

## Research Article

# Recruitment in Swarm-Founding Wasps: *Polybia occidentalis* Does not Actively Scent-Mark Carbohydrate Food Sources

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Scent marking food resources is expected to enhance foraging efficiency reducing search time. Many social bees exhibit this behavior, but scent-marking is absent in social wasps, except for *Vespa mandarinia*. We tested for scent marking in the swarm-founding wasp, *Polybia occidentalis*. This wasp has moderately large colonies and utilizes resources that are concentrated in time and space, making scent marking profitable. Also, this wasp uses chemical markings to lead nestmates to a new nest site during swarm emigration, making it possible that it could use the same behavior to recruit nestmates to a food source. Foragers from 11 colonies were given a choice between a previously visited feeder and an unvisited one, both containing a rich, unscented sucrose solution. There was no difference in the number of visits to the two treatments. However, some individuals chose the feeder on one side more often. We conclude that foragers of this species of wasp do not use odor marks left behind by nestmates to find food, but they do exhibit the tendency, when returning to a food source that has not been depleted, to choose a resource based on its relative position, presumably by using visual cues.

## 1. Introduction

Recruitment is communication that brings nestmates to an area where work is required, and in social insects it enhances the efficiency of colony resource acquisition by increasing the number of foragers exploiting a food source [1]. A number of recruitment mechanisms have evolved, including the well-known waggle dance of honey bees [2] and the trail pheromones of ants [3] and stingless bees [4, 5]. Both the occurrence and sophistication of recruitment mechanisms tend to correlate positively with colony size [6].

In contrast to the bees and ants, no recruitment signals that encode distance or direction have been found in the social wasps [7, 8], but foragers in some species utilize social cues. Olfactory cues from the food brought back by successful foragers can stimulate foraging and bias a colony's collection efforts to resources with the same scent in the field. This behavior has been demonstrated in yellowjackets [9–12]

and the swarm-founding wasp *Polybia occidentalis* [13, 14]. In addition to this nest-based information, wasps also utilize social, field-based information; many species are attracted to food sources where others are feeding (local enhancement) [8, 13, 15, 16].

The majority of social wasp colonies have populations in the  $10^2$ – $10^3$  range, but some species reach the  $10^4$ – $10^5$  range [17], and individuals number as many as 7 million in *Agelaia vicina* colonies [18], far beyond the colony sizes of honey bees, stingless bees, and many ant species. It is puzzling that wasps have not evolved food recruitment behavior despite achieving colony sizes that exceed those of other recruiting insects. The reason for the unequal distribution of recruitment mechanisms across the social Hymenoptera has not been explained. However, the range of recruitment mechanisms also has not been fully explored, especially for the social wasps. Thus, there remains the possibility that food recruitment exists in species that have

not been thoroughly studied, or for which the full gamut of recruitment mechanisms has not been examined.

Chemical markings (either repellent or attractive) left at food sources by previous visitors can also play a role in the rejection or acceptance of a resource. These marks are beneficial because attractive marks can increase the rate of exploitation of a resource, while repellent marks can prevent useless probing of depleted sources. These markings can be categorized as either signals, which are actively left at food sources to convey information, or cues, which provide information but are left passively as a byproduct of sender behavior. Evidence for both attractive and repellent marks has been adduced for some bumble bees [19, 20] and stingless bees [21, 22]. Recent evidence suggests that these marks are cues, footprints of cuticular hydrocarbons left behind passively by foragers walking on food sources [5, 23–26]. The rejection or acceptance of a resource is a context-dependent, learned association between the marking and the presence or absence of a reward. Thus, when a bee encounters a scent mark on a resource that is paired with a reward, she positively associates the scent mark with the presence of a reward and visits scent-marked flowers more frequently. The opposite occurs when a flower has previously been visited and depleted.

Repellent and attractive marks are also left on food by foraging honey bees [27–29]. Studies comparable to those performed on bumble bees and stingless bees have not been carried out to determine whether these marks are cues or signals. However, foraging honey bees actively release Nasonov gland pheromone at some resources, which is attractive to other foraging bees [29, 30]. This pheromone is most often released at water sources, unscented artificial feeders, and highly profitable resources [30, 31]. Taken together, the foraging contexts under which Nasonov pheromone is released suggest that its function is to pinpoint the location of profitable, unscented resources to potential recruits.

