

Aggressive behaviour of the two European Argentine ant supercolonies (Hymenoptera: Formicidae) towards displaced native ant species of the northeastern Iberian Peninsula

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Abstract

The present study attempts to analyse the aggressive behaviour of the two European supercolonies of the Argentine ant, *Linepithema humile*, in confrontations between them and with several native ant species, to assess if there are differences in their aggressiveness, and consequently, in their competitive ability.

Workers from the Main supercolony were more aggressive than workers from the Catalan supercolony. They showed a higher significant aggressiveness index in confrontations with workers from the Catalan supercolony and with two of the three native ant species studied: in *Tapinoma nigerrimum* (NYLANDER, 1856) and *Lasius cinereus* SEIFERT, 1992, but not in *Pheidole pallidula* (NYLANDER, 1849). They also mainly initiated the aggressive encounters and responded aggressively to attacks during confrontations both with the Catalan supercolony and with the native ant species. As compared to the Main supercolony, workers from the Catalan one showed a reduced aggressive behaviour in confrontations with the native ant species studied. Moreover, the native ant species attacked workers from the Catalan supercolony more frequently than workers from the Main one. These results may support the hypothesis of a weaker competitive ability of the Catalan supercolony, and therefore, a minor invasiveness power, and could also partially explain why that supercolony is clearly less widely distributed throughout Europe than the Main supercolony.

Key words: Aggressiveness, competitive ability, *Lasius cinereus*, *Linepithema humile*, *Pheidole pallidula*, *Tapinoma nigerrimum*.

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Introduction

The Argentine ant (*Linepithema humile* MAYR, 1868), well known as an invasive ant species (MCGLYNN 1999), has spread worldwide (HÖLLDOBLER & WILSON 1990, SUAREZ & al. 2001) as a result of human commercial activities in habitats usually associated with human modification (HOLWAY 1998a, SUAREZ & al. 2001). However, its ability to occupy non-altered habitats has also been reported (COLE & al. 1992, HOLWAY 1998a, GÓMEZ & al. 2003). Its distribution range includes areas with Mediterranean-type climates throughout the world (PASSERA 1994, SUAREZ & al. 1998) and in the specific case of the Iberian Peninsula it is found over the entire coastal band (WETTERER & al. 2009).

In its introduced range, the Argentine ant has impacted native ant faunas leading to changes in arthropod communities (HUMAN & GORDON 1996, 1997, HOLWAY 1998b, SUAREZ & al. 1998), ant-vertebrate interactions (SUAREZ & al. 2000) and ant-plant relationships (BOND & SLINGSBY 1984, VISSER & al. 1996, GÓMEZ & OLIVERAS 2003, BLANCAFORT & GÓMEZ 2005). Its presence has also had negative effects on crops and plantations due to its mutualistic interactions with hemipterans, which reduce plant growth and production (BUCKLEY 1987, NESS & BRONSTEIN 2004).

As with most invasive species, there are several characteristics that contribute to their success in their introduced ranges. One of them is unicoloniality (PASSERA 1994), an

extreme case of polydomy and polygyny in ants. Unicolonial ants have huge colonies formed by a complex network of hundreds or thousands of nests, each with multiple queens (HELANTERÄ & al. 2009). This behaviour gives to the Argentine ant the ability to create enormous aggregations of nests that are non-aggressive among each other. These large aggregations are called "supercolonies" and can range over thousands of kilometers (SUAREZ & al. 1999, TSUTSUI & al. 2000, TSUTSUI & CASE 2001, GIRAUD & al. 2002, SUNAMURA & al. 2009, VAN WILGENBURG & al. 2010).

This unusual social structure allows them to obtain high densities of workers and numerical dominance over native ant species. It is widely recognised that the European population of the Argentine ant consists of two supercolonies: the Main supercolony, which follows the entire coastal band from Italy to the Iberian Peninsula, and the Catalan supercolony, which is smaller than the Main supercolony and apparently restricted to the eastern part of the Iberian Peninsula but mainly present in Catalonia (GIRAUD & al. 2002). There is a total absence of intraspecific aggression between workers from the same supercolony, despite the long distance that can separate them (as many as 6000 kilometers in the Main supercolony). However, there is high aggression between the two supercolonies (GIRAUD & al. 2002).

