

# A native ant armed to limit the spread of the Argentine ant

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**Abstract** Argentine ants (*Linepithema humile*) usually actively displace native ants through a combination of rapid recruitment, high numerical dominance and intense aggressive fights. However, in some cases, native ants can offer a strong resistance. In Corsica, a French Mediterranean island, local resistance by the dominant *Tapinoma nigerrimum* has been proposed as a factor limiting Argentine ant invasion. With the aim of evaluating the abilities of *T. nigerrimum* in interference and exploitative competition, this study tested in the laboratory the aggressive interactions between this native dominant ant and the invasive Argentine ant. We used four different assays between *L. humile* and *T. nigerrimum*: (1) worker dyadic interactions, (2) symmetrical group interactions, (3) intruder introductions into an established resident colony, and (4) a competition for space and food. This study confirms the ability of Argentine ants to compete with native species, by initiating more fights, using cooperation and simultaneously deploying physical and chemical defenses. However, despite Argentine ant fighting capabilities, *T. nigerrimum* was more efficient in both interference and exploitative competition. Its superiority was obvious in the space

and food competition assays, where *T. nigerrimum* dominated food in 100% of the replicates after 1 h and invaded Argentine ant nests while the reverse was never observed. The death feigning behavior exhibited by Argentine ant workers also suggests the native ant's superiority. Our study thus demonstrates that *T. nigerrimum* can offer strong competition and so may be able to limit the spread of Argentine ants in Corsica. This confirms that interspecific competition from ecologically dominant native species can affect the invasion success of invaders, notably by decreasing the likelihood of incipient colony establishment and survival.

**Keywords** *L. humile* · *T. nigerrimum* · Competition · Bioassays · Propagule · Invasion process

## Introduction

The introduction of exotic species to a previously unoccupied region is considered to be a key threat to the integrity of many natural habitats and ecosystems worldwide (Vitousek et al. 1997). Among invasive arthropod species, ants are considered as serious ecological and economic pests (Holway et al. 2002a). These invasions are multi-step processes and occur when species are transported and become established

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in a new range in which they persist, proliferate and spread (Kolar and Lodge 2001; Mack et al. 2002). The earliest stage of the invasion process after arrival, i.e. the dynamics of establishment and initial persistence of an incipient colony, is a critical stage in the success of invasive ants. The differences in success not only among genera but also for one species in different field contexts suggest that several factors such as propagule pressure (Lockwood et al. 2005), specific ecological characteristics (e.g. nesting habits, Suarez et al. 2005), abiotic conditions (Holway 1998; Holway et al. 2002b; Thomas and Holway 2005) and competition from ecologically dominant or functionally similar species (Walters and Mackay 2005) may influence species establishment and survival. As soon as exotic ants arrive in new habitats, they compete for resources (food and space) with native ants. Their ability to survive long enough and to displace enough native colonies is critical to their becoming dominant and invasive. Sometimes they succeed (Human and Gordon 1996), sometimes they fail (Walters and Mackay 2005).

Like many invasive ant species, *Linepithema humile* (*Dolichoderinae*) spreads easily around the world from its native range in South America, mainly through trade (Suarez et al. 2001). Argentine ants generally prosper in disturbed or modified habitats such as agricultural land and urban environments. They are one of the most damaging invaders both in ecological and in economic terms (Vega and Rust 2001). They invariably reduce the number of native ant species (Rowles and O'Dowd 2007; Suarez et al. 1998). They can also negatively affect other non-ant invertebrates (Cole et al. 1992; Human and Gordon 1997) and can disrupt important ant-plant mutualistic relationships (Carney et al. 2003; Christian 2001; Gomez and Oliveras 2003). *L. humile* displays characteristics typical of tramp species, such as small size, monomorphism of worker caste, high polygyny, reproduction by budding and unicoloniality (Hölldobler 1990; Passera 1994). Argentine ants are strong competitors in both forms of competition occurring in ant communities, i.e. exploitative competition and interference competition (Holway 1999; Human and Gordon 1996; Rowles and O'Dowd 2007). Exploitative competition involves the ability of an ant species to locate a resource quickly and recruit large numbers of workers to the resource before other species of ants arrive (Hölldobler 1990). Interference

