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Interspecific displacement mechanisms by the invasive little fire ant *Wasmannia auropunctata*

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Abstract Competition between invasive species and native ones in the new environment was found to be significant and to affect both animal and plant species. Invasive ants are notorious for displacing local ant species through competition. Competitive displacement of native species can occur through interference and or resource competition. However, for invasive ants, little is known about the relative importance of competitive displacement. We studied competitive interactions of the little fire ant, *Wasmannia auropunctata*, one of the most destructive invasive ant species, with two other ant species, *Monomorium subopacum* and *Pheidole teneriffana*. We compared the species' foraging behavior and studied their aggressive interactions around food baits for the short

(2 h) and long (21 days) term in the laboratory. Surprisingly we found that in short term experiments *W. auropunctata* had the poorest foraging abilities of the three species studied: it took the workers the longest to locate the bait and retrieve it; in addition they retrieved the lowest amount of food. When both *W. auropunctata* and *M. subopacum* were foraging the same bait, in the short term competition experiment, *W. auropunctata* workers did not defend the bait, and ceased foraging when encountered with competition. The long-term experiments revealed that *W. auropunctata* had the advantage in aggressive interactions over time; they eliminated seven of nine *M. subopacum*'s nests while consuming some of the workers and brood. According to our laboratory studies, *W. auropunctata* cannot be considered an extirpator species, unless it has a substantial numerical advantage, in contrast with previous assumptions. Otherwise it may behave as an insinuator species, i.e. the workers do not initiate aggression and by staying undetected they can continue foraging adjacent to dominant species.

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Introduction

Although only a fraction of established invasive species compete with native species, the ones that do

so can cause extensive damage to native ecosystems (Dickman 2011). Most studies on competition between native and invasive species are focused on plants and a few on reptiles. Competition between native and invasive plants is highly important at different stages of the invasion; competition with native species may prevent invasives from being established, but once established, many invasive plants compete with native species on various limiting resources, often leading to biodiversity loss (Gurevitch 2011). According to Rejmánek et al. (2005), the best plant invaders to natural or semi-natural environments are efficient competitors for limiting resources. A number of studies investigated the competition mechanisms used by invasive lizards when competing with native species; the invasive house gecko *Hemidactylus frenatus* displaces native species from the genus *Nactus* by displacing them from safer habitats (Cole et al. 2005), a parthenogenetic species (*H. garnotii*) by sexual interference (Dame and Petren 2006), and another parthenogenetic species (*Lepidodactylus lugubris*) by resource competition (Petren and Case 1996).

Invasive ants are well known for their high ability to displace local ant species in their introduced range, for various species and habitats (reviewed by Holway et al. 2002; Reitz and Trumble 2002), but little is known about the mechanisms involved in interspecific displacement (Morrison 2000; Holway et al. 2002; Kenis et al. 2009). A better understanding of the mechanisms behind biological invasions will enable better predictions of which species have higher probabilities of invading and causing negative impact to novel environments (Levine et al. 2003).

Interspecific competition is an important component of ant biology (Hölldobler and Wilson 1990), and one of the major determinants of ant foraging strategies (Traniello 1989). Two main mechanisms are recognized: resource competition and interference competition. Resource competition occurs when several species use the same limiting resources (e.g. food, nesting sites, etc.); interference competition occurs when these species harm each other's populations (Krebs 2001). Interference competition is a significant factor in invasive species establishment (Sakai et al. 2001); it may involve direct aggressive interactions, such as biting, charging, spraying defensive secretion, and stinging (Parr and Gibb 2010). Success at resource competition is determined by various aspects of

foraging strategies; such as food detection abilities, rapid and effective worker recruitment, etc.

Both interference competition and resource competition are known mechanisms of interspecific displacement by invasive ants, but their relative importance is unknown (Holway et al. 2002). While in native ant communities a trade-off between the two types of competition may exist (Lynch et al. 1980; Fellers 1987; Morrison 1996; Davidson 1998; Reitz and Trumble 2002), invasive ants often excel in both types (Holway 1998, 1999). Invasive ants have high resource competition abilities compared to the local species they displace, including rapid discovery of food, rapid recruitment, and mass recruitment (reviewed by Holway et al. 2002). Different studies on several invasive ant species suggest that numerical advantage is of great importance to competitive ability (Krushelnycky et al. 2010, and references therein). The Argentine ant (*Linepithema humile*), for example, does better in large group interactions compared with one-on-one interactions (Holway 1999). Larger numbers of recruited workers are also believed to enable the ants to remove food faster as well as to dominate the food resources for longer periods (Jones and Phillips 1990).