Aggressive behaviour is an important component of ecological dominance, because it allows exclusive access to resources such as food or nesting sites (ROWLES & O'DOWD 2007, CARPINTERO & REYES-LÓPEZ 2008). In the case of the Argentine ant, the combination of its highly aggressive behaviour in comparison with native ants (HÖLLDOBLER & WILSON 1990, HUMAN & GORDON 1999) and its numerical dominance caused by unicoloniality (HUMAN & GORDON 1996, OLIVERAS & al. 2005) make this species very competitive, which is likely the key to its high level of invasiveness. For this reason, its nestmate recognition system has been studied in depth. Intraspecific aggression in this species may be influenced by several factors. On the one hand, it seems that both genetic and environmental cues can affect its nestmate-discrimination ability (LIANG & SILVERMAN 2000, TSUTSUI & al. 2000, CHEN & NONACS 2002, SUAREZ & al. 2002). On the other, the frequency and intensity of aggression between non-nestmates can also be influenced by behavioural factors. THOMAS & al. (2005, 2006, 2007) reported that workers close to colony boundaries exhibit higher levels of aggression than those living further away, and concluded that the intensity of the intraspecific aggression of these ants may change depending on the history of contact and the nature of those interactions. Moreover, it was also reported that the levels of aggression of this species may, in some cases, change temporally (CHEN & NONACS 2002, SUAREZ & al. 2002). These studies mainly focus on the aggressive interactions among Argentine ant workers belonging to different United States supercolonies, but up to now, not a single study has examined possible differences in the aggression level of supercolonies towards native ants. It seems that the presence of native ants in the Argentine ant's advancing front can offer resistance to the invasion progress (HELLER & al. 2006). Therefore, the degree of competitiveness exhibited by the invader against local ants can play an important role in terms of the invasion success of the species. Against this background, the present study aims to analyse the aggressive behaviour of the two European Argentine ant supercolonies in confrontations between each other and with several native ant species to assess if there are differences in their level of aggressiveness, and consequently, in their potential invasiveness.

Material and methods

Ant colonies and sampling: In May and June 2008, we collected foraging workers from nests of the Argentine ant. The ants were collected from ten different locations in the north-east of the Iberian Peninsula. Previous unpublished studies let us know the exact supercolony to which they belonged. Five of these locations belong to the Main supercolony: Cassà de la Selva (CS), Castell d'Aro (CA), Girona (GI), Llagostera (LLG) and St. Sadurn de l'Heura (SSH); the other five belong to the Catalan supercolony: Fornells de la Selva (FS), Girona-Campus (GIC), Parlavà (PV), Riudellots de la Selva (RS) and St. Cugat del Vallès (SCV) (Fig. 1).

We also collected foraging workers of *Pheidole pallidula* (NYLANDER, 1849) (from 4 nests), *Tapinoma nigerimum* (NYLANDER, 1856) (from 4 nests) and *Lasius cinereus* SEIFERT, 1992 (from 3 nests). Note that *T. nigerimum* currently is placed in synonymy with *T. erraticum* (LATREILLE, 1798) (see BOLTON & al. 2007); we here nev-

ertheless use the name *T. nigerimum* because the male genitalia of the taxon we used differ from *T. erraticum* (cf. SEIFERT 1984; confirmed by comparison with type material deposited at the Museu de Ciències Naturals de Catalunya) and because of distinct chromosome numbers in *T. nigerimum* and *T. erraticum* (PALOMEQUE & al. 1988), but we do not propose a formal taxonomic act here. We chose these three native ant species because they are successfully displaced by the Argentine ant in natural invaded areas (OLIVERAS & al. 2005), and therefore can be of use to compare the potential invasiveness of each supercolony in terms of their ecological dominance. These native ant species were sampled from the non-invaded area in Castell d'Aro (CA) (Fig. 1).

The level of aggression in the Argentine ant can vary in response to the presence of competitors. Repeated encounters with neighbouring individuals may result in a habituation process leading to a reduction in the aggression levels of workers, the so-called "dear-enemy phenomenon" (CHEN & NONACS 2002). Conversely, the Argentine ant can also increase its aggressiveness as a consequence of repeated exposure to individuals from foreign colonies (THOMAS & al. 2007) leading to changes between the intensity of aggression of workers from the colony boundaries and that of workers far away from this contact zone. Due to this plasticity in its recognition system, we collected all the Argentine ant workers of this study from the invasion centre, far from the contact zones. Conversely, we also collected all the native workers from non-invaded areas; therefore, they had had no contact with the invader prior to this study.

