Bulletin of Entomological Research (2018) **108**, 406–412 doi:10.1017/S0007485317000918

Foraging behaviour of the exotic wasp *Vespula germanica* (Hymenoptera: Vespidae) on a native caterpillar defoliator

A.L. Pietrantuono[1]*, S. Moreyra[2] and M. Lozada[2]

[1]CONICET- INTA EEA-Bariloche, Modesta Victoria 4450, CC 277. San Carlos de Bariloche (8400) Río Negro, Argentina: [2]Laboratory Ecotono, INIBIOMA – CONICET- Universidad Nacional del Comahue, Quintral 1250. San Carlos de Bariloche (8400), Río Negro, Argentina

Abstract

Vespula germanica is a social wasp and an opportunistic predator. While foraging, these wasps learn and integrate different kinds of cues. They have successfully invaded many parts of the world, including native *Nothofagus* and *Lophozonia* forests located in the Andean-Patagonian region, where they forage on native arthropods. *Perzelia arda*, a lepidopteron defoliator of *Lophozonia obliqua*, uses the foliage to hide in and feed on. The purpose of this work is to study whether *V. germanica* use olfactory cues when foraging on *P. arda*. To do this, we used a Y-tube olfactometer and established three treatments to compare pairs of all combinations of stimuli (larvae, leaves with larval traces, and leaves without larval traces) and controls. Data were analysed via two developed models that showed decisions made by *V. germanica* and allowed to establish a scale of preferences between the stimuli. The analysis demonstrates that *V. germanica* wasps choose *P. arda* as larval prey and are capable of discriminating between the offered stimuli (deviance information criterion (DIC) null model = 873.97; DIC simple model = 84.5, $n = 152$). According to the preference scale, *V. germanica* preferred leaves with traces of larvae, suggesting its ability to associate these traces with the presence of the prey. This may be because, under natural conditions, larvae are never exposed outside their shelters of leaves and therefore *V. germanica* uses indirect signals. The presence of *V. germanica* foraging on *P. arda* highlights the flexible foraging behaviour of this wasp which may also act as a positive biological control, reducing lepidopteran populations.

Keywords: invasive wasp, odour cues, olfactometer, patagonian forest, phytophagous

(Accepted 12 August 2017; First published online 19 September 2017)

Introduction

During the process of prey search and selection, predatory insects integrate different kinds of cues (visual, spatial, and olfactory) (Price *et al.*, 2011). The way in which foraging wasps use cues depends on the type of prey and type of context in which foraging takes place (Raveret Richter & Jeanne, 1985). Initially, wasps are guided by global and local landmarks and, once near the goal, other cues such as odour become more attractive to wasps than visual cues for inducing landing responses (Moreyra *et al.*, 2006). A forager's ability to discriminate odours and to associate indirect cues of the prey such volatile compounds emitted by the host plant where the prey develops (green-leaf volatiles-GLVs) improves its success (Brodmann *et al.*, 2008). This selective process helps predators reduce the costs of finding food in terms of time and energy, as it allows them to locate and even identify the quality of the resources (Matthews & Matthews, 2010). The use of indirect cues during foraging behaviour has been studied in depth in parasitoid wasps, although they have different requirements from predatory wasps. Both types of search for a prey have evolved

---

*Author for correspondence
Phone/Fax: (+54 294) 4422731
E-mail: pietrantuono.ana@inta.gob.ar

within a multitrophic context and have similar foraging strategies (Vet & Dicke, 1992; Turlings *et al*., 1993). Vet *et al*. (1991) argued that parasitoid wasps during foraging behaviour face a dilemma between the reliability and detectability of cues, since the stimuli emitted by preys are of high reliability but low detectability and the stimuli released from the food of host are the opposite. Prey indirect cues (silk and/or faeces) may act as reliable indicators of host presence (Agelopoulos *et al*., 1995).

Vespula germanica (Fab.) (Hymenoptera:Vespidae) is a social wasp and opportunistic predator. Foraging wasps search for carrion or preys to feed their developing larvae and search for carbohydrates to satisfy their own energy requirements (Spradbery, 1973). Several studies have demonstrated that during their foraging behaviour, wasps learn and integrate different kinds of cues (Free, 1970; D'Adamo & Lozada, 2003; Moreyra *et al*., 2006; El-Sayed *et al*., 2009; Wilson-Rankin, 2015), displaying complex cognitive processes (D'Adamo & Lozada, 2007, 2008, 2009, 2011, 2014; Lozada & D'Adamo, 2009, 2014; Moreyra *et al*., 2012, 2014, 2016). It has been proposed that these characteristics might have contributed to the successful invasion of *V. germanica* in many parts of the world, including the native forests in the Andean-Patagonian region (Farji-Brener & Corley, 1998; D'Adamo *et al*., 2002; Beggs *et al*., 2011; Lozada & D'Adamo, 2014).

