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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