Cognitive Processes in *Vespula germanica* Wasps (Hymenoptera: Vespidae) When Relocating a Food Source

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Ann. Entomol. Soc. Am. 105(1): 128–133 (2012); DOI: http://dx.doi.org/10.1603/AN11097

ABSTRACT The German yellowjacket *Vespula germanica* (F.) (Hymenoptera: Vespidae), an invasive wasp, is a highly efficient forager. We studied wasp cognitive ability while varying landmark disposition and cue conspicuity. Learning flights were used as an indicator of forager cognition while relocating a food source. We recorded the number of learning flights (circling above the food location) performed after each visit by each wasp. We studied the effect of modifying a learned location and analyzed how the addition of conspicuous cues affected wasp learning. Cognitive ability also was studied in relation to food manipulation efficiency, i.e., the time taken to extract a piece of meat and fly away. We found that one feeding visit was sufficient for wasps to learn relevant cues associated with a rewarded location, as shown by the reduction of learning flights after just one experience. Moreover, wasps reached asymptotic levels in food manipulation after only one feeding visit. The introduction of a contextual change, such as moving the food location a few centimeters from the original feeding site, affected returning foragers, who increased the number of learning flights when leaving the array. Interestingly, enriched contexts with conspicuous cues seemed to facilitate wasp cognition as they performed fewer learning flights than in nonenriched ones. Learning flights seem to be a good cognitive indicator, reflecting wasp experience with a certain context, thus revealing their sensitivity to landmark cue conspicuity. This study highlights the cognitive capacities of *V. germanica* foragers.

KEY WORDS social wasp, learning flight, foraging, food manipulation

Learning capacities vary widely in the animal kingdom (Shettleworth 1998), and it seems that the animal's cognitive abilities are intricately linked to its biotic and abiotic environment, i.e., learning capacities are related to the animal's experience of certain scenarios (Raine and Chittka 2008). *Vespula germanica* (F.) (Hymenoptera: Vespidae) is a highly invasive social wasp that inhabits diverse environments around the world (Archer 1998). When exploiting a food source, foraging hymenopterans learn contextual cues to retrieve the appropriate memories at the appropriate time (Collett and Zeil 1998, Cheng 2000, Jarau and Hrncir 2009). Information about local landmarks is learned within a certain environment, where contextual signals prime the correct local memory. It has been shown that wasps revisit a previously learned feeding location more frequently when foraging in closed habitats (i.e., with dense vegetation) than when foraging in open ones (i.e., with scarce vegetation) (D'Adamo and Lozada 2007). Considering that landmarks help wasps relocate a food source (Collett and Zeil 1996), closed habitats offer more references that guide foragers to the feeding site than open ones. The acquisition of landmark information occurs through specialized learning flights during which the wasp examines the location and stores relevant cues that will enable it to return (Zeil et al. 1996).

Wasps departing from the feeding site perform learning flights, i.e., a series of arcs roughly centered on the goal (Collett and Baron 1994, Collett and Rees 1997, Zeil et al. 1996). Similarly, ants display learning walks in which they turn and look back as they return from a feeding site (Nicholson et al. 1999). As insects become familiar with feeding site cues through repetitive experiences, these inspections become less frequent. In bees and ground nesting wasps, visual characteristics around the hive are learnt during the first orientation flight (Capaldi and Dyer 1999, Tinbergen 1932). Searching behavior in social insects mainly has been studied at the nest site (Wehner and Räber 1979, Brünnert et al. 1994, Capaldi and Dyer 1999, Åkesson and Wehner 2002, Narendra et al. 2007) but less, to our knowledge, at their feeding location (Collett and Rees 1997, Nicholson et al. 1999). In the current study we will evaluate wasps' learning at the feeding location, analyzing orientation flights after collecting meat from an undepleted food source. An individual wasp is often unable to carry an entire piece of food and therefore has to make several trips between the food location

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and the nest where larvae are fed, systematically returning to the learned site. During food relocation, *V. germanica* learns to associate cues— odor, spatial, and visual (color and patterns)—with food (D'Adamo and Lozada 2003, 2008, 2011; Moreyra et al. 2006; Lozada and D'Adamo 2011). This relocating behavior has been studied in diverse environmental conditions, and there is ample evidence to support the existence of complex learning mechanisms in this species (D'Adamo and Lozada 2011, Lozada and D'Adamo 2011). The experience of relocating a particular food source implies the strengthening of certain sensory-motor circuits, evidenced in perception and action patterns. In this way, learning might be the outcome of integrating previous and novel experiences, by developing new sensory-motor patterns.

