



Review Paper

Learning in an exotic social wasp while relocating a food source



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ABSTRACT

In this paper we review several studies on *Vespula germanica* behavioral plasticity while relocating a food source in natural environments. This exotic social wasp, which has become established in many parts of the world, displays diverse cognitive abilities when foraging. Given its successful invasiveness worldwide, our initial hypothesis was that this species has great behavioral plasticity, which enables it to face environmental uncertainty. In our work we have analyzed foraging behavior associated with undepleted resources. Throughout several experiments, rapid learning was observed in this species; after few learning experiences they associate diverse contextual cues with a food source. However, by exploring wasp behavior when food suddenly disappeared, either because it had been removed or displaced, we found that they continued searching over a no longer rewarding site for a considerable period of time, suggesting that past experience can hinder new learning. Particularly surprising is the fact that when food was displaced nearby, wasps persisted in searching over the empty dish, ignoring the presence of food close by. We propose that this species could be a suitable model for studying cognitive plasticity in relation to environmental uncertainty.

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1. Introduction

In social species, learning while foraging can occur both at individual and collective levels. Social wasps frequently make several trips between the nest and undepleted food sources while collecting food to feed their larvae. This relocating behavior, which implies that learning mechanisms are at work in order to navigate from the nest to the feeding place, has been previously studied in

vespid species (Collett and Lehrer, 1993; Collett and Baron, 1995; Collett and Rees, 1997; Raveret-Richter, 2000; Jeanne and Taylor, 2009). During the last decade we have studied cognitive abilities, focusing on this behavior in the exotic wasp *Vespula germanica* (D'Adamo and Lozada, 2003, 2007, 2009, 2011, 2014; Lozada and D'Adamo, 2006, 2009, 2011), thus contributing to the understanding of learning processes of vespids during foraging.

Associative learning is a widespread capacity that involves the establishment of a temporal or spatial link between two stimuli or between a stimulus and a response. Animals learn to associate a neutral stimulus (e.g. contextual cues, conditioned stimulus

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[CS]) with a biologically relevant stimulus (e.g. food, unconditioned stimulus [US]). As a result of experience, associative learning enables predictive relationships to be made between contingent events. Associative learning is known to occur in a variety of insects and has been shown among Hymenoptera, in ants (e.g. Hölldobler and Wilson, 1980), bees (e.g. Menzel and Müller 1996) and wasps (e.g. Raveret-Richter, 2000).

Learning contextual cues helps guide animals while foraging. In the case of social insects, context has been considered a set of cues relating to the time and place feeding takes place; it can involve the physical surroundings, the time of day and motivational state (e.g. leaving the nest or returning to it) (e.g. Collett and Rees, 1997; Cheng, 2005). Positional cues, which we focus on in this study, are landmarks that characterize a certain site, and can help insects identify a previously rewarding location.

By means of specialized flights that wasps perform when leaving an undepleted food source, foragers learn about the positional cues of the location they will return to (Collett and Lehrer, 1993; Collett and Baron, 1995; Zeil et al., 1996). These learning flights permit the association of local landmarks with a certain food source (Moreyra et al., 2012). Local cues learned by free-flying wasps involve visual, spatial and odor cues (D'Adamo and Lozada, 2003, 2009; Moreyra et al., 2006; Lozada and D'Adamo, 2006, 2009). Odor is an important cue for *V. germanica* foragers while searching for a food source, as it elicits landing responses on both protein and carbohydrate resources (Moreyra et al., 2006). Different patterns of relocating behavior were observed depending on whether wasps were foraging in open habitats (without vegetation) or closed ones (with conspicuous vegetation); wasps collecting food in closed habitats returned to the original feeding site more frequently than those feeding in open ones. Interestingly, the addition of five sticks with flagging to the original feeding site in an open habitat elicited a similar response as when foraging in a closed habitat, without these references (D'Adamo and Lozada, 2007). Therefore, it seems that sites that encompass protruding landmarks, like trees or shrubs, facilitate foragers' guidance during re-location. Similarly, it was found that protruding visual cues prevail over flat ones for directing solitary wasps (Tinbergen and Kruyt, 1938). Visual memories can be primed by contextual cues, such as distant panoramic views, time of day, and motivational state (Collett and Rees, 1997; Menzel, 2009; Graham et al., 2007). Furthermore, context can facilitate both learning and memory retrieval (Collett et al., 2003). Context modification can also facilitate the release of previously acquired memories, as found in Cheng's research (2005) when studying the learning of two successive conflicting tasks in bees. He observed a reduction in the performance of one of the tasks. This interference was neutralized when contextual cues differed from one learning condition to the other (Cheng, 2005).

