON 1971, BREED & BENNETT 1987, VANDER MEER & MOREL 1998). The antennation frequency of *L. neglectus* and the respective other *Lasius* species did not differ (GLMs, 24 df; *L. neglectus* - *L. grandis*: $P = 0.57$; *L. neglectus* - *L. emarginatus*: $P = 0.84$; *L. neglectus* - *L. cinereus*: $P = 0.37$), whereas *L. neglectus* and its respective *Lasius* competitor performed the behaviours characterizing aggressive interactions at different frequencies.

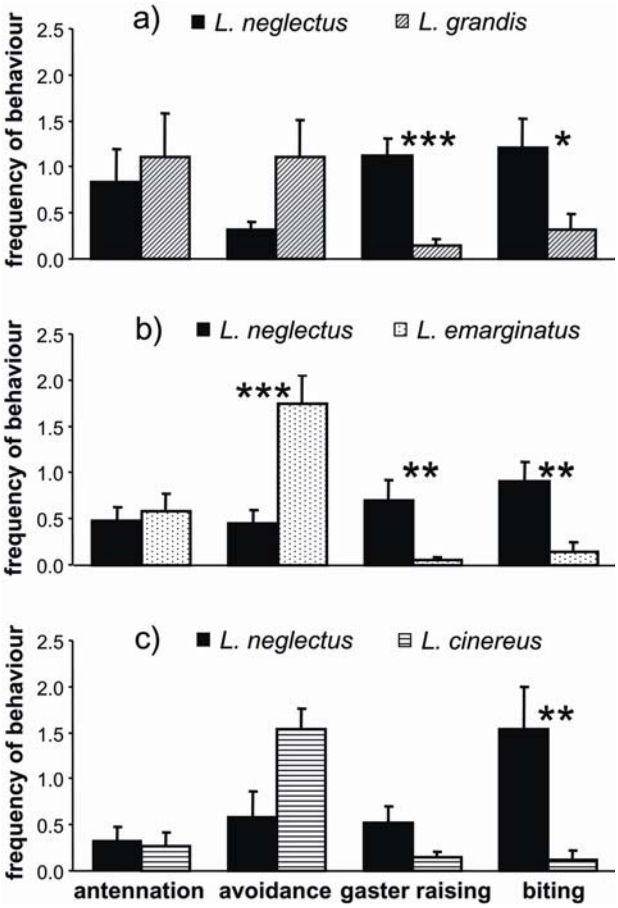

Fig. 3: Frequencies of different directed behaviours (mean ± s.e.m.; antennation, avoidance, gaster raising, and biting) performed by *Lasius neglectus* and a) *L. grandis*, b) *L. emarginatus* and c) *L. cinereus*. There was no difference in antennation behaviour between *L. neglectus* and any of its native competitor species, but the native *Lasius* species performed more avoidance behaviour and *L. neglectus* more gaster raising and biting. Significant differences are indicated (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

Fighting, the non-directed behaviour, in which both ants were at the same time biting and sometimes spraying each other, was the most frequent behaviour in all encounters, occurring approximately 10 times more frequent than unidirectional biting (mean ± s.e.m.: *L. neglectus* - *L. grandis*: 11.6 ± 0.6; *L. neglectus* - *L. emarginatus*: 11.2 ± 0.7; *L. neglectus* - *L. cinereus*: 10.6 ± 0.7).

The level of aggression (total frequency of gaster raising, biting and fighting and avoidance behaviour performed by both species) did not differ in encounters of *L. neglectus* with each of the three species (Repeated Measure ANOVAs, 35 df; gaster raising: $F = 1.92$, $P = 0.17$; biting: F = 0.84, P = 0.45; fighting: F = 0.37, P = 0.70). However, avoidance behaviour occurred less frequently when *L. neglectus* was paired with *L. grandis* than with *L. cinereus* (see second columns of Figs. 3a and 3c; Repeated Measure ANOVA, 35 df; F = 4.36, P = 0.025; Post Hoc Tukey Test all pairwise comparisons: *L. grandis* - *L. cinereus*: P < 0.05; *L. grandis* - *L. emarginatus* and *L. emarginatus* - *L. cinereus*: P > 0.05). Antennation behaviour, on the other hand, occurred more frequently when *L. neglectus* interacted with *L. grandis* than with *L. cinereus* (see first columns of Figs. 3a and 3c; Repeated Measure ANOVA, 35 df; F = 3.86, P = 0.04; Post Hoc Tukey Test: *L. grandis* - *L. cinereus*: P < 0.05; *L. grandis* - *L. emarginatus* and *L. emarginatus* - *L. cinereus*: P > 0.05).

