

Introduction of a scented carbohydrate resource into the nest increases departure rate in *Polybia occidentalis*

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Abstract Social wasps do not possess a sophisticated, signal-based mechanism for recruiting foragers to food resources. Instead, in some species naïve potential foragers use cues, specifically the scent of a resource obtained from successful foragers, to help locate the resource in the field. Prior studies have focused on the effectiveness of this mechanism on increasing the number of foragers at an artificial resource in the field; the increase is typically modest. Here, we focus on the activity at the nest in *Polybia occidentalis*, a tropical social wasp, and quantify the magnitude of the effect an influx of a known amount of scented carbohydrate solution added directly to the nest has on activating foragers to leave the nest in search of the resource. Under our experimental conditions, adding a scented 2.0 M sucrose solution to the nest doubled the average rate of departure. No increase occurred when the same amount of water was added as a control. This mass activation of foragers may give colonies of this species a competitive edge by enhancing their ability to rapidly exploit new resources.

Keywords *Polybia occidentalis* · Cues · Trophallaxis · Recruitment · Foraging rates

Introduction

Colonies of social insects must compete for food sources that last for finite periods of time. To capitalize on an especially profitable source of food, it would be advantageous for foragers to alert colony mates to the presence of a newly discovered resource, lest it be exploited by competitors. Accordingly, many species of social insects have evolved mechanisms that inform nestmates of the location of particularly valuable resources through recruitment behavior. Examples include the honey bee waggle dance (von Frisch, 1967) and the pheromone trails of many ants (Hölldobler and Wilson, 1990) and some stingless bees (Nieh, 2004; Jarau, 2009). In other species, communication of information about distance and direction is absent, but returning foragers produce signals that stimulate nestmates to leave in search of food. In some bumble bees and stingless bees, for example, successful returning foragers make excited runs through the nest, bumping others and increasing the number of departing foragers (Dornhaus and Chittka, 1999, 2001, 2005; Hrncir, 2009). In bumble bees, these excited runs are accompanied by the distribution of a pheromone that stimulates foraging (Dornhaus and Chittka, 2001, 2005; Dornhaus et al., 2003; Molet et al., 2008). Jarau and Hrncir (2009) review this and other food-finding behavior in social insects.

For the social wasps, there is no evidence for signals that communicate the distance or direction of food to nestmates, nor have any forager-activation signals been reported. Surprisingly, this appears to be true even for species of tropical swarm-founders that form very large colonies, for

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which effective food-recruitment signals might be expected to confer a fitness advantage (Jeanne et al., 1995; Hrnčir et al., 2007; Jeanne and Taylor, 2009; Taylor et al., 2011). This group even produces pheromones that are used during swarm emigration to create a trail of scent-marks leading colony mates to a new nest site, but this form of recruitment is not used in a foraging context (Jeanne et al., 1995; Taylor et al., 2011). However, in some wasp species there are other sources of nest-based information that have the effect of increasing the colony's foraging effort on high-quality resources. In particular, food-associated olfactory cues are used by several species to help locate resources in the field. For example, when *Vespula* spp. foragers are making repeated visits to a scented carbohydrate solution at an experimental feeder near the nest, naive foragers from the same colony visiting a second feeder choose the solution with a scent matching the experimental feeder more often than a solution with a control scent (Maschwitz et al., 1974; Overmyer and Jeanne, 1998). Thus, information about foraging opportunities is acquired at the nest and stimulates foragers to seek out rich food sources by searching for resources that match the scent of those brought in by successful foragers. The information that alerts naïve nestmates to the new resource could simply come from the cues associated with the food itself during trophallactic transfer from forager to nest wasp, or it could require some form of alerting behavior or other stimulation by the successful forager. However, the same result is obtained even if forager input is eliminated, as for example by placing the scented solution directly into the nest, thus indicating that behavioral alerting of nestmates by the forager is not a necessary component (Jandt and Jeanne, 2005; Schueller et al., 2010; Taylor et al., 2010).

Similar use of nest-based cues has been reported for swarm-founding epiponines. In a study on *Polybia occidentalis*, a neotropical swarm-founding wasp, Hrnčir et al. (2007) found that foragers accumulated at a food source only when the nestmates were trained to it during 2-h trials, suggesting that input from successful foragers at the nest stimulated foraging. When scented sugar solution was placed directly into nests, naive foragers arriving at a feeding station alighted more often on the dish containing the scent they were exposed to in the nest than on a control-scented dish (Schueller et al., 2010). These studies show clearly for epiponines that, as for vespines, food-associated odor provides a nest-based cue utilized by foragers to locate the source of the food in the field and that the impetus to visit these food sources can occur without any behavioral input from returning successful foragers.

In the majority of these studies, data were collected on foragers arriving at dishes set on feeders away from the nest. The numbers of arrivals at the test dishes in the field in these experiments were typically low, in the range of 1–15 per day

(Maschwitz et al., 1974; Overmyer and Jeanne, 1998; Hrnčir et al., 2007; Schueller et al., 2010; Taylor et al., 2010), raising the question of the source of these new arriving foragers. One possibility is that they are already-active foragers that shift their foraging effort from naturally occurring resources to the new, probably richer, resource provided by the experimenter. This might account for the relatively low numbers of new recruits. Alternatively, the influx of a rich resource may stimulate currently inactive foragers to become active and go in search of the new source. *P. occidentalis* and many other social wasps store excess nectar supplies as droplets in open brood cells (Richards, 1971; Jeanne, 1991; Hunt et al., 1998), suggesting that opportunistic exploitation of rich food supplies benefits the colony by providing a cushion in the event of lean foraging in the future. In the only study bearing on this question, Forsyth (1978) asserted without data that numbers of active foragers in *P. occidentalis* colonies swell from the normal 10–20% of the workers to three to four times that number when the short-lived dispersal flights of termite reproductives provide a super-abundance of prey.