The little fire ant, *W. auropunctata*, is considered to be one of the most destructive invasive ant species (Lowe et al. 2000; Holway et al. 2002). It is an omnivorous ant which nests in the ground and inside plant material; it is polygynous and unicolonial (Clark et al. 1982; Passera 1994). The ant is native to South and Central America, from which it has been introduced mainly into tropical and subtropical localities, including some Caribbean and Pacific islands, and Mediterranean and even desert climate zones in Israel (McGlynn 1999; Wetterer and Porter 2003; Vonshak et al. 2010).

In its introduced range, *W. auropunctata* was frequently shown to displace local ant species and negatively affect other arthropods as well as vertebrate species, causing population decline (Clark et al. 1982; Lubin 1984; Jourdan et al. 2001; Romanski 2001; Armbrecht and Ulloa-Chacon 2003; Le Breton et al. 2003; Wetterer and Porter 2003; Vonshak et al. 2010). *W. auropunctata* is also an agricultural pest and a health nuisance. In addition it inflicts great financial expenses for control (Wetterer and Porter 2003).

Field studies suggest that *W. auropunctata* uses a combination of interference competition, resource

competition, and predation on the other ants (Clark et al. 1982; Meier 1994; Achury et al. 2008). However, interactions between species were not monitored continuously, so it is difficult to discern between possible mechanisms involved.

The Israeli population provides a good opportunity to study mechanisms of competition: it forms a single supercolony that exhibits no intraspecific aggression, yet shows high levels of interspecific aggression (Vonshak et al. 2009). It is a rather recent introduction (past 13 years), but colonies have already spread to at least 100 localities. In areas with dense *W. auropunctata* populations in Israel, there is a marked decrease in ant abundance and species diversity (Vonshak et al. 2010). In an attempt to investigate interspecific displacement by *W. auropunctata*, we studied in the laboratory several parameters that may be involved in resource or interference competition. Although laboratory experiments may yield unrealistic results (Skelly 2002), artificial laboratory settings constitute a well-recognized research methodology for ant ecological research (Morrison 2000; Holway and Case 2001; Holway and Suarez 2004; Walters and Mackay 2005). The laboratory settings allow us to control for factors that may affect foraging activity, such as colony size, hunger level (Morrison 2000), and environmental conditions.

We chose two ant species, the native *Monomorium subopacum* and the invasive *Pheidole teneriffana*, both of which are displaced by *W. auropunctata* in its invasive range in Israel (Vonshak et al. 2010), to study the displacement mechanisms involved. We asked whether *W. auropunctata* displaces the other species by resource or interference competition. Specifically we asked whether *W. auropunctata* uses resource competition, studying its foraging abilities in comparison to the above species: the time it took workers to locate food, their recruitment dynamics, and their food retrieval ability. We compared these parameters for each species separately. In addition, we studied interference competition, by allowing pairs of species to forage in a common foraging arena for 2 h. We particularly investigated whether *W. auropunctata* was able to defend its food resources against competitors, and if it can take over food sources defended by other species. We carried out this experiment for 2 h and for 21 days in order to reveal the interactions between the species over short and long term.

Methods

Ant colonies

Ants were collected during 2007–2008; *W. auropunctata* from distinct nests at different localities in Israel, and *M. subopacum* and *P. teneriffana* in Tel Aviv. The latter are polygyne species that are abundant throughout *W. auropunctata*'s introduced range in Israel, and are displaced by it (Vonshak et al. 2010). In areas of low *W. auropunctata* densities, these species may be found adjacent to *W. auropunctata* colonies. *W. auropunctata* is smaller than the other two species, but they are fairly similar in size.

Each colony collected included a few thousands workers, several queens and brood. The colonies were kept in artificial nest boxes (30 × 10 × 6 cm) with plaster bottoms, in which an embedded plastered Petri dish served as a nest, while the box itself served as a foraging arena. All colonies were fed twice a week with dead domestic crickets (*Acheta domestica*) and sugar water (1:1 water and sugar). Additional water was supplied in cotton-plugged glass tubes. The colonies were kept in a temperature room under constant conditions (25°C, 70% RH, 14:10 L:D). The experiments were conducted during 2007–2009.

About a week before experiments, 3,200 workers, 2–3 queens and some brood were transferred to a new nesting box, as the ones described above. Worker number was estimated by weighing four groups of 100 workers using an analytical balance. In a few cases when the original nest did not contain enough brood, it was supplemented by brood from other nests. Such brood was accepted without any signs of aggression.