In this work we studied wasp cognitive abilities in diverse experimental conditions. Learning flights were used as an indicator of spatial learning. We recorded the number of learning flights performed by a single wasp during several consecutive feeding visits in relation to cue conspicuity and landmark disposition. We also evaluated wasp food manipulation efficiency by analyzing handling time during consecutive feeding visits. We hypothesize that as wasps obtain more experience feeding from a location with certain cues, the time taken to learn about this context will decrease. In the same way, as wasps gain experience in manipulating food, they will require less time to handle it. We expect to find that: 1) during consecutive visits the number of wasp learning flights will decrease if contextual conditions remain unaltered, 2) the introduction of a modification in the learned context will increase the number of learning flights in a subsequent visit, 3) wasps foraging in enriched contexts with conspicuous cues will perform fewer learning flights than wasps foraging in nonenriched ones, and 4) food handling time will decrease during consecutive feeding visits.

Materials and Methods

All experiments were carried out under natural conditions near San Carlos de Bariloche (41° S, 71° W), Argentina, during the most active flight period of *V. germanica* (February–April) in 2004, 2006, 2007, 2008, 2009, and 2010. The experiments were conducted in suburban areas in similar weather conditions (sunny and still), where temperature ranged from 22 to 27°C. In all experiments, an individual forager was allowed to feed from a white plastic dish (7 cm in diameter) containing 20 g of raw bovine minced meat, placed on the ground. An observer sat close to this array at a 0.5-m distance. When a forager arrived at the dish and was collecting food, it was marked distinguishably with a dot of washable paint on the abdomen for identification. This marking procedure caused minimal disturbance to wasps as they were not captured. Any other wasp visiting the dish was removed to work with only one individual per experiment. At each trial, the studied wasp collected food from the dish, then departed for the nest, and returned a few minutes later. We considered the wasp departure to have occurred when it flew away from the dish with a piece of meat within its mandibles. An orientation flight was completed when the wasp directed its flight in a straight line instead of circling above the experimental setting. An individual wasp was used for only one experiment and one treatment. Each experiment consisted of three or four feeding trials, (depending on the experiment). Each feeding trial involved one discrete visit by a forager to the feeding dish, demarcated from the next feeding trial by a return to its nest. The visit during which the wasp was marked counted as the first visit. For each feeding trial we recorded the number of learning flights and the duration of each visit, measured from the wasp's landing on the dish to its departure with a piece of meat. We considered learning flights as arcs of increasing radius and height, roughly centered over the feeding location (Collett and Zeil 1996, Raveret-Richter 2000). When leaving the feeding location, wasps circle high above the ground and then fly away (Raveret-Richter 2000). During each foraging bout, when the wasp leaves the feeder, it backs away from the feeder, in a series of arcs that gradually increase in radius and height. Then, the count of learning flights refer to the number of circles the wasp flew in a continuous bout of flight. To record different wasps from different colonies, we displaced the experimental setting >200 m from one assay to another one.

Experiment 1. Each wasp was allowed to collect food four consecutive times from a dish placed at the center of a 30- by 30-cm square delimited by a yellow cylinder placed at each corner, 2 cm in diameter and 60 cm in height (Fig. 1a). The number of learning flights was recorded after each visit.

Experiment 2. Each wasp was allowed to collect food four consecutive times from a dish. The cylinders were arranged as the corners of a square of 30-cm side length, as in experiment 1, and four dishes were placed at the four edges of the square, one of which contained food (Fig. 1b). The wasp collected food consecutively from the same place twice and when it left the food location after its second visit and before it returned for its third visit, the dish with food was displaced 60 cm from the original feeding location to the opposite point on the array. The wasp was allowed to feed two more consecutive times, i.e., if first the food was located to the east (position A), before the third visit it was placed to the west (position B). Therefore, when the wasp returned on its third visit, it encountered a scenario that differed from the learned one, as the feeder was placed in a different location and a clean empty dish took its place. We recorded the number of learning flights after each visit.

