Insect. Soc. (2016) 63:381–384
DOI 10.1007/s00040-016-0477-z

Insectes Sociaux

RESEARCH ARTICLE

Learning in *Vespula germanica* social wasps: situations of unpredictable food locations

S. Moreyra[1] · P. D'Adamo[1] · M. Lozada[1]

Received: 6 November 2015 / Revised: 27 January 2016 / Accepted: 17 February 2016 / Published online: 12 March 2016

Abstract *Vespula germanica* is a social wasp that frequently forages on carrion, making several trips between un-depleted resources and the nest. In the present study, we analyze this food relocation behavior, evaluating *V. germanica* response in situations of successive changes in food location. To this end, we allowed individual wasps to feed five consecutive times from a dish located within an array of landmarks. After each return, the feeder was randomly displaced 60 cm from the previous location, so that when the wasp retuned to the array it encountered a different scenario. We found that on their first return to the new situation, wasps first went to the previously learned location and took some time to find the displaced feeder. Interestingly, during the following returns, wasps discovered the novel food location more rapidly, even though its location randomly changed at each return. Thus, after the first experience of food absence, wasps seem to have learned that food would not necessarily be present at the previous site. Free-flying wasps use past experience of food position change to reduce searching time at previously learned locations. These findings illustrate wasp behavioral plasticity in uncertain foraging contexts.

Keywords Foraging behavior · Unpredictable contexts · Learning · Social wasps

✉ S. Moreyra
sabrimoreyra@hotmail.com

M. Lozada
mariana.lozada@gmail.com

[1] Laboratory Ecotono, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250 (8400), Bariloche, Argentina

Introduction

Foraging behavior is regulated by the spatiotemporal availability of food and internal state, such as hunger, and the needs of the offspring (e.g., Wilson-Rankin 2014). Resource location can be unpredictable or suffer changes in natural contexts, so learning processes need to account for and are shaped by uncertainty (e.g., Shettleworth 2001; Lozada and D'Adamo 2014). In scavenging social species, once a forager finds a rich resource it makes several trips between the food and the nest, where larvae are fed. During this relocating behavior, foragers learn landmarks and contextual cues associated with rewarding sites, which enable them to return to the resource (e.g., Graham et al. 2003; Zeil 2012; Collett et al. 2013).

It has been demonstrated that *Vespula germanica* (Fab.) (Hymenoptera: Vespidae) is a social wasp which frequently returns to previously visited food sources, displaying diverse learning abilities associated with this relocation behavior (e.g., D'Adamo and Lozada 2011; Moreyra et al. 2012; Lozada and D'Adamo 2011, 2014). Furthermore, it has been shown that this wasp foraging behavior varies in relation to the type of resource exploited (e.g., D'Adamo and Lozada 2003; Wilson-Rankin 2014). Other studies found that food unpredictability can be a recurrent experience when this wasp forages on un-depleted resources such as carrion, or in human settings. It is common to see larger animals (e.g., dogs, birds of prey) displace or remove resources that wasps are feeding on (Lozada and D'Adamo 2011), and in certain anthropic scenarios, such as picnics, barbecues or camp sites, food and contextual cues (e.g., cutlery, glasses, bottles) are continually changing position (D'Adamo and Lozada 2014; Lozada and D'Adamo 2014).

Behavioral response towards changes in food location has been studied in other Hymenopteran species (e.g., Toh and Okamura 2003; Durier et al. 2004; Graham et al. 2007). For example, when food is displaced from the learnt micro-site, the wood ant (*Formica rufa*) performs several trials before aiming for the new location; i.e., it will take them some time to change search direction (Graham et al. 2007). When the novel food location is relatively near the previously learnt one, these ants gradually rotate their search from aiming directly to the learnt location to aiming for the second food site (Graham et al. 2007). Moreover, it has been found that when food is displaced, hornet foragers (*Vespa mandarinia*) take some time to aim at a novel site, showing that previous foraging experience has a great influence on future decision making (Toh and Okamura 2003). Recent research on *V. germanica* foraging behavior has shown that once wasps find carrion in a certain place, they continue looking for it in this location even when food is no longer available (e.g., Lozada and D'Adamo 2006, 2011, 2014; D'Adamo and Lozada 2007, 2011, 2014). That is, when food is removed, the time that wasps continue looking for it depends on the number of successful visits formerly experienced. They eventually stop searching after spending more than 1 h visiting the no longer rewarding site (Lozada and D'Adamo 2006). Moreover, other studies show that when food is displaced, *V. germanica* foragers continue to look for it in the previously learnt location even when the resource has been displaced nearby (Lozada and D'Adamo 2011; D'Adamo and Lozada 2014). In these studies, *V. germanica* relocating behavior was evaluated after a single food displacement (Lozada and D'Adamo 2011; D'Adamo and Lozada 2014). The present work analyzes this behavior further and explores wasp response when facing several changes in food position, we assess whether learning processes take place in this situation involving recurrent uncertainty. Given the high cognitive plasticity of this species (e.g., Moreyra et al. 2012; D'Adamo and Lozada 2014; Lozada and D'Adamo 2014), we hypothesize that wasps will learn to change their foraging behavior when food unpredictability is repeated. We expect to find a decrease in searching time at previously rewarded sites as wasps gain more experience of recurrent contextual modifications.