competition involves the ability of an ant species to defend a resource from other ant species or dominate a resource by aggressively displacing the ants already at the resource (Hölldobler 1990). Within the introduced range, *L. humile* exhibits unicolonial colony structures consisting of large colonies that lack boundaries due to absence of aggression (Blight et al. 2010; Giraud et al. 2002; Tsutsui et al. 2000). They compensate for their mortality rate with high worker numbers, forage more efficiently and may allocate more resources to colony growth, providing this invader with a numerical advantage allowing rapid recruitment of many workers and thus making them strong competitors for resources exploitation (Holway 1999; Human and Gordon 1996, 1999). Among the contributing factors which may explain the interference competitive asymmetry between Argentine ants and native ants, numerical superiority (Holway 1999; Human and Gordon 1999), aggressiveness (Carpintero and Reyes-Lopez 2008; Holway and Case 2001; Human and Gordon 1999) and fight strategies such as cooperation or defensive techniques are thought to be the most important (Buczowski and Bennett 2008; Holway 1999). For instance, their ability to use simultaneously mechanical and chemical defenses influences the outcome of fights against *Tapinoma sessile* (Buczowski and Bennett 2008).

Native ants are affected by *L. humile* to varying degrees due to different intensities of competitive and aggressive interactions (Carpintero et al. 2007; Human and Gordon 1996). For instance, Holway (1999) observed that Argentine ants reduced the numbers of several native ant workers, with the notable exception of *Monomorium ergatogyna*. In some cases, local ants can offer strong resistance and can delay or prevent the spread of Argentine ants (Walters and Mackay 2005; Way et al. 1997; Wetterer et al. 2006). This strong competition usually occurs when the invader encounters an ecologically dominant or functionally similar native species. In Corsica, a French Mediterranean island, two ant species from the genus *Tapinoma*, *Tapinoma nigerrimum* and *Tapinoma simrothi*, can be described as dominant in the sense that they are widespread and abundant forming large polygynous and polydomous colonies with interconnected nests with thousands of workers and displaying mass recruitment to a food source (personal observation). They belong to the subfamily

*Dolichoderinae* and have polymorphic workers ranging from 2.5 to 5.1 mm (Gomez and Espadaler 1998). They share numerous features of foraging with the Argentine ant (e.g. mass recruitment and similar diet, with a preference for hemipterans exudates). *T. nigerrimum* was considered as dominant when competing for food with *L. humile* in Portuguese open land (Way et al. 1997). Given the morphological, behavioral, and ecological characteristics of the two *Tapinoma* species, local resistance has been proposed to explain Argentine ant distribution in Corsica (Blight et al. 2009; Casevitz-Weulersse and Brun 1999). While *L. humile* and the two *Tapinoma* species usually share the same habitat, and are present along the Corsican coast, only two co-occurrences have been observed between small colonies of both species. An almost systematic exclusion seemed to arise between Argentine ants and *Tapinoma*. Despite a marked spread over the last decade, Argentine ants are found discontinuously along the coastal strip (Blight et al. 2009). This observation is interesting considering the relative fragility of island populations (Williamson 1996) and the invasiveness of the Argentine ant notably in Mediterranean Island ecosystems (Gomez and Espadaler 2006).

With the aim of evaluating the performance of Corsican *Tapinoma* in both interference and exploitative competition, this laboratory study tested aggressive interactions with the invasive Argentine ant. Due to the close biological, behavioral, morphological and ecological similarities between the two *Tapinoma* species present on the island, we performed our experiments using *T. nigerrimum* the most common species along the Corsican coast. We conducted four different assays: (1) worker-dyad interactions and (2) symmetrical group interactions to test species' capacity for interference competition, (3) intruder introductions into an established resident colony to test the defense capabilities of whole colonies against individual workers and vice versa and (4) a resource competition assay focusing on competition for food and nesting space to help explain species' capacity for exploitative competition. These bioassays were conducted to answer the following questions: is *T. nigerrimum* armed and able (1) to compete with the Argentine ant and (2) to limit the success of this invader establishment, survival and spread?

## Materials and methods

### Study context and field collection

Argentine ants and *T. nigerrimum* colony fragments were both collected in the north of Corsica in June 2008. A minimum of 10,000 workers and 20 queens were collected from one nest of each colony. Nest fragments were kept in a plastic nest container (360 × 240 × 110 mm) filled with original nest material. In addition to proteins provided by arthropods caught with their original substrate, ants were fed with honey. Colonies were maintained in the laboratory at  $23 \pm 2^\circ\text{C}$  with the appropriate soil moisture.