The western area of Patagonia, located at the southern end of South America and including the territories of Argentina and Chile, is characterized by a temperate-cold climate and the presence of trees of the Nothofagaceae (Fagales) family. These trees represent a high quality resource for *V. germanica*, as they provide wood pulp, honeydew, and prey insects (Harris, 1991). According to several authors, *V. germanica* wasps are capable of foraging on arthropods that inhabit the native environments, causing significant ecological impact (Moller *et al*., 1988; Sackmann *et al*., 2008; Brockerhoff *et al*., 2010; Beggs *et al*., 2011). Currently, *V. germanica* is one of the most abundant insects found in the Patagonian Andes, and to date, specific predators of this wasp have not been reported in this region and there is little information on the effects they may have on the native insects on which it feeds (Farji-Brener & Corley, 1998; Raveret Richter & Tisch, 1999; Sackmann *et al*., 2008).

Foraging behaviour of non-native insects can alter the host environment in ways that affect native species; for instance, if the predator is very efficient, then the prey populations can be substantially reduced (Davis, 2009). Therefore, non-native insects may have a potential impact on the dynamics of native insect populations that inhabit the Andean- Patagonian forest, as well as on other animals competing for the same food resource (Harris, 1991; Sackmann *et al*., 2000; Masciocchi *et al*., 2010). However, there is a lack of knowledge about the native entomofauna of the region, as there are many species that are unknown or have not yet been taxonomically identified, making it difficult to analyse the real impact of these predatory insects (McQuillan, 1993). Studying the foraging behaviour of invasive insects, particularly in a native environment, as the Andean Patagonian forest, provides valuable information that can be used for the development of conservation plans and even for pest management of different species of phytophagous insects associated with Nothofagaceae trees.

Perzelia arda (Lepidoptera: Oecophoridae) is an abundant native insect inhabiting the Andean- Patagonian forest (Argentina), which may represent an important food source for *V. germanica*. These larvae consume seeds and leaves of *Lophozonia obliqua* (Fagales: Nothofagaceae) (previously named *Nothofagus obliqua* Heenan & Smissen (2013)), and according to Carrillo & Cerda (1987), they can become a potential pest of the Nothofagaceae family. Damage caused to leaves may lead to a reduction in reproductive and photosynthetic rates, affecting the vigour and health of these trees which represent a high-quality wood resource with socio-economic importance. *Perzelia arda* caterpillars use the foliage of *L. obliqua* to hide in and feed on. They produce silk for quick escape and for leaf tying when they build their shelter. When these caterpillars detect the presence of a threat, they leave this shelter, leaving traces of silk and faeces within, and build a new one (Pietrantuono *et al*., 2017). Therefore, we suppose that olfactory cues are essential for *V. germanica* during foraging of *P. arda* prey, as the wasps cannot observe the presence of the larva because they are hidden in the shelter made of leaves.

The purpose of this work is to study whether *V. germanica* use olfactory cues when foraging on *P. arda* caterpillars. We expect to find that during their search, *V. germanica* will detect different types of olfactory signals emanating from their prey.

Materials and methods

The study was conducted at different sites located in the North-western Patagonian native forests in Argentina (41°S, 71°W), where *Nothofagus* and *Lophozonia* trees are abundant. Diverse sites where wasps had been observed preying on larvae were sampled.

Each wasp was captured while collecting meat from a dish and was marked with a dot of washable paint on the abdomen for identification to avoid using the same specimen again after its use in the experiment and later release. Only female specimens were used in the experiments.

Several individuals of *L. obliqua* were selected in North-western Patagonian forest for the collection of samples. We collected several branches, which had healthy leaves and leaves glued by the silk with larvae and faeces inside. From these branches, we obtained *P. arda* larvae, leaves without traces and leaves with traces. From the total larvae collected only those that were in the last larval instar were used in the experiments in order to homogenize as much as possible experimental conditions. To select the larvae we took into account that, in their last stage, they change their colour from pale yellow to an intense green, reaching a length of 11 mm and a width of 2 mm (Donoso *et al*., 2006). We selected the leaves that were mature, have a similar size (5–5.5 cm of length and 2.5–3 cm of width), were not chewed/or with another mechanical damage, or with the presence of fungi. Usually when a larva puts together two leaves only feeds on one of them, allowing us to use the other healthy leaf with traces for the experiment. Immediately after the selection of the stimuli, the experiment was started.

Experimental design

The experiments were carried out in natural conditions from February to April 2016, around noon.

To evaluate *V. germanica* foragers' behaviour a sequence of paired comparisons was performed and a glass Y-tube olfactometer (base: 13 cm, arms: 7 cm, diameter: 2 cm, angle between minor arms: 90°) was used. This device was connected to an air pump generating an air flow of 1 cm s^{-1}. Before entering the system, the air was filtered through activated charcoal. The stimuli containers consisted of two Plexiglas boxes ($10 \times 10 \times 10$ cm^3) covered with white paper (to eliminate the possibility of visual cues) attached to the

Table 1. Average time in minutes that *V. germanica* wasp remained on each stimulus and Standar Error (SE). The asterisk indicates significant differences.

