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Foraging Behavior Interactions Between Two non-Native Social Wasps, *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae): Implications for Invasion Success?

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Abstract

Vespula vulgaris is an invasive scavenging social wasp that has very recently arrived in Patagonia (Argentina), a territory previously invaded – 35 yrs earlier – by another wasp, *Vespula germanica*. Although *V. vulgaris* wasps possess features that could be instrumental in overcoming obstacles through several invasion stages, the presence of preestablished populations of *V. germanica* could affect their success. We studied the potential role played by *V. germanica* on the subsequent invasion process of *V. vulgaris* wasps in Patagonia by focusing on the foraging interaction between both species. This is because food searching and exploitation are likely to overlap strongly among *Vespula* wasps. We carried out choice tests where two types of baits were presented in a pairwise manner. We found experimental evidence supporting the hypothesis that *V. germanica* and *V. vulgaris* have an asymmetrical response to baits with stimuli simulating the presence of each other. *V. germanica* avoided baits with either visual or olfactory cues indicating the *V. vulgaris* presence. However, *V. vulgaris* showed no preference between baits with or lacking *V. germanica* stimuli. These results suggest that the presence of an established population of *V. germanica* may not contribute to added biotic resistance to *V. vulgaris* invasion.

Key words: foraging behavior, biological invasion, invasive insects, Vespidae

Investigation of the main factors that contribute to the successful invasion of introduced species remains a vibrant area of much ecological research (Lodge 1993). Some studies have suggested that species-specific characteristics of the invader are probably the key factors determining their success in novel habitats (Moller 1996, Rejmánek and Richardson 1996, Richards et al. 2006, Di Vittorio et al. 2007). Others, however, have proposed that the drivers of invasion success are instead features of the invaded ecosystems that make them more or less susceptible to specific invasions (Davis et al. 2000, Keane and Crawley 2002). Other approaches have related the attributes of invaders to those of the new ecosystems, proposing that successful biological invasions involve complex interactions between both the invading species and the physical and biological characteristics of the invaded environment (Heger and Trepl 2003).

Social insects possess a number of attributes that may contribute to their success in invading new locations, especially during the establishment phase. For example, social insects are characterized by several cooperative behaviors, excellent dispersal abilities, high rates of queen production, broad habitat ranges, efficiency at feeding, effective predator defense, competitive abilities, and broad diets, among others (Simberloff 1989, Moller 1996, Liebert et al. 2006).

One attribute commonly invoked to explain the success of invasive animals is their foraging behavior, a complex process that has also been proposed as an important factor explaining the success in social insect invasions (Holway and Suarez 1999). For example, the use of olfactory and visual stimuli to attract nest mates to new food sources, as well as aggregation of workers at resource patches, are bait discovery strategies often employed by some social wasps (Reid et al. 1995, Holway 1999, D'Adamo et al. 2004).

Several species of social wasps (Hymenoptera: Vespidae) have been highly successful invaders of new territories around the world (Spradbery and Richards 1973, Clapperton et al. 1989, Wilson and Holway 2010, Masciocchi and Corley 2013). In Patagonia (Argentina), *Vespula germanica* (Fabricius; Hymenoptera), a species native to Europe and North Africa, was first observed in 1980 (Willink 1980) and since then, it has established in a wide variety of habitats and spread throughout most of the Patagonia at a remarkable rate (Masciocchi and Corley 2013). In 2010, another wasp of the same genus and also native to Europe, *Vespula vulgaris* (Linnaeus; Hymenoptera), was found in NW Patagonia (Masciocchi et al. 2010).

Sequential invasion by these two eusocial wasps has also been observed elsewhere. In New Zealand, invasive *V. germanica* spread

widely throughout the country after its arrival in 1945, until some 30 yrs later when *V. vulgaris* arrived and displaced it from many environments (Sandlant and Moller 1989, Harris et al. 1991). Feeding activities of both wasp species were disrupted by each other rather than by conspecifics, suggesting that these two species could interfere directly. It has been suggested that differences in foraging behavior may give *V. vulgaris* a competitive advantage over *V. germanica* (Harris et al. 1994).

In their native range, both *Vespula* wasps coexist and show a considerable overlap in their distribution, although *V. germanica* has a narrower altitudinal foraging range than *V. vulgaris* (Archer 1978). The latter appears to have taken longer to colonize the higher altitudes than the lower altitudes, but once there, it accounts for a larger proportion of the wasp population than at lower altitudes. In contrast with the invaded community, when in their native range, both wasp species share the area with a number of other Vespidae, and are exposed to the presence of a suite of nest associates, parasites, and predators that may limit the impacts of competition among these species (Spradbery and Richards 1973).