### Behavioral assays

For the purposes of comparison with the findings of Buczkowski and Bennett (2008), who studied interactions between the Argentine ant and the odorous house ant, *Tapinoma sessile*, we performed behavioral assays analogous to theirs.

#### *One-on-one*

The one-on-one bioassays were conducted in plastic dishes of 5.5 cm of diameter, with the aim of determining the fighting abilities of individual workers of both species. Behavioral tests were videotaped for 15 min and saved on a storage unit. From the recording videotape, we monitored behavioral interactions between workers, using the following classification of ant interactions: 1 = ignore, 2 = avoid, 3 = aggression (lunging, brief bouts of biting, and/or pulling), 4 = fighting (prolonged aggression, also abdomen curling to deposit defensive compounds) (Suarez et al. 2002). We conserved the maximum score per trial, averaged across forty replicates. We also recorded the fight initiator, the fight winner (a species was considered as winner when it killed the other species) and the techniques employed by both species (i.e. physical aggression, chemical defenses, or both). Physical aggressions were defined as commencing as soon as workers opened their mandibles to bite the enemy and the use of chemical defenses (toxic venom) was defined as when we observed gaster flexions.

### *Symmetrical group confrontation*

The objective of this symmetrical group confrontation assay was to test the competitive ability of the two species in equal groups. Twenty-five randomly selected workers of both species were transferred simultaneously to a plastic dish (9 cm diameter) with moist plaster. We monitored behavioral interactions between workers during a 10 s scan every 2 min for 20 min and then another 10 s scan at 40 min, 1, 2, 3, 4 and 5 h after the bioassay began, using the previous ant interaction classification. We conserved the maximum score per trial, averaged across sixteen replicates. At each time point we also recorded the number of dead workers.

### *Intruder introduction*

An individual was introduced into a resident colony of the other species. This experimental design was used to simulate introduction *in natura* of individuals into the enemy territory and to highlight differences in the reaction of resident colonies of a native species and an invasive species toward enemy introductions. The intruder was removed from the colony 5 min after the first contact with the workers of the resident colony. We noted: the maximum level of aggression, the fight initiator and the number of resident colony workers involved in the fight. Forty introductions of Argentine ants into a resident colony of *T. nigerrimum* and forty introductions of *T. nigerrimum* into a resident colony of Argentine ants were performed.

### *Competition for space and food*

500 workers, queens and brood from each of the two species were placed in closed artificial nests with moist plaster (250 × 215 × 40 mm). Artificial nests were connected via plastic tubes to a common foraging arena (360 × 240 × 140 mm). Ants were acclimated to their nests for 2 days without food. On day 3, artificial nests were opened, allowing the workers to access the foraging arena where honey was placed in the center. After the nests were opened, we monitored the colonies every hour over 8 h the first day and then twice a day (morning and afternoon) for 5 days to determine which species discovered the food first, which species dominated the food resource over the 6 days of interactions and

where both species nested. At the end of the test (day 8), we recorded the distribution of workers of both species, noting whether the ants nested in their own nest and/or the nest of the opposing species and recording the number of dead ants. Eight replicates of this resource competition test were conducted.

### *Statistical analyses*

Prior to statistical analysis, we examined all data distributions using the Shapiro–Wilk *W* test for normality. Except for differences in number of dead workers at the end of the group confrontation, data did not conform to a normal distribution even after log transformation. Differences in mortality at the end of the group confrontation were analyzed using a Student *t*-test. Differences in levels of aggressive interactions and in number of ants involved in fights were compared using the non-parametric Mann–Whitney *U* test for independent data. Differences in mortality in the competition for space and food bioassay were compared using the non-parametric Wilcoxon signed-rank test for dependent data. Differences in the proportion of fight winner, fight initiator and defensive techniques employed in fights were analyzed using Fisher's exact test and Chi-square test. All data analyzes were performed using the software Statistica v.6 (Statsoft 2001).

## **Results**

### *One-on-one*

One-on-one bioassay showed moderate aggression. The maximum aggression score was on average  $3.3 \pm 0.1$  SE between *L. humile* and *T. nigerrimum*. Acts of aggression chiefly consisted of brief aggressive contacts. We counted 253 aggressive interactions among the 40 replicates. An average of seven interactions was recorded per replicate. *T. nigerrimum* initiated 103/253 (41%) whereas Argentine ants initiated 150/253 (59%) ( $df = 1$ ,  $P < 0.0001$ , Chi-square test) (Table 1).