Experiment 3. Each wasp was allowed to collect food three consecutive times from a dish placed at the center of a square, delimited by four protruding cylinders as in experiment 1 (Fig. 1c). Located in an open habitat, this array was enriched with five wooden sticks placed around it, each 1.5 m high with 50 cm of blue flagging draped from the top. These sticks were placed at a distance of 1 m from the array. In the

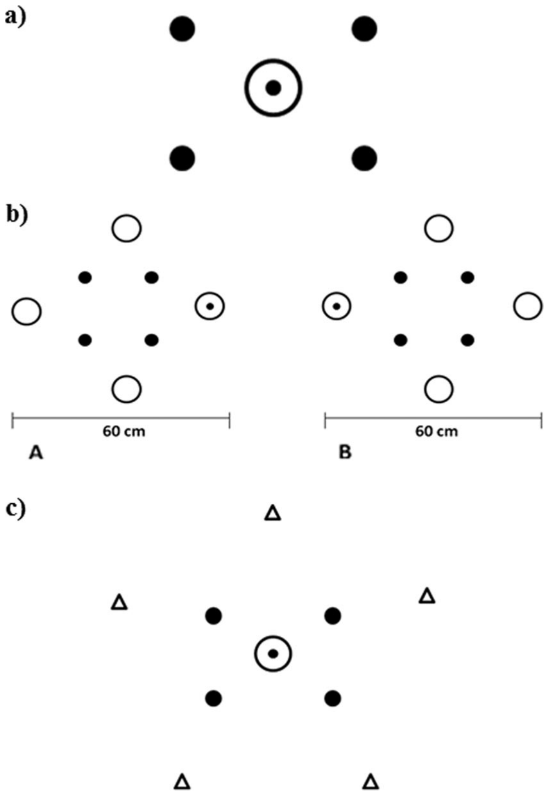

Fig. 1. (a) Experimental array used for training *V. germanica* wasps in experiment 1. Each wasp was allowed to collect food from a dish placed at the center of a square of 30 cm a side, delimited by four protruding cylinders. ⊙ Dish with food; ● cylinders. (b) Experimental array used in experiment 2. A) Food was placed at position A. B) Food was shifted to position B, at 60 cm in opposite direction from the original feeding site. ○ Empty dish, ⊙ dish with food, ● cylinders. (c) Experimental array used in experiment 3. Food was placed at the center of a square surrounded by five wooden sticks. ⊙ Dish with food, ● cylinders, △ wooden sticks with blue flagging. Wooden sticks were added in experimental conditions, whereas in control conditions these were absent.

control group the array was not surrounded by these wooden sticks (i.e., nonenriched context). We analyzed the effect of adding conspicuous cues by comparing wasps' learning flights between the control and the experimental group. Experiments were replicated 41 times in nonenriched and 39 in enriched contexts.

Experiment 4. Each wasp was allowed to collect food four consecutive times from a dish placed at the center of a square delimited by four cylinders as in experiment 1. To evaluate food manipulation time, i.e., the time taken for the wasp to arrive, extract a piece of meat and fly away; we recorded the duration of each visit from wasp arrival until departure. We expected this time to decrease if wasps had learned to handle the food more efficiently.

Data Analysis. The number of learning flights performed at consecutive wasp visits was compared using Friedman analysis of variance (ANOVA) and Kendall Coefficient of Concordance. Paired comparisons were made with Wilcoxon matched pair tests. Learning flights in enriched and nonenriched contexts were compared by means of Mann–Whitney test. Manipulation time during consecutive wasp visits was compared with Friedman ANOVA and Kendall Coefficient of Concordance, and paired comparisons were conducted using Wilcoxon matched pair tests. When quoting statistical analysis, N refers to the number of wasps observed per experiment, and df, the degrees of freedom for each statistical analysis.