Single species foraging experiments

The foraging strategies of each of the three species were compared under the same conditions; each nest was tested three times, every second day, in order to minimize the effect of learning by workers. Five such replicates using different nests were made for each species.

Each experiment started by connecting the nests via a cardboard bridge (21 × 3 cm) to a foraging arena made of Plexiglass (30 × 80 × 10 cm), with Fluon-coated walls. The floor of the foraging arena was covered with filter paper that was replaced before each trial to avoid odor contamination. At the onset of each

experiment the ants were allowed to explore the arena for 3 h without food; subsequently the bridge was disconnected and all ants were collected and placed back in their nest. On the rare occasions when ants did not enter the foraging arena, the experiment was canceled.

In order to control for the level of hunger, we supplied the ants with sugar-water and crickets following the bridge's disengagement, to avoid the effect of hunger on foraging behavior (Fourcassie and Deneubourg 1994). Two hours later the ants were allowed to forage, by reconnecting the bridge, to a bait consisting of 1 day old freshly killed crickets. It was placed on a 5 cm diameter round cardboard at the far end of the foraging arena. Preliminary observations showed that workers of each of the species are able to carry alone a single cricket. We observed the ants' behavior for 1 h with an unlimited amount of crickets at the bait, followed by another hour after bait removal, and measured the following parameters:

- Time elapsed from first worker entry to the arena until food was located;
- Food retrieval time, from food location until the first cricket was brought inside the nest;
- Amount of food taken—the bait was weighted at the beginning and at the end of the experiment, deducting weight loss due to evaporation (measured under similar conditions);
- The number of workers exiting and entering the nest toward the foraging arena, counted every 3 min on the bridge;
- General recruitment response—the number of workers at the bait, counted every 3 min.

Between species comparisons of the different parameters were done for each day separately using One-way ANOVA, and afterwards the probabilities of the individual ANOVA results were combined (Sokal and Rohlf 1981, p. 779). All statistical analyses were carried out using Statistica 7.1 (StatSoft Inc., Oklahoma, USA), unless stated otherwise.

Short term competition experiment

These experiments were done using *W. auropunctata* and *M. subopacum*. The experimental setup was similar to the above foraging experiment, except that here nests of both species were simultaneously connected to the foraging arena. Before each trial,

each species was allowed separately to explore the foraging arena for 1 h, and afterwards all ants were retrieved to their nest and both nests were given food and water. After a 2 h pause the observation started by reconnecting the bridge in the following order (five replicates using different nests for each set): (a) *W. auropunctata* released first to the foraging arena for 15 min of foraging (starting when the food was located), before connecting the arena to the *M. subopacum* nest; (b) *M. subopacum* was released first, and after 15 min *W. auropunctata* was released; (c) both species were released at the same time. In addition to the parameters measured in the above-described foraging experiment, we counted the number of dead and live workers of each species in the foraging arena at the end of each experiment.

We used *t* test for dependant samples to compare the measured parameters of the two species, and Wilcoxon Matched Pairs Test to compare the numbers of dead and live workers between the species.

Long term competition experiment

For the long-term experiments we connected two nests, one of *W. auropunctata* and one of *M. subopacum* at the opposites of a common foraging arena (24 × 24 × 15 cm) for 21 days. Before the experiment began we counted and removed all dead workers from the nests and removed the food source. The ants were thereafter supplied each morning with sugar water and 1 day old crickets in the middle of the common arena to encourage interactions between the species. Twice a day, every morning and evening, both nests and common arena were photographed for accurate counting of the ants. We counted the number of live or dead ants in the common arena and inside the nests, and noted the location of the brood and queens of each species. All dead ants were removed after each counting. We performed nine replicates using different, never experimented before, nests except for one (experiment no. 5) that was conducted with a pair of nests that were used 10 days earlier in the short-term experiment. Control experiments constituted of a pair of *W. auropunctata*'s nests connected together as above (n = 4 pairs). In these experiments we marked the queens individually.

Unless otherwise mentioned, each experiment lasted 21 days. We defined dominance when one species had at least 2.5 times more active workers per

observation (twice a day). We used the cumulative cases in which one of the species dominated the other in a binomial test (according to Morrison 2000), assuming that both species had equal chance of dominating the other. The survival of workers at the end of the experiment was measured by subtracting the total number of dead workers from their initial number. The proportion calculated was Arcsin-transformed and compared by dependant *t* test. These tests were performed in VassaStat website (Lowry 2009).

