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Differences in behavioural traits among native and introduced colonies of an invasive ant

Olivier Blight · Roxana Josens · Cleo Bertelsmeier ·
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Abstract Identifying the factors that promote the success of biological invasions is a key pursuit in ecology. To date, the link between animal personality and invasiveness has rarely been studied. Here, we examined in the laboratory how Argentine ant populations from the species' native and introduced ranges differed in a suite of behaviours related to species interactions and the use of space. We found correlations among specific behavioural traits that defined an explorative-aggressive syndrome. The Main "European" supercolony (introduced range) more readily explored novel environments, displayed more aggression, detected food resources more quickly, and occupied more space than the Catalanian supercolony (introduced range) and two other Argentine

supercolonies (native range). The two native supercolonies also differed in their personalities; one harbouring the less invasive personality, while the other is intermediate between the two introduced supercolonies. Therefore, instead of a binary pattern, Argentine ant supercolonies display a behavioural continuum that is independent on their geographic origin (native/introduced ranges). Our results also suggest that variability in personality traits is correlated to differences in the ecological success of Argentine ant colonies. Differences in group personalities may facilitate the persistence and invasion of animals under novel selective pressures by promoting adaptive behaviours. We stress that the concept of

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animal personality should be taken into account when elucidating the mechanisms of invasiveness.

Keywords Animal personality · Behavioural syndrome · Supercolony · Invasive ant

Introduction

The introduction of non-native species to a previously unoccupied region is considered to be a key threat to the integrity of many natural habitats and ecosystems worldwide, driving loss of biodiversity (Clavero and García-Berthou 2005). Among the pool of species that are transported outside their native range, a small subset is able to establish and spread, leading to major modifications in ecosystem functioning (Simberloff et al. 2013). Identifying the traits that promote the success of invasive species is therefore a key pursuit in ecology.

Differences in success not only among species but also among different populations within a single species (Fogarty et al. 2011) suggest that multiple traits may influence species' invasion success. These traits can be a pre-adaptation of a population (e.g. high productivity) or be developed and expressed after the introduction. Evolutionary processes such as genetic drift resulting from bottlenecks (Tsutsui et al. 2000) or new selection pressures (Giraud et al. 2002) contribute also to changes in important traits (Mooney and Cleland 2001; Sakai et al. 2001), such as social organisation and competitive abilities (Holway and Suarez 1999).

Recent studies suggest animal personality (i.e., inter-individual behavioural differences that are consistent over time and across different contexts) and behavioural syndromes (i.e., suites of correlated behaviours consistent across contexts) can provide novel insights into biological invasions (Wolf and Weissing 2012). Inter-individual variation within species could result in differential abilities manifesting themselves at each invasion stage, thus allowing certain individuals to invade and impact ecosystems (Chapple et al. 2012). Such traits like sociality, boldness, or activity have been proposed as related to the invasion process (Sih et al. 2004; Pintor et al. 2008; Chapple et al. 2012; Wolf and Weissing 2012; Carere and Gherardi 2013). For example, high

boldness and exploratory activity may enhance the likelihood of being transported to and dispersing in a new habitat (Cote et al. 2010). By comparing the personality of different individuals of an invasive species in their native and introduced ranges, it may be possible to shed new light on the factors that promote invasion success (Carere and Gherardi 2013). However, such comparisons are uncommon, particularly in group-living species.

Variation in group personalities has recently been described in many non-invasive species including fish (Dyer et al. 2009), birds (Aplin et al. 2013, 2014), and insects: ants (Chapman et al. 2011; Gordon et al. 2011; Pinter-Wollman et al. 2012; Scharf et al. 2012; Bengston and Dornhaus 2014; Hui and Pinter-Wollman 2014; Kleeberg et al. 2014; Modlmeier et al. 2014; Blight et al. 2016); bees and bumble bees (Wray et al. 2011; Wray and Seeley 2011); and spiders (Keiser et al. 2014; Pruitt and Keiser 2014) (reviewed in Jandt et al. 2014 and Kralj-Fišer and Schuett 2014). In social species, personality traits are expressed at both the individual- and group-level (Jandt et al. 2014) and can affect the efficiency of group-level processes and performance (Webster and Ward 2011). For instance, in the gypsy ant *Aphaenogaster senilis*, proactive colonies that contained bold individuals who more readily explored novel environments, exhibited aggressive behaviours and demonstrated higher food-retrieval efficiency during intraspecific competition trials (Blight et al. 2016). Group personality is also related to differences in collective foraging in social spiders (Wright et al. 2015). As a consequence, we might expect group-level personality traits to be related to invasiveness in invasive social species (Fogarty et al. 2011).

