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Field preferences of the Social Wasp *Vespula germanica* (Hymenoptera: Vespidae) for Protein-rich Baits

Ana Julia Pereira · Maité Masciocchi · Octavio Bruzzone · Juan C. Corley

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Abstract Food preferences displayed by foraging insects are important from a fundamental perspective and in pest control. We studied the preference of an invasive wasp, *V. germanica,* for protein foods in field conditions. Preferences were evaluated by placing baits in a paired design in different habitats and analyzing wasp visits, using a Bayesian approach to the Thurstone model. *V. germanica* workers display a clear rating of preferences, but were affected by the presence of competitors at the bait. These results contribute knowledge aimed at toxic baiting protocols for this wasp and suggest that food choice is a complex process subject to the influence of diverse factors. We emphasize the importance of on-site paired comparisons in preference studies to fully understand the drivers of food choice by insects.

Keywords Patagonia · yellow jackets · social insect management · invasive wasps

Introduction

Food preference studies have been the subject of much research in animal behavior, due to the adaptive implications related with foraging (see Hahn and Wheeler 2002, Hemerik, et al. 2003, Butin, et al. 2004, Ekmen, et al. 2010, Nyamukondiwa and Addison 2011, Pirk and Lopez de Casenave 2011). In pest control, such studies may be particularly important. For example, knowing the degree of specificity shown by natural enemies used in biological control can minimize the possible impacts these may have on non-target species. When toxic baits are used to control pests (i.e. chemical control), knowledge of pest food preferences may be critical to establish the relative attractiveness of alternative baits in order to optimize their use in terms of specificity and exposure time, as well as of their efficacy.

A. J. Pereira (✉) · M. Masciocchi · O. Bruzzone · J. C. Corley
CONICET, Grupo de Ecología de Poblaciones de Insectos, INTA EEA Bariloche (8400), Bariloche, Argentina
e-mail: apereira@bariloche.inta.gov.ar

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The German wasp *Vespula germanica* is a social vespid native to Eurasia and Northern Africa that invaded NW Patagonia 30 years ago (Willink 1980). It has also invaded and become established in New Zealand, Tasmania, Australia, South Africa, the USA, Canada, and Chile (Archer 1998). Since the first detection of *V. germanica* to date, these wasps have become established in a wide variety of habitats, displaying a notably high rate of geographical spread (Masciocchi and Corley 2012). Wasps in high numbers may negatively affect economic activities such as beekeeping, horticulture, tourism and cattle rearing. Moreover, the sting may interfere with human outdoor activities (Sackmann, et al. 2001 and 2008).

A range of control strategies have been tested to manage invasive *V. germanica* populations. Among these, chemical control has proven consistently to be the most effective method to date (Beggs, et al. 2011). Several studies in different regions, using different baits, have shown satisfactory results (Grant, et al. 1968, Wagner and Reierson 1969, Ennik 1973, Perrot 1975, Chang 1988, Spurr 1991, Beggs, et al. 1998). Baits are typically protein-rich foods such as minced beef, fish or chicken meat, varying among regions in part due to their local retail availability or handling facilities. Bait attraction is determined empirically by registering wasp numbers and response time to the offered product and rarely through rigorous comparisons among potential baits or else in a given environment (Spurr 1995, Wood, et al. 2006, Sackmann and Corley 2007). However, the success of chemical control is determined, not only by the attractiveness of the baits used, but also by the context in which wasps forage which can be site-specific (for example: presence of other food sources or competitors).

Even though most baits have shown some degree of attraction, a comparison between some studies shows that bait appeal can vary between different sites or regions, and that this could be because of diverse weather conditions, local wasp populations or else the timing of the wasp flight season (Harris, et al. 1991, Spurr 1995, Wood, et al. 2006). Also, foods tested were different and preferences may vary with geographical location and species. In Hawaii, for example *V. pensylvanica* preferred tuna baits over meat baits (Chang 1988). However, experiments from North America showed that this specie preferred lean meat there (Grant, et al. 1968, Reid and MacDonald 1986, Akre 1991). This observation is presumably associated with intrinsic features of each site inhabited by studied wasp populations, for example the presence of different competing species or of alternative food sources. Note that for *V. germanica*, it has been suggested that local environmental features can influence behavioral traits such as chemical communication among nest mates or spatial learning (D'Adamo and Lozada 2003, 2005, Wood, et al. 2006, D'Adamo and Lozada 2007).