Results

Foraging dynamics

The recruitment dynamics of all three species showed a similar pattern during the 3 days of experiment: following bait location the number of workers at the bait increased to reach a constant number of workers at the bait (Fig. 1). *W. auropunctata* recruited a higher number of workers to the bait compared to the other species. Following bait removal, the numbers of workers of all species declined sharply, and in the following hour only a few workers were found near the bait. *P. teneriffana* workers recruited big workers (majors) as well, but the majors were rarely seen retrieving food to the nest.

Significant differences were found between the three species with regard to time to locate food and time to retrieve food. Compared to the other species, *W. auropunctata* workers were the slowest to locate the bait ($\chi^2 = 38.39$, $df = 6$, $P < 0.0001$, Fig. 2; Table 1), and to retrieve it ($\chi^2 = 35.19$, $df = 6$, $P < 0.0001$, Fig. 2). In addition, *W. auropunctata* workers carried less food to the nest (0.18 ± 0.04 g \pm SE, compared to 0.71 ± 0.22 for *P. teneriffana* and 0.36 ± 0.11 for *M. subopacum*; $\chi^2 = 21.93$, $df = 6$, $P = 0.0012$).

Short term competition experiment

When *W. auropunctata* were released first, they located the bait after 3.4 ± 1.02 min, reached a maximum of 146 ± 56.36 ants at the bait after 21 min, and carried 8.97 ± 5.99 crickets back to the nest (Fig. 3a). However, when *M. subopacum* workers arrived to the bait 15 min later, the presence of *W. auropunctata* workers at the bait area declined rapidly, and even before losing their numerical

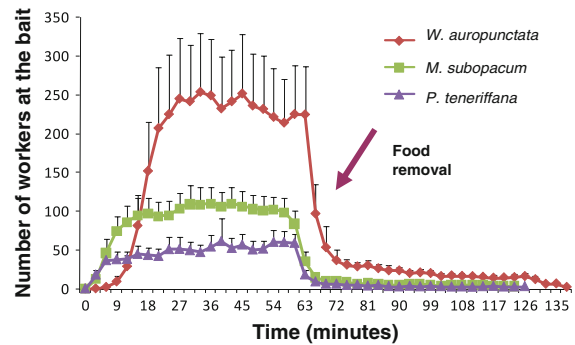


Fig. 1 Foraging dynamics of *W. auropunctata*, *M. subopacum*, and *P. teneriffana* during the 2 h foraging experiment (expressed as average number of workers at the bait). The three species were studied separately. Error bars are standard errors of the mean

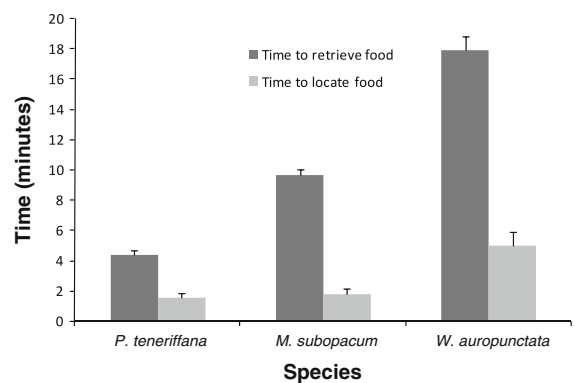


Fig. 2 Time to locate food and time to retrieve food by workers of each of the three species in the foraging experiments. Error bars are standard errors of the mean

advantage they stopped carrying food back to the nest. *M. subopacum* workers located the food slightly faster than *W. auropunctata* workers (after 1.8 ± 0.75 min), however the difference was not significant (Table 2. Dependent *t* test, $t = -2.66$, $P = 0.056$). The time to retrieve food was similar for both species (Table 2. Dependent *t* test, $t = -2.27$, $P = 0.1$). Nonetheless, food uptake by *M. subopacum* workers was significantly higher than that of *W. auropunctata* (Table 2. Dependent *t* test, $t = 3.49$, $P = 0.025$).

When *M. subopacum* were released first, they quickly located the bait (1.8 ± 0.71 min) and maintained high worker presence at it and continued to transport large amounts of food to the nest, even after the release of *W. auropunctata* workers. *W. auropunctata* workers that entered the arena took longer

Table 1 Statistical analyses results for the foraging experiment: days were tested by separate ANOVA, probabilities of the separate ANOVA were combined using χ^2 test

Parameter	ANOVA analyses						χ^2 tests		
	Day 1		Day 2		Day 3		χ^2	df	P
	F	P	F	P	F	P			
Food weight	7.97	0.006	2.16	0.158	5.79	0.017	21.93	6	0.0012
Time to locate food	12.29	0.001	7.75	0.007	15.06	0.001	38.39	6	<0.0001
Time to retrieve food	14.94	0.001	9.1	0.005	7.19	0.009	35.19	6	<0.0001

time to locate the food than *M. subopacum* workers (12.2 ± 8.13 min. Dependent t test, $t = -3.16$, $P = 0.034$), and they did not retrieve any food (significant difference in food uptake: dependent t test, $t = 4.79$, $P = 0.017$) (Fig. 3b; Table 2).

