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ORIGINAL ARTICLE

Behavioral syndrome in a native and an invasive hymenoptera species

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Abstract Recent studies have focused on the role of behavior in biological invasions. Individuals may differ consistently in time for several behavioral traits (personality) which covary (behavioral syndrome) resulting in different behavioral types, some of them favoring invasion. Social hymenopterans have a strong potential to be invaders and their success depends primarily on the foundresses' ability to found viable colonies. They are expected to be active, explorative and bold for optimally establishing their nest. In Europe, 2 hornet species coexist: the native *Vespa crabro* and the invasive *Vespa velutina*. These 2 species may compete for nesting sites and we suggest that the initial success of *V. velutina* has been favored by its behavior in outperforming *V. crabro* for the traits involved in nest initiation. Here, we (i) defined the personality of *V. crabro* and *V. velutina*, (ii) tested for the existence of behavioral syndrome in these species, and (iii) compared their performances using an open-field test. Our results show that *V. crabro* foundresses behave consistently but not *V. velutina*; this lack of consistency being mainly due to reduced variance among individuals. This result questions the possibility of detecting consistent behavioral differences in species having recently undergone a strong bottleneck. Both species exhibit the same correlations between activity, boldness and exploration and *V. velutina* clearly outperforms *V. crabro* for all traits. Our results suggest that activity, boldness, and exploration are implicated in both hornet nest initiation and invasion process which contributed to explain why social hymenopterans are so successful at colonization.

Key words animal personality; biological invasion; invasion syndrome; *Vespa crabro*; *Vespa velutina*; Vespidae

Introduction

Alien species are defined on their ability at completing invasion process, from the transportation out of their native range to the spread in another area (Chapple *et al.*, 2012). Individuals may survive transport, establish themselves, compete with the native species and then spread in a novel environment. Thus, invasion process acts as a filter which may select individuals for several traits especially those promoting dispersal, establishment, and proliferation. Usually, invasive species exhibit *r*-selected life history traits such as high fecundity and growth rate, but also high dispersion ability (Sakai *et al.*, 2001). For example, a recent population genetic study on invasive monk parakeets (*Myiopsitta monachus*) in the United States reveals that invasive individuals dispersed over longer distance than do their native counterparts (Gonçalvez da Silva *et al.*, 2010). In the last decade, researchers have also been interested in understanding the contribution of behavior to biological invasion (see for review Holway & Suarez, 1999; Sih *et al.*, 2004; Chapple *et al.*, 2012). Especially, recent works considered that individuals differ

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consistently for several behavioral traits also known as personality (Réale *et al*., 2007). Such traits like sociality, boldness, or activity have been proposed as related to invasion process (Sih *et al*., 2004; Pintor *et al*., 2008; Chapple *et al*., 2012; Wolf & Weissing, 2012; Carere & Gherardi, 2013). For example, recently founded island and mainland populations of *Rana temporaria* display clear differences in their behavior; island populations are bolder and more explorative than individual from mainland (Brodin *et al*., 2013). Additionally, these behavioral traits can be correlated forming a so-called behavioral syndrome (Sih *et al*., 2004; Bell, 2007). For example, in the invasive mosquitofish, *Gambusia affinis*, sociability, boldness, exploration and activity are positively correlated (Cote *et al*., 2010a). These traits are linked to dispersal (Dingemanse *et al*., 2003; Cote *et al*., 2010b; Hoset *et al*., 2011).

Social hymenopterans are well-known to be successful at invading new environments: sociality provides flexibility which promotes invasiveness and thus results in successful colorizations worldwide (Moller, 1996; Farji-Brener & Corley, 1998; Cervo *et al*., 2000; Matthews *et al*., 2000; Chapman & Bourke, 2001; McGlynn, 2002; Wilson *et al*., 2009; Beggs *et al*., 2011; Monceau *et al*., 2014). They usually display high fecundity, a single queen producing hundreds to thousands of offspring, depending on the species (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). In these species, the success of the invasion depends primarily on the ability of the foundress to survive transport from the native to the introduced area and to establish colonies. Indeed, colony initiation is considered the most critical step in hornet life cycle, especially in haplometrotic species (i.e., a single queen founds the colony; Spradbery, 1973; Moller, 1996). Foundresses may find a suitable place for establishing their nest, laying eggs, and feeding their larvae until the first workers emerge to ensure all the tasks for the maintenance of the colony (Spradbery, 1973). Foundresses are thus expected to be active, explorative, and bold to found viable colonies. Therefore, foundresses in invasive hymenopteran species are supposed to exhibit higher level of exploration, activity, and boldness than native queens.