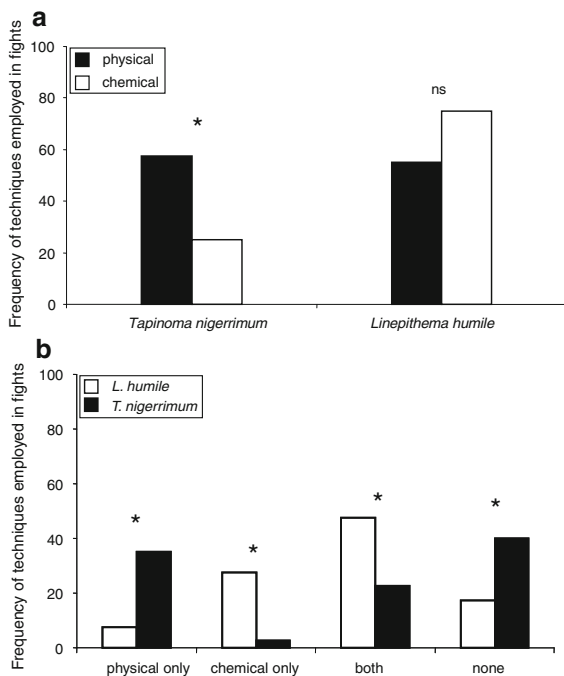
Although *T. nigerrimum* initiated less aggressive interactions, they won (death of the Argentine ant worker) 7/40 (17.5%) of the replicates and Argentine ants won (death of the *T. nigerrimum* worker) only 1/40 (2.5%) of the replicates ( $df = 1$ ,  $P < 0.05$ ,

Fisher's exact test) (Table 1). In 31/40 (77.5%) no winner was identified at the end of the 15 min and one encounter led to the death of both species.

Both species used physical aggression and chemical defensive compounds in fights. Argentine ant workers used chemical defense (either alone or in conjunction with physical defenses) in 30/40 (75%) replicates and they used physical aggression (either alone or in conjunction with chemical defenses) in 22/40 (55%) ( $df = 1$ ,  $P = 0.05$ , Fisher's exact test) (Fig. 1a). *T. nigerrimum* used chemical defense (either alone or in conjunction with physical defenses) in 10/40 (25%) and they used physical aggression

**Table 1** Frequency of fight initiations and fight winner in the one-on-one bioassay, fight initiator ( $n = 253$ ), fight winner ( $n = 40$ )

	Fight initiator	Fight winner
<i>T. nigerrimum</i>	103/253 (41%)	7/40 (17.5%)
<i>L. humile</i>	150/253 (59%)	1/40 (2.5%)



**Fig. 1** The frequency of use **a** of physical and chemical defenses in the Argentine ant and *T. nigerrimum* and **b** of physical defense alone, chemical defense alone, physical and chemical defense simultaneously and lack of any defensive techniques ( $n = 40$ ), ns indicates non significant, \*  $< 0.05$

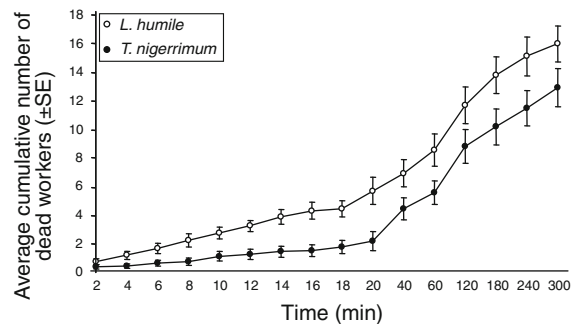
(either alone or in conjunction with chemical defenses) in 23/40 (57.5%) of the replicates (Fig. 1a) ( $df = 1$ ,  $P < 0.01$ , Fisher's exact test) (Fig. 1a).