In *V. germanica*, one experience seems to be sufficient to establish an association between diverse cues and food reward in different contexts (D'Adamo and Lozada, 2007, 2011; Lozada and D'Adamo, 2006, 2009, 2011). In line with this, a significant reduction in the number of learning flights is observed after just one feeding visit (Moreyra et al., 2012), a pattern previously observed in honeybees (Lehrer and Collett, 1994). Overall, the studies conducted on *V. germanica* demonstrate that one learning experience significantly influences wasp behavior, suggesting cognitive plasticity in this invasive species.

2. *V. germanica* invasiveness and biology

V. germanica, originally from Eurasia and Northern Africa, has invaded several regions of the world, becoming a major pest in the invasion sites (Edwards, 1976; Akre and MacDonald, 1986).

In Argentina it has spread rapidly throughout the country, becoming established in different types of environments, such as steppe, forest, lake shore, transition zone, urban and suburban areas. This truly social species has an annual cycle, i.e., colonies grow at a rapid rate during a short period of time (summer), after which wasps become very abundant, and then perish with the first frosts. Following this, new queens hibernate until the next spring, when the cycle begins again. During the growing period, foragers collect protein to feed the larvae and the queen, and carbohydrates for their own maintenance; therefore, efficient foraging behavior is an important trait for colony development. These wasps obtain their food from a variety of sources that require diverse foraging strategies, such as scavenging, preying on live arthropods, consuming fruit, honeydew from aphids, and human garbage (Akre, 1982). The flexibility observed in *V. germanica* behavior might be associated with this eclectic diet as well as with the ample diversity of environments it inhabits.

Social communication could contribute to successful food exploitation. Within social communication, recruitment is an important mechanism which leads conspecifics to a certain site (Wilson, 1971). Although there is no evidence of which mechanisms are used, the odor of a rich food source inside the nest orients naïve wasps' search towards that resource (Overmyer and Jeanne, 1998; Jandt and Jeanne, 2005). In addition, social learning while foraging has been described in the bumble bees *Bombus impatiens* (Worden and Papaj, 2005), *Bombus terrestris* (Leadbeater and Chittka, 2009) and in *V. germanica* wasps (D'Adamo et al., 2000, 2001, 2003, 2004; D'Adamo and Lozada, 2005). In the last mentioned studies, we found that naïve foragers are attracted by the presence of conspecifics at a certain location, i.e. attraction to an undepleted protein resource is increased by the presence of live conspecifics. When both visual and olfactory cues of conspecifics occur together, wasp response is much greater than if either visual or olfactory cues are presented alone, suggesting the synergistic action of these cues (D'Adamo et al., 2003).

3. Unpredictability, variability, contextual change

This invasive species constantly deals with artificial scenarios related to human settings. Moreover, as scavengers, *V. germanica* natural environments usually entail uncertainty, as food may be unexpectedly removed or displaced by other predators. It is frequently observed that dogs or birds of prey move carrion which wasps are feeding on, removing the food or displacing it, thus changing positional cues (pers. obs.). Furthermore, when wasps collect resources from human settings at picnics or outdoor activities, food position continuously changes. Picnickers not only shift food location constantly, but also local cues such as camping equipment, cutlery, dishes, beverage recipients, and colored cans. Therefore, the modification and displacement of locational cues is a frequent experience for this species when relocating undepleted food sources.