Aggressiveness tests: In order to quantify aggressiveness between the two Argentine ant supercolonies and between these supercolonies and the native ant species, we adapted the protocol employed by GRANGIER & al. (2007). To avoid possible changes in the aggression levels of workers through time (CHEN & NONACS 2002, SUAREZ & al. 2002), we carried out all the aggression tests on the same day we collected them from the field. In the lab, we chose at random one worker from each supercolony or species and placed them in a neutral arena (diameter = 2.5 cm, height = 1 cm). The ants were prevented from escaping by coating the walls with Fluon®. The tests began with the first interaction and continued for 5 minutes. We noted: a) the duration of each interaction, b) the supercolony or species that initiated the interaction, and c) the type of behavioural interaction, which was scored as follows:

- (1) Indifference: After making contact with its antagonist, the individual shows neither aggressive nor submissive behaviour.
- (2) Antennation: Repeated tapping of the antennae somewhere on the other ant.
- (3) Escape: The individual moves quickly away after making contact with its opponent.
- (4) Gaster flexion: The individual raises its gaster to a vertical position as a chemical defense.
- (5) Biting: The attacker bites quickly at the body or appendices of its antagonist.
- (6) Fight: Prolonged aggression with amputation of members and / or death of at least one of the contestants.

Furthermore, we classified the above behavioural interactions in two categories: "aggressive behaviour", consisting of levels 4 to 6; and "submissive behaviour", consisting of levels 1 to 3.

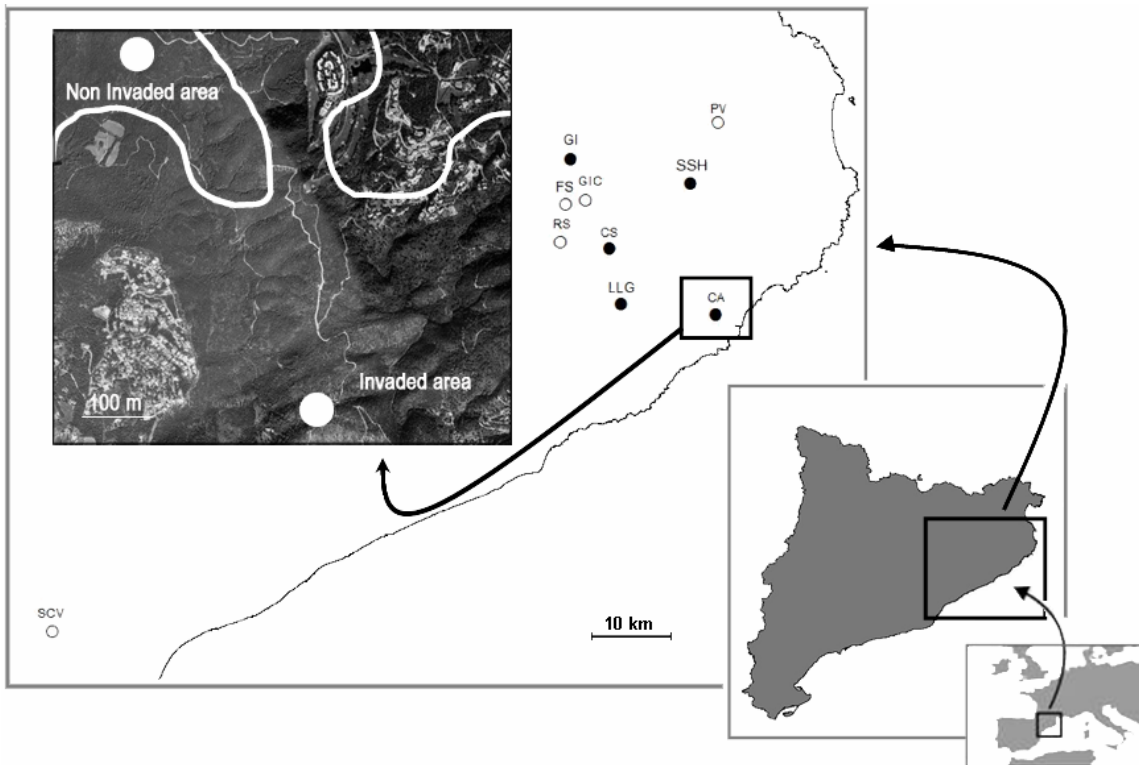


Fig. 1: Collection sites of the Argentine ant colonies in the north-eastern part of Catalonia used in the laboratory aggressiveness tests; abbreviations as in Material and methods. Black circles indicate colonies from the Main supercolony and white circles colonies from the Catalan supercolony. The map on the left illustrates the non-invaded area where the three native ant species were sampled (white spot), while the white spot in the invaded area refers to the place where the Argentine ant workers from the Main supercolony of CA were sampled.

We carried out at random a total of five combinations between the nests belonging to each of the two supercolonies. In order to identify each worker we marked them with Uni paint marker pens (Mitsubishi Pencil Co., LTD.) on the dorsal surface of their thorax. The final combinations were (CS-FS, LLG-GIC, SSH-PV, GI-SCV, and CA-RS). Distances between collection sites in confrontation ranged from 7.2 km (CS-FS) to 84.4 km (GI-SCV).