In NW Patagonia (Argentina), past work has shown that toxic baits, using minced beef can reduce *Vespula germanica* populations locally (Sackmann, et al. 2001, Sackmann and Corley 2007). Additional studies tested the attraction of different baits, comparing protein-rich baits against carbohydrate based foods as it is known that *V. germanica* workers preferences change with nest development (D'Adamo and Lozada 2005). However, these results, although carried out in the field, were obtained in a single habitat type with low human presence (human refuse is attractive to wasps) and did not test alternative protein baits. In addition, this research, cannot assess the attractiveness of new baits, without repeating the experiments fully. It should also be

considered that, in this region, native ants may outcompete wasps at baiting stations (minced beef baits), especially in more open areas were wasps may also be abundant (Masciocchi, et al. 2010). Together, these findings suggest that generalizations about bait preferences (attraction + acceptance) may not be straight forward in invasive *Vespula germanica* populations.

We studied the preferences of *V. germanica* workers for a set of protein-rich baits in the field. Our aim was to establish a robust bait preference rating, that may allow future addition of baits and that considers the effects of the environment (biotic and abiotic habitat characteristics and human presence) in which baits are normally used, to manage yellow-jacket populations.

Methods

Study Area

The study was carried out in the Nahuel Huapi National Park, Patagonia, Argentina (41°S, 72°W). This area is dominated by an abrupt west-to-east decrease in precipitation, with the mean annual precipitation 3.500 mm in the western zone and 500 mm in the eastern. The vegetation reflects this climatic pattern, showing three distinct habitats, along the west-to-east gradient: forest, scrubland, and steppe.

Biology of *Vespula Germanica*

The social wasp *Vespula germanica* is an opportunist predator and scavenger. It feeds on flower nectars, honey, aphids excretions, fruits, carrion and a variety of insect prey (Akre and MacDonald 1986, Harris 1991, Harris and Oliver 1993, Barr, et al. 1996, Harris 1996, Farji-Brener and Corley 1998). Foraging in this species is part of a strong social behavior. Workers search for foods, and carry them back to the nest, where they feed developing larvae. Although *V. germanica* workers search for food individually, a strong aggregative behavior after the discovery a profitable food source may be observed (local enhancement, see D'Adamo, et al. 2000). This behavior allows nest mates to find and exploit food more efficiently. *V. germanica* wasps usually build underground nests and show a foraging range of approximately 200 m, from their nests (Edwards 1980). Foragers of this species tolerate low temperatures, showing a wide daily and seasonal foraging activity (Akre, et al. 1989).

Experimental Design

In order to establish the food rating of *Vespula germanica*, considering the local context, 10 sites representative of scrubland, forest and urban environments, were chosen within the study area. The choice of sites was arbitrary -habitat type was identified visually-, constrained by the abundance of wasps during the time of sampling and their accessibility. Because, worker foraging activity is affected by several local environmental variables (e.g.: temperature, light intensity, visual range) in order to consider this (Kasper, et al. 2008, Contrera, et al. 2011), we established at

each site: the type of environment (qualitatively as scrubland, forest or urban), the presence of other species foraging at the baits (competitors) and the (qualitative) degree of human traffic. From these variables, and through a multiple combination of these, 24 possible models were proposed. A null model with no effect of the independent variables, 6 models with a single independent variable and 17 with more than one of the above mentioned variables.

To obtain independent data from each replicate, the minimum distance between sampling sites was established at 500 m. In each site, the different baits were offered in a paired manner -two plastic dishes separated by 50 cm-, so that each was compared against every other, at a time. It has been suggested that this type of paired design is the most efficient method to understand animal preferences (Bruzzone and Corley 2011). The baits used were different types of minced meet: hake (here after fish), beef, chicken and a commercially available freeze-dried minced beef poisoned bait (Amaxis; Fipronil 0.1 %). As all paired comparisons were done in every site, a total of 60 assays were carried out. The experiments were conducted in the field, between 10 a.m. and 5 p.m. during March and April of 2011. The response variable measured was the bait on which the first *V. germanica* worker landed on. It should be noted that *V. germanica* workers are known to hover over the foods before landing, this latter behavior being a sign of acceptance (D'Adamo and Lozada 2003, Lozada and D'Adamo 2006). This, and the reported local aggregation, as well as the faster response when foods are closer to the nest, are important behaviors observed in these insects that limit the interpretation of other response variables (e.g.: time until first arrival; number of workers on a dish after a given time) when measuring bait choice. All bait stations were open to other animals foraging within the area.