Argentine ants used both types of aggression simultaneously in 19/40 (47.5%) of the replicates whereas *T. nigerrimum* used both types of aggression in only 9/40 (22.5%) of the replicates ( $df = 1$ ,  $P < 0.05$ , Fisher's exact test) (Fig. 1b). *L. humile* used only physical aggression in 3/40 (7.5%) of the interactions and *T. nigerrimum* used only physical aggression in 14/40 (35%) of the interactions ( $df = 1$ ,  $P < 0.01$ , Fisher's exact test). Both species also used only chemical aggression, Argentine ants in 11/40 (27.5%) of the interactions and *T. nigerrimum* in 1/40 (2.5%) of the interactions between the two species ( $df = 1$ ,  $P < 0.01$ , Fisher's exact test) (Fig. 1b). Finally, Argentine ant and *T. nigerrimum* workers used no aggressive defenses respectively in 7/40 (17.5%) and 16/40 (40%) of the replicates ( $df = 1$ ,  $P < 0.05$ , Fisher's exact test).

### Symmetrical group confrontation

Although these confrontations started with an equal number of 25 individuals, the fights became asymmetrical, *T. nigerrimum* gaining an advantage over Argentine ant workers (Fig. 2). At the end of the test, differences in the mean number of dead workers were nearly significant, with an average of  $16 \pm 1$  SE (64%) Argentine ants and  $13 \pm 1$  SE (52%) *T. nigerrimum* dead workers ( $n = 16$ ) ( $t = -1.92$ ,  $df = 15$ ,  $P = 0.07$ ).

The maximum aggression score was on average 4, the maximum level which corresponded to long



**Fig. 2** Average cumulative number of dead ( $\pm$ SE) of Argentine ant and *T. nigerrimum* workers in symmetrical group confrontations ( $n = 16$ )

intense fights. The average maximum aggression score was higher in the 25 versus 25 than in the one-on-one biosassay ( $3.3 \pm 0.1$  SE) ( $n = 40$  for one-on-one assay and  $n = 16$  for 25 versus 25 assay,  $P < 0.0001$ , Mann–Whitney  $U$  test).

#### Intruder introduction

Aggression was always high when Argentine ants were defending their nest from the intruder. The maximum aggression score was on average  $3.8 \pm 0.1$  SE toward the intruder whereas it was on average  $3.3 \pm 0.1$  SE when *T. nigerrimum* were defending their territories from Argentine ants ( $P < 0.001$ ,  $n = 40$ , Mann–Whitney  $U$  test).

We recorded more aggressive interactions, 282, when *T. nigerrimum* was the intruder than when the Argentine ant worker was the intruder (162 aggressive interactions) (Table 2). As intruder, Argentine ant workers were more aggressive, initiating 60 of the 162 (37%) aggressive interactions, as compared to *T. nigerrimum*, which initiated 35 of the 282 (12.4%) aggressive interactions. In the same way, the Argentine ant colony initiated more aggressive interactions, 247/282 (87.6%) than the *T. nigerrimum* resident colony 102/162 (63%). These two species had different aggressive behaviors, *L. humile* initiated significantly more fights both as intruder and as resident colony than *T. nigerrimum* ( $df = 1$ ,  $P < 0.001$ , Fisher's exact test).

Argentine ants cooperated in 24/40 (60%) of the replicates whereas *T. nigerrimum* cooperated only in 8/40 (20%) of the replicates ( $df = 1$ ,  $P < 0.001$ , Fisher's exact test). On average,  $2.2 \pm 0.1$  SE *L. humile* workers attacked the *T. nigerrimum* worker (range 1–8 Argentine ant workers). In contrast only  $1.2 \pm 0.1$  SE *T. nigerrimum* workers attacked the intruder Argentine ant worker (range 1–4 *T. nigerrimum* workers) ( $P < 0.001$ ,  $n = 40$ , Mann–Whitney  $U$  test).

**Table 2** Frequency of fight initiations by *T. nigerrimum* and *L. humile* as intruder and as resident colony, ( $n = 40$ )

	Fight initiator	
	Intruder	Resident colony
<i>T. nigerrimum</i>	35/282 (12.4%)	102/162 (63%)
<i>L. humile</i>	60/162 (37%)	247/282 (87.6%)

An interesting behavior was observed for the Argentine ant intruder. In some replicates, they adopted a pupal posture, feigning death. They fooled the *T. nigerrimum* workers into picking the intruder up and carrying it to the *T. nigerrimum* dead worker location. A few seconds after the *T. nigerrimum* workers had gone, the Argentine ant intruder started to move again.