We also confronted each of the supercolonies with the three native ant species mentioned above. We made a total of four combinations for each supercolony (Main supercolony = CA, CS, GI, and SSH; Catalan supercolony = FS, GIC, PV and SCV) using workers from four different nests of *Pheidole pallidula* and *Tapinoma nigerrimum*, and a total of three combinations with workers from three nests belonging to *Lasius cinereus* (Main supercolony = CA, CS and GI; Catalan supercolony = FS, GIC and SCV).

A total of 15 trials were performed for each combination using different individuals each time. The trials were all carried out one by one and always by the same person.

To estimate 1) the aggressiveness level of each opponent in confrontations between the supercolonies and between the supercolonies and the native ant species, and 2) the intensity of aggression demonstrated by each opponent in the above-mentioned confrontations, we used an aggressiveness index obtained from ERRARD & HEFETZ (1997):

$$\frac{\sum_{i=1}^n \delta_i t_i}{T}$$

where δ_i and t_i are the interaction index and the duration of each act, respectively, and T is the total time during which the ants were in physical contact.

To estimate the aggressiveness level of each opponent, we calculated the index using all the interactions observed in the confrontations (levels 1 - 6), whereas to estimate the intensity of aggression exhibited by each opponent in the confrontation, we calculated the index using only the levels included in the "aggressive behaviour" category (levels 4 to 6).

We compared data on aggressiveness between the supercolonies and among the supercolonies and native species by means of generalised linear mixed models (GLMMs) with nest as a random factor and colony identity as a fixed factor. We used data collected on the supercolony / species that initiated the encounters to report the frequency of initiations of aggressive acts by each supercolony and native species. We compared the results obtained using binomial probability tests. We also analysed the individual behaviour of each supercolony and native ant species, and reported the frequency of acts involving aggressive or submissive behaviour in individuals initiating or responding to encounters. We compared the results obtained using Fisher's exact test. We used the S-Plus statistical package version 6.1 for all analyses.

Results

Initiations of aggressive acts: The Main supercolony usually attacked first in encounters with the Catalan supercolony, and also with each of the native ant species studied (Tab. 1). On the other hand, the Catalan supercolony did not show significant differences in the frequency of initiations of aggressive acts with *Pheidole pallidula* and *Tapinoma nigerrimum*, but it did with *Lasius cinereus*, which

Tab. 1: Proportion of aggressive encounters during which the Argentine ant supercolonies / native ant species initiated the first aggressive act. Sample sizes are in parenthesis. Significance level at * $P < 0.025$, ** $P < 0.005$ and *** $P < 0.0005$ after the application of Bonferroni Correction Probabilities.

	Aggression initiation (%)
Main supercolony vs. Catalan supercolony	91 / 9 (75) ***
Main supercolony vs. <i>P. pallidula</i>	67.5 / 32.5 (60) *
Catalan supercolony vs. <i>P. pallidula</i>	47 / 53 (60)
Main supercolony vs. <i>T. nigerrimum</i>	95 / 5 (60) ***
Catalan supercolony vs. <i>T. nigerrimum</i>	33 / 67 (60)
Main supercolony vs. <i>L. cinereus</i>	80 / 20 (45) ***
Catalan supercolony vs. <i>L. cinereus</i>	15 / 85 (45) ***

tended to initiate the attacks when confronted with the Catalan supercolony (Tab. 1). Moreover, all native ant species studied attacked first more frequently in encounters with the Catalan supercolony than with the Main supercolony (Tab. 1).

Initiation and response to encounters: During a trial, when workers from the Main supercolony initiated the aggressive behaviour, they were more aggressive than the Catalan supercolony with *P. pallidula* and *T. nigerrimum* (Tab. 2: "aggressive action": proportion of aggressive acts (level 4 - 6) for individuals initiating aggressive encounters; "aggressive response": proportion of aggressive acts (level 4 - 6) for individuals responding to aggressive encounters; "non-aggressive action": proportion of submissive acts (level 1 - 3) for individuals initiating aggressive encounters; "non-aggressive response": proportion of submissive acts (level 1 - 3) for individuals responding to aggressive encounters). Workers from the Main supercolony also responded to the aggression of *P. pallidula* with higher frequencies of aggressive acts than the Catalan supercolony.

On the other hand, although the Catalan supercolony also tended to be aggressive when initiating attacks during a confrontation with workers belonging to the Main supercolony and *L. cinereus*, this was not so clear with workers from *P. pallidula* and *T. nigerrimum*. The frequencies of aggressive encounters when its workers initiated the attacks in confrontations with these species were similar to the frequencies of non-aggressive encounters (Tab. 2).