Data Analysis

Preferences were tested according to the Thurstone model, by paired comparisons of the different baits (Thurstone 1928, David 1988, De Vries 1998). To assemble the Thurstone scale, the minced beef was used, randomly, as a reference value. This bait was valued as zero and preferences for the rest of baits were positioned following their scalar values, ranking from lowest to highest. Data were analyzed using a model selection system in a Bayesian approach. Given a set of plausible candidate models, we found the best balancing fit and complexity model, using the deviance information criterion (DIC). The best selected model is the one with the lowest DIC value of all candidates (Burnham and Anderson 2002, Johnson and Omland 2004, McGrory and Titterington 2007).

The *a posteriori* distribution of the parameters for each model was calculated using Markov Chain Monte Carlo methods. Given we did not have a priori information for the studied variables, we used a normal distribution with mean 0 and deviance 10, as an uninformative starter for all the parameters. For each model, we performed two million iterations, from which we discarded the first million as a burn-in. From the remainder, we chose one in 1,000 to avoid autocorrelation. Convergence was tested using Geweke plots (Geweke 1992), and visual inspection of the traces of the variables.

All analyzes were performed, using the pymc library for Bayesian estimation (Patil, et al. 2010) in the Python programming language.

Results

The model that best explained bait choice by *V. germanica* workers in the field was the one which included the presence of ants (Table 1). Models with other competitors and the null model, fitted the data poorly (A, A2, B1.1, B2.2, I). In Model A, both competitors (*Dorymyrmex tener* ants and *Vespula vulgaris* wasps) were added as a factor, also had some support but comparatively less than models with ants only. In turn, the remaining models, which evaluated the degree of human traffic, type of environment, different sites and the combination of these, had essentially no support from the data. There were no differences between models which included the presence of ants and the bait type (models A1.1–14). Therefore, for the analysis of Thurstone scale we considered only model A1, which takes into account the presence of ants at the baited dishes.

Then, we determined the preference rating of *V. germanica* for baits, both with and without ants (Fig. 1). This rating is, in ascending order, chicken, minced beef, freeze-dried minced beef and fish. It is important to recall that, minced beef is used as a reference value. Figure 1a shows a greater distance between bait preferences than in Fig. 1b. The preference patterns, while remaining essentially similar, become more diffuse when ants were present at the baits.

Table 1 Values of deviance information criterion (DIC) for the various models proposed

Model	Measured parameter	DIC
I	No effect of context or site	29.1415
B3	Site	33.6887
B2.1	Human transit + Environment	31.9915
B1	Environment	31.1120
B2	Human transit	30.4302
B1.1	Environment + Competitor	29.1526
B2.2	Human transit + Competitor	27.4049
A	Competitor	25.1794
A2	*Vespula vulgaris*	27.6012
A1	Ants	22.4075
A1.1	Ants + Meat	22.5255
A1.2	Ants + Amaxis	22.6069
A1.3	Ants + Chicken	22.6069
A1.4	Ants + Fish	22.4570
A1.5	Ants + (Meat, Amaxis)	22.4028
A1.6	Ants + (Meat, Chicken)	22.7588
A1.7	Ants + (Meat, Fish)	22.4055
A1.8	Ants + (Amaxis, Fish)	22.9109
A1.9	Ants + (Amaxis, Chicken)	22.7192
A1.10	Ants + (Chicken, Fish)	22.1586
A1.11	Ants + (Chicken, Fish, Amaxis)	22.6352
A1.12	Ants + (Chicken, Fish, Meat)	22.6352
A1.13	Ants + (Meat, Amaxis, Chicken)	22.4886
A1.14	Ants + (Meat, Amaxis, Fish)	22.5768