Previous work on *Vespula germanica* wasps suggested that feeders are attractive to foragers after being visited heavily over a period of days or walked over extensively [32, 33]. However, a better-controlled study on this species found that feeders visited 50 or 100 times are no more attractive than unvisited ones [34]. The only wasp that has been found to actively apply scent marks to food sources is the hornet *Vespa mandarinia*, which applies secretions from the sixth sternal (van der Vecht's) gland that are attractive to nestmates [35]. This behavior occurs during autumn raids on honey bee and wasp colonies, when these hornets switch to group hunting and attack these colonies en masse [35, 36].

In contrast to the vespine wasps, food site marking has not been studied in the swarm-founding Polistinae. Swarm-founding wasps may be more likely to exhibit scent-marking behavior than independent-founding species. Many species of the swarm-founding Polistinae, including *Polybia occidentalis*, deposit attractive scent marks that guide nestmates to a new nest site during colony emigration [37, 38]. During emigration, scout wasps drag their gasters on leaves to deposit an attractive pheromone from a gland at the base of the fifth gastral sternite [37, 38]. This pheromone could easily be co-opted for use in a foraging context.

The benefits of food-site marking are expected to be greater for species with large colony size. Larger colonies have more foragers and therefore are more likely to find scent-marked resources quickly. *Polybia occidentalis*, like many wasps, exploits a variety of carbohydrate resources that are often concentrated in time and space, including fruit, human refuse, honeydew, and extrafloral nectaries ([39], B. Taylor pers. obs.). *Polybia occidentalis* also gathers nectar from flowers of at least 15 families of plants, and the families of plants preferred by wasps tend to be those that produce large numbers of flowers [40]. Furthermore, *P. occidentalis* forms moderately large colonies, numbering up to several thousand individuals [38]. Thus, in addition to the presence of scent-marking glands used during swarm emigration, the large colony sizes and the types of resources exploited by *P. occidentalis* suggest this species may benefit from food-site marking.

Here, we test the hypothesis that the swarm-founding wasp *Polybia occidentalis* marks carbohydrate food sites using a chemical attractant signal. We also test whether foragers use a visual cue—relative position on a feeder stand—to relocate food upon return.

## 2. Methods

The study was performed at Centro de Rescate Las Pumas, approximately 5 km west of Cañas, Guanacaste, Costa Rica (10°25'N, 85°7'W). Experiments were conducted between 23 June and 9 July 2008. This is the wet season in this area of Costa Rica, and colonies were in a stage of active growth.

To facilitate training and following of foragers, nests were moved into a field with scattered trees, where they were attached to branches at eye level using either nylon cable ties or wire. Tanglefoot (The Tanglefoot Co., Grand Rapids, MI, USA) was applied to the branches to prevent predation by ants. All nests were moved at night to minimize the number of workers lost. Experimental trials were conducted between the hours of 08:00 and 14:00. Rain often occurred in the late afternoon, so conducting trials during this time was specifically avoided.

**2.1. Forager Marking and Training.** A pool of 50 individually marked workers was established for each nest at least one day prior to testing to differentiate individuals and members of different nests. A sucrose-filled feeding dish atop a tripod stand was placed directly against the nest. As workers stepped onto it from the nest to feed, they were caught, placed in vials on ice until immobile, and marked on the thorax using paint pens (Decocolor, Uchida of America, Corp. Torrance, CA, USA). The markings encoded a unique number for both nest and individual. After marking, individuals were returned to the tripod stand, where they warmed up before flying back to the nest.

Before each experimental trial, foragers were trained to feed from a round, 4.5 cm-diameter tin dish that was covered by a lid. The side of each dish had an opening through which a glass microscope slide projected, providing a landing platform down which foragers could walk to access the liquid

(see [34] for details). The feeder was filled with a 2 M sucrose solution and placed against the nest in the same fashion as during the marking process. Foragers crawled down from the nest and fed from the dish. After 15–20 workers started feeding from the dish, we began moving it upwind from the nest in increments of approximately 1 m until it was 10 m from the nest. During this time, the number of foragers coming to the feeder often dropped considerably. If fewer than two marked foragers arrived, the feeder was again moved near the nest until at least two marked foragers made repeated visits. Because there is some evidence that scented solutions are less likely to be marked [30], we did not scent the solution with any extracts.