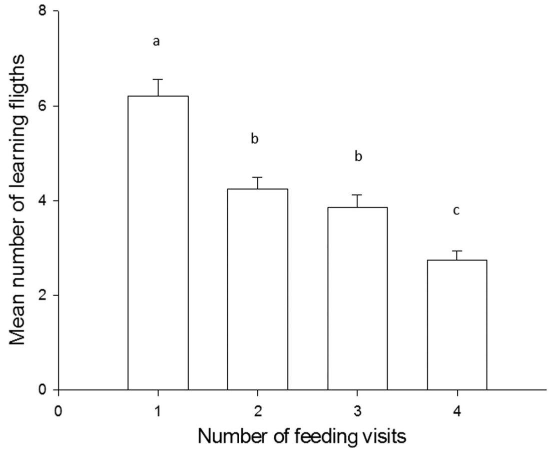

Fig. 2. Mean numbers of learning flights after each feeding visit during the training session when the feeder remained at the same position. (experiment 1) Different letters denote significant differences ($P < 0.05$).

Results

After a foraging wasp collected a piece of meat, it flew away and performed learning flights, i.e., arcs of increasing radius over the location where it had fed.

Experiment 1. The number of learning flights decreased with feeding visits ($\chi^2 = 52.81$, $N = 32$, $P < 0.0001$). More learning flights were observed after the first feeding visit than after the second one ($Z = 3.99$, $N = 32$, $P < 0.0001$). Similarly, more learning fights were found after the second than after the fourth visit ($Z = 4.06$, $N = 32$, $P < 0.0001$) (Fig. 2). However, nonsignificant differences existed between the number of learning flights after the second and the third visit ($Z = 1.17$; $N = 33$, $P > 0.05$).

Experiment 2. In this case, wasps fed two consecutive times from a certain feeder position (e.g., position A) before feeding twice from a different position (e.g., position B). Significant differences were observed in the number of learning flights of the four feeding visits ($\chi^2_{(N = 13, df = 3)} = 22.45$, $P < 0.00005$), (Fig. 3). As in experiment 1, the number of learning flights was significantly lower after the second visit than after the first one ($Z = 2.54$, $N = 13$, $P < 0.01$). However, after the third visit, the number of learning flights increased, reaching similar levels to the first one as nonsignificant differences were found between

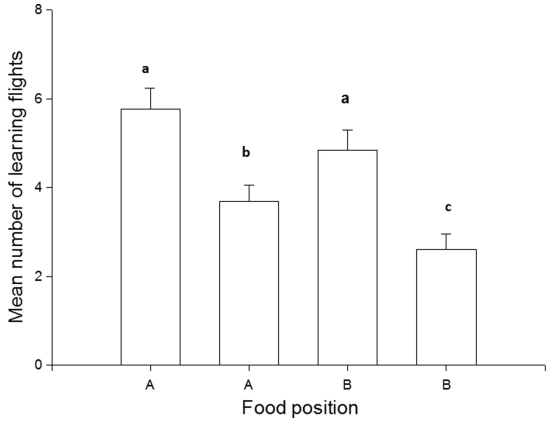

Fig. 3. Mean number of learning flights during consecutive feeding visits when the feeder was displaced after the second wasp's visit. (experiment 2) A) Food was located to the East "position A". B) Food was placed to the West "position B" in opposite direction to the original feeding site. Different letters denote significant differences ($P < 0.05$).

them ($Z = 1.78$, $N = 13$, $P > 0.05$). Moreover, significantly fewer learning flights were found after the fourth feeding visit than after the second one ($Z = 2.19$, $N = 13$, $P < 0.05$). As expected, significantly more learning flights were observed after the third feeding visit than after the fourth one ($Z = 3.00$, $N = 13$, $P < 0.005$).