V. germanica and *V. vulgaris* both share a broad diet that includes carbohydrates (from flower nectars, honey, and ripe fruits) and protein-rich foods (live insects and – more importantly – carrion) (Harris 1991, Sackmann et al. 2000, 2008). Foraging by both these species is part of a strong, well-developed social behavior that relates directly to colony success. This is because workers search for foods that they carry back to the nest, where they feed developing larvae which will become future workers and reproductives. While workers search for food individually, a strong aggregative behavior, mediated by olfactory and visual cues, after the discovery a profitable food source has been observed in *V. germanica* (i.e., local enhancement, see D'Adamo et al. 2000). A study on olfactory cues found that head, rather than abdomen pheromones, were shown to attract *V. germanica* foragers to baits, eliciting landing a transportation to the nest (D'Adamo et al. 2001). These behaviors allow nestmates a rapid food location and efficient exploitation which, in turn, may give them an increased capacity to adapt to rapidly changing environmental conditions (Free 1970, Reid et al. 1995, Farji-Brener and Corley 1998, Raveret Richter and Tisch 1999, Brown et al. 2014). This important foraging behavior may favor the potential for these wasps to invade new habitats. While *V. vulgaris*, as other social insects, possesses features that may contribute to their establishment in new territories such as NW Patagonia, their arrival occurred in areas previously invaded by *V. germanica*. Thus, *V. vulgaris* invasion success implies not only dealing with the potential biotic resistance offered by the native community but also with the addition of a preestablished social invasive wasp.

The sequential and recent invasion by two very similar wasps in NW Patagonia offers a unique opportunity to study the interaction between these two invaders at an early stage of the invasion process. A standing question is whether both invaders will coexist in given environmental conditions. With this in mind, in this study, we explore the potential role played by *V. germanica* on the invasion process of *V. vulgaris* wasps in Patagonia. We focused on their foraging behavior since there is an overlap in their feeding habits (Harris 1991) and carrion searched by both – likely a key to wasp success – is a highly preferred source, yet temporary and rapidly changing in its characteristics. Given that these wasps share overlapping foraging niches and in the light of the competitive exclusion noted in some areas of New Zealand, we hypothesize that *V. vulgaris* and *V. germanica* do not display the same response when foraging in presence of the other wasp species. The main contribution of this work arises from the possibility to study the interactions between the invader, the invaded environment, and a previously established similar invader, during the early stages of the invasion process.

Materials and Methods

Study area
The study was carried out under natural conditions, within the *Nahuel Huapi National Park*, Patagonia, Argentina (41°S, 72°W). This area is characterized by an abrupt west-to-east gradient in rainfall – mean annual precipitation is 3,500 mm in the western end and 500 mm in the East. The vegetation reflects this climatic pattern, determining three distinct habitats: forest, scrubland, and steppe.

Experimental design
In order to test foraging interactions between *V. germanica* and *V. vulgaris*, we assessed the behavior of each one in the presence of workers of the other. Accordingly, we selected similar sites (separated a minimum of 500 m from one another to ensure sampling from different nests) where only one species was present and simulated the presence of the other one using visual and odor cues. At each site, paired choice tests were conducted to compare the preference of foraging wasps for treated or untreated food baits, placed 50 cm away from each other. Treated baits consisted of the application of odor or visual stimuli of the absent species onto minced beef. The response variable measured was the bait on which the first worker landed. In each site, only one wasp was used per experiment. We used minced beef as food bait because it has proved highly attractive for *Vespula* spp. (Spurr 1995, Wood et al. 2006). We deployed experiments between 10 a.m. and 5 p.m. during March, April, and May, autumn in Argentina, of 2012–2013 and 2013–2014 (period of peak wasp abundance). Visual cues were dead workers with cuticular odors extracted (hereafter, dummies) and odor cues were wasp head pheromone extracts. Previous work has shown that head glands of *V. germanica* secrete pheromones that are responsible for intraspecific communication and promote local enhancement (D'Adamo et al. 2001, 2004).