**2.2. Experimental Trials.** After at least two marked foragers were trained to the feeder and it was 10 m from the nest, the feeder was replaced with a clean one in the center of the tripod stand. If a resource is actively marked with a chemical signal, then few visits should be required to make a feeder more attractive. Therefore, the trained foragers were allowed to visit the new feeder (hereafter referred to as the test feeder) a total of five times (i.e., a total of five visits distributed among all the trained foragers). This process occurred very quickly, usually taking less than 2 minutes. Immediately thereafter, the test feeder was moved to one side of the stand, and an identical but unvisited feeder (hereafter referred to as the control feeder) was placed on the opposite side of the stand, 9.5 cm from the test feeder. The stand was rotated so that the line connecting the two dishes was perpendicular to wind direction.

A trial consisted of 40 choices made by a colony (distributed among 2–5 foragers, each making 1–25 choices). All choices made by arriving, marked foragers were recorded for use in the analysis until 40 visits were reached. All unmarked foragers were captured and held until the conclusion of the trial. To avoid the biasing effects of local enhancement, foragers that arrived while another forager was feeding were not counted [13, 15]. The position of the test feeder on the tray (either right or left as viewed from downwind) was determined by a coin flip and switched between visits. If the control feeder was visited, its slide was replaced, and if other portions of the control feeder were walked on, they were also replaced. An observer sat crosswind, approximately 1 m from the feeders, to minimize interference with any scent plumes left behind by foragers.

**2.3. Statistical Analysis.** The food-site-marking hypothesis predicts that the test feeder will receive more visits than the control feeder. If no scent marking has occurred, then both feeders should be visited equally. Therefore, we let  $Y_i$  = proportion of landings on the test feeder for each colony and conducted a  $t$ -test with  $H_0: \mu = 0.5$ . A 95% confidence interval for the mean was also constructed. We conducted further tests to explore the roles of previous visits and positional fidelity on feeder choice. For each individual making at least eight choices during a trial, we conducted two Fisher’s exact tests. The first tested whether there was any preference for the previously visited test feeder, and the

TABLE 1: The proportion of landings on the test feeder (40 visits per colony) for the eleven colonies tested.

Colony no.	Proportion of landings on test feeder
08-003	0.475
08-012	0.525
08-024	0.550
08-027	0.550
08-030	0.475
08-045	0.625
08-057	0.500
08-058	0.550
08-059	0.550
08-072	0.475
08-073	0.500
Mean	0.525

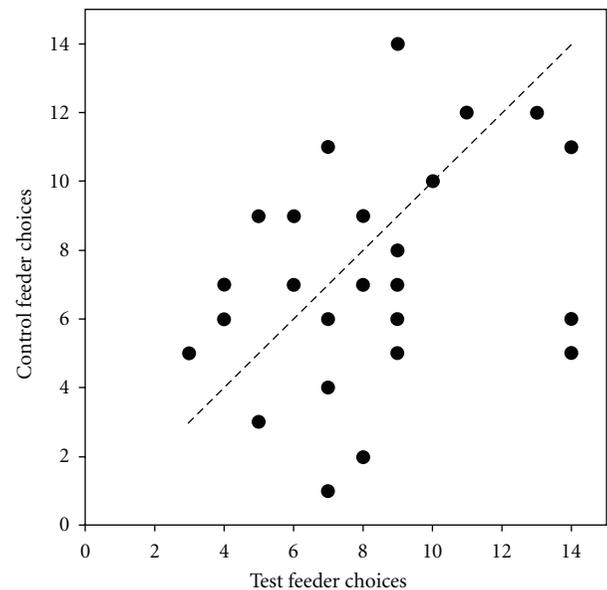


FIGURE 1: The number of choices for the test feeder and control feeder made by individuals that made at least eight choices during a trial. Each symbol represents an individual. The dotted line represents choices of 1 : 1.

second tested whether foragers showed any positional bias (i.e., chose the feeder associated with the left or right side more often during their visits).