Among the 22 known *Vespa* species, only 2, *V. crabro* and *V. velutina* are considered invasive (Beggs *et al*., 2011). The European hornet, *V. crabro*, native to Eurasia, has been introduced into the United States in the 19th century and is also invasive in Canada (Akre *et al*., 1980; Buck *et al*., 2008; Kimsey & Carpenter, 2012). *Vespa velutina*, the yellow-legged hornet, native to Asia, has been recently introduced into Western Europe in a single event of a single foundress (see Monceau *et al*., 2014 for a review). Thus, the interaction of these 2 predators, *V. crabro* and *V. velutina*, is very interesting but the nature of these interactions (competition or not) is unknown. In *Vespa* sp., although interspecific competition is rare or underreported, it can occur for nesting sites (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). Basically, *V. crabro* foundresses establish their nest in closed sites such as tree cavities (Edwards, 1980; Matsuura & Yamane, 1990) and previous studies suggest that this species displays high nest site fidelity, foundresses being able to reuse old nests (Hoffmann *et al*., 2000; Langowska *et al*., 2010). In *V. velutina*, little is known about the dispersal of the gynes from their parent nests. However, *V. velutina* foundresses establish their nests in both closed and open sites, from the underground to the tree tops (Monceau *et al*., 2013, 2014). Therefore, the nesting habits of the native species (closed sites) overlap with those of the invasive species (closed and open sites).

Although the spread of *V. velutina* may have been favored by its high fecundity since it produces larger colonies than *V. crabro* (Edwards, 1980; Matsuura & Yamane, 1990; Archer, 1993; Hoffmann *et al*., 2000; Martin, 1995; Monceau *et al*., 2014), we suggest that the initial success of *V. velutina* at establishment has been favored by its behavior and that this invasive species outperforms the native species for the behavioral traits involved in nest initiation. In this study, wild hornet foundresses were tested for 3 major behaviors involved in nest initiation, that is, activity, boldness, and exploratory tendency using an open-field test (Réale *et al*., 2007). We aimed at (i) defining the personality of *V. crabro* and *V. velutina* (i.e., if they behave consistently), (ii) testing the existence of behavioral syndrome in these 2 species, and (iii) comparing the performances of the native and the invasive hornet species.

Materials and methods

Hornet foundress captures and laboratory rearing

Twenty six *V. crabro* and 29 *V. velutina* foundresses were captured between February and April 2013 by sweet bait traps (Monceau *et al*., 2012) or directly in their wintering woodpile shelters at different locations near Bordeaux (south–west France, see details in Table S1), invaded since 2004–2005. In laboratory, foundresses were maintained individually in plastic box (23.2 × 15.3 × 16.6 cm) including a refuge (egg carton), food (honey) and water provided *ad libitum* and were placed at 23 ± 1 °C in 16 L : 8 D photoperiod. All foundresses were kept at least during a week (range: 7–13 days, median: 8 d) in acclimatization before the experiments in order to keep all individuals in the same conditions prior to behavioral experiments. After the experiments, *V. crabro* foundresses were released *in natura* while *V. velutina* foundresses were kept in the laboratory for further experiments (but were never released in the field due to their invasive status).

Experimental design

Following Cote *et al*. (2010a), 3 behavioral traits (activity, boldness, exploration) were measured at the same time using an open-field apparatus (Réale *et al*., 2007). It consisted in an experimental arena constituted of an opaque acclimatization box (dimension: 14 × 14 × 14 cm) connected via a trapdoor (5.3 × 10.8 cm) to a transparent test box (dimension 25 × 25 × 25 cm) divided in 27 equivalent sections. Each part of the apparatus was carefully washed with 96% ethanol between trials. Each foundress was tested twice in a 1 week interval and at the same time of the day in a random sequence among foundresses of the 2 species. Foundresses were kept between trials in the same conditions as described above. The foundress was first introduced in the opaque box for 5 min of acclimatization; the trapdoor was then opened to allow the female to explore freely the test box for 5 min or to return to the opaque box as a refuge. The foundresses were video recorded (Canon Digital Ixus 870 IS, 640 × 480 resolution, 30 FPS) and videos were analyzed by the same person (KM) using JWatcher (Blumstein *et al*., 2006). Three behaviors were measured: (i) the latency to the first exit from the acclimatization box after the trapdoor opening was used as a measure of *boldness* (i.e., the lower is the score, the more the individual is bold); (ii) the total time the female stayed in motion in the test box was used as a measure of *activity* (i.e., the time spend motionless, dedicated to preening or in the acclimatization box was discarded); and (iii) the number of different sections visited was used as a measure of *exploration* (maximal score = 27).