#### Competition for space and food

As soon as artificial nests were opened (day 3), *T. nigerrimum* discovered the food first in 50% (4/8) of the replicates. In 25% (2/8) of the replicates, the two species shared the food station and in 25% (2/8) of the replicates Argentine ants discovered the food first. *T. nigerrimum* dominated in 100% (8/8) of the replicates after 1 h and until the end of the test.

At the end of the test, *T. nigerrimum* invaded and nested in *L. humile* nests in 50% (4/8) of the replicates, whereas *L. humile* never invaded *T. nigerrimum* nests. It took on average 3 days for *T. nigerrimum* workers to invade Argentine ant nests. In six replicates, Argentine ant workers and queens found refuge on the top of the central arena. We never observed this behavior for *T. nigerrimum*.

On day 8, we recorded significantly more dead Argentine ants,  $378.1 \pm 45.1$  (75.6%) than *T. nigerrimum*,  $313.5 \pm 31.7$  SE (62.7%) ( $P < 0.05$ ,  $n = 8$ , Wilcoxon signed-rank test). In one replicate, 100% of *L. humile* workers were dead on day 8, body fragments attesting to the intense nature of the fighting.

#### Discussion

Our study offers support for the hypothesis that the distribution of Argentine ants in Corsica may be limited by the presence of an ecologically dominant native species. Indeed, the results of all four biosassays point to the fact that *T. nigerrimum* is superior to the invasive Argentine ant in exploitative and interference competitions.

Competition is the mechanism by which Argentine ants usually displace native ant species (Holway 1999; Human and Gordon 1996). They actively displace local ants through a combination of rapid recruitment, high numerical dominance and intense aggressive fights (Human and Gordon 1996; Rowles and O'Dowd

2007). This success may be explained by Argentine ant colony sizes (Holway and Case 2001) and by their effective fighting strategies (Holway 1999). Among these tactics, the capacity of fighting in groups is a successful strategy for a positive outcome. By joining forces, workers decrease the risk of injury or death, quickly kill enemies and quickly create a numerical advantage. It allows Argentine ants to compete much larger and ecologically dominate local ant species in invaded areas (Holway 1999; Human and Gordon 1999). Cooperative fighting was recorded in our intruder introduction assay where an average of 2.2 Argentine ant workers attacked the intruder whereas *T. nigerrimum* workers rarely received help. In addition to their cooperation against the enemy, Argentine ant workers use effective chemical compounds and physical aggression against local ants, generally with success (Buczowski and Bennett 2008; Holway 1999). Both species are able to use both techniques at the same time but not in the same proportions. The Argentine ant workers frequently used both techniques in fights (47.5%) whereas *T. nigerrimum* less often used them simultaneously (22.5%). Buczowski and Bennett (2008) consider that after the ability to cooperate, the use of efficient defense techniques is the second most important factor in wins by Argentine ants against *T. sessile*.

However, despite similarities in the results of Buczowski and Bennett (2008) and ours, notably in terms of Argentine ant fight strategies and aggressive behaviors, we demonstrate a clear divergence in the results of the two studies. Indeed, despite the Argentine ant fighting ability observed previously, in our study *T. nigerrimum* was more efficient in interference and exploitative competitions than Argentine ants. In the one-on-one bioassay, while Argentine ant workers initiated more fights and in 40% of the interactions the native ant did not use defense techniques, *T. nigerrimum* killed the Argentine ant worker in seven replicates whereas Argentine ants only once killed the *T. nigerrimum* worker. A number of studies have shown that invasive ants are not particularly successful in one-on-one competition with native species (Buczowski and Bennett 2008; Holway 1999; Holway and Case 2001). However, whereas these studies indicated that Argentine ants have the advantage in group confrontations, here we observed the reverse. In the 25-on-25 assay, contrary to *T. sessile* (Buczowski and Bennett 2008), *T. nigerrimum* gained an

