

The cues have it; nest-based, cue-mediated recruitment to carbohydrate resources in a swarm-founding social wasp

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Abstract This study explores whether or not foragers of the Neotropical swarm-founding wasp *Polybia occidentalis* use nest-based recruitment to direct colony mates to carbohydrate resources. Recruitment allows social insect colonies to rapidly exploit ephemeral resources, an ability especially advantageous to species such as *P. occidentalis*, which store nectar and prey in their nests. Although recruitment is often defined as being strictly signal mediated, it can also occur via cue-mediated information transfer. Previous studies indicated that *P. occidentalis* employs local enhancement, a type of cue-mediated recruitment in which the presence of conspecifics at a site attracts foragers. This recruitment is resource-based, and as such, is a blunt recruitment tool, which does not exclude non-colony mates. We therefore investigated whether *P. occidentalis* also employs a form of nest-based recruitment. A scented sucrose solution was applied directly to the nest. This mimicked a scented carbohydrate resource brought

back by employed foragers, but, as foragers were not allowed to return to the nest with the resource, there was no possibility for on-nest recruitment behavior. Foragers were offered two dishes—one containing the test scent and the other an alternate scent. Foragers chose the test scent more often, signifying that its presence in the nest induces naïve foragers to search for it off-nest. *P. occidentalis*, therefore, employs a form of nest-based recruitment to carbohydrate resources that is mediated by a cue, the presence of a scented resource in the nest.

Keywords *Polybia occidentalis* · Recruitment · Foraging behavior · Communication · Signals · Cues

Introduction

Recruitment is communication that brings individuals to a site where work is needed (Wilson 1971). In many groups of social insects, successful foragers recruit unemployed nest mates to forage at a profitable carbohydrate source by relaying information about the resource's location, quality, or scent (Seeley 1995). Carbohydrates are essential energy sources for both adults and brood, and the ability to quickly exploit profitable, sometimes transient, carbohydrate resources can be expected to increase the colony's foraging rate and consequent development rate (Raveret Richter and Tisch 1999). This may be especially true for groups that store nectar and thus use a quickly-garnered windfall over an extended period of time (Hrnčir et al. 2007).

By definition, recruitment involves communication, which some authors narrowly define as the transfer of information via signals (Otte 1974; Lloyd 1983; Dawkins 1995). Signals are actions or structures shaped by natural selection to convey information that benefits both the

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sender and receiver (Seeley 1989). Recruitment via signals is epitomized by the honey bee “waggle dance” by which a returning successful forager encodes the distance and direction of a resource to colony mates (Seeley 1995; von Frisch 1967).

Since food-recruitment signals are unknown in wasps, by this narrow definition of communication social wasps lack recruitment to carbohydrate resources. Nevertheless, wasps do have the ability to integrate colony-wide food-foraging efforts through the use of cues (Jeanne and Taylor 2009). Cues are information-bearing structures or actions not shaped by natural selection, have equal or greater importance than signals in colony integration (Seeley 1995, 1998), and as such, are vehicles of communication (Seeley 1995; Anderson and McShea 2001; Jeanne 2003). Even though they lack food-recruitment signals, social wasps are able to recruit to carbohydrate resources via cues. Naïve German yellowjacket (*Vespula germanica*) foragers use nest-based cues to locate carbohydrate resources (Overmyer and Jeanne 1998; Jandt and Jeanne 2005). They associate an incoming food reward with its scent, and are stimulated to leave the nest and search for a food source with the same scent (Overmyer and Jeanne 1998; Jandt and Jeanne 2005). Although unemployed foragers can locate a like-scented food source off-nest, there is no evidence that either distance or direction information is communicated inside the nest. In addition, some groups use resource-based cues in the form of local enhancement. Both *P. occidentalis* and *V. germanica* utilize local enhancement; naïve foragers are attracted to the presence of conspecifics at a site (Raveret Richter and Tisch 1999; Parrish and Fowler 1983; Jeanne and Taylor 2009; Hrnčir et al. 2007; D’Adamo and Lozada 2005).

The wasp *P. occidentalis* is a member of the large group of swarm-founding Polistinae. This group occurs only in the Old and New World tropics and subtropics, and has social traits unlike wasps of the temperate zones. As is the case for many polistine wasp species, *P. occidentalis* stores nectar in its nests (Hrnčir et al. 2007; Hunt et al. 1998; Kojima 1996; Sugden and McAllen 1994; Jeanne 1991). For these groups, the ability to recruit nest mates to carbohydrate resources would be beneficial because it would allow colonies to quickly gather ephemeral resources, store them, and use them as needed over time (Hrnčir et al. 2007). They will thus be buffered from severe feast or famine effects.