Statistical analyses

For each species, the behavior of foundresses caught in traps was first compared to the behavior of those caught in their wintering shelter to discard potential differences due to trapping and/or sheltering. No difference between groups was detected so the catching method was not included in the analyses. The consistency of behavioral differences across time (personality) was tested independently for *V. crabro* and *V. velutina* using Linear Mixed-effects Models (LMM for boldness and activity) and Generalized LMM (GLMM for exploration) (Nakagawa & Schielzeth, 2010). The correlations between the 3 averaged behavioral traits (mean score over the 2 trials) were assessed using Spearman's rank correlation tests for *V. crabro* and *V. velutina* separately and then compared between species based on their 95% confidence intervals. Even though the strength of the correlation could be overestimated due to the measurement of the behavioral traits during the same trial (see Cote *et al*., 2010a for a discussion), only a late exit from the acclimatization box can constrain the correlations because it limits activity and exploration duration. At the opposite, an early exit does not necessary mean that the hornet will move the rest of the test, neither will explore the whole apparatus. These points (early exit, i.e., bold individuals) determine the strength of the correlations. The variance of each averaged behavioral traits was compared between species using Brown–Forsythe tests (nonparametric Levene-type tests based on the absolute deviations from the median). An effect size estimator (assorted with 95% confidence interval, thereafter noted 95%CI) was further used to compare the 3 averaged traits between *V. crabro* and *V. velutina* (Nakagawa & Cuthill, 2007). Cliff's delta estimator was preferred to usual Cohen's *d* because our data were nonparametric (Cliff, 1996; Nakagawa & Cuthill, 2007; Macbeth *et al*., 2010; Ivarsson *et al*., 2013). The score of Cliff's delta estimator represents the proportion of scores obtained in *V. velutina* which do not overlap with those obtained in *V. crabro*. The performances of *V. crabro* and *V. velutina* are considered to be different if Cliff's delta 95%CI does not integer 0 and effect size is considered large if Cliff's delta >0.47 (Romano *et al*., 2006). Contrary to classical nonparametric tests such as Mann–Whitney U test, effect size estimators can be compared between tests (here between behaviors) using their 95%CI to know if the strength of the differences between species is equivalent for each behavior. All statistical analyses were performed with R software (v. 3.0.1, R Development Core Team, 2013) implemented with *effsize* package.

Results

In *V. crabro*, activity and boldness were consistent between trials within individuals (Table 1). Exploration also tended to be consistent although the significant threshold was not reached probably due to our small sample size (Table 1). In *V. velutina*, none of the behavior was repeatable (Table 1). The 3 traits were positively correlated with

Table 1 Repeatability (R) of the 3 behaviors in *Vespa crabro* and *V. velutina*, assorted with their *P*-values (*P*). Linear mixed-effects models (LMM) based on restricted maximum likelihood were used for activity, boldness and sheltering behaviors and generalized LMM based on link-scale repeatabilities was used for exploration (see Nakagawa & Schielzeth, 2010).

Behavior	*Vespa crabro*		*Vespa velutina*	
	R	*P*	R	*P*
Activity	0.33	0.04	0.00	0.58
Boldness	0.39	0.03	0.00	0.95
Exploration	0.27	0.08	0.00	0.95

Table 2 Spearman's rank correlation tests in *Vespa crabro* (above diagonal) and *V. velutina* (below diagonal) between the 3 behaviors assessed in this study.

	Activity	Boldness	Exploration
Activity	–	0.85*** [0.63–0.95]	0.91*** [0.76–0.97]
Boldness	0.73*** [0.43–0.90]	–	0.84*** [0.60–0.95]
Exploration	0.73*** [0.47–0.88]	0.68*** [0.39–0.86]	–

Correlation coefficients are given with 95% confidence interval.
All *P*-values were highly significant (***$P < 0.0001$).