### 3. Results

For the population of foragers from the 11 nests tested, the mean proportion of visits to the test feeder was 0.525, with a confidence interval that included 0.5 (95% CI: 0.494–0.556) (Table 1). A  $t$ -test revealed that colonies did not choose the test feeder any more or less often than expected by chance ( $t = 1.80$ ,  $df = 10$ ,  $P = .102$ ). There were 25 foragers that made at least eight choices during the trials. Of these, none chose the test feeder significantly more often (Figure 1), but

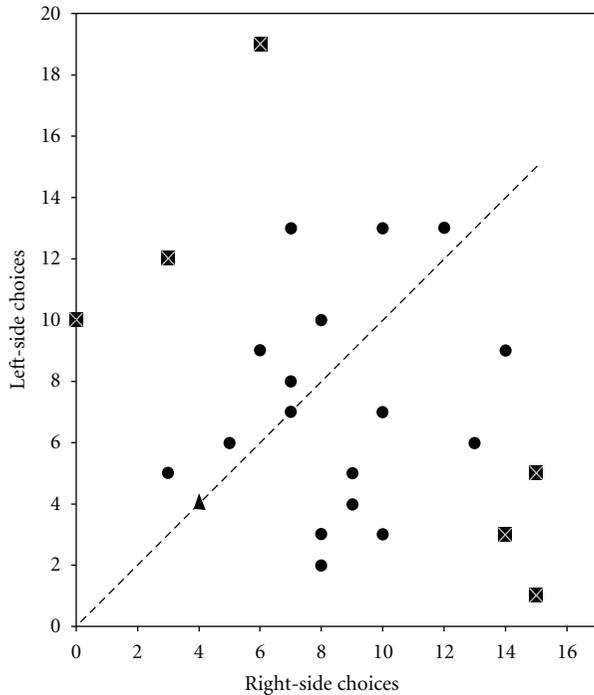


FIGURE 2: The number of choices for the feeder on the left or right side made by individuals that made at least eight choices during a trial. Each symbol represents an individual. The dotted line represents choices of 1 : 1. The triangle represents two overlapping individuals that chose the right and left equally (4 times each); the squares containing an X represent individuals that showed a significant bias for one side ( $P < .05$ ).

six of the 25 showed a side preference (Figure 2). This is sufficient to reject the null hypothesis that no individuals had a side preference ( $P = .0012$ ). Foragers approached the feeders from downwind but did not fly in a zig-zag pattern as they approached and did not hover before entering a feeder. Instead, foragers flew directly to a feeder before landing and entering. During the trials, no dragging of the gaster on the feeders was seen, except when foragers exited the feeders. However, because there was no evidence that exiting foragers actively wiped the gaster on any portion of the feeder as described for swarm emigration [37, 38], the dragging was likely due to the mass of the imbibed liquid weighing the gaster down. The average time between visits to the test feeder by successive foragers during testing was 1 minute 20 seconds (maximum time: 6 minutes 25 seconds). This figure is slightly inflated because the choices of foragers were scored only if no other forager was present.

#### 4. Discussion

We found no evidence that attractive scent marks were actively applied to the food dishes, and thus we conclude that scent marking does not occur in the context of carbohydrate foraging in *P. occidentalis*. In addition, foragers were observed taking direct lines of flight from the nest to the feeders, and no hovering near the feeders occurred before

landing. This is in contrast to the behavior of wasps using olfactory cues to locate food [10, 12]. In these studies, wasps approached the feeders using zig-zag patterns and hovered before landing at the resource [10, 12]. It is unlikely that scent markings applied to the feeders would have deteriorated during the trials. Chemical signals evolved in this context should be long-lasting. Markings laid down by bumble bees and stingless bees can last for more than an hour [41–43]. Here, the maximum time between visits to the test feeder was only 6 minutes 25 seconds.

It is also unlikely that the feeders did not exceed a threshold of profitability required to elicit scent marking. The concentrations of dissolved sugar in the carbohydrate resources often exploited by wasps (floral and extrafloral nectar, fruit, and honeydew) range from approximately 0.5 M to 2.5 M [44–47]. Thus, it is likely that a 2 M solution located a mere 10 m from the nest would be perceived as highly profitable to the wasps and therefore likely to be marked if the behavior indeed did exist. However, if wasps only switch to marking at greater distances, similar to honey bees switching to waggle dances only when food sources are >100 m from the nest [2], our test would not have detected its presence.

Because we tested only for responses to signal-based, active scent marks, we cannot entirely rule out the possibility of passive footprint cues, such as those utilized by stingless bees and bumble bees, that might accumulate after many repeated visits [5, 23–26]. The number of visits required to make a feeder more attractive varies among species. A foraging honey bee need land only briefly on a feeder to leave an attractive scent mark [30]. However, in some stingless bees, 20–40 visits are required to make a visited feeder more attractive than an unvisited one [23, 43]. *Vespula germanica* foragers did not choose a feeder visited 50 or 100 times any more often than an unvisited one [34]. On the other hand, these wasps were shown to follow a trail in the nest entrance tunnel after it had been walked over by more than 200 individuals [48]. However, if such a large number of visits is required to mark a food site with a footprint cue, it would be of little value to foragers.