4. Relocating behavior when food is removed or displaced

We evaluated relocating behavior in *V. germanica* foragers when facing changes, analyzing wasp response in three different instances: (1) when food is removed after a certain number of rewarding experiences, (2) when food is displaced nearby after a certain number of rewarding experiences, (3) when food is displaced nearby after a certain number of rewarding experiences, and contextual cues associated with the food are modified.

The experimental design was similar in these three instances: we worked under natural conditions, on pebble beaches of lake shores, where we placed an array consisting of four cylinders

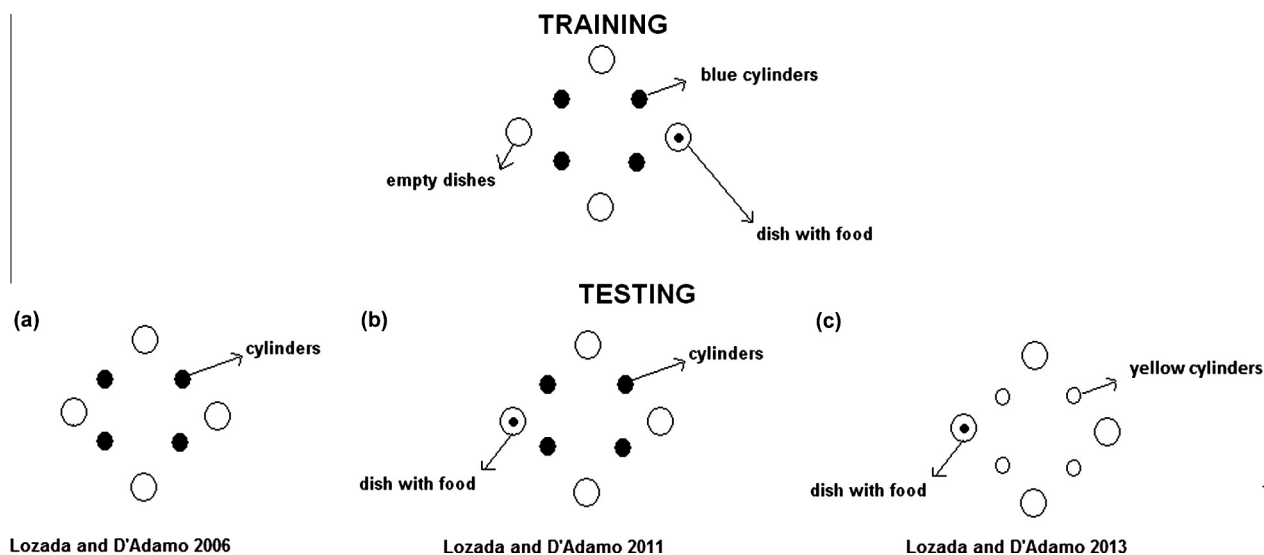


Fig. 1. Experimental design: in all cases individual wasps were trained to feed from one of four dishes which were placed around an array composed of four colored cylinders. During training, wasps fed at a certain location during one, two, three or four consecutive visits. During testing: (a) food was removed and the experimental design was maintained, (b) food was displaced to the opposite location and (c) food was displaced to the opposite location and cylinder color was changed (non-matching group).

arranged as the corners of a square, and four dishes placed at the four sides of this square, one of which contained food (Fig. 1). We waited until one wasp spontaneously landed on the dish, and while the wasp was collecting food it was marked with washable paint. Any other wasp that approached the feeder was removed. At each training session, the studied wasp fed and collected food from the dish, then departed to the nest and returned a few minutes later. An individual wasp was used for only one experiment and one treatment.