Treatments	Larvae (minutes ± SE)	Leaves with traces (minutes ± SE)	Leaves without traces (minutes ± SE)	Nothing (minutes ± SE)	*P* value (Wilcoxon)
Larvae vs. leaves with traces ($n = 25$)	0.63 ± 0.11	1.00 ± 0.17	–	–	$P > 0.05$
Larvae vs. leaves without traces ($n = 27$)	0.85 ± 0.11	–	0.65 ± 0.09	–	$P < 0.05$*
Leaves with traces vs. leaves without traces ($n = 25$)	–	1.43 ± 0.25	0.82 ± 0.14	–	$P < 0.05$*
Larvae vs. nothing ($n = 30$)	0.88 ± 0.12	–	–	0.59 ± 0.08	$P < 0.05$*
Leaves with traces vs. nothing ($n = 18$)	–	1.67 ± 0.37	–	0.56 ± 0.12	$P < 0.05$*
Leaves without traces vs. nothing ($n = 27$)	–	–	1.00 ± 0.17	0.82 ± 0.14	$P > 0.05$

end of each arm of the olfactometer. Furthermore, the device was placed inside a large white box ($50 \times 50 \times 25$ cm^3) covered by a detachable, transparent and red cover (all made in Plexiglas of 5 mm thickness).

For each assay, one female individual of *V. germanica* was placed in the base of the olfactometer and kept there during 1 min (i.e. adaptation period). It was then released for 3 min to choose between stimuli. Given the diameter of the Y-tube, the wasp had to make its choice while walking. A forager's choice was considered effective when the wasp performed rapid antennal movements (i.e. active search) (El-Sayed *et al.*, 2009) and its full body passed a line set at 1 cm into each minor arm after the dichotomous division. The wasps that did not pass this line or not performed an active search were not considered. The Plexiglas boxes were positioned at random during the experiments and after each experiment, the olfactometer was washed to avoid wasp pheromone trails (first with ethylic alcohol, then with a 5% solution of ionic detergent and finally rinsed with distilled water). Two researchers, sat at a distance of 0.5 m from this device, recorded the length of time that the wasp spent in each arm of the olfactometer after crossing the line set 1 cm from the beginning of the minor arm.

Three treatments were performed to compare pairs of all combinations of stimuli (larvae vs. leaves with larval traces ($n = 25$), larvae vs. leaves without larval traces ($n = 27$) and leaves with larval traces vs. leaves without larval traces ($n = 25$)). It should be noted that we considered as larval traces the presence of silk and/or faeces of *P. arda*. In addition, three control treatments were performed (nothing = empty box vs. Larvae ($n = 30$), nothing vs. leaves without larval traces ($n = 27$) and nothing vs. leaves with larval traces ($n = 18$)). Because *P. arda* larvae tend to cluster in natural conditions, we offered as a stimulus five larvae simultaneously (Pietrantuono *et al.*, 2017). Five entire mature leaves of similar size were used for the leaf stimulus. After six assays both stimuli were renewed to keep them fresh. In total we evaluated the response of 175 female wasps (one per assay).

Data analysis

The paired comparisons were analyzed using a two-step methodology. First, we performed a Wilcoxon matched pair test (Bonferroni corrected) to determine whether there were differences between treatments and second we developed a model using a Bayesian approach to establish a scale of preferences between stimuli. This procedure provides a more straightforward way to determine the degree of attraction between stimuli and it is widely used by ecologists in animal behaviour studies (Ellison, 2004; McNamara *et al.*, 2006; Valone, 2006; Pereira *et al.*, 2013; Pietrantuono *et al.*, 2014, 2015, 2017).

In order to analyse decisions made by *Vespula germanica* through the time that elapsed in each arm of the olfactometer, we developed two models based on the Thurstone model of comparative judgments case V (Thurstone, 1927/1994; Bradley & Terry, 1952; Tsukida & Gupta, 2011). Through these models we were able to determine the gradient of preference for each stimulus. This scale is used in various types of experimental designs and is the most well-known tool for estimating object preferences through the observed frequency of paired comparisons (Lipovetsky, 2007; Angulo & O'Mahony, 2009). Not only does it provide a ranking of preferences for all the options offered, but it also provides the position of each of these options in one-dimensional space of preferences. It should be noted that when a preference scale is established, the magnitude of the quality of the options is in relation to an arbitrarily established reference value (Tsukida & Gupta, 2011). This is why we define the zero position and the unit of measure as arbitrary.

The first of the models or 'null model' establishes that there are not preferences between the stimuli offered. While in the second model or 'simple model' there is a scale of preferences (based on the Thurstone model). This linear scale expresses the degree of attraction or preference that an experimental subject shows for one of the available options. Higher values indicate an increasing preference, and lower/negative values indicate rejection. Because the Thurstone scale is an 'interval scale' (Stevens, 1946), we used one of the stimuli (larvae) as the reference value (origin ordinate) of the scale system. This stimulus was arbitrarily chosen as the reference value (corresponds to zero); therefore, it has no estimation error. In addition, the units of this scale were expressed in terms of the standard deviations of the discriminal dispersion of the reference stimulus. Thus, the preference for each stimulus within the scale was positioned relative to this value, and its values were expressed in terms of the discriminal dispersion (Pietrantuono *et al.*, 2017).

For the development of the model, 110,000 iterations were performed, from which 10,000 were discarded as a burn-in. From the remainder, one in 100 was chosen to avoid autocorrelation. To test convergence, Geweke plots were used, and a visual inspection of the variable traces was carried out (Geweke, 1992). The analyses were performed using the PyMC library for Bayesian estimation (Patil *et al.*, 2010) in the Python programming language. Finally, the model with the lowest value of the deviance information criterion (DIC) was selected (Gelman *et al.*, 2004).