As for the individual behaviour of the native ant species when initiating or responding to attacks, we observed some differences in their behaviours depending on the supercolony that they had as an opponent (Tab. 2): *Pheidole pallidula* responded non-aggressively to the attacks from the Main supercolony, whereas with workers of the Catalan supercolony they tended to respond aggressively. *Lasius cinereus* when responding to the attacks by the Argentine ant, acted submissively more frequently with the Main supercolony than with the Catalan supercolony. When encountering workers of the Main supercolony, *T. nigerrimum* tended to show non-aggressive behaviour (main-

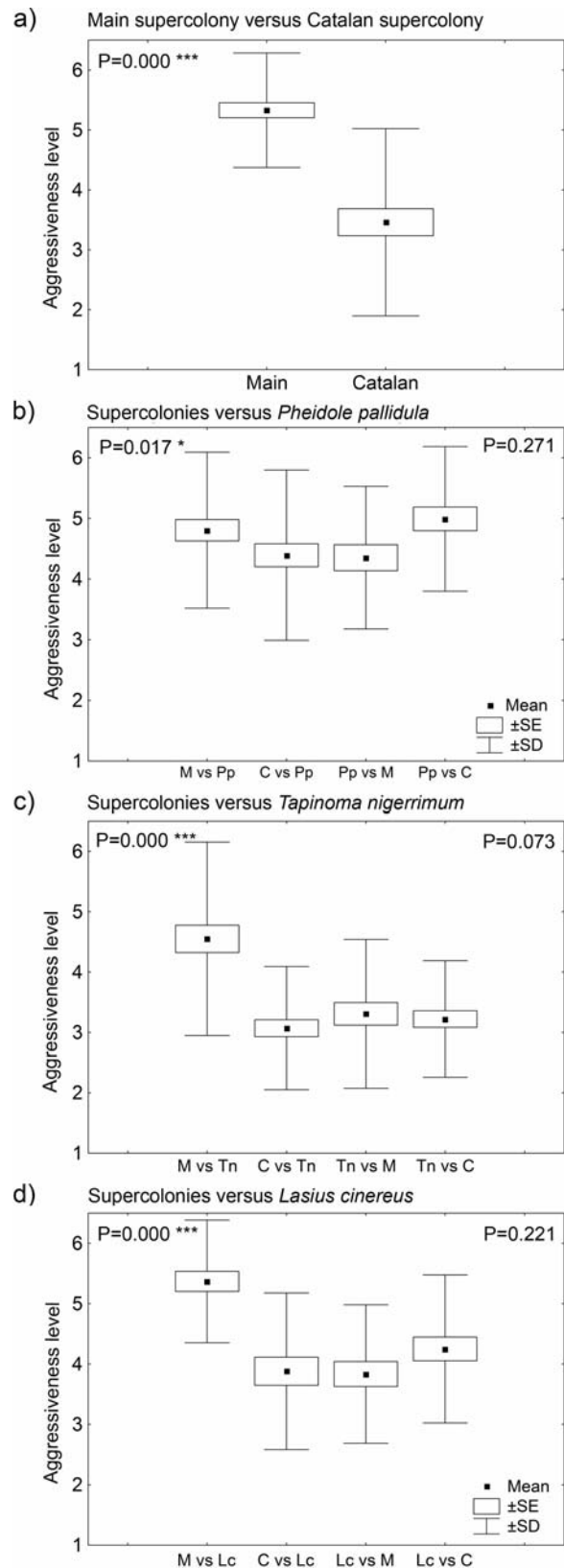


Fig. 2: Aggressiveness level recorded during confrontations between the Argentine ant supercolonies / native ant species under study. P_{adj} = Adjusted probabilities following sequential Bonferroni Correction with a significance level of * $P_{adj} < 0.025$, ** $P_{adj} < 0.005$ and *** $P_{adj} < 0.0005$, respectively. M = Main supercolony; C = Catalan supercolony; Pp = *P. pallidula*; Tn = *T. nigerrimum*; Lc = *L. cinereus*.

Tab. 2: Proportion of acts involving aggressive (physical or chemical attack) or submissive (indifference, antennation and escape) behaviour in individuals initiating or responding to attacks. Frequencies of aggressive / non-aggressive acts between the species / supercolonies in confrontation. Samples sizes are in parenthesis. Significance level at * $P < 0.025$; ** $P < 0.005$ and *** $P < 0.0005$ after the application of Bonferroni Correction Probabilities.