Recruitment to carbohydrate resources in *P. occidentalis* is still only partially understood. *P. occidentalis* foragers arrive in numbers at profitable resources and are able to return to them using learned color cues (Shafir 1996). They have been shown to employ resource-based cues: foragers are attracted to the presence of conspecifics at a site (Hrnčir et al. 2007). Although resource-based recruitment is effective in attracting nest mates to a resource, it is a blunt

tool in that it can also attract non-nest mates and even heterospecific foragers. Nest-based recruitment would be more efficient (Hrnčir et al. 2007), but it is not known whether or not *P. occidentalis* employs nest-based recruitment. If it does, it is likely to be cue-based because *P. occidentalis* does not appear to have food-recruitment signals (Jeanne and Taylor 2009).

We investigated whether *P. occidentalis* has nest-based recruitment by testing whether foragers are induced to search for the scent of a profitable resource in the field after encountering it at the nest. Foragers chose a dish scented with the training scent more frequently than one scented with an alternate scent. We conclude that *P. occidentalis* uses a form of nest-based, cue-mediated recruitment to carbohydrate sources. As a resource is brought into the nest, exposure to it induces naïve foragers to learn to associate a scent with a rich reward and search for the scent off-nest.

Methods

The investigation was conducted at La Fundación Hagnauer Centro de Rescate Las Pumas, near Cañas, Guanacaste, Costa Rica (10°25′N, 85°07′W) during June–July 2008 and July 2009. *P. occidentalis* colonies are abundant at this site and are readily found in shrubs and small trees on the edges of the disturbed land.

Twenty-five *P. occidentalis* colonies were used for this study. Each colony was used for one experimental trial. After sundown, suitable nests were moved from their natural locations to sites where they could be easily accessed. Nighttime transport ensured that all individuals were present in the nest, as the wasps do not fly in the dark. The supporting twig was clipped about 5 cm from each side of the nest. The nest was then carried by hand to its new location and attached to a new branch via binder clips, zip ties, or wire. A thin, 2.5-cm wide band of Tanglefoot® was applied to the new supporting branch between the tree trunk and the nest to prevent predation of the brood by ants.

Training began at least 12 h and up to 7 days after the colony was transplanted to its new site and was initiated between 7:30 and 10:30 am. Foragers from each colony were trained to forage at an unscented 2.0 M sucrose solution in a glass feeding dish (6.5 cm diameter, 1.75 cm deep) on a Plexiglas table (43 × 30 cm) attached to a tripod. Training began with the tripod placed such that the dish was in contact with the front of the nest just below the entrance. At this point, many wasps reached from the nest into the dish to imbibe the sugar solution. After about 5 min of direct contact, the dish was moved down and away from the nest in increments of 1–2 cm approximately every 5 min, as long as sufficient numbers of individuals were arriving. The critical point in the training process came

when the wasps could no longer reach the dish from the nest, and often it had to be restarted several times before sufficient numbers began flying to the dish. Once this threshold was crossed, the table and dish were moved away from the nest in larger steps until the dish was 5 m away from the nest entrance. After this distance was reached, training criteria were fulfilled when within a 2-min period there were at least ten landings with feedings at the dish.

After the initial training, the experimental portion of the protocol was initiated. The sucrose-filled dish was removed from the table for a minimum of 10 min, or until no foragers were arriving at the table. At this point, two dishes each containing water (no sucrose) and a scent solution (2% v/v), one with the training scent and the other with the alternate scent, were placed 11 cm apart on the table perpendicular to the direction to the nest. Extracts of raspberry, pure almond, and anise (McCormick & Co, Inc., Hunt Valley, MD, USA) were used in 2008; organic extracts of green apple and blueberry (Nature's Flavors, Orange, CA, USA) were used in 2009. Each colony was randomly assigned a training and an alternate scent. That resulted in six combinations of training and alternate scents in 2008, because three scents were used, and two combinations in 2009, because two scents were used. Observer #1 collected all wasps arriving at either dish for 1 h, noting the content and position of the chosen dish and the arrival time of the forager. An arrival was scored when the wasp landed on the rim of the dish. The positions of the dishes were randomly assigned after each arriving forager was collected. Collected foragers were placed in uniquely numbered vials and stored on ice until the end of the experiment. This insured that no forager returned to the nest, thus eliminating possible recruitment behavior.

At the same time as the two dishes were being presented in the field, another observer began adding a 2.0 M sucrose solution with the 2% training scent to the outside and inside of the nest with a plastic pipette. For the next hour, 2 mL of the training-scented sucrose solution were added at 5-min intervals to the nest by dripping approximately equal amounts outside on the nest envelope and just inside the nest entrance.