Results

Based on the data analysis performed with the Wilcoxon test we found significant differences ($P < 0.05$) when

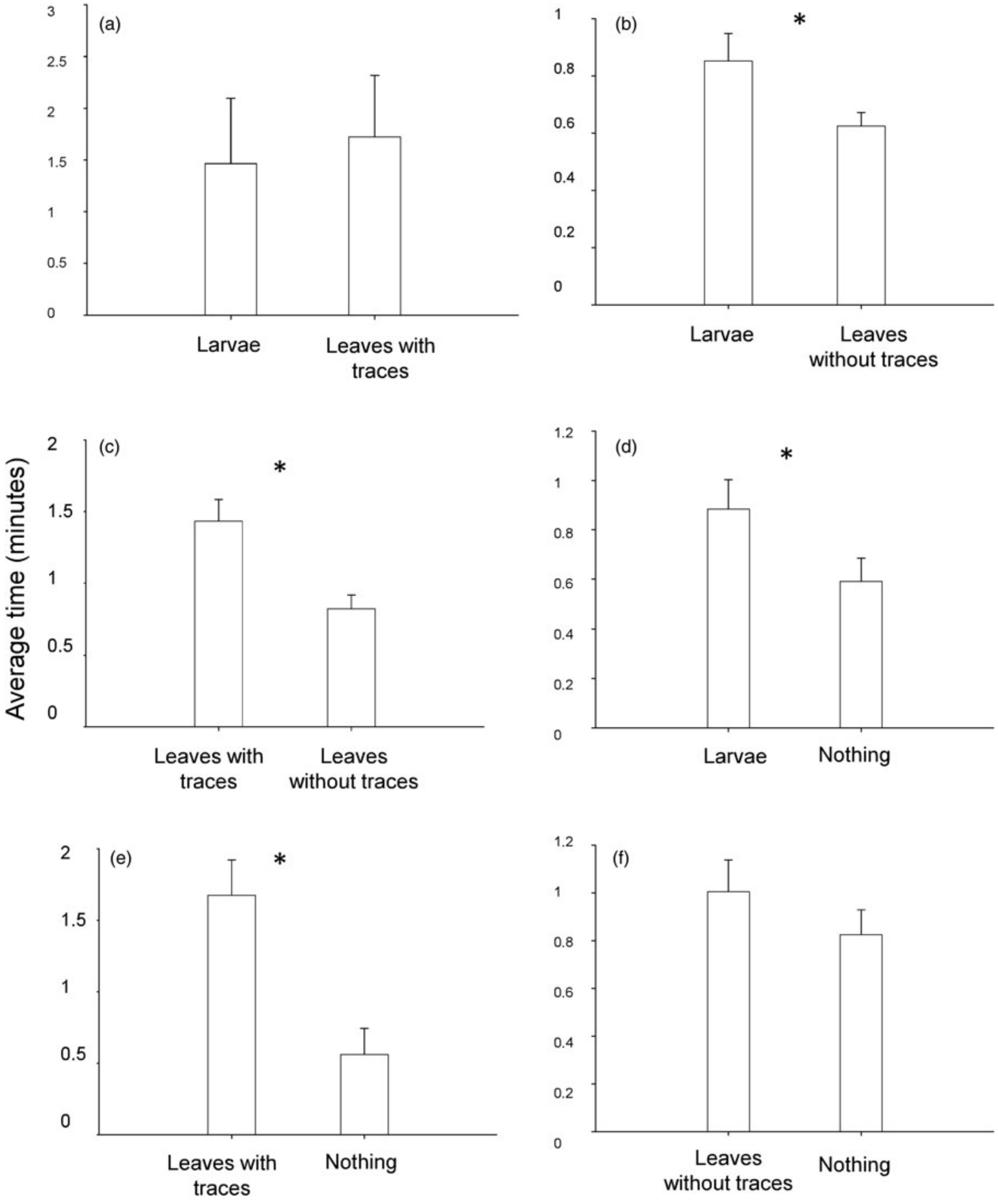

Fig. 1. Average time in minutes that *V. germanica* wasp remained on each stimulus offered: (a) Larvae *vs.* Leaves with traces ($n = 25$, $P > 0.05$); (b) Larvae *vs.* Leaves without traces ($n = 27$, $P < 0.05$); (c) Leaves with traces *vs.* Leaves without traces ($n = 25$, $P < 0.05$); (d) Larvae *vs.* Nothing ($n = 30$, $P < 0.05$); (e) Leaves with traces *vs.* Nothing ($n = 18$, $P < 0.05$); (f) Leaves without traces *vs.* Nothing ($n = 27$, $P > 0.05$). The asterisk indicates significant differences.

comparing larvae vs. leaves without larval traces ($n = 27$); leaves with larval traces vs. leaves without larval traces ($n = 25$); larvae vs. nothing ($n = 30$) and leaves with larval traces vs. nothing ($n = 18$). However, non-significant differences ($P > 0.05$) were found when comparing larvae vs. leaves with larval traces ($n = 25$), and leaves without larval traces vs. nothing ($n = 27$) (table 1 and fig. 1).