4.1. Relocating behavior once food is removed

We investigated how long wasps continue searching for a food source that is no longer available (Lozada and D'Adamo, 2006). Training sessions consisted of either one or three feeding trials, depending on treatment. One treatment consisted of one feeding trial, and after the wasp's departure, the feeding dish was immediately replaced by an empty one. The other treatment consisted of three consecutive feeding trials, after which the feeding dish was replaced by an empty one. During the testing phase, we analyzed the wasp's behavior when it returned to the experimental array, by recording the number of visits (i.e., hovers and landings) to the clean dish. We found that wasps continued visiting the feeder for a period of time that ranged from approximately 60 min (with 1 feeding trial) to 200 min (with 3 feeding trials) (Figs. 2 and 3). This shows that wasps learnt to associate food with the experimental array after only one trial, although searching increased when wasps had previously had a higher number of learning episodes. What might be happening is differential weighting of location and olfactory cues, which affects wasp behavior differently depending on their number of previously rewarding experiences. This is in accordance with a huge body of evidence demonstrating that the repetition of a rewarding experience greatly influences future decision-making (e.g. Bitterman et al., 1983; Hall, 1994; Gallistel et al., 2004).

While in the above described experiment the empty feeder and the array remained in place and wasp behavior was evaluated from food disappearance until they no longer returned, in a later study both the feeder and the array were removed for one hour (Moreyra et al., 2013). After this period, the array was re-installed, but this time with two baited feeders. We hypothesized that if

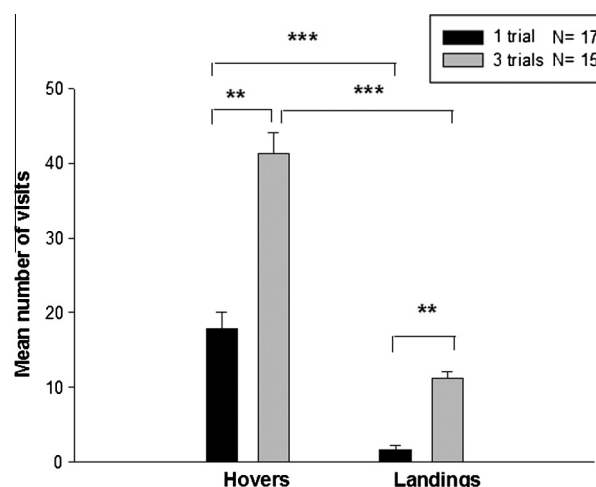


Fig. 2. Mean number of wasp visits (i.e. hovers and landings), \pm standard error, during the testing phase, over the array where wasps were previously trained with one or three feeding trials. From Lozada and D'Adamo (2006).

wasps chose the previously learnt location this would indicate memory retrieval; whereas if they chose both feeders in similar proportions, this would indicate that the location cue was not so strong. Wasps trained with four feeding trials collected food from the previously learned feeder significantly more frequently than from the non-learned one. In contrast, wasps that had been trained only once showed no preference between feeders. Thus, memory retrieval could be observed one hour after wasps had collected food on four consecutive occasions, but not after only one, demonstrating that one hour does not impair memory retention if four previous feeding experiences have occurred. We would like to highlight that this experimental design, which implies offering two baited feeders at the testing phase, could be a novel way of analyzing memory processes in social wasps.

Comparing both studies (Lozada and D'Adamo, 2006; Moreyra et al., 2013), we can infer that wasps are able to learn an association with only one rewarding experience; moreover, when contextual cues remain, they continue searching for food for 60 min.