advantage over *L. humile* by means of numerical superiority. Even though this advantage was not great it was maintained throughout the test. This superiority was even more marked in the resource competition assay, where *T. nigerrimum* workers clearly gained the upper hand. They more rapidly located the food resource and dominated it throughout the 6 days of experimentation. They also aggressively displaced Argentine ants from their nest, whereas the reverse was never observed. This competition bioassay demonstrates clearly that *T. nigerrimum* dominate all aspects of the competition with the Argentine ant for food source and space (nests + foraging arena). *L. humile* exhibited two interesting submissive behaviors which tend to confirm *T. nigerrimum* dominance. In the cases where *T. nigerrimum* invaded nests of Argentine ants, we invariably found Argentine ant workers and queens on the top of the central arena while *T. nigerrimum* dominated space and food. Such escape behavior may be a strategy employed to improve the survival prospects of small incipient colonies (Sagata and Lester 2009). The interesting death-feigning behavior that we observed in the intruder assay may be additional evidence of the *T. nigerrimum* superiority. Thanatosis (death-feigning) is a method of self-defense generally used by prey species when threatened by predator species and generally occurs in encounters between two species. Argentine ants may use this behavior to avoid fights and so to diminish the risk of injury and death. In ants, very few death-feigning behaviors are mentioned in the literature and to our knowledge this is the first time that such behavior has been reported for *L. humile*. Cassill et al. (2008) recorded death-feigning in *Solenopsis invicta* during intraspecific aggression among neighboring fire ant workers.

These differences in the competition abilities of *T. nigerrimum* and *T. sessile* are interesting, in view of the fact that the two species are similar. These two dominant species belong to the subfamily *Dolichoderinae* and have comparable biology, behaviors and colony attributes. Both species form large polygynous and polydomous colonies with interconnected nests containing thousands of workers and are both well-armed for fighting. However, only *T. nigerrimum* seems to be armed to compete with the invasive Argentine ant. The outcome of an interference interaction between two workers often depends on disparities in worker size and agility (Fellers 1987) or

on whether repellent chemical defensive compounds are used (Holway 1999). Nowbahari et al. (1999) showed that the size of individuals is an important factor affecting the result of aggression interactions among ants. *T. nigerrimum* workers being bigger than *T. sessile* workers, respectively 2.5–5.1 mm and 2.4–3.2 mm, body sizes may explain these disparities in the competitive abilities of the two *Tapinoma* species. Another explanation for the resistance of the Corsican native ant in bioassays may be better resistance to the toxic venom of Argentine ants. The toxicity of ant venoms can differ among target ant species. For instance, the venom of *Crematogaster scutellaris* has very different effects on different species, killing some after an application of only three droplets, while others can withstand a dose of 90 droplets (Marlier et al. 2004). The ability of the *T. nigerrimum* worker to survive in fights against Argentine ants even when the later cooperated prevented Argentine ants from gaining the numerical advantage which usually leads to their success.

Competition is an important factor shaping ant communities (Hölldobler 1990) and there is evidence that interspecific competition affects distribution in ant communities (Holway 1999; Human and Gordon 1996). Local resistance has usually been associated with local dominant ant species. *Lasius grandis* in Madeira (Wetterer et al. 2006), native *Iridomyrmex* in Australia (Walters and Mackay 2005), *T. nigerrimum* in arable and pasture Portuguese habitats (Way et al. 1997), and *T. simrothi* in North Africa (Bernard 1983), all these species were described as offering potential resistance to Argentine ants and were assumed to limit their spread. Native dominant ant species probably affect the invasion success of Argentine ants at the earliest stage of the invasion process, i.e. the dynamics of establishment and initial persistence of a colony. Although incipient colonies of Argentine ants composed of queens and 10 workers can grow quickly (Hee et al. 2000), a colony introduction experiment in Australia showed that even substantially larger colonies (5,000) of *L. humile* were unable to displace *Iridomyrmex 'rufoniger'* from baits (Walters and Mackay 2005). This is what may occur in Corsica between the dominant native *T. nigerrimum* and the Argentine ant. In a context of numerical advantage for *T. nigerrimum*, such as an accidental introduction of Argentine ant propagules, the main mechanism for new infestations in Corsica

(Blight et al. 2009), our findings indicate that this native dominant ant is armed to offer strong competition. *T. nigerrimum* may be able to limit the survival of small incipient colonies of Argentine ants, before they have time to begin forming the huge colonies that make them so dominant, capable of displacing native ants. Our results therefore strengthen our previous hypothesis (Blight et al. 2009) that the Argentine ant distribution in Corsica may be shaped by the presence of the dominant native *Tapinoma nigerrimum*. These behavioral results seen in the light of the distribution of both species in Corsica (Blight et al. 2009) appear to confirm that interspecific competition from ecologically dominant native species can affect the invasion success of invaders, notably by decreasing the likelihood of incipient colony establishment and survival.

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