Species pair	ACTION (Aggressive / Non-aggressive actions)			RESPONSE (Aggressive / Non-aggressive actions)		
	Sp1	Sp2	Fisher's exact test	Sp1	Sp2	Fisher's exact test
Main supercolony ^{sp1} vs. Catalan supercolony ^{sp2}	81 / 19 (141)	83 / 17 (12)	ns	80 / 20 (5)	20 / 80 (50)	***
Main ^{sp1} / Catalan ^{sp2} supercolony vs. <i>P. pallidula</i>	76 / 24(116)	60 / 40 (65)	*	79 / 21 (43)	34 / 66 (56)	***
<i>P. pallidula</i> vs. Main ^{sp1} / Catalan supercolony ^{sp2}	88 / 11 (26)	96 / 4 (53)	***	36 / 64 (11)	73 / 27 (15)	***
Main ^{sp1} / Catalan ^{sp2} supercolony vs. <i>T. nigerrimum</i>	93 / 7 (134)	50 / 50 (26)	***	25 / 75 (4)	20 / 71 (34)	ns
<i>T. nigerrimum</i> vs. Main ^{sp1} / Catalan supercolony ^{sp2}	22 / 78 (9)	53 / 47 (43)	***	21 / 79 (42)	100 / 0 (9)	***
Main ^{sp1} / Catalan ^{sp2} supercolony vs. <i>L. cinereus</i>	88 / 12 (85)	86 / 14 (7)	ns	67 / 33 (12)	67 / 33 (24)	ns
<i>L. cinereus</i> vs. Main ^{sp1} / Catalan supercolony ^{sp2}	54 / 46 (46)	56 / 44 (89)	ns	20 / 80 (30)	50 / 50 (4)	***

ly escape) both after initiating and as a response to the confrontation, but showed higher frequencies of encounters involving aggressive behaviour as a response to the attacks with workers belonging to the Catalan supercolony.

Level and intensity of aggressions: The Main supercolony was significantly more aggressive than the Catalan supercolony (GLMM: $F = 183.43$; $P < 0.0005$) (Fig. 2a), but the two supercolonies attacked with the same intensity (GLMM: $F = 0.94$; $P = 0.71$).

With regard to the aggressiveness of each supercolony when encountering native ant species, we observed that, in general, the Catalan supercolony showed a lower level of aggressiveness when facing these species than did the Main supercolony. In the case of confrontations with *T. nigerrimum* and *L. cinereus*, the Main supercolony was significantly more aggressive than the Catalan supercolony (GLMM *T. nigerrimum*: $F = 81.62$; $P < 0.0005$; GLMM *L. cinereus*: $F = 26.03$; $P < 0.0005$), whereas with *P. pallidula* there were no detected differences (GLMM: $F = 1.79$; $P = 0.27$) (Fig. 2b). Instead, we observed significant differences in the aggressiveness level shown by *P. pallidula* towards the supercolonies. This species was more aggressive with the Catalan supercolony than with the Main supercolony (GLMM: $F = 57.31$; $P < 0.025$) (Fig. 2b). With respect to the other native ant species observed, there were no detected differences in their aggressiveness towards the two supercolonies (GLMM *T. nigerrimum*: $F = 7.28$; $P = 0.073$; *L. cinereus*: $F = 3.11$; $P = 0.22$) (Fig. 2c, d).

There were no differences in the intensity of aggression between all the confrontations studied except for *T. nigerrimum*, which attacked the Main supercolony more intensely than the Catalan one (GLMM *T. nigerrimum*: $F = 28.18$; $P < 0.0005$). These differences in the intensity of

attack may be a product of the high aggressiveness shown by the Main supercolony towards workers of this native species, which induces them to respond as fiercely as they do.

Other observed behaviour: The most common form of aggressive behaviour was physical attack. In the case of confrontations between the two supercolonies, all the aggressive behaviour was in the form of physical attack, whereas, the confrontations of the Argentine ant with *P. pallidula*, *T. nigerrimum* and *L. cinereus* represented 89.2%, 97% and 96.2%, respectively, of physical attacks as opposed to chemical attacks, which were only observed to be carried out by the Argentine ant.

In the case of *P. pallidula*, we frequently observed another form of aggressive behaviour. Workers tended to stay immobile with the mandibles opened, threatening the intruder. We also observed this behaviour with the Argentine ant, during the confrontations between supercolonies and also with *L. cinereus*, but this was less frequent (only five occasions in total) than in the case of *P. pallidula*, and also less apparent.

The most common non-aggressive behaviour observed in all confrontations was escape, which accounted for 94.2% of all non-aggressive encounters. The remaining 5.8% of non-aggressive encounters fell into the "other behaviour" category, composed of level 1 and 2 behavioural interactions.