Discussion

Our results show that the invasive garden ant, *L. neglectus*, is highly aggressive against all three tested native *Lasius* species (*L. grandis*, *L. emarginatus*, and *L. cinereus*) that it encounters at the edge of its supercolony in Seva, Spain. This is expressed both in a higher attack rate of *L. neglectus* than the native *Lasius* species (Fig. 1) and in a behavioural dominance expressed throughout the aggressive encounters (Fig. 3). All three native *Lasius* species show avoidance behaviour in higher frequencies than the invasive garden ant, which on the other hand shows aggressive behaviour in higher frequencies. *Lasius neglectus* does not only bite more, it also performs more "gaster raising", a behaviour tightly linked to the spraying of formic acid, its chemical defence compound. Extensive use of chemical defences in addition to physical defence has also been described in a number of other invasive ants (*A. gracilipes*: FLUKER & BEARDSLE 1970, HAINES & HAINES 1978, *L. humile*: HUMAN & GORDON 1996, HOLWAY 1999, HUMAN & GORDON 1999 and *S. invicta*: MORRISON 2000). Also, MORRISON (2000) reports that *S. invicta* proved to be initially more aggressive in encounters with two native ant species, and eventually dominating most food resources. However, this was only the case when worker biomass of the rival colonies was the same, and not when they had equal numbers of workers.

Lasius neglectus achieves this dominance in direct competition against the native *Lasius* species despite its pronounced smaller body size between 20 % and 35 %. The low frequency of avoidance behaviour performed by *L. grandis* (Fig. 3, second column) could follow from its relatively larger superiority in body size. However, despite or maybe because of the size difference being largest between *L. neglectus* and *L. grandis*, it is against this species that the attacks occur most frequently and fastest (Fig. 2), and also the antennation frequencies between these two species are highest (Fig 3, first column). An explanation why *L. neglectus* is extremely aggressive against *L. grandis* could come from the more overlapping ecological niche use of the two species. *Lasius grandis* occupies the most humid microhabitats of the three tested native *Lasius* species (SEIFERT 1992) and likewise, *L. neglectus* prefers humid microhabitats, hence in Spain it is only able to prosper in irrigated gardens and parks (X. Espadaler, pers. comm.). In contrast, *L. cinereus* is the most xerothermous of the three native *Lasius* species, which might lead to the lowest conflict over habitat use with *L. neglectus* and could explain the longer delay until aggression occurs between this species and *L. neglectus* (Fig. 2). Interestingly, this delay until overt aggression is negatively correlated to the difference in body size of *L. neglectus* to the respective other species.

Our data show a non-significant trend that workers of *L. neglectus* from the colony edge had somewhat increased attack rates towards the three native competitors relative to the ants collected from central nests (Fig. 1). There was no difference between the central and peripheral ants in their timing of attacks and in their dominance behaviour throughout the fights. This might be explained by a regular exchange of ants between the centre and the edge of the colony. A complete mix, however, might be unlikely given the large size of the supercolony.

Our results thus give a weak support for the hypothesis that *L. neglectus* workers from the centre of the 17 ha large supercolony, who do not interact with other ant species, might be less aggressive in interspecific competition than workers from the periphery that are likely to interact with native species on a daily basis. We cannot confirm the "dear enemy effect", which would have led to decreased aggression in ants from peripheral than central nests. However, our experimental setups were artificial as they forced the two ant species to interact with each other within a small arena. In nature, given the choice of interacting or not, workers at the nest periphery might avoid too many aggressive interactions with the native species (TARTALLY 2000), and instead invest more energy in the less costly indirect competition, e.g., by high foraging activity. The chosen method is therefore limited to assess direct competitive ability in one-to-one interactions, whereas colony-level competitive ability is likely influenced by several other additional parameters (see Introduction and ROULSTON & al. 2003).