Each captured forager was removed from the ice at the end of the trial and marked with an individual color code to insure that the foragers arriving at the feeder were members of the focal colony. Each was held in forceps for a few seconds at the entrance and then placed just inside the entrance. The reaction of the other colony members was noted as to whether the forager was accepted or rejected. If there was ambiguity in the reaction of the colony members, a 5-min scan the following day was used to confirm residence. Individual foragers that elicited rejection behavior and that were not present on the nest the following day were assumed to be from another colony and were not used in the analysis.

Due to a previously unknown preference for anise, which confounded all trials using anise, we divided our data into two groups: (a) all trials in which anise was not used and (b) all trials in which anise was one of the scents used. We performed a “primary” analysis on group (a) and a “secondary” analysis on group (b). The primary analysis focused on quantifying the effect of training, whereas the secondary assessed innate scent preference.

Each analysis was conducted using a two-factor ANOVA model; this analysis was chosen to account for scent pair (and year) as a blocking factor. For the primary analysis, the response variable was the proportion of foragers arriving at a particular scent during the 1-h test period. The response was the proportion arriving at the scent to which the foragers were trained. In the primary analysis, the particular scent chosen for the response was raspberry (vs. almond) and blueberry (vs. apple).

For the primary analysis, the predictor factors were (1) an indicator of whether or not the foragers were trained to the scent of the dish of the response, (2) a grouping variable (described below), and (3) the interaction of these two factors. For the secondary analysis, the predictor variables were (1) an indicator of “particular scent” (using the designations in the previous paragraph), (2) a grouping variable, and (3) the interaction.

For group (a), those trials without anise, the grouping variable was year. Since different pairs of scents were used in 2008 and 2009, the grouping variable includes both year and scent pair. For group (b), trials with anise, all trials were conducted in 2008. Here, the grouping variable was scent pair: anise vs. almond and anise vs. raspberry.

There was considerable variability in the total number of arrivals at the table with the scents due in part to different colony sizes; we therefore used a weighted analysis where the weights were proportional to the absolute counts of arrivals. Since our response variable in all cases was a proportion, we used standard practice by making the arcsin (square root (proportion)) transformation of the proportion (Lehner 1996).

Results

The primary analysis was performed on the data from the 14 colonies without anise. A larger proportion of individuals arrived at the test dish containing the training scent than the dish with the alternate scent (Fig. 1a—proportion arriving at training scent=0.71—test for equality: $F=11.47$; $n=14$; $df=1$; $P=0.0069$). An approximate standard error for this estimate is 0.07. Neither the year ($F=0.32$, $P=0.58$) nor the interaction between year and training scent ($F=$

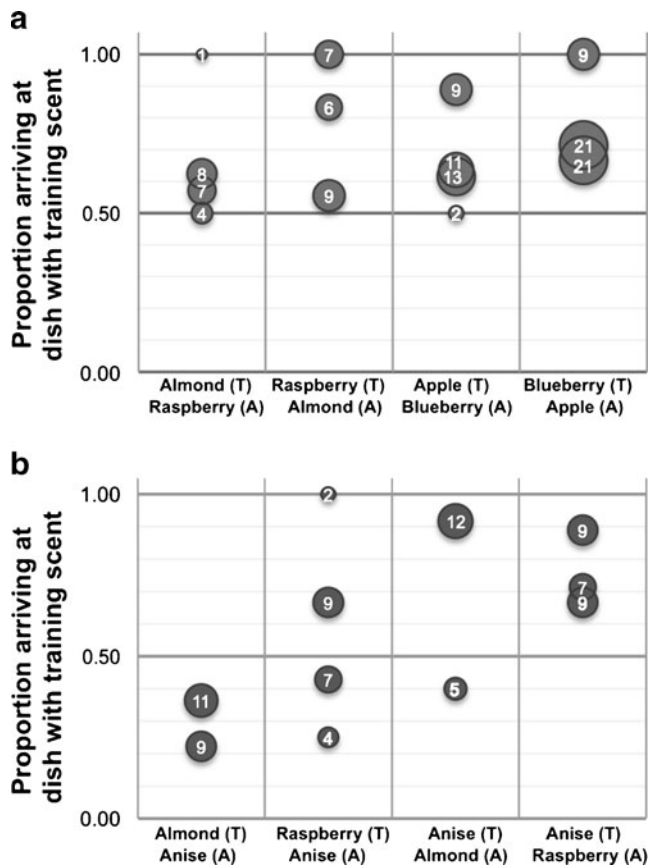


Fig. 1 The proportion of *Polybia occidentalis* foragers arriving at the dish containing water and the training scent. Each circle represents one colony. The area of the circle is proportional to number of foragers arriving from the colony, also indicated within the circle. (T) denotes the training scent and (A) denotes the alternate scent for each set of colonies. **a** $N=14$, nests for which anise was neither the test nor alternate scent. **b** $N=11$, nests for which anise was either the test or alternate scent

0.00, $P=0.95$) had significant effects on the proportion of foragers arriving at the dishes.