Experiment 3. Significant differences were found when comparing the number of learning flights after the first, second, and third visit, between enriched and nonenriched contexts ($N1,2 = 41, 39$, $Z = 1.99$, $P < 0.05$; $N1,2 = 40, 39$, $Z = 2.21$, $P < 0.05$; $N1,2 = 39, 38$, $Z = 2.45$, $P < 0.05$, respectively) (Fig. 4). A significantly higher number of learning flights were observed after the first visit than after the second one, and after the second than after the third within each environment ($Z = 5.05$, $N = 39$, $P < 0.05$; $Z = 4.75$, $N = 40$, $P < 0.05$; $Z = 5.30$, $N = 38$, $P < 0.05$; $Z = 4.64$, $N = 38$, $P < 0.05$ for enriched and nonenriched contexts, respectively).

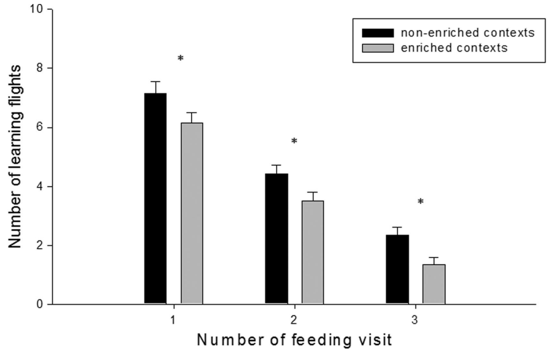

Fig. 4. Mean number of learning flights performed after consecutive feeding visits in enriched and nonenriched contexts. Gray bars refer to enriched contexts and black bars to nonenriched ones. Asterisks denote significant differences between numbers of learning flights for each feeding visit and between different contexts, ($P < 0.05$).

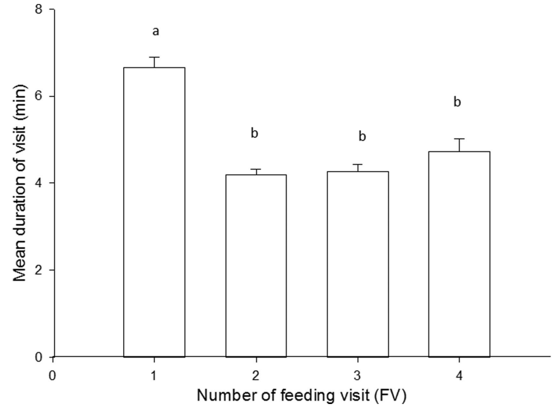

Fig. 5. Food manipulation time during each consecutive feeding visit. Different letters denote significant differences ($P < 0.05$).

Experiment 4. We found significant differences between all consecutive feeding visits when analyzing food manipulation time ($\chi^2_{(N = 102, df = 3)} = 50.27$, $P < 0.0001$) (Fig. 5). Wasps spent significantly more time manipulating the food during the first visit than during the following visits ($N = 278$, $Z = 10.51$, $P < 0.000$). There were no differences between the second, third, and fourth visits ($N = 254$, $Z = 1.20$, $P > 0.05$; $N = 105$, $Z = 0.42$, $P > 0.05$ respectively), indicating that wasps learned to manipulate the food efficiently mainly during the first visit, reaching an asymptotic level at this point.

Discussion

In this study we found that while relocating a food source, *V. germanica* wasps rapidly learn to associate certain sensory motor experiences with a particular foraging context. One experience seems to be sufficient for wasps to learn relevant cues associated with a rewarded location as evidenced in the reduction of learning flights after just one feeding visit. Moreover, wasps reached asymptotic levels in food manipulation after only one experience with food. As wasps gain more experience in feeding from a certain site, the number of learning flights decreases. However, the introduction of a contextual change, such as moving food location some distance from the original feeding site, is recorded by returning foragers, which increase the number of learning flights when leaving the array. Interestingly, enriched contexts with conspicuous cues facilitate cognition as wasps perform fewer learning flights than in nonenriched ones.