In conclusion, our study shows that despite its small body size, the invasive garden ant, *L. neglectus*, shows an impressive competitive ability in one-to-one encounters with the native species *L. grandis*, *L. emarginatus* and *L. cinereus*, promoted both by physical aggression and the use of chemical weapons. High aggression in one-to-one encounters is probably one cause of the rapid expansion of the invasive garden ant. We do not know as yet how frequent these aggressive interactions occur in the field and thus cannot estimate the relative importance of direct competition by aggressive behaviour compared to indirect benefits gained by its large worker densities (TARTALLY 2000) and its high activity patterns (ESPADALER & BERNAL 2004). But we know that the strong competitiveness of *L. neglectus* in both direct and indirect interspecific competition leads to a high ecological dominance of this invasive ant over native species communities, especially other ant species, in its introduced range (reported by VAN LOON & al. 1990, ESPADALER 1999, TARTALLY 2000, DEKONINCK & al. 2002). Consequently, despite its currently limited distribution, this invasive species represents a major threat to the biodiversity in European and Asian ecosystems, so that monitoring and biocontrol (REY & ESPADALER 2005) of the invasive garden ant should be taken very seriously.

Acknowledgements

We thank Xavier Espadaler and Carolina Paris for help in ant collection. This manuscript benefited from discussion with Jacobus J. Boomsma, Xavier Espadaler, and Bernhard Seifert, and from comments of Laurent Keller and an anonymous referee. This study was supported by the European Community's Improving Human Potential Programme under contract HPRN-CT-2000-00052 "INSECTS" and a Feodor-Lynen postdoctoral stipend by the Alexander von Humboldt Foundation (S.C.), and by the Danish National Science Research Council (J.S.P.).

Zusammenfassung

Das Aggressionsverhalten der invasiven Gartenameise, *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, gegenüber drei nativen *Lasius* Arten (*L. grandis* FOREL, 1909, *L. emarginatus* (OLIVIER, 1792) und *L. cinereus* SEIFERT, 1992) wurde in einer spanischen Population (Seva) untersucht. Es wurde getestet, ob *L. neglectus* in der direkten aggressiven Auseinandersetzung mit anderen Arten eine dominante Rolle einnimmt, und ob sich Arbeiterinnen, die an der Expansionsgrenze der invasiven Superkolonie gesammelt wurden, aggressiver gegenüber fremden Arten verhalten, als Arbeiterinnen aus dem Zentrum der Kolonie, die in der Regel nur Artgenossinnen antreffen.

Unsere Studie zeigt, dass *L. neglectus* in der Tat häufiger als die natürlich vorkommenden *Lasius*-Arten eine Attacke initiiert, und auch den Kampf dominiert. Letzteres ergibt sich daraus, dass alle drei nativen Ameisenarten häufiger Fluchtverhalten an den Tag legen als die invasive Gartenameise, welche wiederum häufiger beißt und chemische Waffen (Spritzen von Ameisensäure) im Kampf einsetzt. Es ergab sich kein Unterschied im Kampf von *L. neglectus* gegen die drei verschiedenen Arten, außer dass bei der Interaktion mit *L. grandis* seltener Fluchtverhalten auftrat, die Antennierungsfrequenz aber erhöht war. Außerdem kennzeichneten sich die Kämpfe zwischen diesen beiden Arten durch die kürzeste Zeit aus, die zwischen Zusammensetzen der Ameisen und der ersten Attacke verstrich. Somit kann geschlussfolgert werden, dass *L. grandis* möglicherweise durch die Beanspruchung der ähnlichsten ökologischen Nische den größten natürlichen Konkurrenten von *L. neglectus* in der spanischen Population darstellen könnte. Außerdem könnte der große Größenunterschied zwischen den beiden Arten das starke Aggressionsverhalten erklären. Das Verhalten von *L. neglectus*-Arbeiterinnen im Zentrum und an der Peripherie der Superkolonie unterschied sich nur sehr wenig. So zeigten Ameisen von der Nestgrenze eine höhere (aber nicht signifikant höhere) Tendenz, fremde Ameisenarten anzugreifen.

Insgesamt betrachtet zeigt *L. neglectus* trotz seiner viel kleineren Körpergröße im Vergleich zu den drei natürlich vorkommenden *Lasius*-Arten sehr starke Aggression und deutliche Dominanz gegenüber diesen Arten. Zusammen mit den Vorteilen, die die unikoloniale Populationsstruktur invasiven Ameisen gegenüber nativen Ameisen verleiht, scheint also die direkte aggressive Auseinandersetzung mit natürlichen Konkurrenten eine große Rolle für die Dominanz von *L. neglectus* über natürliche Artengesellschaften in den eingeführten Regionen zu spielen.

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