The Argentine ant (*Linepithema humile*) provides a good example of the invasion success of a social species. This invader has successfully spread across the globe in regions with Mediterranean and subtropical climates, through the intensification of human activities over the last century (Suarez et al. 2001). The Argentine ant is one of the most devastating invaders in the world (Holway et al. 2002), as attested by its registration on the '100 of the world's worst invasive alien species' list (Lowe et al. 2000). Interestingly, in its introduced range, the Argentine ant often forms a single geographically vast supercolony—large networks of integrated polygynous (multiple queens) nests exhibiting no aggression

within supercolonies but high aggression between supercolonies (Helanterä et al. 2009)—that dominates several smaller supercolonies.

Considering its biology and invasiveness, *L. humile* represents an ideal species model to investigate personality traits in invasive social species. In the current study, we investigated using a series of individual- and group-level behavioural tests, if supercolonies of Argentine ants from the introduced range (Spain) differ from those of the native range (Argentina) in a suite of behaviours: aggression, exploratory activities, and spatial distribution.

Materials and methods

Colony collection and maintenance

In May 2014, we sampled two Argentine ant supercolonies in the species' native range (Buenos Aires, Argentina) [we were allowed to import to Spain only two boxes of Argentine ants (import license 09 April 2014 from the Spanish Ministry of Agriculture, Food, and the Environment)]. The supercolonies (hereafter BA1 and BA2) were located 1 km apart. At the same time (May 2014), we also sampled two supercolonies in the species' introduced range: the Main European supercolony (hereafter the MAIN supercolony) in Doñana National Park (Huelva, SW Spain) and the Catalan supercolony (hereafter the CATA supercolony) at Caldes d'Estrac (Barcelona, NE Spain). We sampled two locations separated from at least 500 m of both introduced supercolonies. The MAIN supercolony is one of the world's most successful invasive populations; its members have been transported and established at least in the USA, Europe, Japan, Australia, and South Africa (Vogel et al. 2010). This supercolony dominates other supercolonies of *L. humile* that are restricted to small areas (Thomas et al. 2006; Brandt et al. 2009; van Wilgenburg et al. 2010). This is the case in Europe where the Catalonian supercolony is restricted to a small region in eastern Spain whereas the MAIN supercolony spans for thousands of kilometres in southern Europe (Giraud et al. 2002; Blight et al. 2012). Fragments from these four supercolonies were set up in artificial nests (30 × 15 × 6 cm) in the Doñana Biological Station and kept in a climate chamber (Aralab, Fitoclima 5000; 25 ± 1 °C, 50 ± 10% RH). They were fed the

same diet (honey and meal worms) and given water ad libitum. All behavioural experiments were conducted at room temperature (26 ± 1 °C) in June 2014.

Bioassays

1. *Aggressiveness towards allospecifics* We randomly collected five *L. humile* workers and put them in a Petri dish (ø5.5 cm). After 2 min, we introduced an *Aphaenogaster senilis* worker. *Aphaenogaster senilis* is a subordinate species native to Spain. All the *A. senilis* workers used in the trials came from the same colony, which had been collected in Doñana National Park in an area that has not yet been invaded by *L. humile*. The behaviour of the resident *L. humile* workers towards the introduced *A. senilis* worker was monitored for 3 min and classified as: (1) touch; (2) avoidance; (3) open mandibles; and (4) fighting. For each encounter, we calculated an aggression index, which was the number of aggressive acts (classes 3 and 4) divided by the number of peaceful interactions (classes 1 and 2). We conducted ten replicates per *L. humile* supercolony using each time naïve individuals. The Petri dish was cleaned between each trial.
2. *Aggressiveness towards conspecifics* We assessed intraspecific aggression by staging pairwise one-on-one confrontations in plastic petri dishes (ø5.5 cm) using ants from each of the three other *L. humile* supercolonies. We recorded during a 5-min period which ant initiated and/or won the fight (an ant “won” when it injured or killed its opponent). We conducted six replicates per supercolony pair using each time naïve individuals. To identify individuals during the trials, we collected from the same colony half-time individuals with a large gaster (fed with honey) and half-time individuals with a small gaster (unfed). The Petri dish was cleaned between each trial.
3. *Exploration* We placed 150 workers, 1 queen, and a batch of larvae in a box (ø4 × 10 cm) containing moist cotton. After 30 min of acclimation, the ants were allowed access to a novel environment, which comprised a row of five circular chambers that were interconnected in series (ø4 × 10 cm). We noted the farthest chamber visited by the ants during a 10-min period and the total number of