Because we used a carbohydrate food source, our experiment cannot rule out the possibility that scent marks are deposited on protein resources. Several swarm-founding wasps scavenge on carrion [49–51], especially those in the genera *Agelaia* and *Angiopolybia*. On the other hand, the scent of rotting meat may render active marking of a resource superfluous [8]. Indeed, recruitment was not found in *Agelaia multipicta* or *A. hamiltoni*, two species known to exhibit necrophagy [7]. In the tropics, these wasps must also contend with stingless bees and ants that feed on carrion [3, 4, 52]. Wasps may not be able to compete with these insects, especially those that can amass large numbers of foragers at these highly profitable sources using recruitment.

Foragers also did not choose the test feeder any less often than the control, suggesting that *P. occidentalis* does not leave behind repellent scent marks, either. There remains the possibility, however, that repellent scent marks may be left behind if a feeder is depleted. When repellent behavior has been found in bees, the experiments utilized real flowers or

artificial flowers that were depleted after feeding. In contrast, our feeders remained filled.

Although we found no evidence for the role of scent marks in forager resource choice, we did find an effect of feeder position for some individuals. Presumably, these wasps learned the relative position of the feeder on the tripod stand using local landmarks and subsequently returned to that same feeder more often. Because scent was weak, visual cues may have been the only reliable cues available. Indeed, visual cues are known to be used by wasps upon return if a food source has not been depleted [53–55]. However, not all individuals displayed a side preference. It is possible that these individuals encountered other foragers at the feeders during a trip, and this interaction caused them to choose a different feeder on subsequent trips. Alternatively, the strength of positional fidelity may have varied among individuals. A study addressing the phenomenon directly is needed to resolve the issue.

The apparent absence of scent marking in wasps and its presence in some bees may be related to differences in food sources utilized. Bees derive much of their carbohydrate sustenance from flowers, while wasps get theirs from a variety of sources including fruit, extrafloral nectaries, honeydew, and human refuse [39]. Repellent scent marks left by bees on depleted flowers allow subsequent visitors to discriminate between visited and unvisited flowers (i.e., each flower represents a point source). In contrast, a repellent marking on a non-point source, such as honeydew, would not be as beneficial for a foraging wasp. Yet, like most bees, wasps feed on flowers ([39, 40], B. Taylor, pers. obs.). However, because wasps are restricted by their short glossas to flowers with short corollas or cup-like morphologies, flowers likely make up a smaller portion of their diet compared to bees, and therefore, selective pressure favoring scent marking of these sources may be weak. The application of attractive scent marks to clustered food sources, such as concentrations of honeydew-producing Hemiptera or human refuse, could be beneficial for wasps. However, fruit and human refuse may be similar to rotting carrion in that they could be easily detected by means of their scents alone. Also, the overall distribution of these resources in the environment near *P. occidentalis* nests, though unknown in this study, may select for an opportunistic foraging strategy. Johnson [56] reasoned that environments with an abundance of small resources and few large, transient resources would select for opportunism, rather than recruitment and defense of resources. An opportunistic strategy may also allow foragers to find resources more quickly [56].

The seemingly anomalous presence of scent marking in *Vespa mandarinia* may be explained by this wasp's unique food [8, 36]. These hornets attack and overwhelm colonies of other social wasps and of honey bees. It is highly unlikely that a single hornet would succeed at this, but by coordinating and attacking en masse they can overcome the strong defenses of colonies that can contain up to tens of thousands of individuals. This coordination is facilitated by the scent marking [35]. For wasps such as *P. occidentalis* that do not utilize such well-defended food sources, scent marking may not be adaptive.

Despite having the machinery for scent-marking swarm emigration routes, *P. occidentalis* does not utilize it in the context of carbohydrate foraging. This suggests that the benefit-to-cost ratio of the behavior must fall heavily on the cost side. Unlike nest-based recruitment mechanisms that remain cryptic to non-nestmates, field-based mechanisms are subject to eavesdropping by non-nestmates and heterospecifics. Indeed, some foraging stingless bees, honey bees, and bumble bees use marks by individuals from other nests and even other species [28, 57]. Thus, the cost of olfactory eavesdropping may render scent-marking behavior unprofitable to most wasp species.