From the total number of the tested individuals ($n = 175$), 152 wasps actively chose between two stimuli offered (i.e. each wasp passed the line set at 1 cm into each arm of the

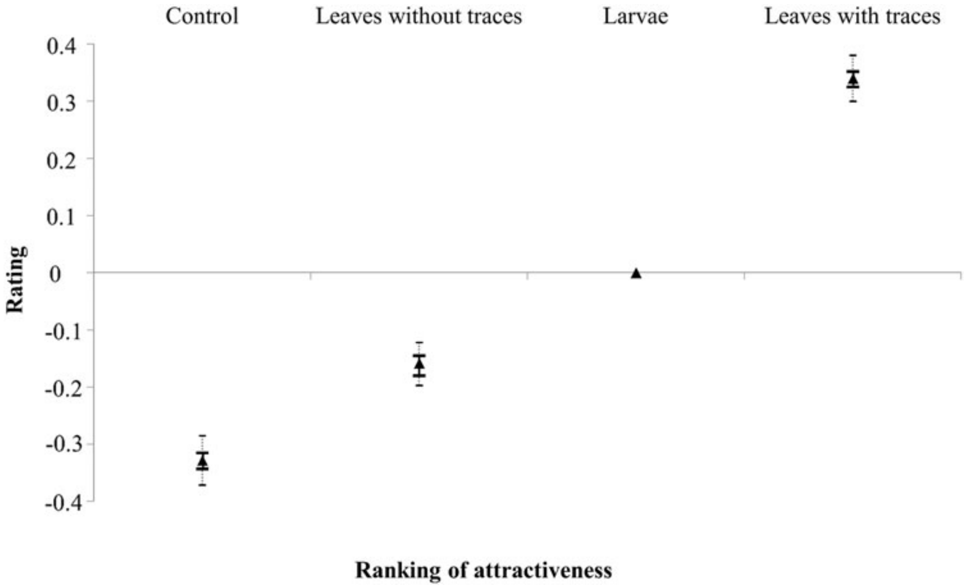

Fig. 2. Ranking of attractiveness as a function of the choices made by *Vespula germanica*. Leaves with traces of *Perzelia arda* were the most attractive stimulus. The black lines indicate the error estimates for the mean value for each point on the Thurstone scale. The grey dotted lines indicate the discriminal dispersion according to case V of the Thurstone model (Thurstone, 1927/1994).

olfactometer and produced rapid antennal movements) and were included in the data analysis. The wasps that did not respond ($n = 23$) belonged to different treatments.

The analysis of the proposed models showed that *V. germanica* wasps choose *P. arda* as larval prey and are capable of discriminating between the offered stimuli (DIC null model = 873.97; DIC simple model = 84.5). According to the preference scale (fig. 2), leaves with traces of larvae were preferred or were the most attractive stimulus for *V. germanica* as shown by its first ranking; while larvae were in the second most attractive stimulus. These results could suggest that the main olfactory cue could be unrelated to larvae itself but rather to the products of its activity (silk and/or faeces). However, the control (i.e. the empty box) was the least attractive stimulus.

Discussion

To our knowledge this is the first study that evaluates the behaviour of the exotic wasp *V. germanica* when foraging on *P. arda*, a native folivorous insect from the Andean-Patagonian forest. The present research demonstrates that *V. germanica* is able to differentiate between the offered stimuli and use a variety of signals to locate and choose *P. arda* as larval prey. Particularly, *V. germanica* is able to associate the traces of faeces and/or silk as a sign of the presence of the prey. This may be because, under natural conditions, larvae are never exposed outside their shelters of leaves, and therefore, the presence of these traces is a strong indicator that the larvae must be there.

Similarly, Cornelius (1993) demonstrated that the behaviour of the predatory wasp *Mischocyttarus flavitarsis* (Hymenoptera: Vespidae) was influenced by cues that are associated with prey but are not emitted directly by the prey (i.e. wasps preferred leaves previously damaged by caterpillars than leaves without leaf damage). Raveret Richter & Jeanne (1985) argued that the way in which foraging wasps use cues for prey location depends on both the context in which the hunt takes place and on the types of prey for which the wasp is hunting. Even though in this work the visual cues were avoided, we hypothesize that in this study system, *V. germanica* uses olfactory cues in a greater proportion than visuals cues (Hendrichs *et al.*, 1999; D'Adamo *et al.*, 2000). For this reason, further research is needed to discern which volatile compounds of the indirect cues as silk, faeces, or leaves are involved in this behaviour (Bergelson & Lawton, 1988; Jones *et al.*, 2002; Chuche *et al.*, 2006). There were certain variables (such as age and previous experiences) that were not evaluated in the current work, given the nature of the experimental design used here which may have had importance in the learning and behaviour of the wasp (Papaj & Lewis, 1993). Indeed, several studies have demonstrated the high plasticity with which *V. germanica* responds to unpredictable contextual changes while foraging and how wasps integrate old and new memories while foraging on un-depleted food sources (D'Adamo & Lozada, 2009; Lozada & D'Adamo, 2009; Moreyra *et al.*, 2014). In future research it would be interesting to evaluate whether age and previous experience influence wasps' foraging behaviour on *P. arda* (Papaj *et al.*, 1987).