ants in the chambers at the end of those 10 min. The ants were then returned to the box awaiting the foraging activity test to begin. We conducted five replicates per supercolony using each time naïve individuals. The chambers were cleaned at the end of the test.

4. *Foraging activity* Thirty minutes after the exploration trials, we put honey in the centre of the third chamber and allowed ants access to the chambers. We recorded the time they took to detect the food and the total number of workers in the chamber over a 15-min period.
5. *Spatial brood and queen distribution* We connected three glass tubes ($\varnothing 2 \times 10$ cm) containing water and covered by red paper to a circular arena ($\varnothing 10 \times 10$ cm). Five hundred workers, five queens, and a batch of larvae were placed in the arena and allowed to settle in one tube while the other two tubes were closed. After 48 h, we opened them and monitored whether the workers transported queens and larvae to the new tubes at day + 1, day + 5, day + 10, day + 24, and day + 30. We conducted five replicates per supercolony using each time naïve individuals.

Statistical analysis

General linear models (GLMs) were used to determine whether the nine behavioural variables (1) aggressiveness towards allospecifics (bioassay 1); (2) fight initiation; and (3) fight success (bioassay 2); (4) exploration of a novel environment; (5) number of chambers explored (bioassay 3); (6) time to food detection; (7) level of foraging activity (bioassay 4); (8) distribution of queens; (9) distribution of larvae (bioassay 5); differed among the four supercolonies. GLMs 1–7 were fitted using Poisson or quasi-Poisson distributions, while GLMs 8 and 9 were fitted using a binomial distribution.

To identify suites of correlated behaviours, we performed a Principal Component Analysis (PCA). The PCA was performed to build synthetic variables (components of the PCA) summarising the nine behavioural variables. The variables included in the PCA were the average of the behavioural scores for each supercolony. Because the nine variables differed in their units (e.g. number of individuals or time in seconds), we normalised the data using the option

“scale = TRUE” of the `prcomp` function. We also calculated Spearman correlation coefficients between the behavioural scores for the experiments conducted on the same individuals (i.e. tests 4, 5, 6 and 7). All statistics were carried out using R (R Core Team).

Results

Ants from the MAIN supercolony were systematically the most aggressive. During allospecific encounters, MAIN ants were more aggressive than CATA ($z = 5.04$; $P = 0.0001$), BA1 ($z = 4.04$; $P = 0.0001$), and BA2 ($z = 3.29$; $P = 0.005$), but the latter three did not differ significantly ($P > 0.05$) (Tables 1, 2). Moreover, during the intraspecific pairwise encounters, MAIN ants initiated significantly more fights (71 ± 7) than CATA (38 ± 10) ($z = 3.17$; $P = 0.008$) and BA1 (38 ± 7) ($z = 2.61$; $P = 0.04$) ants, but not BA2 ants (54 ± 10) ($z = 0.51$; $P = 0.95$) (Tables 1, 2). The proportion of fights won by the different colonies did not differ ($P > 0.05$).