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## References

- [1] E. O. Wilson, *The Insect Societies*, The Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1971.
- [2] K. von Frisch, *The Dance Language and Orientation of Bees*, The Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1967.
- [3] B. Hölldobler and E. O. Wilson, *The Ants*, The Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1990.
- [4] J. C. Nieh, "Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini)," *Apidologie*, vol. 35, no. 2, pp. 159–182, 2004.
- [5] S. Jarau, "Chemical communication during food exploitation in stingless bees," in *Food Exploitation In Social Insects: Ecological Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., pp. 223–249, CRC Press, Boca Raton, Fla, USA, 2009.
- [6] R. Beckers, S. Goss, J. L. Deneubourg, and J. M. Pasteels, "Colony size, communication and ant foraging strategy," *Psyche*, vol. 96, pp. 239–256, 1989.
- [7] R. L. Jeanne, J. H. Hunt, and M. G. Keeping, "Foraging in social wasps: *Agelaius* lacks recruitment to food (Hymenoptera: Vespidae)," *Journal of the Kansas Entomological Society*, vol. 68, no. 3, pp. 279–289, 1995.
- [8] R. L. Jeanne and B. J. Taylor, "Individual and social foraging in social wasps," in *Food Exploitation In Social Insects: Ecological Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., pp. 53–79, CRC Press, Boca Raton, Fla, USA, 2009.
- [9] U. Maschwitz, W. Beier, I. Dietrich, and W. Keidel, "Futterverständigung bei Wespen der Gattung *Paravespula*," *Naturwissenschaften*, vol. 61, no. 11, p. 506, 1974.
- [10] S. L. Overmyer and R. L. Jeanne, "Recruitment to food by the German yellowjacket, *Vespa germanica*," *Behavioral Ecology and Sociobiology*, vol. 42, no. 1, pp. 17–21, 1998.