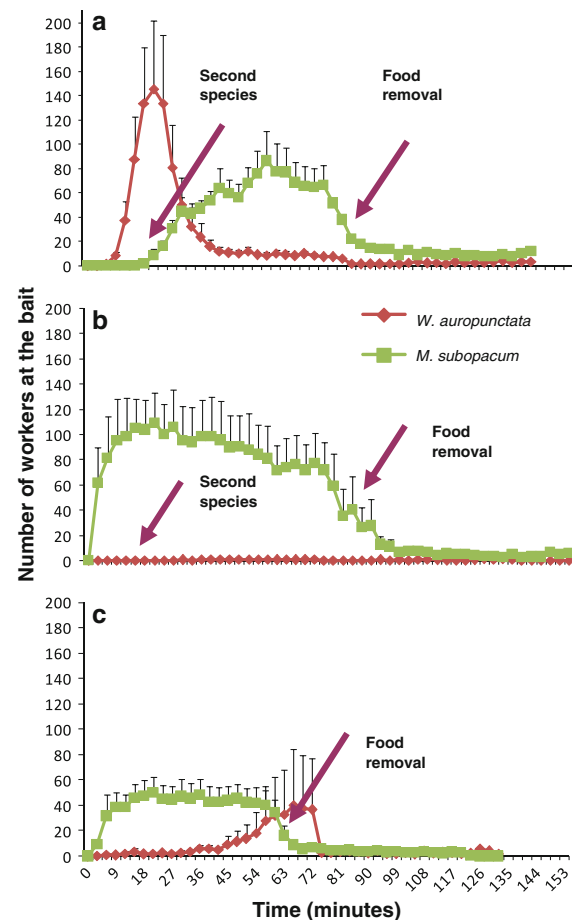


Fig. 3 Foraging dynamics during the short-term competition experiment (expressed as average number of workers at the bait). **a** *W. auropunctata* released first, after 15 min *M. subopacum* released. **b** *M. subopacum* released first, after 15 min *W. auropunctata* released. **c** Both species released at the same time. Error bars are standard errors of the mean

When both species were released simultaneously, *M. subopacum* workers rapidly became dominant at the bait area, while *W. auropunctata* workers were present in low numbers. The numbers of *W. auropunctata* increased only briefly just before the bait was removed when the numbers of *M. subopacum* were on the decline and thus *W. auropunctata* workers hardly collected any food (Fig. 3c). Although *M. subopacum* workers were not faster to locate the food compared with *W. auropunctata* workers (2.4 ± 0.49 and 4.4 ± 1.5 min, respectively. Dependent t test, $t = -2.39$, $P = 0.075$), they collected a significantly greater amount of food (dependent t test, $t = -2.39$, $P = 0.02$). Workers of *W. auropunctata* were able to retrieve food only in two replicates, and it took them longer than *M. subopacum* workers.

Monomorium subopacum workers retrieved a significantly greater amount of food in all three sets (averages of the three experiments): 0.29 ± 0.06 g \pm SE ($=635 \pm 124.88$ crickets), compared with 0.002 ± 0.00 g ($=5.07 \pm 7.54$ crickets) taken by *W. auropunctata* workers (Table 2). In a quarter of the replicates *W. auropunctata* workers did not carry any crickets to their nest. In some of the replicates *W. auropunctata* workers carried dead *M. subopacum* workers back to their nest, or the latter entered the nest and were killed there.

A higher number of *M. subopacum* workers died in the foraging arena in each of the experiments compared with *W. auropunctata* workers (Fig. 4a. Wilcoxon, $P = 0.043$). In experiments 1 and 3, but not in 2, a significantly higher number of live *W. auropunctata* workers were present in the foraging arena at the end of the experiment (Fig. 4b. Wilcoxon, $P = 0.043$).