Works focusing on prey and predator interactions in the Andean- Patagonian forests represent a challenge since they are systems poorly studied and are difficult to develop under laboratory conditions. Therefore, in the present work we contributed to the recognition of chemically mediated interactions and to the understanding of the complexity of invasive processes and their potential impact on biodiversity and ecosystem function (Beggs & Rees, 1999; Vet, 1999). On one hand, the availability of prey may influence the success of wasps and developing larvae (Raveret Richter, 1990). On the other hand, wasps may have an important role as a positive biological control because they reduce the populations of lepidopteran that damage Nothofagaceae trees (Lawson *et al.*, 1961; Gould & Jeanne, 1984; Cornelius, 1993).

Our work highlights the importance of studying in more depth the interaction between exotic and native species coexisting in a natural environment. These findings also provide a starting point for phytosanitary care and the conservation of systems containing native species.

Acknowledgements

The authors are very grateful to Marcela Maldonado for revising the English text. The authors like to thank the two anonymous reviewers for useful comments on previous versions of this manuscript. They also acknowledge support from the INIBIOMA-CONICET, INTA EEA-Bariloche and Universidad Nacional del Comahue.

References

Agelopoulos, N.G., Dicke, M. & Posthumus, M.A. (1995) Role of volatile inforchemicals emitted by feces of larvae in host-. searching behavior of parasitoid *Cotesia rubecula* (Hymenoptera: Braconidae): a behavioral and chemical study. *Journal of Chemical Ecology* **21**(11), 1789–1811.

Angulo, O. & O'Mahony, M. (2009) Las pruebas de preferencia en alimentos son más complejas de lo imaginado. *Interciencia* **34**(3), 177–181.

Beggs, J.R. & Rees, J.S. (1999) Restructuring of Lepidoptera communities by introduces *Vespula* wasps in a New Zealand beech forest. *Oecologia* **119**, 565–571.

Beggs, J.R., Brockerhoff, E.G., Corley, J.C., Kenis, M., Masciocchi, M., Muller, F., Rome, Q. & Villeman, C. (2011) Ecological effects and management of invasive alien Vespidae. *BioControl* **56**, 505–526.

Bergelson, J.M. & Lawton, J.H. (1988) Does foliage damage influence predation on the insect herbivores of birch? *Ecology* **69**, 434–445.

Bradley, R.A. & Terry, M.E. (1952) Rank analysis of incomplete block designs. I. The method of paired comparisons. *Biometrika* **39**, 324–345.

Brockerhoff, E.G., Barratt, B.I., Beggs, J.R., Fagan, L.L., Kay, M. K., Phillips, C.B. & Vink, C.J. (2010) Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems. *New Zealand Journal of Ecology* **34**(1), 158–174.

Brodmann, J., Twele, R., Fracke, W., Hölzler, G., Zhang, Q.H. & Ayasse, M. (2008) Orchids mimic green-leaf volatiles to attract prey-hunting wasps for pollination. *Current Biology* **18**(10), 740–744.

Carrillo, R. & Cerda, L. (1987) Zoofitófagos en *Nothofagus* chilenos. *Bosque* **8**(2), 99–103.

Chuche, J., Xuéreb, A. & Thiéry, D. (2006) Attraction of *Dibrachys cavus* (Hymenoptera: Pteromalidae) to its host frass volatiles. *Journal of Chemical Ecology* **32**, 2721–2731.

Cornelius, M.L. (1993) Influence of caterpillar-feeding damage on the foraging behavior of the paper wasp *Mischocyttarus flavitarsis* (Hymenoptera: Vespidae). *Journal of Insect Behavior* **6**, 771–781.

D'Adamo, P. & Lozada, M. (2003) The importance of location and visual cues during foraging in the German wasp (*Vespula germanica* F.) (Hymenoptera: Vespidae). *New Zealand Journal of Zoology* **30**, 171–174.

D'Adamo, P. & Lozada, M. (2007) Foraging behavior related to habitat characteristics in the invasive wasp *Vespula germanica*. *Insect Sciences* **14**, 383–388.

D'Adamo, P. & Lozada, M. (2008) Foraging behaviour in *Vespula germanica* wasps re-locating a food source. *New Zealand Journal of Zoology* **35**, 9–17.

D'Adamo, P. & Lozada, M. (2009) Flexible foraging behavior in the invasive social wasp *Vespula germanica* (Hymenoptera: Vespidae). *Annals of the Entomological Society of America* **102**, 1109–1115.

D'Adamo, P. & Lozada, M. (2011) Cognitive plasticity in foraging *Vespula germanica* wasps. *Journal of Insect Science* **11**(103), 1–11.

D'Adamo, P. & Lozada, M. (2014) How context modification can favor the release of past experience in *Vespula germanica* wasps, enabling the detection of a novel food site. *Journal of Insect Behavior* **27**, 395–402.

D'Adamo, P., Sackmann, P., Lozada, M. & Corley, J.C. (2000) Local enhancement in the wasp *Vespula germanica*. Are visual cues all that matter? *Insectes Sociaux* **4**, 289–291. DOI: 10.1007/PL00001717.