To create the dummies, we collected 20 workers of some *V. vulgaris* nests from different sites, using a vacuum directly into the nest entrance, and removed from these specific cuticular odors (Raveret Richter and Tisch 1999). Wasps collected were posed in a life-like foraging posture (that is mimicking live foragers on a bait, Fig. 1), air dried, and then deodorized by 1) immersion in a 50 ml beaker containing 30 ml of hexane for 1 hour, 2) immersion in a second beaker containing 30 ml of hexane for another hour, and 3) immersion in a third beaker containing 40 ml hexane for 17 hours (overnight). The hexane was allowed to evaporate at room temperature for at least 1 week before experiments were conducted.

Head pheromone extracts were obtained from approximately 800 workers collected from several nests, using an adapted vacuum bag. Pheromone extraction followed the protocol of D'Adamo et al. (2004). Heads were cut with scissors, crushed with a mortar and pestle with 16 ml of ethanol, and then fractionated in Eppendorf tubes and centrifuged for 10 min at 14,000 rpm. Then, the supernatant was pipetted into a 30 ml glass vial and brought back up to a 16 ml volume of ethanol.

Choice test
Olfactory choice cues. To assess the response of *V. germanica* to *V. vulgaris* odors cues, we selected 51 sites where *V. germanica* was abundant. The offered treated and untreated baits consisted of: 10 g of minced beef with 100 μl of ethanol and 10 g of minced beef with
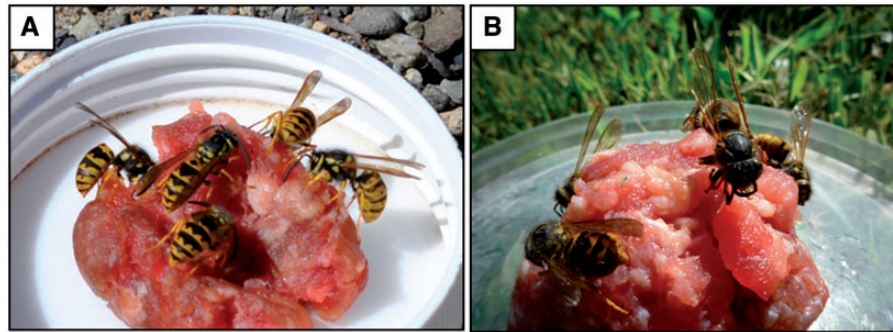
Fig. 1. Baits with wasps. (A) Live wasps foraging on the bait. (B) Dead wasps (dummies) in a life-like foraging posture.

100 µl head pheromone extract of *V. vulgaris* (approx. equivalent to five wasps). We chose this value because it is a dose that can be detected by foraging wasps with a minimum of extract usage (see D'Adamo et al. 2004). Once we placed the paired dishes, both the 100 µl of extract and ethanol were measured and placed on the minced beef with a 1 ml syringe. After we offered the baits, we waited until the first wasp landed. Workers of both *Vespula* species hover over food before landing (Collett and Lehrer 1993, Pereira et al. 2013), with the latter behavior a sign of food acceptance.

To assess the response of *V. vulgaris* to *V. germanica* odors, we selected 42 sites where *V. vulgaris* was abundant. The experimental procedure is the same as that done to evaluate the response of *V. germanica*.

Visual choice cues. To evaluate the response of *V. germanica* to visual cues of *V. vulgaris* workers, we tested baits of the first choice in 42 sites. Treated and untreated baits consisted of: 10 g of minced beef and 10 g minced beef to which we added *V. vulgaris* dummies, which consisted of five odorless dead workers simulating foragers (Fig. 1B). Since we offered the baits, we waited until the first wasp landed.

To assess the response of *V. vulgaris* to *V. germanica* visual cues, we selected 45 sites where *V. vulgaris* was abundant. We assessed the response to *V. germanica* dummies – odor extracted, posed, dried, and pinned wasp forager – by the same procedure as above.

Control. Controls were done exactly at the same time as each olfactory and visual choice test, for both species in 40 sites. The control consisted of the same experimental set up – baits offered in a paired manner – but without any kind of stimuli. This allows us to compare with treatments and to take into account differences between sites, as for example, nest location regarding baits or wind direction. In this setup, therefore, wasps had to choose between two dishes with only minced beef on them. As for the experimental group, the response variable measured was the bait on which the first *V. germanica* or *V. vulgaris* worker landed. Here, we expected wasp to choose equally among baits. Then, we compared the frequency of choices between experiments and controls.