Long term competition experiments

High aggression between *W. auropunctata* and *M. subopacum* was characteristic of all replicates, especially

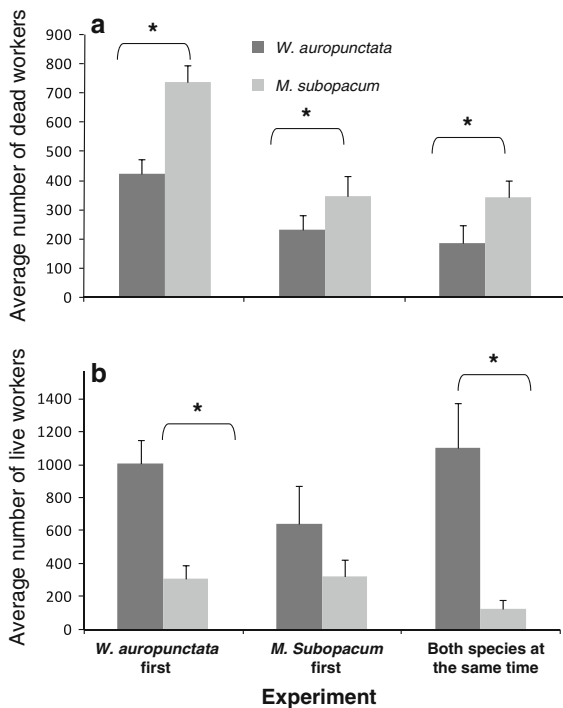
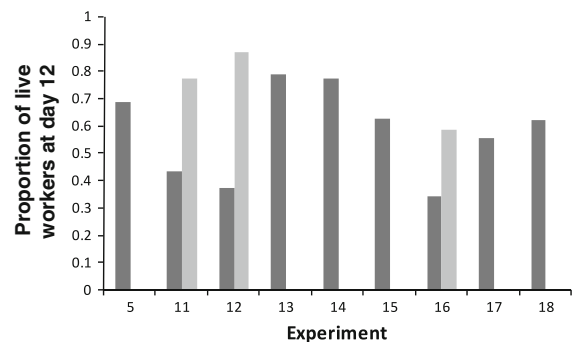
Table 2 Mean \pm standard errors of the mean of the following parameters: amount of food taken by the workers to the nest, time to locate food, and time to retrieve food, in the short-term competition experiment

Parameter	Experiment					
	<i>W. auropunctata</i> first		<i>M. subopacum</i> first		Both at the same time	
	<i>W. auropunctata</i>	<i>M. subopacum</i>	<i>W. auropunctata</i>	<i>M. subopacum</i>	<i>W. auropunctata</i>	<i>M. subopacum</i>
Food weight	0.003 \pm 0.001	0.217 \pm 0.069	0	0.538 \pm 0.112	0.004 \pm 0.004	0.129 \pm 0.062
Time to locate food	0:03 \pm 0:00	0:01 \pm 0:00	0:12 \pm 0:04	0:01 \pm 0:00	0:03 \pm 0:01	0:03 \pm 0:01
Time to retrieve food	0:19 \pm 0:04	0:19 \pm 0:12		0:07 \pm 0:01	0:33 \pm 0:08	0:17 \pm 0:06

during the first five days, resulting in increasing numbers of dead workers of both species (supplementary material, Fig. S1a, b). In six out of nine replicates increasing numbers of *W. auropunctata* workers invaded *M. subopacum*'s nest-box during each of the first 4 days, and after 7 ± 2.96 days on average ($n = 7$) *W. auropunctata* workers were seen moving at least part of their brood and queens into the inner nest of *M. subopacum* while it was still occupied with the latter (supplementary material, Fig. S2). By the 11th day, all *M. subopacum* were killed in seven out of

nine replicates (Fig. 5), at which point *W. auropunctata* workers usually gathered all remaining *M. subopacum* larvae into the inner nest and kept them near their own larvae and queens. These larvae however were not tended despite the presence of *W. auropunctata* workers nearby. Since no new workers of *M. subopacum* emerged thereafter, these larvae were probably consumed.

Wasmannia auropunctata workers were dominant (see materials and methods for definition of dominance) in higher number of observations both in the respective species nest boxes and the common foraging arena compared with *M. subopacum* workers (number of observations—dominant: total number of observations, *W. auropunctata* box: 207:207, foraging arena: 179:198, *M. subopacum* box: 135:203; binomial test for each box: $P < 0.0001$). Additionally, there was a significantly greater survival of *W. auropunctata* throughout the first 12 days of the experiment (T test for Dependent Samples, $t = 2.62$, $df = 8$, $p = 0.03$). It is important to note that in all replicates *M. subopacum* workers were never observed to injure

**Fig. 4** Workers' activity (a as number of active workers) and workers' mortality (b as numbers of dead workers) in the foraging arena at the end of the short-term competition experiment. Error bars are standard errors of the mean**Fig. 5** Proportion of workers' survival after 12 days in the long-term competition experiment (dark columns: *W. auropunctata*; light columns: *M. subopacum*)