MAIN ants also displayed the most exploratory behaviour (MAIN: 89 ± 5 individuals—CATA: 55 ± 4 individuals; $z = 6.51$, $P = 0.0001$; MAIN–BA1: 55 ± 1 individuals; $z = 5.07$, $P = 0.0001$; MAIN–BA2: 69 ± 1 individuals; $z = 2.94$, $P = 0.02$), although the supercolonies did not differ in the number of chambers visited ($P > 0.05$). Similarly, Main ants were the most active during foraging (i.e. the number of ants out of the nest over a 15 min period) with the BA2 ants (MAIN: 87 ± 7 individuals—BA2: 87 ± 4 individuals; $z = 0.08$, $P = 0.99$; MAIN–CATA: 70 ± 3 individuals; $z = 4.32$, $P = 0.0001$; MAIN–BA1: 69 ± 2 individuals; $z = 3.76$, $P = 0.0001$). They also detected the food resource more rapidly than all other supercolonies (MAIN: 233 ± 40 s—CATA: 555 ± 32 s; $z = 6.51$, $P = 0.0001$; MAIN–BA1: 572 ± 32 s; $z = 5.07$, $P = 0.0001$; MAIN–BA2: 363 ± 22 s; $z = 2.94$, $P = 0.02$). Finally, MAIN ants scattered the larvae significantly more than CATA ($z = 3.92$, $P = 0.0001$) and BA1 ants ($z = 4.24$, $P = 0.0001$) but not BA2 ants ($z = 2.1$, $P = 0.15$) (Tables 1, 2). There was no difference in the distribution of the five queens ($P > 0.05$).

The PCA revealed a behavioral syndrome described by two components that accounted for 87% (PC1) and 8% (PC2) of the total variance in the

Table 1 Values (mean \pm SE) obtained from behavioural experiments using native and introduced Argentine ant supercolonies

Behaviour	Native range		Introduced range	
	BA1	BA2	CATA	MAIN
Interspecific aggression ¹	0.90 \pm 0.07 ^a	1.46 \pm 0.37 ^a	1.10 \pm 0.16 ^a	3.74 \pm 0.40 ^b
Intraspecific fights initiated ²	38 \pm 10 ^a	54 \pm 10 ^{ab}	38 \pm 7 ^a	71 \pm 7 ^b
Intraspecific fights won ³	25 \pm 9 ^a	29 \pm 9 ^a	10 \pm 4 ^a	29 \pm 7 ^a
Exploratory activity ⁴	55 \pm 1 ^a	69 \pm 1 ^b	55 \pm 4 ^a	89 \pm 5 ^c
Chambers visited ⁵	3.4 \pm 0.2 ^a	3.6 \pm 0.2 ^a	3.3 \pm 0.3 ^a	4.1 \pm 0.3 ^a
Food detection ⁶	572 \pm 108 ^a	363 \pm 22 ^b	558 \pm 32 ^a	233 \pm 40 ^c
Foraging activity ⁷	69 \pm 2 ^a	87 \pm 4 ^b	70 \pm 3 ^a	87 \pm 7 ^b
Queen distribution ⁸	37 \pm 3 ^a	37 \pm 2 ^a	37 \pm 1 ^a	38 \pm 2 ^a
Distribution of larvae ⁹	33 \pm 0 ^a	37 \pm 2 ^{ab}	35 \pm 1 ^a	41 \pm 1 ^b

Different letters indicate statistically significant differences between supercolonies (GLM analysis, Tukey's post hoc test, $P < 0.05$)

¹ Index of interspecific aggression

² % of fights initiated

³ % of fights won during intraspecific one-on-one tests

⁴ Number of workers outside after 10 min (without food)

⁵ Number of chambers visited by workers during the 10 min of exploration

⁶ Time to food detection (s)

⁷ Number of workers outside after 15 min (with food)

⁸ % of available tubes containing queens

⁹ % of available tubes containing larvae

nine behavioral traits (Fig. 1). The first principal component included aggressiveness towards allospecifics (bioassay 1), fight initiation (bioassay 2), exploration of a novel environment and the number of chambers explored (bioassay 3), time to food detection and level of foraging activity (bioassay 4) and, distribution of queens and distribution of larvae (bioassay 5). The second principal component included fight success (bioassay 2). The Spearman correlation tests detected significant relationships among behaviors forming the first component, which confirms the existence of a complex behavioral syndrome in *L. humile* (Fig. 2; Table 3).