Data analysis
We analyzed the bait preference of the first *V. germanica* and *V. vulgaris* worker in each pair – control comparison, minced beef, and minced beef with visual or odor stimuli – using a binomial test comparing observed visits to those predicted if wasps showed no choice among baits. All analyses were carried out using the R statistical environment (R Development Core Team 2009).

Results

Choice test
We determined that *V. germanica* significantly avoids baits with *V. vulgaris* visual and odor cues. On the other hand, wasps of the latter species were not deterred by stimuli indicating *V. germanica* presence and showed no preference among baits. Throughout the experiments, we observed that workers of both species invariably hovered over the food before landing. Remarkably, *V. germanica* hovered closer, over baits with the simulated presence of *V. vulgaris* but did not land on them. In contrast, *V. vulgaris* workers showed a behavior that was typical for this species (Collett and Lehrer 1993).

Vespula germanica. Wasps made more visits to baits with minced beef than to those with added *V. vulgaris* head pheromone extracts (Binomial test, $P < 0.0001$, $n = 51$) or those with added visual cues (Binomial test, $P < 0.0001$, $n = 42$). Regarding the controls, as expected, there was no significant difference between both minced beef baits offered (Binomial test, $P = 0.7798$, $n = 40$) (Fig. 2).

Vespula vulgaris. Wasps first visits were not significantly different between baits with only minced beef and those with added *V. germanica* head pheromone extracts (Binomial test, $P = 0.7552$, $n = 42$) or visual cues (Binomial test, $P = 0.2327$, $n = 45$). As was the case for *V. germanica*, workers did not distinguish between baits in the control assays (Binomial test, $P = 0.8742$, $n = 40$) (Fig. 2).

Discussion

We found experimental evidence supporting the hypothesis that *V. germanica* and *V. vulgaris* have asymmetrical foraging behavior abilities. *V. germanica* was deterred by cues indicating the presence of *V. vulgaris*. Workers of *V. germanica* were able to detect both visual and olfactory cues used to simulate the presence of a congeneric wasp species, responding to these stimuli and consequently avoiding those baits. In contrast, *V. germanica* cues did not affect the foraging behavior of *V. vulgaris* workers on a given food patch.

A benefit of social living is the opportunity of learning from conspecifics what foods to eat and where to find them (Shettleworth 1994). This process may involve complex behaviors such as worker recruitment as noted in ants and honey bees, or simpler mechanisms such as the local enhancement behaviors observed in some wasps (Wilson 1971, D'Adamo et al. 2000, Raveret Richter 2000, Grüter and Farina 2009). Such behaviors may be especially important in scavenging insects, given that dead or decaying foods, such as dead animals, can be widely scattered and are an unpredictable resource which can be exploited by other animals or is subjected to rapid
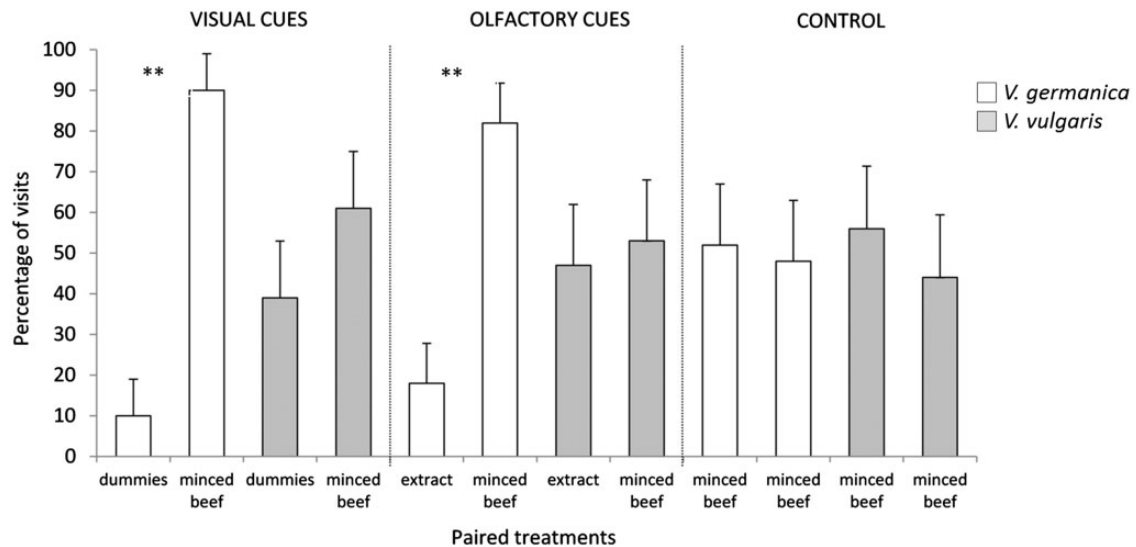
Fig. 2. Percentage of first visits of *V. germanica* and *V. vulgaris* foragers to a given bait in each paired choice tests (visual cues, olfactory cues, and control). Error bars indicate 95% confidence intervals for proportion. *V. germanica* foragers preferentially made their initial landing on baits lacking visual ($N = 4$ vs. $N = 38$) or olfactory stimuli ($N = 42$ vs. $N = 9$) of the other species. Wasps presented with identical baits showed no preference ($N = 19$ vs. $N = 21$) between baits. *V. vulgaris* foragers showed no preference at landing on baits presented with visual ($N = 18$ vs. $N = 27$), olfactory ($N = 20$ vs. $N = 22$), and control baits without *V. germanica* cues. **Indicates significant differences.