In the case of workers from the Catalan supercolony, we also observed some curious submissive behaviour, which was only shown in the presence of the Main supercolony. When the Main supercolony attacked workers from the Catalan supercolony, the latter adopted a pupal posture by folding their antennae and legs in against their bodies and remaining motionless in this posture (this behaviour was

observed during encounters with a frequency of 10.6%). The worker from the Main supercolony usually stopped the aggression when the Catalan worker adopted this posture but, sometimes (in two occasions), it picked up the Catalan worker with its mandibles and carried it around the entire neutral arena. On some occasions (five times of 75 confrontations) we also observed another kind of submissive behaviour shown by workers belonging to the Catalan supercolony when confronted with workers from the Main supercolony. In this case, after a strong aggressive confrontation between the two workers in which the worker from the Main supercolony had been biting the Catalan worker intensely, the Catalan worker became immobile while its opponent climbed over it making quick bites. The Catalan worker responded to this behaviour remaining motionless while crouching and, sometimes, with its mandibles open.

Discussion

In confrontations between the two Argentine ant supercolonies, workers from the Main supercolony exhibited a higher degree of aggressiveness than workers from the Catalan supercolony, both when initiating aggressive behaviour and when responding to attacks. The Catalan supercolony, when confronted with the Main supercolony, showed submissive behaviour. Workers avoided confrontation during encounters and were usually the ones that received the attacks, responding non-aggressively to them. They even resorted to the use of ritualised behaviours to appease their opponent, some of them similar to the dominant behaviour exhibited among queens of the ant species *Nothomyrmecia macrops* CLARK, 1934 or among workers of *Polyrhachis laboriosa* SMITH, 1858 (see HÖLLDOBLER & WILSON 1990, MERCIER & al. 1997). The use of submissive behaviour is a clear indication of a dominance relationship between individuals (DE VRIES 1998), and in the case of the two supercolonies this indicates the dominance of the Main supercolony workers over the Catalan ones.

Recently, a study carried out by SUNAMURA & al. (2009) showed that Argentine ant workers from the dominant supercolonies of California, Europe (corresponding to the Main supercolony) and Japan, together with workers from the Macaronesian populations, did not show aggressive behaviour among them, comprising the largest global supercolony formed by a social insect. All supercolonies which formed this large transcontinental unit are also the largest supercolony present in the invaded area where it is found, being locally dominant as well. One explanation to this is that this supercolony is a superior competitor which displaces the other smaller supercolonies and avoids the establishment of new populations (VAN WILGENBURG & al. 2010). In accordance with this idea, and supported by our findings in the present study, workers from the Main supercolony in Europe may be competitively superior to workers from the Catalan one.

On the other hand, TSUTSUI & al. (2003) found asymmetries in aggression between workers from the larger Californian supercolony and the smaller Californian supercolonies, with the former being more aggressive than the latter. They suggested that these findings are a result of an asymmetry in genetic diversity, thus workers from less genetically diverse colonies are more aggressive and survive antagonistic encounters more often than individuals from

more diverse colonies. Therefore, and according to GIRAUD & al. (2002: Fig. 3) and also to our results, this suggests that the Main supercolony in Europe has less genetic diversity than the Catalan supercolony.

The Catalan supercolony is less abundant and barely spreading in Catalonia in comparison with the Main supercolony (GIRAUD & al. 2002; S. Abril & C. Gómez, unpubl.). Moreover, there is no evidence of its presence in other territories of Europe, its distribution being restricted to the north-east of the Iberian Peninsula (GIRAUD & al. 2002; S. Abril & C. Gómez, unpubl.). Recently, it was shown that the two supercolonies have separate gene pools, even when the respective nests are in close proximity (as close as 27 meters) (JAQUIÉRY & al. 2005). Based on these findings, it was hypothesised that these two European Argentine ant supercolonies came from two different and independent introduction processes from the native South American populations (JAQUIÉRY & al. 2005). Moreover, studies on the mitochondrial haplotype of workers from several worldwide introduced populations of the Argentine ant show that, in the case of the Catalan population, its workers have a unique mitochondrial haplotype which is not found in the other introduced populations (VOGEL & al. 2010). Thus, these results also support the idea that the Catalan supercolony resulted from an independent introduction process. This could explain, in part, why the Catalan supercolony is less widely distributed in Europe than the Main supercolony, which clearly has a wider distribution range: The less abundant Catalan supercolony could have been introduced to Europe at a later date. However, the finding in this study of the greater dominance exercised by the Main supercolony over the Catalan one could be another, non-exclusive explanation of these differences in the distribution range of the two supercolonies in Europe. This dominance may restrict the Catalan supercolony's access to resources such as food or space, leading to a lower dispersal capacity of this supercolony in places where the Main supercolony is also present.