The secondary analysis was used with the 11 colonies that included anise as the training or alternate scent and could not be used to assess a training effect. We discovered that in most trials in which anise scent was used, a higher proportion of individuals arrived at the dish scented with anise (Fig. 1b—proportion arriving at anise=0.67—test for equality: $F=5.78$; $n=11$; $df=1,7$; $P=0.0471$), regardless if it was the training scent or the alternate scent. An approximate standard error for this estimate is 0.08. To rule out the presence of other such preferences for the remaining scents, we carried out an analysis similar to the secondary analysis for the 14 trials with combinations of raspberry vs. almond and apple vs. blueberry. There was no significant difference in the preference for either raspberry or almond when paired ($n=7$; $df=1,5$; $F=1.33$; $P=0.3012$) or for blueberry or apple when paired ($n=7$; $df=1,5$; $F=0.28$; $P=0.6209$; see Fig. 1a). Because we found such a strong preference for anise in our 2008 trials, we did not use it in 2009.

A total of 212 foragers were used in the analyses. An additional 92 foragers were observed, but not used in analyses because their residence in the focal colonies could not be confirmed. To assess if local enhancement influenced dish choice, the time between the arrival of one forager and the next was calculated for 188 foragers. The remaining 24 foragers arriving at the dishes were not used in this calculation because they were either the first forager from a colony to arrive at a dish ($n=20$) or else the arrival time was inadvertently not recorded ($n=4$). The average time between arrivals was 240 s, with a range of 0–1,448 s and a median of 131. Of the 188 foragers, only five arrived less than 5 s after the preceding forager, and thus may have been influenced by the presence of forager at a dish, as it took about 5 s for a forager to circle the dish, land, and be captured. Of these foragers, two arrived at the alternate scent, and three at the trained scent. One of the three arriving at the trained scent did so even though the wasp present at the time or arrival had chosen the alternate scent. The other four foragers arrived at the same dish as the previous forager. While a formal test for local enhancement could not be identified based upon previous literature on the subject, local enhancement had at most a very small effect on dish choice during this investigation.

Discussion

Our results demonstrate that the presence of a scented resource at the nest is sufficient to cause foragers to search for that scent in the field. Nectar foragers strongly prefer the scent associated with a profitable carbohydrate resource they encountered at the nest rather than a novel scent. By catching all foragers arriving at the dish, we removed the possibility of an employed forager returning to the nest and performing recruitment behavior, thus indicating cue-mediated recruitment. We conclude that a probable mechanism for this is that as incoming foragers arrive at the nest with a profitable resource, foragers in the nest are exposed to it, learn to associate the rich reward with its scent, and subsequently search for that scent in the field. Naïve foragers not only receive information about available resources without the use of signals, but they are able to process the information and use it to locate them while off-nest. Although the potential for local enhancement existed in our experiments, its effects at best were weak, with only five of 212 foragers potentially arriving while another was at one of the dishes. However, our findings do not rule out other possible forager-mediated recruitment behavior, for example that flying conspecifics could view the choice of the focal wasp from farther away or could follow a nestmate in flight to the dish.

An unexpected finding of this study was that *P. occidentalis* is innately attracted to the scent of anise.

Although an attraction to anise has also been observed in the honey bee (Seeley 1995), it has not been documented in other social insects. Anise is not known to occur naturally in Costa Rica (Leela and Vipin 2008) so it is unlikely that the *P. occidentalis* foragers used in this study were previously exposed to the scent; thus, their preference appears to be innate rather than learned. The reasons for this preference remain unclear, and surprising, since anise is an effective insecticide against mosquitos (Leela and Vipin 2008). Anise has antibacterial and antifungal properties (Leela and Vipin 2008), which could be beneficial to a colony with stored nectar. Also, its insecticidal properties may not be effective on wasps.

This investigation was performed in the field; therefore, foragers were not constrained to one of two choices, but were actually exposed to a large variety of carbohydrate resources in the environment. Since foragers were free to travel, it is likely that some were visiting other carbohydrate resources and bringing them back to the nest. New recruits arrived at the test-scented dish even though it was possible that competing resources were being brought into the nest. The fact that the experimental dishes contained scented water and not scented sucrose solutions rules out the possibility that foragers arriving at the dishes were randomly searching for new carbohydrate resources. When combined, these two factors demonstrate that foragers arrived at the training-scented dishes because they actively searched in the environment for the scent after encountering it on the nest.