W. auropunctata queens or brood, even when having a numerical advantage.

Aggression was rarely observed after the first few days of conflict. In three replicates the *M. subopacum* nest survived until day 21 with higher endurance compared with *W. auropunctata* workers (Fig. 5). In replicate #5 a small group of *W. auropunctata* settled inside the *M. subopacum* nest, with at least 100 workers and some brood, feeding on the *M. subopacum* workers. To assess whether in such situations *W. auropunctata* workers eventually destroy the whole *M. subopacum* nest, we observed another replicate (#16) that showed a similar scenario until the *M. subopacum* nest was destroyed. In this case *W. auropunctata* workers entered the *M. subopacum* nesting-box on day 8, and the inner nest on day 10, but it took 42 days in total until the last *M. subopacum* worker was dead.

In the control replicates aggression events were rarely observed, and mortality usually occurred on the first 2 days (supplementary material, Fig. S3b). Workers activity was similar on all days, and was a little higher in the foraging arena compared with the nesting-boxes (supplementary material, Fig. S3a). During the 21 days of the experiment the queens and brood location changed frequently between the nest boxes, and foraging trails led from the common arena to both nest boxes. At the end of the experiment, each pair of nests has merged into a single box, where the workers kept all queens and brood together. Queen mortality was not observed, confirming that the nests truly merged.

Discussion

When invasive species compete with natives, inter-specific competition can be an important mechanism for their spread (Dickman 2011). The newcomers outcompete and displace their congeners, with several examples, from invasive tadpoles (Smith 2005), lizards (Dame and Petren 2006), mammals (Harris and Macdonald 2007; Stokes et al. 2009), and plants (Mitchell et al. 2009).

While many studies focus on the impact of invasive ants on the invaded fauna, few studies tested the underlying mechanisms (Morrison 2000; Holway et al. 2002; Reitz and Trumble 2002). A common hypothesis is that the significant impact of invasive

ants, and of *W. auropunctata* in particular, on local ant communities results from their successful foraging strategies compared to native species (Clark et al. 1982; Meier 1994; Holway et al. 2002). However, unlike the Argentine ant which was more proficient in both exploitative and interference competition than the native ant species studied (Holway 1999), our research demonstrates that in laboratory conditions, *W. auropunctata* was not an efficient forager, compared to the two other species studied, *M. subopacum* and *P. teneriffana*. Although *W. auropunctata* workers recruited more workers to the bait, *M. subopacum* and *P. teneriffana* were quicker to arrive at the food resources, and retrieved more of them to their nests, abilities that may reflect their overall larger size. Therefore we can conclude that with an equal number of workers, *W. auropunctata* has no foraging advantage over the other species in laboratory settings. In a similar laboratory experiment, Jones and Phillips (1990) concluded that foraging efficiency is less important for the success of *S. invicta*, in comparison with high reproduction ability and colony size.

During the short-term competition experiments *W. auropunctata* workers were neither able to overtake nor to defend the bait, but abandoned it as soon as *M. subopacum* workers arrived, behaving like a subordinate species. Consequently they carried only a negligible amount of food during all short-term competition experiments. Although the workers of *W. auropunctata* killed and consumed *M. subopacum* workers during these experiments, this was negligible compared with the weight of crickets they carried when foraging without interference. These results are in contrast with previous studies, which found that *W. auropunctata* occupied the highest number of baits, and had the highest percentage of observations as the only species present in a bait, in its invasive range in the Galapagos (Clark et al. 1982).

Our results are not consistent with the hypothesis that *W. auropunctata* is an extirpator species (Hölldobler and Wilson 1990); neither can it be considered an opportunist species because in our experiments the workers moved very slowly and consequently were not very efficient in locating new food resources. We believe that this applies also to field conditions, since we observed such slow movement also in the field (MV, unpublished data). Moreover, in the laboratory when *W. auropunctata* workers encountered a competing species, the few

workers that remained at the bait area “froze” rather than behave aggressively. They responded with aggression only when attacked by *M. subopacum* workers. The few workers that stayed near the bait did not carry any of it back to the nest. Fellers (1987) reported a similar behavior by *Leptothorax curvispinosus*. However, unlike *W. auropunctata*, this species was the first to discover baits during foraging/competition experiments, but was rated the last of eight species in dominance hierarchy, and therefore was considered to be an insinuator forager (Fellers 1987).