decay (Reid et al. 1995). Several studies have reported that foraging by *Vespula* wasps involves odor and visual cues which facilitate the location and exploitation of food resources (Free 1970, Parrish and Fowler 1983, Overmyer and Jeanne 1998, Raveret Richter and Tisch 1999). D'Adamo et al. (2003) found that the addition of *V. germanica* conspecifics to meat baits increased their attractiveness and that this is largely mediated by odor cues. Other previous works showed similar findings but mediated by visual cues (Parrish and Fowler 1983, Raveret Richter and Tisch 1999). In past classical work, Free (1970) attributed asymmetry in the numbers of *V. vulgaris* at equivalent patches to workers being attracted to signals derived from the presence of conspecifics. Knowing that manipulative experiments have their limitations, for example, we are not sure that the deodorizing treatment removes all substances and is equally equivalent for both species, earlier studies, where visual and odor cues have been used, give us some confidence when interpreting the results. The fact that both *V. germanica* and *V. vulgaris* are able to detect and react to their own olfactory and visual cues, leads us to suggest that *V. germanica* avoidance behavior is a plausible outcome of a process mediated by the detection of congeneric stimuli only. Regarding *V. vulgaris*, we would not predict a random choice, as wasps would be either attracted to or repelled by stimuli from *V. germanica*.

Unlike most previous works, where the role played by a variety of stimuli is evaluated by observing the response of conspecific workers, our results suggest that behavioral responses to visual and odor cues may be observed across species with similar foraging habits. These findings are consistent with those reported by Parrish and Fowler (1983) where they observed that *V. maculifrons* workers avoided feeders with both *V. maculifrons* and *V. germanica* olfactory and visual stimuli. Such mechanism was proposed to relate the behavioral differences expressed in *V. germanica* and *V. maculifrons*, suggesting that the first (through local enhancement) was superior to *V. maculifrons* at exploiting large resource patches (Parrish and Fowler 1983). Our results are novel since using cues and behavioral responses to evaluate mechanisms may have implications, not only to further our understanding of social behavior in insects, but also

to further our knowledge on the role played by interspecific competition in modeling behaviors in social wasps.

This study shows that *V. germanica* and *V. vulgaris* respond differently to the presence of individuals of other species on foods. Past work has shown that both these species display different behavioral responses toward competitors. Masciocchi et al (2010) found that *V. germanica* does not forage on baits when the native ant *Dorymyrmex tener* was feeding on them. In contrast, Grangier and Lester (2011) noted that *V. vulgaris* in New Zealand not only will not avoid baits with the native ants *Prolasius sp.*, but may even pick up ants while foraging, using its mandibles, and then fly backward, dropping them at some distance away from the food. These authors suggested then, that one reason for this behavior is the bigger size of wasps compared to that of ants. In the present study, we observed that *V. germanica* avoids baits with the presence of *V. vulgaris*, despite being smaller (see Spradbery and Richards 1973). Perhaps, *V. vulgaris* workers display a more aggressive behavior than *V. germanica* ones. The factors influencing aggressive behavior in wasps and the actual mechanisms involved are poorly known. Future studies should consider observing both species during foraging and evaluating possible aggressive encounters. Another explanation could be that *V. germanica* may identify in *V. vulgaris*, evolutionary phenotypic traits that convey information about the potential competitor, influencing their behavior (Grether et al. 2009). The absence of direct evidence for competitive interactions should not lead us to think that competition is not important. It may well be that competition is manifested as avoidance responses such as those found in this study.