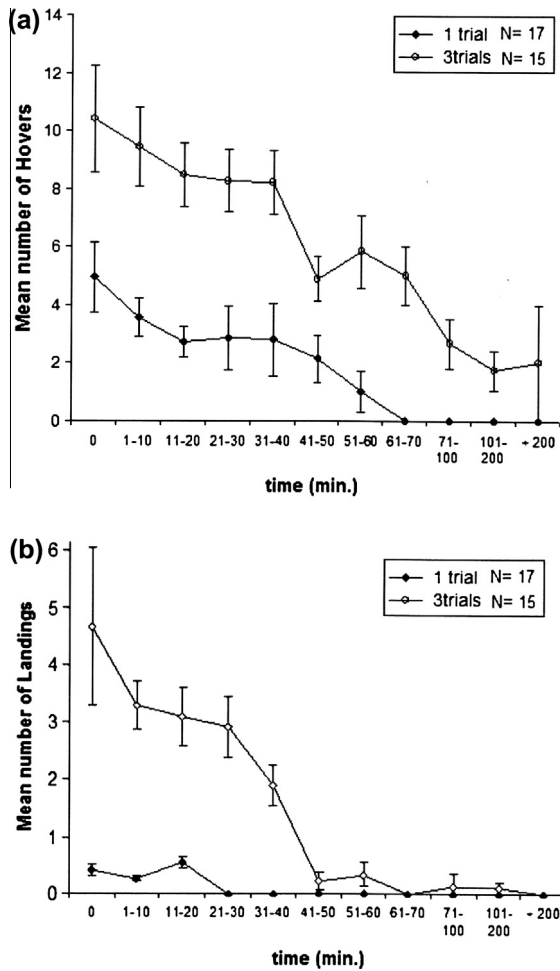


Fig. 3. Time course of wasps' visits over the array without food, when trained with one or three feeding trials; (a) extinction of hovering responses and (b) extinction of landing responses. Means and standard errors are shown. The x-axis indicates time intervals. From Lozada and D'Adamo (2006).

However, if the whole array is removed immediately after one learning episode, one hour later wasps do not show a preference for the learnt feeder (as do wasps with four learning experiences). Nevertheless, the fact that wasps returned could indicate that they remember the approximate location of the feeding site. In our experiment, we observe how the number of learning experience repetitions affects the strength with which wasps can establish associations between landmarks and food, thus enhancing the 'reliability' of the location. Similarly, previous studies in honeybees have demonstrated that one learning trial leads to consolidation processes of several minutes (for review, see Menzel, 1999; Menzel and Müller, 1996), whereas multiple trials facilitate memory consolidation of several days, enhancing resistance to extinction (Menzel, 1990).

4.2. Relocating behavior when food is displaced nearby after a certain number of rewarding experiences

We studied how previous learning experience interferes with the detection of new food sources (Lozada and D'Adamo, 2011). As explained above, wasps persist in visiting a feeder after food removal (Lozada and D'Adamo, 2006), but what would happen if food were displaced nearby? Would wasps return to the empty learned feeder as previously found, or would they go directly to the new food source? In this study we repeated the Lozada and

D'Adamo (2006) experiment, but instead of removing the feeder, it was displaced 60 cm (Fig. 1). Wasps were trained to feed from the array during either one or four consecutive visits, depending on treatment. After these learning trials, the dish with food was displaced from the original feeding location to the opposite point on the array, i.e. if during training food was located to the West, in the testing phase it was placed to the East. Thus, returning foragers encountered a different scenario in the testing phase. We analyzed wasp behavior after food displacement by recording the number of hovers and landings on each empty dish, until the wasp discovered the new food location and collected a piece of meat. The number of hovers was scored by counting the number of times each wasp flew over the dish without landing on it. We compared wasp response in relation to the number of previous learning experiences. We found that after wasps had associated a certain location with food, they returned to this learned location even if food was no longer there, but placed nearby. In contrast, wasps with no previous experience landed on the food source without previously hovering or landing on empty dishes. When wasps had fed from the array only once, they took less time to discover the novel dish of meat than those that had had four previous feeding experiences (Fig. 4). Therefore, in this case it seems that the detection of new food sources is delayed by previous experience. Interestingly, just one feeding experience led wasps to ignore the food and search over an empty feeder. Since meat odor has great saliency for eliciting landing responses in this species (Moreyra et al., 2006), we were surprised that wasps did not directly respond to this cue (i.e., the unconditioned stimulus). We should clarify that the food was uncovered, so it produced attractive odor cues, evidenced by the fact that naïve foragers landed on it without hovering or landing on empty dishes.