Some ant species switch between foraging strategies according to the situation (Morrison 1996), which could be the case with *W. auropunctata*. At low worker densities, as may be the case in its native or at the edges of its invasive range, it behaves as an insinuator species, i.e. the workers do not initiate aggression and by staying undetected they can continue foraging adjacent to dominant species. It is possible that when having a substantial numerical advantage (apparently higher than in the current competition experiment), they behave as an extirpator species, displacing other species. In addition, their observed massive recruitment may help them dominate food resources for a longer period, as suggested for other species (Fellers 1987; Jones and Phillips 1990) and for this species (Achury et al. 2008). The importance of numerical advantage to competitive displacement from food resources was demonstrated in the Argentine ant (Holway and Case 2001; Walters and Mackay 2005), and high workers recruitment abilities are believed to enable the ants to remove food faster and to dominate the food resource for longer periods (Jones and Phillips 1990). Jones and Phillips (1990) also reported that two ant species (*Forelius foetidus* and *Monomorium minimum*) that were less efficient in bait removal compensated by recruiting larger worker numbers to the bait. Additionally, both species were considered to be “timid”, although equipped with effective chemical defense (Jones and Phillips 1990), analogous to *W. auropunctata*.

Despite the fast withdrawal, and inability to retrieve food from the bait when facing the competing species, *W. auropunctata* workers were still the most abundant live ants in the foraging arena at the end of the experiment, following massive extermination of the opponent species. We therefore suggest that if interspecific displacement occurs, it takes longer than the 2 h that the short-term experiment lasted.

Indeed, in the long-term experiment there was a clear advantage to *W. auropunctata*. Although in some of the replicates at the onset of the experiment *M. subopacum* workers quickly invaded the common foraging arena and dominated the shared bait, and even invaded *W. auropunctata*'s nest in high numbers and caused high worker mortality, in none were the queens or brood injured. On the other hand, when *W. auropunctata* workers invaded *M. subopacum*'s nests, albeit at a slower pace, they took over the nest boxes, culminating in total destruction of most of the invaded nests including all queens and brood, 12 days after the experiment began. Invasion attempts by *M. subopacum*'s workers into the *W. auropunctata* nests, at a smaller scale, were also documented in the short-term competition experiments, but these were unsuccessful and ended with high mortality among the invading workers and no harm to *W. auropunctata* queens or brood.

Evidence for nest invasions by invasive ants as a way of competitive displacement is rare in the literature. Dejean et al. (2008) showed that it could be highly important for the spread of *Pheidole megacephala* in its introduced range, where fewer species were able to resist their raids compared with its native range. Holway et al. (2002) stated that nest invasion might be an important mechanism of displacing local ant species, although in these cases there were no evidence that the invaders consumed the resident workers and brood. In another study, Zee and Holway (2006) showed that nest raiding may be an important mechanism when displacing species that differ from the invader in their dietary requirements. Our experiments show that both nest invasion and worker and brood consumption of the invaded species are a feasible mechanism that may be employed by *W. auropunctata* to displace local ant species. We suggest that in the field, when workers of *W. auropunctata* encounter heterospecific nests they can invade and destroy them, slowly but persistently clearing the habitat for their own exploitation.

The nests used in these experiments were standardized by worker number. As the species studied differ in their mass, had we standardized our experiments by worker biomass we would have conferred a greater advantage upon *W. auropunctata*. In addition, the experimental settings presented here may have increased the interspecific aggression levels, by placing nests in close proximity to each other, and forcing the

ants to forage on the same food source. This evidently must be the case also in the field where along the advancing front of *W. auropunctata* heterospecific nests, including nests of the species studied here, surely occur at close proximity and occasionally even nesting under the same stone (M. Vonshak, unpublished data). Finally, behavioral observations in the field, studying interspecific encounters at food baits, could shed more light on the rate of aggressive interactions under more natural conditions, exploring the importance of numerical dominance for aggressive interactions between the species, when the species are not forced to be in the same place. Our laboratory results emphasize the significance of experiment duration when examining exploitation versus interference as mechanism of competitive interactions. Results of the short-term experiments do not reflect the true interference competition abilities of *W. auropunctata*, whereas the long-term experiment clearly demonstrated them (see also Walters and Mackay 2005).

In sum, we found that *W. auropunctata*'s exploitative abilities are lower than those of the other species studied: *W. auropunctata* workers take more time to locate and retrieve food, but they recruit more workers (Fig. 1). On the other hand, their interference ability is very high, both during encounters in small groups (ten by ten; Vonshak et al. 2009), and in encounters with neighboring nests. The number of dead *M. subopacum* was significantly higher at the end of the short and the long term experiments. Moreover, their ability to exploit other species' nests, workers, and brood could be highly valuable for their spread into new habitats, even before reaching a numerical advantage over the opponent species.

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