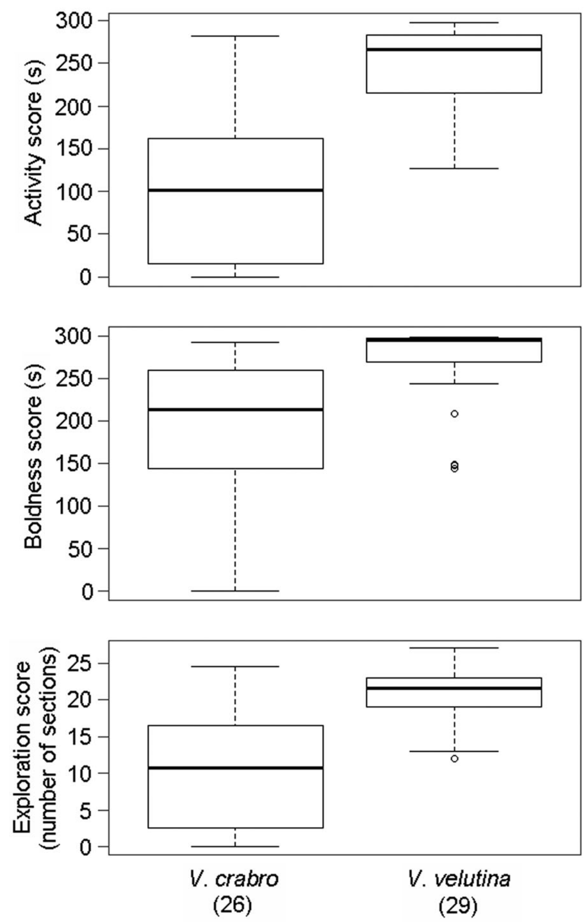

Fig. 1 Activity, boldness and exploration scores in *Vespa crabro* and *V. velutina*. Boxes, plain line, dashed lines, and open circles represent 50% of all values, medians, 1.5 interquartile range and extreme values respectively. Sample sizes for each species are presented in parentheses.

no difference between species since 95%CI overlapped (Table 2). For the 3 traits, variances were larger in *V. crabro* than in *V. velutina* (Brown–Forsythe test; activity: $F = 5.87$, $P = 0.02$; boldness: $F = 11.98$, $P < 0.01$; exploration: $F = 16.13$, $P < 0.001$; Fig. 1). For the 3 behavioral traits, *V. velutina* outperformed *V. crabro* foundresses; Cliff's deltas were always greater than 0.47 and 95%CI were always different from 0 thus representative of large and significant effect sizes (Fig. 2).

Discussion

In this study, we have tested the behavior of the native *V. crabro* and the invasive *V. velutina*, and we show behavioral differences between the foundresses of the 2 species. However, these results should be carefully interpreted before further field and larger scale investigation.

Personality and behavioral syndrome in hornet species

In *V. crabro*, foundresses behaved consistently across time for activity and boldness with also a marked tendency for exploration. This consistency is congruent with the average value obtained by Bell *et al*. (2009) in their meta-analysis, although activity is usually found more repeatable than exploration (Bell *et al*., 2009). Conversely, none of the behavioral traits in *V. velutina* were found repeatable. The repeatability coefficient reflects the proportion of variance which is due to within-individual variance in regards to among-individual variance. In other words, the absence of repeatability is due to equivalent among- and within-individual variance. In the present case, the among-individual variance was lower in *V. velutina* than

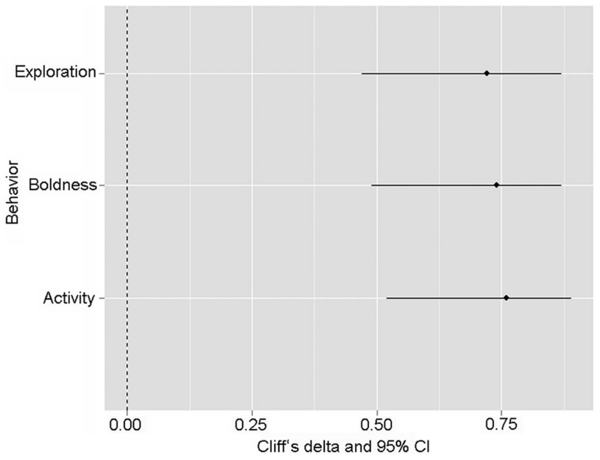

Fig. 2 Effect size estimator (Cliff's delta) of behavioral differences between *V. crabro* and *V. velutina* foundresses for activity, boldness and exploration.