This is the first investigation exploring nest-based recruitment in the swarm-founding Polistinae. Members of this group initiate new nests in groups. Many tasks are carried out by groups of individuals and there is greater worker specialization in comparison to independent-founding wasps. The greater worker specialization requires a correspondingly greater degree of integration among individuals. Without signals that can be used, colonies need to rely upon cues for task integration. The type of cue-mediated, nest-based recruitment we describe for *P. occidentalis* in this investigation is also utilized by a yellowjacket (*V. germanica*) and a bumble bee (*Bombus impatiens*; Overmyer and Jeanne 1998; Dornhaus and Chittka 2004; Jandt and Jeanne 2005; Renner and Nieh 2008; Molet et al. 2009). It increases colony-wide foraging efficiency because it narrows the search for naïve foragers who do not have to search blindly for resources; thus, colonies can quickly exploit profitable, transient resources. When coupled with the ability to store nectar for future use, as is the case for *B. impatiens* and *P. occidentalis*, recruitment is beneficial as it allows a colony to smooth out highs and lows in its food supply (Hrncir 2007).

Although we have shown that the presence of a scented resource on the nest is sufficient to induce foragers to search for like-scented resources off-nest, our results cannot

rule out signal-mediated recruitment for *P. occidentalis*. *P. occidentalis* uses pheromone-mediated recruitment while house hunting. Scouts scent mark landmarks between the awaiting swarm and the new nest site they have selected. When the swarm emigrates to the new site, the naïve nest mates follow the pheromone trail (Sonntag and Jeanne 2009; Jeanne 1991). Stingless bees use a similar mechanism to recruit to food sources, employing tarsal or mandibular gland secretions, or anal droplets to mark the route (Nieh 2004). Although our experiment was not designed explicitly to test whether *P. occidentalis* uses this mechanism in food recruitment, it is not likely that it does. Many hours of observation of foragers arriving, feeding, and departing from our food dishes revealed no evidence of scent marking. With one exception, no other social wasp is known to use food-recruitment signals. The exception is *Vespa mandarinia*, which specializes on attacking honey bee nests for their brood. Single *V. mandarinia* foragers cannot breach the defenses of a honey bee colony. Instead, a forager that has discovered a honey bee hive recruits additional nest mates by scent marking the target nest. Once sufficient numbers of hornets have been recruited, a mass attack is mounted and the bee colony's defenses are overcome (Ono et al. 1995).

In contrast, *P. occidentalis* and most other social wasps typically forage on small, scattered nectar sources and hunt for individual insects, making it possible for a single forager to exploit the resource. Recruiting nest mates to such resources is therefore not likely to enhance the colony's foraging efficiency. In fact, selection may act against the evolution of scent-marking a resource, since it may attract non-nest mate conspecifics and increase inter-colony competition (Jeanne and Taylor 2009). Although some social wasp species forage on non-ephemeral resources, such as carrion or fruit, the scents of these resources alone may be adequate to attract foraging individuals, reducing the adaptive value of pheromonal marking (Jeanne and Taylor 2009).

Nest-based cues other than the presence of a scented resource may also play a role in integrating foragers' efforts in *P. occidentalis*, even in the absence of food recruitment signals. Molet et al. (2009) discovered that when anise scent was experimentally added to the honey pots in bumble bee (*Bombus terrestris*) nests without allowing employed foragers to bring resources to the nest, seventy-five percent of naïve foragers were incited to land on anise-scented flowers; but when employed foragers were allowed to bring anise-scented sucrose to the nest, ninety-three percent of the unemployed foragers landed on anise-scented flowers. They found no indication of recruitment signals, but suggested that unknown cues, in addition to the presence of a scented reward, are being conveyed by successful foragers. Both *B. terrestris* and *P. occidentalis* store nectar within their nests and, in the absence of other

cues or signals being brought in by active foragers, naïve foragers may simply search for the scent of stored nectar when foraging for carbohydrates. This type of recruitment may not be as strong as that of foragers arriving at the nest with a resource, because it does not necessarily represent current availability of a resource, only that the resource was collected sometime in the past. A forager choosing to search for the scent may or may not be successful. In both the Molet et al. (2009) and present studies, this condition was replicated when active foragers were not allowed to return to the nest. Additional cues may be present as active foragers bring in resources, reinforcing those already on the nest and inducing larger numbers of naïve foragers to search for the scent off-nest.

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