D'Adamo, P., Sackman, P., Rabinovich, M. & Corley, J.C. (2002) The potential distribution of German wasps (*Vespula germanica*) in Argentina. *New Zealand Journal of Zoology* **29**, 79–85.

Davis, M.A. (2009) *Invasion Biology*. Oxford, UK, Oxford University Press.

Donoso, P., Donoso, C., Gallo, L., Azpilicueta, M.M., Baldini, A. & Escobar, B. (2006) *Nothofagus Obliqua (Mirb.) Oerst*. Roble, Pellín, Hualle. pp. 471–485 *in* Donoso, C. (*ed*) *Las especies arbóreas de los bosques templados de Chile y Argentina*. Valdivia, Chile, Autoecología.

El-Sayed, A.M., Manning, L.A., Unelius, C.R., Park, K.C., Stringer, L.D., White, N., Bunn, B., Twidle, A. & Suckling, D.M. (2009) Attraction and antennal response of the common wasp, *Vespula vulgaris* (L.), to selected synthetic chemicals in New Zealand beech forests. *Pest Management Science* **65**(9), 975–981.

Ellison, A.M. (2004) Bayesian inference in ecology. *Ecology Letters* **7**, 509–520.

Farji-Brener, A. & Corley, J.C. (1998) Successful invasions of hymenopteran insects into NW Patagonia. *Ecología Austral* **8**, 237–249.

Free, J.B. (1970) The behavior of wasps (*Vespula germanica* L. and *V. Vulgaris* L.) when foraging. *Insectes Sociaux* **17**, 11–20.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*. 2nd edn. EE UU, Boca Raton, Chapman & Hall.

Geweke, J. (1992) Evaluating the accuracy of sampling based approaches to calculating posterior moments. pp. 169–193 *in* Bernardo, J.M., Berger, J., David, A.P. & Smith, J.F.M. (*Eds*) *Bayesian Statistics*. Volume **4**. Oxford, Oxford University Press.

Gould, W.F. & Jeanne, R.L. (1984) *Polistes* wasps (Hymenoptera: Vespidae) as control agents for lepidopteran cabbage pests. *Environmental Entomology* **13**, 150–156.

Harris, R.J. (1991) Diet of the wasps *Vespula vulgaris* and *V. Germanica* in honeydew beech forest of the South Island, New Zealand. *New Zealand Journal of Zoology* **18**(2), 159–169.

Heenan, P.B. & Smissen, R.D. (2013) Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscospora*, *Lophozonia*, and *Trisyngyne* (Nothofagaceae). *Phytotaxa* **146**, 1–31.

Hendrichs, J., Katsoyannos, B.I., Wornoayporn, V., Hendrichs, M.A. (1999) Odour-mediated foraging by yellowjacket wasps (Hymenoptera: Vespidae): predation on leks of pheromone-calling Mediterranean fruit fly males (Diptera: Tephritidae). *Oecologia* **99**, 88–94.

Jones, M.T., Castellanos, I. & Weiss, M.R. (2002) Do leaf shelters always protect larvae from invertebrate predators? *Ecological Entomology* **27**, 753–757.

Lawson, F.R., Rabb, R.L., Guthrie, F.E. & Bowery, T.G. (1961) Studies of an integrated control system for hornworms and tobacco. *Journal of Economical Entomology* **54**, 93–97.

Lipovetsky, S. (2007) Thurstone scaling in order statistics. *Mathematical and Computer modeling* **45**, 917–926.

Lozada, M. & D'Adamo, P. (2009) How does an invasive social wasp deal with changing contextual cues while foraging? *Environmental Entomology* **38**, 803–808.

Lozada, M. & D'Adamo, P. (2014) Learning in an exotic social wasp while relocating a food source. *Journal of Physiology-Paris* **108**, 187–193.

Masciocchi, M., Farji-Brener, A.G. & Sackmann, P. (2010) Competition for food between the exotic wasp *Vespula germanica* and the native ant assemblage of NW Patagonia: evidence of biotic resistance? *Biological Invasions* **12**, 625–631. DOI: 10.1007/s10530-009-9469-5.

Matthews, R.W. & Matthews, J.R. (2010) *Insect Behavior*. 2nd edn. New York, Springer, 514pp.

McNamara, J.M., Green, R.F. & Olsson, O. (2006) Bayes theorem and its applications in animal behavior. *Oikos* **112**, 243–251.

McQuillan, P.B. (1993) *Nothofagus* (fagaceae) and its invertebrate fauna- an overview and preliminary synthesis. *Biological Journal of the Linnean Society* **49**, 317–354.

Moller, H., Tilley, J.A.V., Alspach, P., Millar, I.R. & Plunkett, G. M. (1988) Impact of Vespula wasps on native insects and birds: first year research report. Ecology Division Report No. 13, DSIR, New Zealand.

Moreyra, S., D'Adamo, P. & Lozada, M. (2006) Odour and visual cues utilised by German yellowjackets (*Vespula germanica*) while relocating protein or carbohydrate resources. *Australian Journal of Zoology* **54**, 393–397.