in *V. crabro* and this lower variance may result from the strong bottleneck that *V. velutina* suffered during the single female introduction (Arca, 2012; Monceau *et al*., 2014). Indeed, the invasion is supposed to select for particular behavioral types (Chapple *et al*., 2012) and often results in a loss of genetic diversity depending on the number of introduced founders and gene flow (Nei *et al*., 1975; Dlugosch & Parker, 2008). Therefore, due to the probable strong bottleneck, it is not surprising to find low behavioral variability within *V. velutina* foundresses in this study and consequently to not detect consistent differences between individuals. Because of this strong selection event, the fact that consistency could not be detected does not exclude this trait to be consistent in the native populations. Here, we suggest that such traits should be observed in populations of the native area. To go further, if invasion process selects for some specific behavioral types, that is, highly active, bold, and/or explorative individuals for instance, it is thus questionable to detect personality traits in a recently introduced species because drastic selective processes are supposed to strongly reduce the variance of the trait within the invasive population (see Brodin *et al*., 2013 for another example).

In this study, we found evidence for a behavioral syndrome in both the native and the invasive species. The most active individuals were also the most explorative and the boldest. These traits are classically linked to dispersal success (Dingemanse *et al*., 2003; Cote *et al*., 2010b; Hoset *et al*., 2011). Alternatively, the correlation between boldness and exploration were not significant in *Rana temporaria* neither in recently colonized islands nor in mainland populations (Brodin *et al*., 2013) suggesting that such relationships among behavioral traits remain species-specific and cannot be generalized based on the few studies available. However, we observed the same trends in the native and the invasive hornet species. This suggests that the relation between these behavioral traits may be common in Vespid foundresses because of the implication in nest initiation. Indeed, being highly active, explorative, and bold is advantageous to find a suitable place to initiate the nest, and to search for nest materials and prey to feed the larvae. To go further, the success of the invasion in *Vespa* species should depend upon nest initiation success. Thus, we suggest that nest foundation by Vespid queens can be viewed as recurrent invasion events within an ecosystem and this may also contribute to explain (along with the other life traits, see Moller, 1996) why Vespid are so successful at colonization. Some recent studies strongly highlighted the importance of understanding local processes of dispersal to understand and predict global invasion events (Giometto *et al*., 2013). Thus, integrating behavioral syndromes as a major component of the dispersal pattern is, to our opinion, of major concern to predict the spatial expansion of invasive Vespid.

Ecological implications of behavioral differences within and between hornet species

In *Vespa* species, interspecific competition can occur for nest sites (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). *Vespa velutina* foundresses clearly outperform *V. crabro* foundresses for the 3 behavioral traits and emerge first from overwintering (i.e., before *V. crabro*, Monceau & Thiéry, unpublished data). They thus potentially access the most suitable nest sites first. Consequently, *V. velutina* may force *V. crabro* foundresses to disperse. However, the existence of a mix of behavioral types within the population of *V. crabro* may have allowed coping with the invasive *V. velutina* (Sih *et al*., 2012; Wolf & Weissing, 2012). Indeed, where *V. velutina* is not already established, the most active, explorative and boldest *V. crabro* foundresses should be favored in dispersing for finding free place while those which display the lowest level of activity, boldness and explorative tendencies may either directly compete to coexist with the invasive species or, in the worst case, not be able to establish their nest. This hypothesis deserves further investigation because it may result in a heterogeneous distribution of *V. crabro* behavioral types between free and *V. velutina*-invaded areas (Wolf & Weissing, 2012).

Conclusion

Personality and behavioral syndromes have received a considerable interest in the past 10 years because of their potential important role in ecological and evolutionary processes such as biological invasions (Holway & Suarez, 1999; Sih *et al*., 2004, 2012; Bell, 2007; Reale *et al*., 2007; Chapple *et al*., 2012; Wolf & Weissing, 2012; Carere & Gherardi, 2013). Overall, *V. velutina* outperforms *V. crabro* for each behavioral trait. Nevertheless, foundresses behave similarly although invasion filter has probably selected for a particular behavioral type in *V. velutina* and traits involved in nest foundation may also favor invasiveness. The differences we found in the present experiment would stimulate further field studies on these specific behavioral traits.

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Disclosure

The authors have no conflicts of interest, including specific financial interests and relationships and affiliations relevant to the subject of this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1 GPS coordinates of the sites where the hornet foundresses involved in the present study were caught.