We hypothesize that wasps could be giving a different weight to current and memorized information. Future experiments could elucidate possible mechanisms underlying this phenomenon. Wasps could be detecting but ignoring perceived olfactory information, or perception pathways could be switched off on the return to a previously learned productive site. Another possibility is that wasps have learnt a sequence of linked actions of which a late step is going to the location defined by the four cylinders.

The fact that when wasps had visited the feeder four consecutive times they took longer to find the novel food source than those that had visited it only once, is in accordance with the previously discussed experiment on food removal in which wasps that had experienced one feeding trial spent less time searching over the previously learned location than wasps that had experienced three

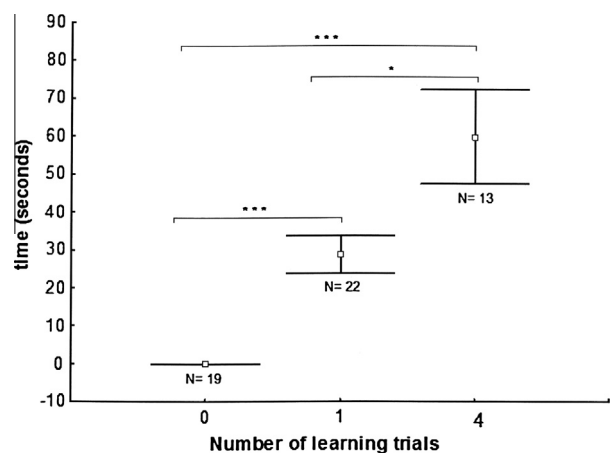


Fig. 4. Time lapse (in seconds) from wasp's arrival at the array to discovery of novel food source. From Lozada and D'Adamo (2011).

(Lozada and D'Adamo, 2006). Thus, in both experiments, whether food was removed or displaced, wasps' search on the empty feeder persisted longer when more feeding experiences had occurred. Moreover, these results also agree with another experiment described, in which wasps with four feeding experiences preferred and chose a learned feeder (over a non-learned one) in a dual choice experiment one hour after training (Moreyra et al., 2013). Conversely, wasps with only one previously rewarding experience did not show a preference, thus choosing the two baited feeders indistinctively. Overall, it seems that one experience has less impact on wasps' future decisions than more learning experiences.

When evaluating decision-making associated with foraging behavior, it might be important to take into account that a wasp's choice implies consideration of both current and remote experience. Going beyond *Vespula* species, earlier research on insects has described how individuals cope with food location change (e.g. Schmidt-Hempel, 1984; Wehner et al., 2004; Durier et al., 2004; Graham et al., 2007). For example, the desert ant *Cataglyphis bicolor* tends to stick to a previous foraging direction, i.e. it exhibits direction fidelity (Wehner et al., 2004). When an individual departs from the nest in search of prey it goes in a certain direction. If it finds food, its next trip will be in the same direction, but if on the subsequent trip no prey is found there, it searches around that location or further in that direction. On its next or next but one trip it will try a new direction which might be more successful. In other words, it takes time to relinquish one memory and search elsewhere. Ants progressively abandon a previously rewarded location in favor of a new site, first aiming at the former, or between both sites and then turn abruptly to the new one (Durier et al., 2004). Another study conducted in this species has shown that the persistence of re-searching in a place where food has been previously encountered is highly variable among individuals (Schmidt-Hempel, 1984). Similarly, when the wood ant, *Formica rufa*, was trained to a food source and after a number of trials the position of the food source was switched, ants persisted in searching at the position of the old site for some time before switching to the new one (Graham et al., 2007). The underlying functional principle of this response could be associated with the fact that remembering the location of a resource may be useful in case it is replenished in the future. Interestingly, it was demonstrated in honeybees that a colony can switch sites more rapidly than do individuals (e.g. Seeley, 1995).