Moreyra, S., D'Adamo, P. & Lozada, M. (2012) Cognitive processes in *Vespula germanica* wasps (Hymenoptera: Vespidae) when relocating a food source. *Annals of the Entomological Society of America* **105**(1), 128–133.

Moreyra, S., D'Adamo, P. & Lozada, M. (2014) The influence of past experience on wasp choice related to foraging behavior. *Insect Sciences* **21**, 759–764.

Moreyra, S., D'Adamo, P. & Lozada, M. (2016) Learning in *Vespula germanica* social wasps: situations of unpredictable food locations. *Insectes Sociaux* **63**, 381–384.

Papaj, D.R. & Lewis, A.C. 1993. *Insect Learning: Ecology and Evolutionary Perspectives*. New York, Springer Science +Business Media Dordrecht, Chapman & Hall.

Papaj, D.R., Prokopy, R.J., McDonald, P.T. & Wong, T.T.Y. (1987) Differences in learning between wild and laboratory *Ceratitis capitata* flies. *Entomologia Experimentalis et Applicata* **45**(1), 65–72.

Patil, A., Huard, D. & Fonnesbeck, C.J. (2010) PyMC: Bayesian stochastic modeling in Python. *Journal of Statistical Software* **35**, 1–81.

Pereira, A.J., Masciocchi, M., Bruzzone, O. & Corley, J.C. (2013) Field preferences of the social wasp *Vespula germanica* (Hymenoptera: Vespidae) for protein-rich baits. *Journal of Insect Behavior* **26**, 730–739.

Pietrantuono, A.L., Fernandez-Arhex, V. & Bruzzone, O.A. (2014) First study of host-plant preferences of *Sinopla perpunctatus* (Hemiptera: Acanthosomatidae) a stink bug from Andean-patagonic forest. *Florida Entomologist* **97**, 534–539.

Pietrantuono, A.L., Enriquez, A., Fernandez-Arhex, V. & Bruzzone, O.A. (2015) Substrates preference for pupation on sawfly *Notofenusa surosa* (Hymenoptera: Tenthredinidae). *Journal of Insect Behavior* **28**, 257–267.

Pietrantuono, A.L., Bruzzone, O.A. & Fernández-Arhex, V. (2017) The role of leaf cellulose content in determining host plant preferences of three defoliating insects present in the Andean-Patagonian forest. *Austral Ecology* **42**(4), 433–441. DOI: 10.1111/aec.12460.

Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. & Kaplan, I. (2011) *Insect Ecology: Behavior, Population and Communities*. New York, University Press Cambridge.

Raveret Richter, M.A. (1990) Hunting social wasp interactions: influence of prey size, arrival order, and wasp species. *Ecology* **71**, 1018–1030.

Raveret Richter, M. & Tisch, V.L. (1999) Presence, size, and species of resident social wasps (Hymenoptera: Vespidae) influence resource choice by foragers. *Insectes Sociaux* **46**, 131–136.

Raveret Richter, M.A. & Jeanne, R.L. (1985) Predatory behavior of *Polybia sericea* (Olivier), a tropical social wasp (Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology* **16**, 165–170.

Sackmann, P., D'Adamo, P., Rabinovich, M. & Corley, J.C. (2000) Arthropod prey foraged by the German wasp (*Vespula germanica*) in NW Patagonia, Argentina. *New Zealand Entomologist* **23**, 55–59.

Sackmann, P., Farji-Brener, A. & Corley, J. (2008) The impact of an exotic social wasp (*Vespula germanica*) on the native arthropod community of north-west Patagonia, Argentina: an experimental study. *Ecological Entomology* **33**, 213–224.

Spradbery, P. (1973). *Wasps: An Account of the Biology and Natural History of Solitary and Social Wasps*. Seattle, WA, University of Washington Press.

Stevens, S.S. (1946) On the theory of scales of measurement. *Science* **103**, 677–680.

Thurstone, L.L. (1927/1994) A law of comparative judgment. *Psychological Review* **101**, 266–270.

Tsukida, K. & Gupta, M.R. (2011) *How to Analyze Paired Comparison Data*. UWEE Technical report. USA, University of Washington.

Turlings, T.C.J., Wäckers, F.L., Vet, L.E.M., Lewis, W.J. & Tumlinson, J.H. (1993) Learning of host-finding cues by hymenopterous parasitoids. *Ecological and Evolutionary Perspectives* **3**, 51–78.

Valone, T.J. (2006) Are animals capable of Bayesian updating? An empirical review. *Oikos* **112**, 252–256.

Vet, L.E.M. (1999) From chemical to population ecology: infochemical use in an evolutionary context. *Journal of Chemical Ecology* **25**(1), 31–49.

Vet, L.E.M. & Dicke, M. (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* **37**, 141–172.

Vet, L.E.M., Wäckers, F.L. & Dicke, M. (1991) How to hunt for hiding hosts: the reliability-detectability problem in foraging parasitoids. *Netherlands Journal of Zoology* **41**(2–3), 202–213.

Wilson-Rankin, E.E. (2015) Level of experience modulates individual foraging strategies of an invasive predatory wasp. *Behavioral Ecology and Sociobiology* **69**, 491–499.