- [11] J. M. Jandt and R. L. Jeanne, "German yellowjacket (*Vespula germanica*) foragers use odors inside the nest to find carbohydrate food sources," *Ethology*, vol. 111, no. 7, pp. 641–651, 2005.
- [12] B. J. Taylor, D. R. Schalk, and R. L. Jeanne, "Yellowjackets use nest-based cues to differentially exploit higher-quality resources," *Naturwissenschaften*, vol. 97, no. 12, pp. 1041–1046, 2010.
- [13] M. Hrncir, S. Mateus, and F. S. Nascimento, "Exploitation of carbohydrate food sources in *Polybia occidentalis*: social cues influence foraging decisions in swarm-founding wasps," *Behavioral Ecology and Sociobiology*, vol. 61, no. 6, pp. 975–983, 2007.
- [14] T. I. Schueller, E. V. Nordheim, B. J. Taylor, and R. L. Jeanne, "The cues have it; nest-based, cue-mediated recruitment to carbohydrate resources in a swarm-founding social wasp," *Naturwissenschaften*, vol. 97, pp. 1017–1022, 2010.
- [15] M. R. Richter, "Hunting social wasp interactions: influence of prey size, arrival order, and wasp species," *Ecology*, vol. 71, no. 3, pp. 1018–1030, 1990.
- [16] P. D'Adamo, J. Corley, P. Sackmann, and M. Lozada, "Local enhancement in the wasp *Vespula germanica*; are visual cues all that matter?" *Insectes Sociaux*, vol. 47, no. 3, pp. 289–291, 2000.
- [17] R. L. Jeanne, "Social complexity in the Hymenoptera, with special attention to the wasps," in *Genes, Behaviors and Evolution of Social Insects*, T. Kikuchi, N. Azuma, and S. Higashi, Eds., pp. 81–130, Hokkaido University Press, Sapporo, Japan, 2003.
- [18] R. Zucchi, S. F. Sakagami, F. B. Noll et al., "Agelaia vicina, a swarm founding polistine with the largest colony size among wasps and bees (Hymenoptera: Vespidae)," *Journal of the New York Entomological Society*, vol. 103, pp. 129–137, 1995.
- [19] U. Schmitt, G. Lübke, and W. Francke, "Tarsal secretion marks food sources in bumblebees (Hymenoptera: Apidae)," *Chemoecology*, vol. 2, no. 1, pp. 35–40, 1991.
- [20] D. Goulson, J. C. Stout, J. Langley, and W. O. H. Hughes, "Identity and function of scent marks deposited by foraging bumblebees," *Journal of Chemical Ecology*, vol. 26, no. 12, pp. 2897–2911, 2000.
- [21] D. Goulson, J. W. Chapman, and W. O. H. Hughes, "Discrimination of unrewarding flowers by bees; direct detection of rewards and use of repellent scent marks," *Journal of Insect Behavior*, vol. 14, no. 5, pp. 669–678, 2001.
- [22] F. G. Barth, M. Hrncir, and S. Jarau, "Signals and cues in the recruitment behavior of stingless bees (Meliponini)," *Journal of Comparative Physiology A*, vol. 194, no. 4, pp. 313–327, 2008.
- [23] V. M. Schmidt, R. Zucchi, and F. G. Barth, "Scent marks left by *Nannotrigona testaceicornis* at the feeding site: cues rather than signals," *Apidologie*, vol. 36, no. 3, pp. 285–291, 2005.
- [24] N. Saleh, A. G. Scott, G. P. Bryning, and L. Chittka, "Distinguishing signals and cues: bumblebees use general footprints to generate adaptive behaviour at flowers and nest," *Arthropod-Plant Interactions*, vol. 1, pp. 119–127, 2007.
- [25] J. Wilms and T. Eltz, "Foraging scent marks of bumblebees: footprint cues rather than pheromone signals," *Naturwissenschaften*, vol. 95, no. 2, pp. 149–153, 2008.
- [26] D. Goulson, "The use of scent marks by foraging bumble bees," in *Food Exploitation In Social Insects: Ecological Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., pp. 251–260, CRC Press, Boca Raton, Fla, USA, 2009.
- [27] J. B. Free and I. H. Williams, "Scent-marking of flowers by honeybees," *Journal of Apicultural Research*, vol. 18, pp. 128–135, 1983.
- [28] J. C. Stout and D. Goulson, "The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees," *Animal Behaviour*, vol. 62, no. 1, pp. 183–189, 2001.
- [29] J. Reinhard and M. V. Srinivasan, "The role of scents in honey bee foraging and recruitment," in *Food Exploitation In Social Insects Ecological Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., pp. 165–182, CRC Press, Boca Raton, Fla, USA, 2009.
- [30] J. B. Free, *Pheromones of Social Bees*, Cornell University Press, Ithaca, NY, USA, 1987.
- [31] P. C. Fernández and W. M. Farina, "Changes in food source profitability affect Nasonov gland exposure in honeybee foragers *Apis mellifera* L.," *Insectes Sociaux*, vol. 48, no. 4, pp. 366–371, 2001.
- [32] W. Beier, "Observations and experimental approach to the foraging behavior of the German wasp *Paravespula germanica*," *Zoologische Beiträge*, vol. 28, pp. 321–348, 1983.
- [33] P. D'Adamo and M. Lozada, "Conspecific and food attraction in the wasp *Vespula germanica* (Hymenoptera: Vespidae), and their possible contributions to control," *Annals of the Entomological Society of America*, vol. 98, no. 2, pp. 236–240, 2005.
- [34] J. M. Jandt, L. Riel, B. Crain, and R. L. Jeanne, "*Vespula germanica* foragers do not scent-mark carbohydrate food sites," *Journal of Insect Behavior*, vol. 18, no. 1, pp. 19–31, 2005.
- [35] M. Ono, T. Igarashi, E. Ohno, and M. Sasaki, "Unusual thermal defence by a honeybee against mass attack by hornets," *Nature*, vol. 377, no. 6547, pp. 334–336, 1995.
- [36] M. Matsuura, "Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae)," *Bulletin of the Faculty of Agriculture Mie University*, vol. 69, pp. 1–131, 1984.
- [37] R. L. Jeanne, H. A. Downing, and D. C. Post, "Morphology and function of sternal glands in polistine wasps (Hymenoptera: Vespidae)," *Zoomorphology*, vol. 103, no. 3, pp. 149–164, 1983.
- [38] R. L. Jeanne, "The swarm-founding Polistinae," in *The Social Biology of Wasps*, K. G. Ross and R. W. Matthews, Eds., pp. 191–231, Comstock Publishing Associates of Cornell University Press, Ithaca, NY, USA, 1991.
- [39] J. P. Spradbery, *Wasps: An Account of the Biology and Natural History of Solitary and Social Wasps*, University of Washington Press, Seattle, Wash, USA, 1973.
- [40] E. R. Heithaus, "Flower visitation records and resource overlap of bees and wasps in Northwest Costa Rica," *Brenesia*, vol. 16, pp. 9–52, 1979.
- [41] U. Schmitt and A. Bertsch, "Do foraging bumblebees scent-mark food sources and does it matter?" *Oecologia*, vol. 82, no. 1, pp. 137–144, 1990.
- [42] J. C. Nieh, S. Ramírez, and P. Nogueira-Neto, "Multi-source odor-marking of food by a stingless bee, *Melipona mandacaia*," *Behavioral Ecology and Sociobiology*, vol. 54, no. 6, pp. 578–586, 2003.
- [43] M. Hrncir, S. Jarau, R. Zucchi, and F. G. Barth, "On the origin and properties of scent marks deposited at the food source by a stingless bee, *Melipona seminigra*," *Apidologie*, vol. 35, no. 1, pp. 3–13, 2004.
- [44] T. D. Seeley, *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*, Harvard University Press, Cambridge, Mass, USA, 1995.
- [45] V. Engel, M. K. Fischer, F. L. Wäckers, and W. Völkl, "Interactions between extrafloral nectaries, aphids and ants: are there competition effects between plant and homopteran sugar sources?" *Oecologia*, vol. 129, no. 4, pp. 577–584, 2001.