4.3. Relocating behavior once food is displaced and contextual cues are modified

In order to further understand the fact that wasps disregard the presence of food, we analyzed how context modification could influence the detection of the displaced resource. As surrounding visual cues are important cues associated during food relocation (Lozada and D'Adamo, 2009), we hypothesized that the modification of the color of local cues would favor the discovery of the novel food site, thus diminishing searching time over the previously rewarded location. In this way, by displacing food and changing local visual cues after wasps had learned a certain task, we would be able to analyze whether wasps found a new food location more rapidly than when contextual cues remained unaltered (D'Adamo and Lozada, 2014).

As in the above experiments, wasps were trained to feed from the array described. After a certain number of rewarding experiences, food was displaced 60 cm from the original feeding location to the opposite point on the array (Fig. 1c). Thus, in the testing phase, wasps had to choose between three empty dishes and one dish with food. We analyzed two treatments: (1) a “matching group”, where the color of the four cylinders was maintained from training to testing conditions, i.e., wasps fed from an array of a

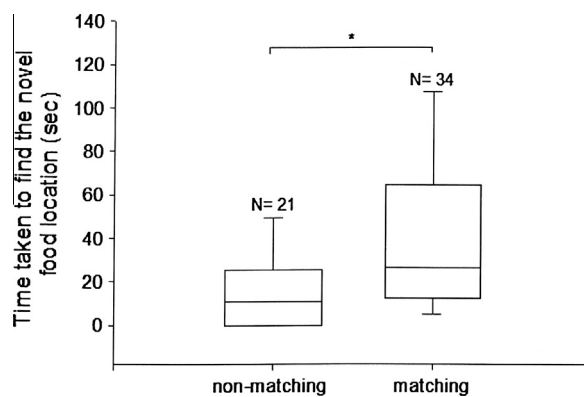


Fig. 5. Median, percentiles and error bars of time taken (in seconds) to find the novel food site for the matching and non-matching groups. From D'Adamo and Lozada (2014).

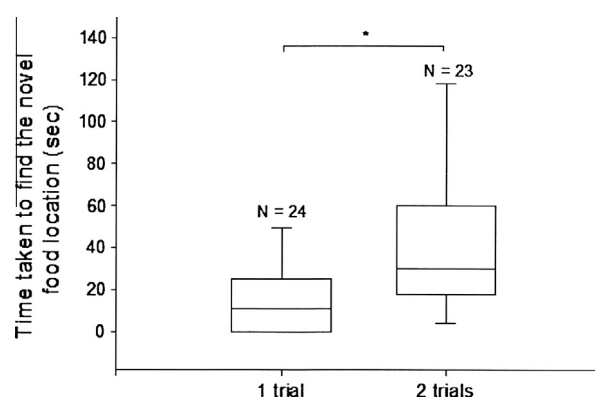


Fig. 6. Median, percentiles and error bars of time taken (in seconds) to find the novel food site for foragers trained with one or two feeding trials under non-matching conditions. From D'Adamo and Lozada (2014).

certain color (e.g. blue), and during testing food was displaced but the other cues remained unaltered (e.g. blue cylinders); (2) a “non-matching group”, where the color of the four cylinders was changed from training to testing. Consequently, if during training wasps fed from an array of a certain color (e.g. blue), during testing, food was displaced and the color of the cylinders changed (e.g. yellow). In non-matching conditions, we also evaluated the effect of experiencing either one or two feeding trials during training on the discovery of the novel food location at testing. Thus, during the two consecutive feeding visits, visual cues remained unaltered, after which the color of the array was changed before the third visit (i.e. for testing).