It has been demonstrated that wasps record contextual landmarks during learning flights, which help foragers to relocate the food source (Zeil et al. 1996). The number of learning flights seems to be a good indicator of learning when wasps return to a previously visited food source. The relative importance of orientation cues varies with experience in other social insects such as ants (Aron et al. 1988, Harrison et al. 1989) and honey bees (Becker 1958, Von Frisch 1967). The current study demonstrates that when wasps feed from the same location, they perform significantly fewer learning flights after each consecutive feeding visit. After their first visit, wasps perform the highest number of learning flights. This means that although they improve landmark learning over several visits, wasps have to learn enough during the first one to guide them to a previously rewarded location (Collett and Zeil 1996). Previous works showed that one visit is sufficient for this species to establish an association between diverse cues and food reward in different contexts (D'Adamo and Lozada 2009, 2011; Lozada and D'Adamo 2009, 2011). The introduction of a contextual change, such as moving food location a few centimeters from the original feeding site, was seen to affect returning foragers, which in response to the new configuration, increased the number of learning flights to the number performed after the initial feeding visit. Interestingly, this increased number of learning flights was similar to the number performed after the first visit. Thus, when wasps fed two consecutive times from each of two different positions, the number of learning flights after the first and third visit was similar, as well as after the second and fourth. When studying landmark stability in learning flight duration, Wei et al. (2002) found that bees performed longer learning flights when landmarks surrounding the food were displaced. However, in their study, the decrease in learning flight duration after reorientation flights was faster than after the original food discovery. This difference with our findings could be because of differences in the recorded variable, given that they evaluated duration instead of number of learning flights. Differences between species also might play an important role.

When wasps fed from enriched environments, they performed fewer learning flights than from nonenriched ones. The addition of protruding artificial cues was correlated with a decrease in the number of learning flights, suggesting that this type of landmark facilitates spatial learning. In accordance with this, it has been previously found that when food is removed, wasps revisit a previously learned location containing protruding landmarks more frequently than contexts without them (D'Adamo and Lozada 2007). This suggests greater associative strength with contexts incorporating conspicuous stimuli. In contrast, Wei et al. (2002) found that learning flight duration in bees increased with visual complexity. In Wei's experimental design, visual complexity was associated with more complex patterns, whereas in the current study, the inclusion of landmarks of greater height might not require greater learning effort on the part of wasps, as these cues seem to be more salient, favoring cognitive recovery. Our results confirm that height could be a relevant landmark feature for *V. germanica* as also found for other wasps and bees (Tinbergen and Kruyt 1938, Lehrer 1996, D'Adamo and Lozada 2007). The higher a stimulus is raised above the ground, the more easily it is detected by honey bees (Lehrer 1996). Moreover, Tinbergen and Kruyt (1938) concluded that the wasp *Philanthus triangulum* (F.) consistently prefers protruding objects to flat landmarks. In view of these studies, it seems that conspicuous cues might facilitate cognition in *V. germanica* wasps when relocating a food source.

Vespula germanica wasps seem to use highly flexible learning mechanisms while exploiting a food source. It is interesting to highlight that in our experimental setting, contextual changes not only implied modifications in perception, but also in wasp action patterns. Therefore, learning might result from the integration of old and new experiences, implying not only the mere acquisition of environmental information but also the development of novel sensory-motor patterns. For example, if a wasp learns to find food to the west of a blue landmark, and to the east of a yellow landmark, then when presented with the blue landmark, the wasp will direct its search to the west of that landmark, as this learned motor response prevails (D'Adamo and Lozada 2009). Moreover, wasps persist in visiting a previously rewarded location even when food is located very close by (Lozada and D'Adamo 2011), indicating the importance of sensory motor patterns configured during this learning situation, which delay novel perceptual-action patterns. Furthermore, rapid learning related to sensory motor circuits seems to be associated with food handling. The experience of manipulating food decreases the time spent in removing a piece of meat. This decrement in time taken reaches asymptotic levels after the first visit. Several studies have demonstrated previously that *V. germanica* foragers can learn diverse tasks in just one learning trial (D'Adamo and Lozada 2009, Lozada and D'Adamo 2009). In conclusion, the current study highlights the cognitive plasticity of *V. germanica* wasps, providing further evidence of the rapid learning abilities of this invasive species.

Acknowledgments

We are very grateful to Audrey Shaw and three anonymous reviewers whose comments highly improved a first version of the manuscript. This study was funded partially through a grant from CONICET (PIP 2009). We also acknowledge support from the CRUB, Universidad del Comahue.

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Received 2 June 2011; accepted 28 October 2011.