These results mean that the MAIN supercolony that readily explored novel environments and demonstrated higher levels of foraging activity, was the most aggressive, and detected the food source more rapidly. In contrast, BA1 and CATA supercolonies that less readily explored novel environments, demonstrated lower levels of foraging activity, detected the food source more slowly and were less aggressive. These correlated behaviors define a proactive-reactive syndrome in *L. humile* where ants from the MAIN supercolony were proactive and both CATA and BA1

were reactive (Fig. 2; Table 3). BA2 ants were intermediate along this behavioural gradient.

Discussion

The MAIN supercolony's personality is consistent with its high degree of invasiveness. In contrast, the Catalanian supercolony, which occupies a much smaller distribution area, was less aggressive and less active. The recent emergence of the concept of behavioural syndrome has stressed the importance of within-species group-personality in collective behaviour and group performance (Webster and Ward 2011). Invasive ants, for example, are accustomed to move to new nest sites when perturbations occur. The speed and accuracy of nest relocation, assumed to contribute to their ecological success (Holway et al. 2002), are influenced by the behavioural type of the group (Hui and Pinter-Wollman 2014). Here, the MAIN supercolony's aggressiveness and its tendency to explore novel environments and scatter larvae may increase its competitive ability, to the detriment of native species or other supercolonies. One hypothesis

Table 2 Results of the GLM analysis to characterise behavioural variation among supercolonies

Colony pairs	df	Z	P
Interspecific aggression^a			
MAIN–CATA	39	5.04	0.0001
MAIN–BA1	29	4.04	0.0001
MAIN–BA2	29	3.29	0.005
CATA–BA1	29	0.51	0.95
CATA–BA2	29	−0.84	0.83
BA1–BA2	19	−1.14	0.65
Intraspecific fights initiated^b			
MAIN–CATA	95	3.17	0.008
MAIN–BA1	71	2.61	0.04
MAIN–BA2	71	1.37	0.52
CATA–BA1	71	0.01	1
CATA–BA2	71	−1.32	0.55
BA1–BA2	47	−1.14	0.66
Exploratory activity^c			
MAIN–CATA	19	6.51	0.0001
MAIN–BA1	14	5.07	0.0001
MAIN–BA2	14	2.94	0.02
CATA–BA1	14	−0.05	0.99
CATA–BA2	14	−2.43	0.07
BA1–BA2	9	−2.02	0.18
Food detection^d			
MAIN–CATA	19	−5.15	0.0001
MAIN–BA1	14	−4.68	0.0001
MAIN–BA2	14	−2.6	0.04
CATA–BA1	14	−0.16	0.99
CATA–BA2	14	2.31	0.09
BA1–BA2	9	−2.2	0.12
Foraging activity^e			
MAIN–CATA	19	4.32	0.0001
MAIN–BA1	14	3.76	0.0001
MAIN–BA2	14	0.08	0.99
CATA–BA1	14	0.31	0.99
CATA–BA2	14	−3.52	0.002
BA1–BA2	9	−3.25	0.006
Distribution of larvae^f			
MAIN–CATA	19	3.92	0.0001
MAIN–BA1	14	4.24	0.0001
MAIN–BA2	14	2.1	0.15
CATA–BA1	14	1.22	0.7
CATA–BA2	14	−1.1	0.7

Table 2 continued

Colony pairs	df	Z	P
BA1–BA2	9	−1.92	0.24

The dependent variables were the nine measures of behaviour. The independent variable was the colony (fixed categorical factor with four levels: BA1, BA2, Main, and Cata). We only report results for the six behaviours for which the four supercolonies differed

Significant results are in bold ($P < 0.05$)

^a Index of interspecific aggression (MAIN and CATA $n = 20$; BA1 and BA2 $n = 10$)

^b N of fights initiated (MAIN and CATA $n = 48$; BA1 and BA2 $n = 24$)

^c N of workers outside after 10 min (without food) (MAIN and CATA $n = 10$; BA1 and BA2 $n = 5$)

^d Time to food detection (MAIN and CATA $n = 10$; BA1 and BA2 $n = 5$)

^e N of workers foraging during 15-min period (with food) (MAIN and CATA $n = 10$; BA1 and BA2 $n = 5$)