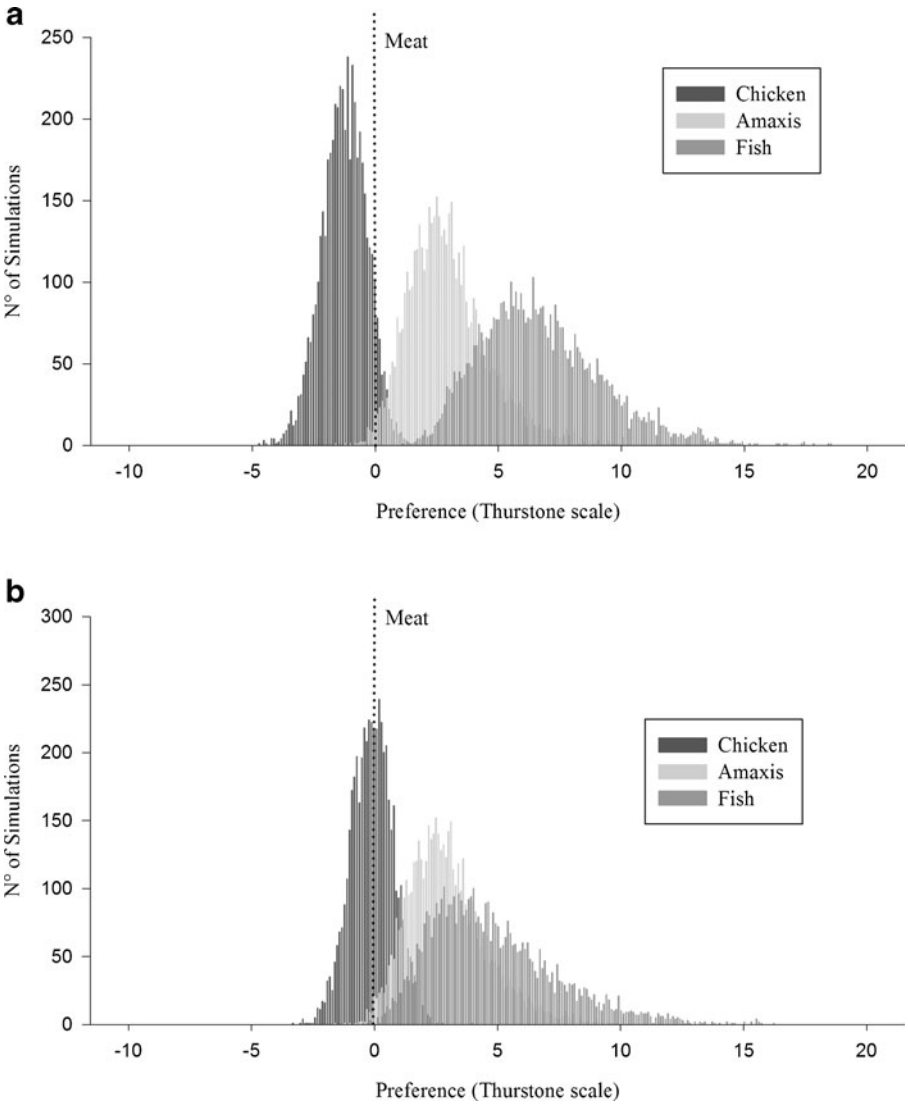

Fig. 1 **a** Rating of protein-rich foods displayed by *Vespula germanica* in the absence of ants. Histogram with *a posteriori* distribution of the parameters for the preference model. The Y axis represents the number of times in which each parameter had a given value during the Monte Carlo simulations. The X axis is the Thurstone scale of preference. Minced beef (*vertical dotted line*) is considered as the reference value (see text for details). Negative values indicate a preference lower that shown for the reference bait. **b** Rating as above, but in the presence of ants

Discussion

The non-native wasp *V. germanica* presents a clear food preference rating in NW Patagonia. Fish turned out to be the most attractive bait, followed by freeze-dried minced beef based commercial baits, fresh minced beef and raw chicken. The preference for these baits was affected by the presence of native ants but not by the presence at the baits, of another, similar exotic wasp, *V. vulgaris*.