- [46] P. Riba-Hernández, K. E. Stoner, and P. W. Lucas, "The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in tropical humid forest in Costa Rica," *Journal of Tropical Ecology*, vol. 19, no. 6, pp. 709–716, 2003.
- [47] A. James, R. Dungan, M. Plank, and R. Ito, "A dynamical model of honeydew droplet production by sooty-beech scale insects (*Ultracoelostoma* spp.) in New Zealand *Nothofagus* forest," *Ecological Modelling*, vol. 209, no. 2-4, pp. 323–332, 2007.
- [48] J. M. Jandt, C. Curry, S. Hemauer, and R. L. Jeanne, "The accumulation of a chemical cue: nest-entrance trail in the German yellowjacket, *Vespula germanica*," *Naturwissenschaften*, vol. 92, no. 5, pp. 242–245, 2005.
- [49] S. O'Donnell, "Necrophagy by Neotropical swarm-founding wasps (Hymenoptera: Vespidae, Epiponini)," *Biotropica*, vol. 27, pp. 133–136, 1995.
- [50] O. T. Silveira, M. C. Esposito, J. N. Dos Santos, and F. E. Gemaque, "Social wasps and bees captured in carrion traps in a rainforest in Brazil," *Entomological Science*, vol. 8, no. 1, pp. 33–39, 2005.
- [51] L. Gomes, G. Gomes, H. G. Oliveira et al., "Occurrence of Hymenoptera on *Sus scrofa* carcasses during summer and winter seasons in southeastern Brazil," *Revista Brasileira de Entomologia*, vol. 51, no. 3, pp. 394–396, 2007.
- [52] D. W. Roubik, "Obligate necrophagy in a social bee," *Science*, vol. 217, no. 4564, pp. 1059–1060, 1982.
- [53] M. A. R. Richter and R. L. Jeanne, "Predatory behavior of *Polybia sericea* (Olivier), a tropical social wasp (Hymenoptera: Vespidae)," *Behavioral Ecology and Sociobiology*, vol. 16, no. 2, pp. 165–170, 1985.
- [54] P. D'Adamo and M. Lozada, "The importance of location and visual cues during foraging in the German wasp (*Vespula germanica* F.) (Hymenoptera: Vespidae)," *New Zealand Journal of Zoology*, vol. 30, no. 3, pp. 171–174, 2003.
- [55] S. Moreyra, P. D'Adamo, and M. Lozada, "Odour and visual cues utilised by German yellowjackets (*Vespula germanica*) while relocating protein or carbohydrate resources," *Australian Journal of Zoology*, vol. 54, no. 6, pp. 393–397, 2006.
- [56] L. K. Johnson, "Foraging strategies and the structure of stingless bee communities in Costa Rica," in *Social Insects in the Tropics*, P. Jaisson, Ed., pp. 31–58, Université Paris-Nord, Paris, France, 1983.
- [57] J. C. Nieh, F. A. L. Contrera, R. R. Yoon, L. S. Barreto, and V. L. Imperatriz-Fonseca, "Polarized short odor-trail recruitment communication by a stingless bee, *Trigona spinipes*," *Behavioral Ecology and Sociobiology*, vol. 56, no. 5, pp. 435–448, 2004.



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