^f % of available tubes containing larvae (MAIN and CATA $n = 10$; BA1 and BA2 $n = 5$)

to explain the success of invasive ants is the violation of the discovery-dominance trade-off in native ant communities (Holway 1999). This trade-off implies that some species are exploitative specialists, while others are interference specialists. We observed here that the MAIN supercolony is better at both discovering and dominating the resources than the other supercolonies. Such competitive advantage over both other supercolonies and local ant species (Holway 1999) may provide a direct mechanism of its invasion success. Our results concur with those of a previous study that compared aggressiveness in the two European supercolonies (Abril and Gómez 2010). This polymorphism in personality traits among native and invasive populations raises interesting questions regarding the evolutionary processes underlying this behavioural pattern. Two non-exclusive hypotheses may be proposed.

First, either evolutionary processes—such as founder effects (Tsutsui et al. 2000) or selection for highly adaptive behaviour (Giraud et al. 2002)—or high levels of phenotypic plasticity (Chown et al. 2007) might account for behavioural differences between populations across biogeographic ranges. For

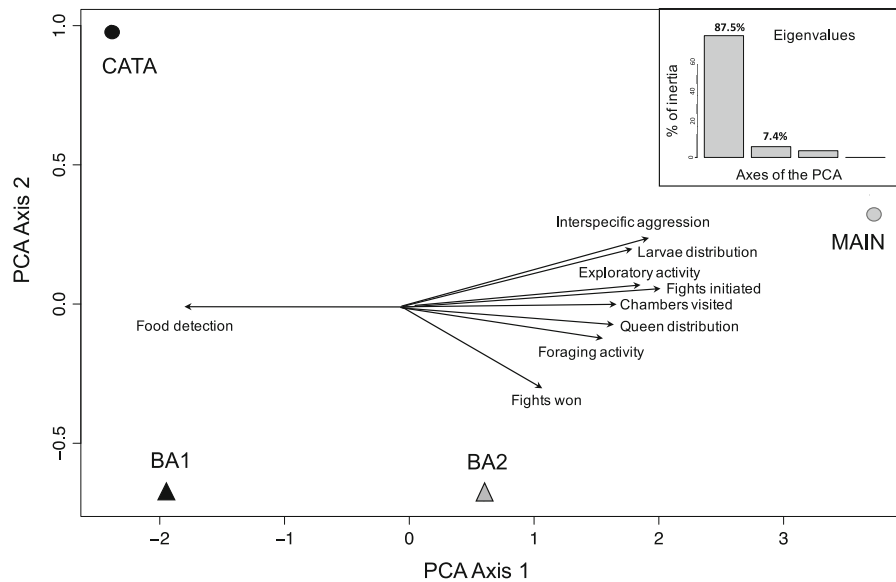


Fig. 1 PCA biplot along the two principal components; associating supercolonies with nine behaviours. In the *upper right corner*, the percentage of the inertia of the first axes of the

principal component analysis is given in an eigenvalues plot. PC1 and PC2 accounted for 87 and 8% of the total variance in the nine behavioral traits