For foraging insects, the presence of competitors may alter food preferences by modifying resource availability (Werner and Hal 1976; Kincaid and Cameron 1982; Persson and Greenberg 1990; Luo and Fox 1995; Sanders and Gordon 2000) and activity (Englund, et al. 1992; Haemig 1996). Experiments with *Aphaenogaster cockerelli* (Formicidae) in Arizona (USA) showed that ants of this species changed their preferences when competitors (other ant species, *Myrmecocystus depilis* and *M. mimicus,* Formicidae) were present (Sanders and Gordon 2003). In the present study, we observed that native ants, visiting exposed foods, may influence the preferences displayed by *V. germanica*. In line with this finding, Masciocchi *et al.* (2010) showed that the presence of *Dorymyrmex tener* ants, negatively affected the foraging activity of *Vespula germanica*, suggesting that aggressive behavior and worker aggregation were the mechanisms by which the ants gained a competitive advantage. Another study, involving competition between *V. vulgaris,* another invasive social wasp, and a native ant (*Prolasius advenus*) in New Zealand, reports a novel form of interference behavior. Unlike the latter, this study shows wasp removing ant from food resources by picking them up using their mandibles (Grangier & Lester, 2011). On the other hand, it has been shown that *Vespula vulgaris* could displace *V. germanica* from *Nothofagus* spp. forests. In this habitat, both wasps co-exist and have similar diets, suggesting that the food competition may be the cause of displacement (Harris 1991, Toft and Rees 1998, Beggs and Rees 1999, Beggs and Wardle 2006).

Vespula germanica food preferences were not influenced by the type of environment in which they forage. In NW Patagonia, different habitats may show different environmental features for the wasps. Scrublands are composed of low shrubs and characterized by having a heterogeneous surface structure that may facilitate visual detection of food. Instead forests, offer a more complex structure being characterized by having several distinct vertical layers, which could make food detection more difficult for wasps. This type of environmental structure could influence, among other things, the ground temperature by reducing sun exposure. Finally, in urban areas, there is a greater supply of alternative foods, due to human refuse. Also, in this latter environment, abundant visual cues (man-made structures) may improve wasp orientation to food sources, allowing them to re-locate resources rapidly (D'Adamo and Lozada 2007). Human presence did not alter food preference of the wasps.

The most common experimental design applied to the study of preference behavior is through complete block designs. There is abundant work on bait preferences shown by *V. germanica*, and all of them resort to multiple choice experiments, in which several stimuli are offer simultaneously (Ross, et al. 1984, Reid and MacDonald 1986, Chang 1988, Spurr 1995, Wood, et al. 2006, Sackmann and Corley 2007). However, as noted by Bruzzone and Corley (2011), experiments carried out with incomplete block designs may prove more informative. A paired design allows managing comparisons among increasing number of stimuli. The resulting rating is thus a robust representation of animal preferences and tolerates, in contrast with multiple choice assays, the addition of new stimuli in latter experiments. The Thurstone scale not only provides a rating of preferences for all the options, but also the position of each of these options in one-dimensional space. In behavioral ecology, this model has been used to estimate dominance relationships in some groups of animals (De Vries and Appleby 2000, Adams 2005, De Vries, et al. 2006) and in preference studies (Boyd and Silk 1983, Stapley 2003, Head, et al. 2008).

The relationship between an animal's food preference with the environmental context in which individuals forage is important when baits are tested. Under laboratory conditions, where interactions with the environment are typically not included, results may not reflect field preferences. For opportunistic foragers, feeding is strongly influenced by the availability of resources in a given area. The presence of other animals or the relationships between competitive abilities can influence bait attractiveness when different species share resources. The response of pest species on baits used in chemical control programs depends on the environmental context in which it is applied.

For *V. germanica*, our results suggest that the presence of competitors may affect the success of particular baits at given sites. Baiting protocols that exclude ants will not only prevent negative effects on non-target species but also increase their efficacy. In this sense, performing robust bait ratings may allow a better use of toxic baiting and more specific pest management protocols. Given the wide distribution and the continued spread of *Vespula* spp. worldwide and the growing public demand for environmentally friendly solutions, it is necessary to advance on site specific preference studies in field that considers the presence of other non-target species. Added value is given by using paired comparisons that allow adding new stimuli as these become available.

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