Materials and methods

The experiments were performed in a natural environment, under similar weather conditions (sunny and still) near Bariloche (41°S, 71°W), Argentina from February to April 2015. The experimental array consisted of four cylinders of 2 cm diameter by 60 cm high, located on the ground to form a square of 30 cm per side. On each of the four sides, we placed a white plastic 7 cm dish, one of which contained 20 gr of minced meat (feeder) (Fig. 1).

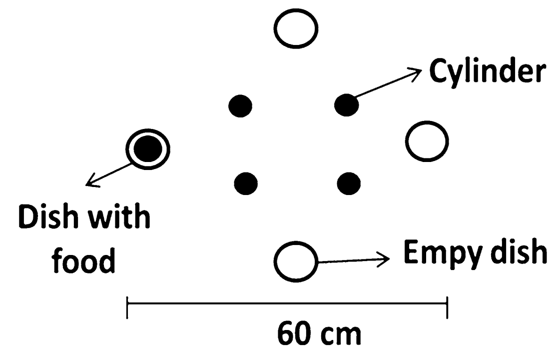

Fig. 1 Diagram of the experimental setting used under natural conditions. The array consisted of four *cylinders* and four dishes, one of which contained food (feeder). Each wasp collected food from the feeder five consecutive times

In all experiments, only one forager wasp was allowed to collect meat from the feeder five consecutive times. To identify this wasp when it arrived and collected food, it was marked with a washable ink dot on the abdomen. This marking procedure caused minimum disturbance to the wasp since it was not captured. That is, we worked with an individual wasp per experiment and any others arriving on the feeder were removed. Each experiment was conducted more than 200 m apart, as in Wilson-Rankin (2014), i.e., we analyzed wasps likely belonging to different colonies. During each trial, the target wasp collected food from a feeder and returned a few minutes later. The time taken between returns was recorded. One of the researchers (the observer), who was always positioned in the same location, at 0.5 m from the array recorded wasp behavior. The wasps' response to the food location change was evaluated with an Experimental and a Control group. Wasps were randomly assigned to the Control or Experimental groups. In the Experimental group, food position was randomly changed following each return. For example, if at the first feeding trial food was located to the East of the experimental array, then when the wasp left to the nest, the food was randomly placed at a different location and an empty dish replaced the baited one. On the following returns, food was displaced again to a new location (different from the previous one). In the Control group, however, food was always left in the same place, i.e., wasps had to choose between three empty dishes never rewarded and one dish with food placed in the same position. That is, control wasps had no previous experience with food location change. Thus, the comparison between the experimental and control groups reflects the effects of each kind of experience.

In each return, we recorded the time taken by the wasp from its return to the array to that of the landing on the feeder, i.e., searching time started when wasps hover over the array and ended when wasps landed on the feeder with all six legs. Experiments were conducted with 22 different wasps per group.

Data analysis

We carried out Kruskal–Wallis tests ($p < 0.05$) to compare the time taken to detect the novel food site of wasps which collected food from the feeder located on the right, left, bottom or top of the array (i.e., to control whether the position of the feeder conditioned wasp response). Time taken to detect the new food location on consecutive returns was compared using the Friedman analysis of variance (ANOVA) and Kendall Coefficient of Concordance. Paired comparisons were made with Wilcoxon matched pair tests (Bonferroni corrected) and differences in time taken to detect food on consecutive returns between experimental and control groups, were carried out with the Mann–Whitney *U* test.