According to our results, *V. germanica* and *V. vulgaris* display different foraging behaviors on baits with cues simulating the presence of congeneric workers. While this could suggest some degree of improved competitive abilities of *V. vulgaris* when compared to *V. germanica*, such behavior may have important implications for the establishment and spread of either invasive wasp species. We observed that highly attractive protein-rich foods were avoided by *V. germanica* whenever there was some indication suggesting the presence of *V. vulgaris*. In sites where both species have successfully established, *V. vulgaris* could outcompete *V. germanica* and lead to

the displacement of the latter species when food sources become limiting, as may occur at the end of the summer season, or when populations of *V. vulgaris* reach very high numbers as has been observed in the honeydew beech (*Nothofagus* spp.) forests of New Zealand (Harris et al. 1991, Clapperton et al. 1994). Also, monopolization of the best foods by *V. vulgaris* could affect the invasion process by slowing down the population spread of *V. germanica*, via a reduction of population growth. In sites where *V. vulgaris* arrived first, such behaviors could affect the probabilities of the establishment of arriving *V. germanica* populations. In all *Vespula* spp., the quality of the queens is critical to population growth. Fertilized new queens appear at the end of the summer and look for dry and protected sites to overwinter until the following spring (Spradbery and Richards 1973). Reproductive females must thus gain weight – usually through feeding by workers during the larval stage – to face the winter.

In New Zealand, where both invasive wasps are also found, some studies have related the invasion process of these wasps (Harris 1991, Harris et al. 1991). *V. germanica* was widely spread throughout the country when *V. vulgaris* arrived, some 30 yrs later, displacing the former from many – yet not all – environments (Clapperton et al. 1994). Only in a few given environmental conditions, *V. germanica* is still more abundant and both species coexist (Sandlant and Moller 1989, Harris et al. 1991). Although both species are generalists, *V. germanica* commonly foraged for protein resources on the forest floor, while *V. vulgaris* foraged on shrubs and tree saplings (Harris et al. 1991). However, both species compete for honeydew resources allowing *V. vulgaris* to displace *V. germanica* in honeydew beech forests. This probably is explained by the superior foraging efficiency of *V. vulgaris* in these habitats. *V. vulgaris* foragers were more active and fed at a faster rate than those of *V. germanica*. This greater feeding rate reduced the time needed by *V. vulgaris* to obtain a load of honeydew and return to its nest. A greater foraging rate may lead to improved quality and number of queens produced, and an increased probability that they will survive the winter and produce successful colonies in the following season (Harris et al. 1994).

Competition for food resources between established species and a new invader is believed to be an important mechanism affecting the establishment probability, acting as biotic resistance (Elton 1958, Simberloff 1989, Davis et al. 2000). For *V. vulgaris*, a wasp species that shares with *V. germanica* foraging habits and foods, establishment, and spread of their populations in invaded regions implies dealing with an additional biotic element: the prior successful arrival of *V. germanica*. While our experiments did not test biotic resistance, evidence of the avoidance foraging behavior shown by *V. germanica* coupled with a rapid population growth of *V. vulgaris* (A.J.P. et al. unpublished data) suggests that the former invader is unlikely to provide significant biotic resistance to the spread of *V. vulgaris* in NW Patagonia. Generally, we detect a new invasion when new species have already become established or even are spreading and the reasons behind such success are likely several (e.g., disturbances, environmental heterogeneity, enemy release, etc.) (Lockwood et al. 2013). However, to determine if the responses detected by this experiment are species-specific or a more general response to *Vespula* sp. cues, additional studies on competitive relationships between *V. germanica* and *V. vulgaris* are needed.

Improving our understanding of foraging interactions between invading species may help to predict the establishment of new invaders. Most past studies focus on the interactions among invaders with natives species and there are few works where interactive processes among invaders are analyzed (McClure 1980, Braks et al.

2004, Simberloff and Von Holle 1999). Our study shows how the foraging behavior of an established invasive species can be affected by visual and olfactory cues simulating the presence of a later invader. Testing the mechanisms behind the establishment and displacement of invaders by evaluating individual behavior may lead to new insights on invasion success.

Acknowledgments

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