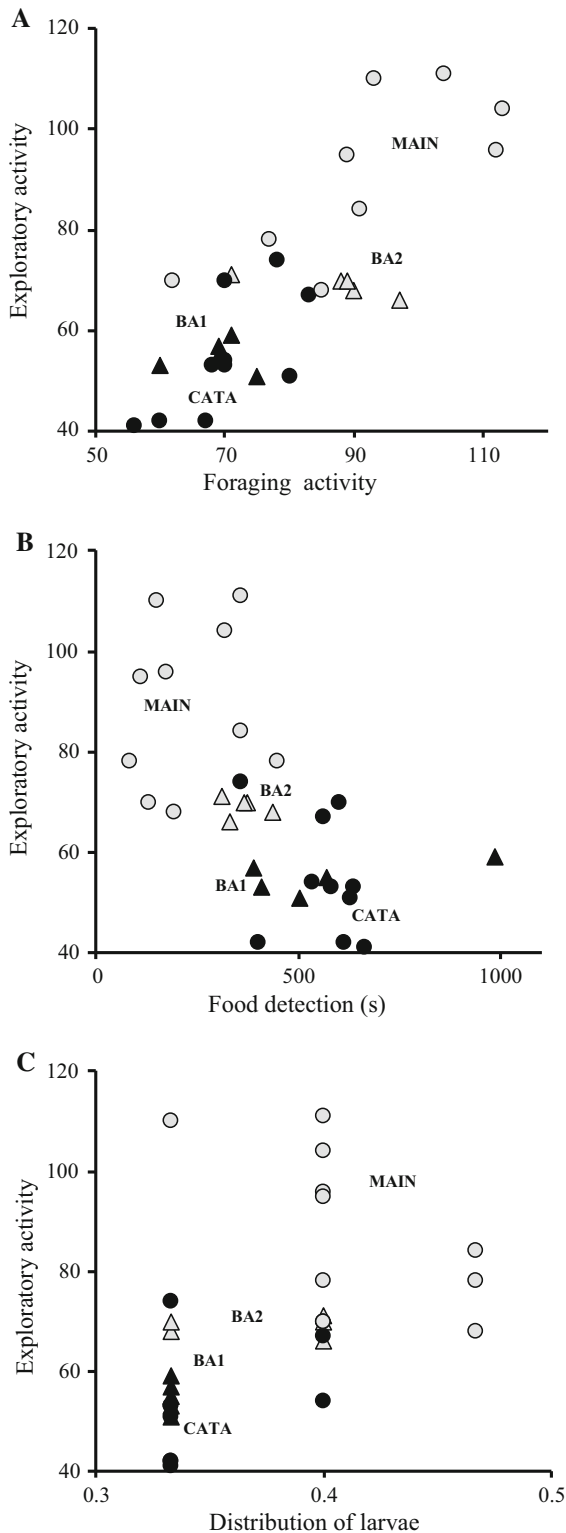
Table 3 Correlations between the behaviours in the experiments using native and introduced Argentine ant supercolonies

	Exploratory activity	Foraging activity	Chambers visited	Food detection
Foraging activity	0.64	–		
Chambers visited	0.25	0.3	–	
Food detection	–0.72	–0.52	–0.42	–

Significant correlations are in bold (Spearman's r , $P < 0.05$)

example, island and mainland populations of the European common frog, *Rana temporaria* display clear differences in their behaviour; island populations are bolder and more explorative than populations from the mainland (Brodin et al. 2013). Similarly, native and introduced populations of the invasive crayfish, *Pacifastacus leniusculus*, differ in a series of behavioural traits (Pintor et al. 2008; Pintor and Sih 2009). In the case of the Argentine ant, we expected to find a behavioural type specific to each range. Instead of a binary pattern, however, Argentine ant supercolonies display a behavioural continuum that is not influenced by geographic origin (native/introduced range). There are less active, less aggressive supercolonies (the Catalonian supercolony in the introduced range and BA1 in the native range) and highly active and aggressive supercolonies (the MAIN supercolony in the introduced range). The BA2 (native) supercolony is intermediate along this behavioural continuum.

Second, colony-level variation in behavioural type may be inherent to native populations and maintained after introduction events. In support of this argument, although the two native supercolonies (BA1 and BA2) were located only 1 km apart, they were not behaviourally similar to each other; BA1 workers showed a greater resemblance to workers from the Catalonian supercolony than to BA2 workers. Interestingly, these two supercolonies differ in size, BA1 and BA2 range over 6 and 11 ha respectively. It seems that the personality polymorphism is also related to differences in group's success in the native range, because BA2 has the greater range and the more aggressive personality. Differences in supercolonies' age might be an alternative explanation for differences in spatial occupation. However, despite multiple surveys, they both have been detected in late 2000s (Josens R; Pers. Comm.), suggesting that they are of a similar age. Group-level personalities are known from



may facilitate the persistence and invasion of animals under novel selective pressures by promoting adaptive behaviours relevant to their ecology such as higher aggressiveness and exploratory activity. Natural selection may favour certain behaviours over others when animals are confronted with different ecological challenges posed by their introduction to new biogeographic regions. Therefore, we stress the necessity of taking the concept of animal personality into account when addressing the issue of invasive species.

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