With regard to the behavioural interactions of the two Argentine ant supercolonies with the native ant species studied, workers from the Main supercolony are more aggressive towards the native ant species than workers from the Catalan supercolony. Although the two supercolonies attack the native ant workers with the same intensity, the aggressiveness level of the Main supercolony is significantly higher than that of the Catalan supercolony in confrontations with *T. nigerrimum* and *L. cinereus*, and with *P. pallidula* it is also somewhat, though not significantly, higher. Workers from the Main supercolony also initiate far more aggressive interactions in confrontations with the native species than workers from the Catalan supercolony do.

The individual behaviour of native ant workers also varied depending on the supercolony that they were confronting. Workers from the species *P. pallidula* were more aggressive towards workers from the Catalan supercolony than towards workers from the Main supercolony. The aggressive behaviour of this native species towards the two supercolonies is surprisingly different. While in confrontations with workers from the Main supercolony they do not tend to attack their opponent, with workers from the Catalan supercolony, they are the main initiators of aggressions. They also respond to aggressions from the Catalan supercolony mainly with aggressive behaviour, while their re-

sponse is radically different with workers from the Main supercolony since they tend to escape rather than to return the attack. *Tapinoma nigerrimum* and *L. cinereus* are less aggressive than *P. pallidula*. Workers of *P. pallidula* are always threatening their opponent with ritualised behaviours, such as staying immobile with the mandibles open and always ready to attack, while workers of *T. nigerrimum* and *L. cinereus* present a less aggressive behaviour, trying more frequently to escape from their opponents than to attack. Attacks are in the form of quick bites, and constant attempts to flee from the rival. Despite this more submissive behaviour, they also present some differences in their behavioural interactions with the two supercolonies. Both *T. nigerrimum* and *L. cinereus* workers initiate more aggressive interactions with workers from the Catalan supercolony than with workers from the Main one. They also present a higher frequency of encounters involving aggressive behaviour with the Catalan supercolony when initiating the attacks and when responding to them, respectively. All this clearly shows a strong tendency of the native ant species to attack workers from the Catalan supercolony more frequently than workers from the Main supercolony. This could result in a weaker invasive ability of the Catalan supercolony in relation to the Main one, and could also partially explain the apparent smaller dispersion capacity of the Catalan supercolony. All this leads us to raise new questions: Are native ant species more resistant to the Catalan Argentine ant supercolony invasion? Can the areas invaded by the Catalan supercolony be recolonised by certain more dominant native ant species?

Further research is necessary to respond to these questions. Although our results provide some support for the hypothesis that the Catalan supercolony might have a less competitive ability than the Main supercolony, our experimental procedure was artificial as it forced the two ant species to interact with each other in a small neutral arena. This method allows us to evaluate the direct competitive ability of each supercolony in one-to-one confrontations between them and also with some native ant species, but not the colony-level competitive ability, which is likely to be influenced by several other factors. Therefore, studies on the relationship between aggressiveness and competitive ability for the two European supercolonies are needed to shed light on their exact ecological interactions in the field.

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Zusammenfassung

Die vorliegende Arbeit untersucht das aggressive Verhalten von zwei europäischen Superkolonien der Argentinischen Ameise, *Linepithema humile*, in Konfrontationen zwischen ihnen und mit einigen einheimischen Ameisenarten, um Unterschiede in Aggressivität und folglich Konkurrenzfähigkeit der zwei Superkolonien zu erfassen.

Arbeiterinnen der größeren Superkolonie ("Main supercolony") waren aggressiver als Arbeiterinnen der katalanischen Superkolonie. Sie wiesen einen höheren Aggres-

sionsindex in Konfrontationen mit Arbeiterinnen der katalanischen Superkolonie und mit zwei der drei untersuchten einheimischen Ameisenarten auf, nämlich mit *Tapinoma nigerrimum* (NYLANDER, 1856) und *Lasius cinereus* SEIFERT, 1992, jedoch nicht mit *Pheidole pallidula* (NYLANDER, 1849). Außerdem begannen sie häufiger aggressive Interaktionen und reagierten aggressiv auf Attacken während der Konfrontationen mit der katalanischen Superkolonie und mit den einheimischen Ameisenarten. Verglichen mit der größeren Superkolonie zeigten Arbeiterinnen der katalanischen reduziertes Aggressionsverhalten in Konfrontationen mit den untersuchten einheimischen Ameisenarten. Des Weiteren attackierten die einheimischen Ameisenarten häufiger Arbeiterinnen der katalanischen als solche der größeren Superkolonie. Diese Ergebnisse könnten die Hypothese einer schwächeren Konkurrenzfähigkeit und einer dadurch geringeren Fähigkeit zur Invasion der katalanischen Superkolonie unterstützen und könnten somit zumindest teilweise erklären, warum die katalanische Superkolonie in Europa deutlich weniger weit verbreitet ist als die größere Superkolonie.

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