Results

We found that the average time that wasps took between returns was 6.8 min (SE: ±0.72, $n = 88$) for experimental group and 7.8 min (SE: ±0.83, $n = 88$) for the control group. The average time taken to detect the novel food site in each return was; 0.44 min (SE: ±0.09, $n = 22$) for the first return, 0.16 min (SE: ±0.03, $n = 22$) for the second return, 0.25 min (SE: ±0.05, $n = 22$) for the third return, and 0.14 (SE: ±0.03, $n = 22$) for the fourth return. The time taken to detect the novel food site did not differ between groups of wasps which collected food from the feeder located on the right, left, bottom, or top of the array ($x^2_{(22,3)} = 3.0$, $p > 0.39$). In the first foraging visit of both the experimental and control group, wasps approached to the bait directly, immediately landing on the meat.

In the experimental group, we found that wasps' searching time over the first learned food location differed between consecutive returns ($x^2_{(22,3)} = 20.69$, $p < 0.001$). Wasps spent more time looking for food in the previously rewarded site in the first return than in the second one ($z = 3.28$, $n = 22$, $p < 0.05$). Moreover, they took longer searching for food in their first return than in the third ($z = 2.29$, $n = 22$, $p < 0.05$); and fourth return ($z = 2.97$, $n = 22$, $p < 0.05$). However, searching times did not differ between the second and the third return ($z = 1.42$, $n = 22$, $p > 0.05$), between the second and fourth ($z = 1.44$, $n = 22$, $p > 0.05$) and between the third and fourth ($z = 1.79$, $n = 22$, $p > 0.05$) (Fig. 2). In the control group, we found that the average searching time of wasps was approximately 0.01 min (SE: ±0.04, $n = 22$), i.e., foragers tended to direct their landing directly on the resource.

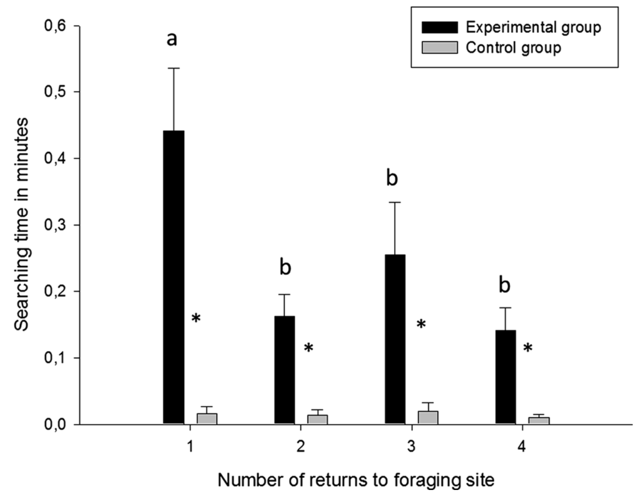

Fig. 2 Searching time (in minutes) until wasps discovered the novel food position, in relation to the number of returns to foraging site. *Different letters* denote significant differences throughout successive returns of the experimental group, and *asterisks* illustrate significant differences between Experimental and Control groups (Mann–Whitney *U* test, $p < 0.05$)

When comparing searching time between the experimental and control groups, we found significant differences in the first ($z = 5.54$, $n = 22$, $p < 0.05$), second ($z = 5.36$, $n = 22$, $p < 0.05$), third ($z = 5.35$, $n = 22$, $p < 0.05$) and fourth return ($z = 5.24$, $n = 22$, $p < 0.05$). In the first return of the experimental group, wasps spent 4.3-fold more time searching for the novel food location than wasps of the control group.

Discussion

In the present study, we found that *V. germanica* learnt to detect a novel food location more rapidly after experiencing recurrent changes in food position. When the wasp experienced the first food location displacement it looked for the source in the previously rewarded site for a longer period of time than on the following returns. This suggests that wasps learn about food unpredictability, indicating behavioral plasticity to cope with change.

In our investigation, we evaluated wasp response to recurrent food location changes in "natural" environments, a relatively common situation for this species given that other predators or human beings often move carrion it is feeding on (Lozada and D'Adamo 2011). In addition, movement of artificial elements such as picnic gear and barbecue grills frequently occurs due to human activities (Lozada and D'Adamo 2014). Interestingly, our experimental design which involved objects such as cylinders and dishes did not seem to constitute an artificial scenario for these wasps.

During the successive changes in food location, free-flying wasps returned to the previously rewarded site in a greater proportion than foragers from the control group, showing that past experience influences their search. So after one feeding experience wasps returned to the "learned" location, spending some time searching there (i.e., the time taken to detect the novel site, approximately 1–2 s) before moving on to the newly rewarded site. This agrees with an earlier study in which food was displaced only once (Lozada and D'Adamo 2011) rather than four consecutive times, as in the present work. Using the current experimental design we found that when wasps faced repeated changes in food position they tended to reduce the time taken to discover the novel food site. This reduction was most notable after the first experience of food absence in the expected location. Repeated changes in food location did not continue to significantly diminish searching time. Further research could elucidate whether more experiences with food displacement might promote learning of the alternation rule in response to recurrent changes.