Results showed that color modification of the array facilitated the discovery of the new food location. Wasps spent less time searching over the empty feeder, detecting the novel food location more rapidly when the cylinder color had been changed in the testing phase (non-matching group) than if it remained the same (matching group) (Fig. 5). Wasps found the novel food site more quickly when the color of the array differed from the previously learned one. Hence, color modification of the array facilitated the discovery of the novel food location, releasing a previous association more rapidly than if local cues had been maintained. This improvement in food detection when color was modified could be understood in terms of visual guidance. If wasps use the colored cylinders as local cues, when these change, wasps' memories would match less with this novel situation, thus facilitating the discovery of the new food location. In *V. germanica*'s natural environments, the change of local cues, together with food, is a

common experience while relocating resources, as explained above. Moreover, when local cues were changed, i.e., non-matching conditions, wasps trained with two learning trials spent significantly more time searching over the previously learned location than those trained with only one (Fig. 6). These findings highlight the impact of associative learning on the observed relocating behavior. Earlier studies in honeybees have demonstrated that color and spatial layout of landmarks are learnt and taken into account when trying to find a previously rewarded site (e.g. Cartwright and Collett, 1983; Cheng et al., 1986; Fry and Wehner, 2005).

It is interesting to note that in our study, although the change in contextual cues favored the discovery of the new food location, wasps still visited the empty dish first, in spite of the fact that food was present nearby. This result strengthens the previous finding related to how past experience can affect the detection of novel food resources (Lozada and D'Adamo, 2011).

5. Conclusion

In summary, wasps exploiting a rich food source which suddenly disappears continue visiting that site for a certain period of time once food is removed (Lozada and D'Adamo, 2006). How long wasps continue searching in this location depends on the number of feeding visits wasps had previously experienced. As natural environments imply uncertainty, and particularly, in the case of *V. germanica* foragers, food may suddenly be removed, it would be beneficial for the species to have the plasticity to extinguish a previously established association that is no longer rewarding. It is significant that this memory extinction depends on the number of previous experiences with a certain resource. Possibly, the wasp's uncertainty about the location of a food site decreases with the number of visits to that site. The ability to differentially extinguish an association between a stimulus and a food resource could be one of the various behavioral mechanisms in *V. germanica* that contributes to the effective foraging behavior of this invasive species.

On the other hand, the fact that foragers return straight to the no longer rewarding site, even when food is present nearby, evidences the strength of past experience, since wasps respond as if food were present there (Lozada and D'Adamo, 2011). This attraction to a no longer rewarding site even occurs when local cues are modified (D'Adamo and Lozada, 2014). Thus, it seems that not only do certain stimuli elicit a response, but the whole experience that includes those stimuli is also associated with that response; this suggests how strong location cues are compared to cues from a novel food location. Our findings contribute to previous knowledge on how insect species change feeding sites when resources fail (e.g. Wehner et al., 2004; Schmidt-Hempel, 1984; Durier et al., 2004; Graham et al., 2007).

The fact that *V. germanica* is a social species adds further complexity to the analysis of its relocating behavior, as individual learning overlaps with social communication. For example, in earlier work with this species, we observed the attraction of conspecifics at a resource, a fact that indicates relocating behavior is affected by social mechanisms (D'Adamo et al., 2000, 2001, 2003, 2004; D'Adamo and Lozada, 2005). It is likely that individual cognition contributes to colony performance by the integration of local and global scales, i.e. individual and social levels. The study of these two levels of analysis in an integrated manner could shed new light on the cognitive plasticity of *V. germanica* and other social wasp behavior. Throughout our research we have prioritized working with free-flying wasps under natural conditions, a situation whose importance has been highlighted in the study of learning processes related to foraging behavior (Shettleworth, 2001).

Our studies carried out on this exotic, social species suggest that *V. germanica* could be a suitable and interesting model for analyzing cognitive plasticity related to environmental uncertainty.

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