The present findings tie in well with a previous investigation which demonstrated that *V. germanica* foragers return to a learned visual configuration previously associated with food (Lozada and D'Adamo 2009). In that study, after training, the resource was removed and the visual array was displaced 60 cm from the original feeding site. A second array of a different color was placed 60 cm from the original location at the opposite side of the array. Returning wasps searched over the colored array most recently associated with food (Lozada and D'Adamo 2009). Similarly, in another work, D'Adamo and Lozada (2008) found that when food was removed and the array displaced after the first food collection, wasps tended to search in the previously learnt location. This behavioral pattern is in agreement with results of the present research, showing that foragers tend to revisit past rewarding sites even if the array or the food are displaced. In both cases, analysis of learning flights could complement these results.

Previous studies exploring insect behavior in relation to food location change also demonstrated that individuals delay their redirection to a new location, evidencing how past experience conditions their next search (Toh and Okamura 2003; Durier et al. 2004; Graham et al. 2007). Likewise, food displacement in *Vespa mandarinia* shows a similar pattern; when a feeder is moved after several learning trials, returning hornets look for food at the previously learned site (Toh and Okamura 2003). Another study which evaluated relocating behavior with landmark displacement in *Vespula pensylvanica* revealed that wasps initially fly to the displaced landmarks, and then reorient their flights towards the bait (Wilson-Rankin 2014).

The present work contributes to the understanding of how *V. germanica* deals with repeated food location changes, a topic that to our knowledge, has not been explored in depth in social wasps. In conclusion, we demonstrated that wasps use past experience of change to reduce search time in previously learned locations, adjusting their behavior to changing contexts. This work provides new evidence of *V. germanica* learning processes associated with food relocation behavior in natural environments.

Acknowledgments We are very grateful to Marcela Maldonado for revising the English text and two anonymous reviewers who highly improved the first version of our manuscript. We also acknowledge support from the INIBIOMA-CONICET and CRUB, Universidad Nacional del Comahue.

References

Collett M, Chittka L, Collett TS (2013) Spatial memory in insect navigation. Curr Biol 23:R789–R800

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 Zeal J Zool 30:171–174

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

D'Adamo P, Lozada M (2008) Foraging behavior in *Vespula germanica* wasps re-locating a food source. New Zeal J Zool 35:9–17

D'Adamo P, Lozada M (2011) Cognitive plasticity in foraging *Vespula germanica* wasps. J Insect Sci 11:103

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. J Insect Behav 27:395–402

Durier V, Graham P, Collett TS (2004) Switching destinations: memory change in wood ants. J Exp Biol 207:2401–2408

Graham P, Fauria K, Collett T (2003) The influence of beacon-aiming on the routes of wood ants. J Exp Biol 206:535–541

Graham P, Durier V, Collett T (2007) The co-activation of snapshot memories in wood ants. J Exp Biol 210:2128–2136

Lozada M, D'Adamo P (2006) How long do *Vespula germanica* wasps search for a food source that is no longer available? J Insect Behav 19:591–600

Lozada M, D'Adamo P (2009) How does an invasive social wasp deal with changing contextual cues while foraging? Environ Entomol 38:803–808

Lozada M, D'Adamo P (2011) Past experience: a help or a hindrance to *Vespula germanica* foragers? J Insect Behav 24:159–166

Lozada M, D'Adamo P (2014) Learning in an exotic social wasp while relocating a food source. J Physiol Paris 108:187–193

Moreyra S, D'Adamo P, Lozada M (2012) Cognitive processes in *Vespula germanica* wasps (Hymenoptera: Vespidae) when relocating a food source. Ann Entomol Soc Am 105:128–133

Shettleworth SJ (2001) Animal cognition and animal behavior. Anim Behav 61:277–286

Toh Y, Okamura J (2003) Foraging navigation of hornets studied in natural habitats and laboratory experiments. Zool Sci 20:311–324

Wilson-Rankin EE (2014) Level of experience modulates individual foraging strategies of an invasive predatory wasp. Behav Ecol Sociobiol 69:491–499

Zeil J (2012) Visual homing: an insect perspective. Curr Opin Neurobiol 22:285–293