The present study was undertaken to quantify the effect on foraging rate of a known amount of scented carbohydrate food introduced directly into the nest of *P. occidentalis* with the aim of testing between the two hypotheses described above. The first hypothesis predicts that introducing a rich new resource into the nest will not cause an increase in the number of foragers departing the nest. Workers may simply utilize the added food either by ingesting it or storing it in the nest. In this case foraging rates may well stay the same (if the distribution is carried out by nest workers), or even decrease (if distribution is carried out by active foragers that temporarily switch to this task). The second predicts that an influx of a rich new resource will trigger an increase in the colony's overall foraging effort, as new foragers are mobilized to opportunistically exploit the source. Our results support the latter outcome.

Methods

The study was performed approximately 5 km west of Cañas, Guanacaste, Costa Rica (10°25'N, 85°7'W). Detailed descriptions of the study site can be found in Bouwma et al. (2003). Nests used for the study were often in dense vegetation or in tall trees. We moved nests to small, isolated trees in an open area to facilitate clear videotaping of foragers departing from the nest. These wasps do not fly at night, so the nests were moved after dark to minimize the number of workers lost. At the new site, the nests were attached to branches at eye level using either nylon cable ties or wire. Tanglefoot® was applied to the branch between the nest and the tree trunk to prevent predation by ants.

Trials were conducted between the hours of 1000 and 1600 from 29 June to 12 July 2008. Each trial was videotaped using a Sony HDR-HC7 camcorder with 1080i HD visual resolution and a frame rate of 30 frames/sec. Videotapings were made in such a way that the entire nest was encompassed in the field of view, framed with enough surrounding negative space to see arriving and departing wasps clearly against the distant background. Accordingly, precise data on departure rates could be extracted from the tapes during playback. For each trial, a colony was videotaped continuously for 1 h. The first 20 min were used to obtain a baseline (unmanipulated) departure rate. Then 2 mL of 2.0 M sucrose solution was added to the nest entrance via pipette, and an equal amount was dripped onto depressions on the outside of the nest envelope. We added food directly via pipette to control the total amount of food given to each nest and to eliminate behavioral interactions from returning foragers, thereby limiting the stimulus to the scented food itself. The mean crop size of *P. occidentalis* is approximately 6.6 μ L (Jeanne, 1986), making the total amount of sucrose solution added the equivalent of about 600 forager loads. This large volume was used to ensure that a response could be detected against the background rate of departures. The solution was scented with 1% v/v of pure orange extract (extract contained alcohol 79%, water, and oil of orange; McCormick[®], McCormick & Co., Inc., Hunt Valley, MD, USA). Recording continued for a further 40 min.

Fifteen colonies were used in the study. Each received two treatments, one of the sucrose solution and one of water as a control. Other than the substitution of water for sucrose, all aspects of the procedure were the same for both treatments. Only one treatment was administered per colony per day, and in most cases the two treatments for a given colony were administered on consecutive days, with the order of treatments randomized for each colony. All colonies were treated identically with the following exceptions. Inclement weather caused postponement of the second treatment from the second day to the third day for one colony and to the fourth day for another. In five cases, rain forced termination 5 min (one colony) or 10 min (four colonies) short of the full 60-min trial. Of the 15 colonies that were used in the study, only one was engaged in active nest construction. That colony was repairing sections of envelope that had been damaged during the relocation process. All nests were collected and dissected following the experiments.

To analyze the videotapes, a macro was created in Microsoft Excel[®] that recorded date and time when a key-stroke was performed. This made it possible to record departures in real time as the videotape played, without taking one's eyes off the screen. Departures were binned in 5-minute intervals. The 30 frames per second of the video recordings were more than sufficient to allow us to see all departures from the nest.

We used a mixed-model ANOVA to assess differences in departure rates, treating colony within treatment as the subject variable in a repeated-measures design. The model contained fixed factors for treatment (between-subject factor), time, and the interaction between these factors (within-subject factors). Colony and its interaction with treatment were treated as random, between-subjects factors. Several different covariance structures were considered for the model, and their fits were assessed using the Akaike Information Criterion (AIC) (Akaike, 1974). From these assessments, we opted to use a model that incorporated a first-order autoregressive covariance structure on square-root-transformed departure rates. However, the majority of the assessed covariance structures produced similar *p* values, suggesting the results were robust. Degrees of freedom were determined using the Kenward–Roger method which reduces the probability of type-I errors when longitudinal data are missing from some experimental trials (Kenward and Roger, 1997; Padilla and Algina, 2004; Spilke et al., 2005).

We conducted further tests to determine how long the effects of each treatment lasted by comparing each 5-min time interval to the baseline rate within each treatment. To accomplish this, we first used contrasts to test the hypothesis that the departure rate was constant during the 20-min baseline period before the start of the manipulation. We found no significant differences in departure rates among any of the baseline time intervals within either treatment (all *p* > 0.05, Fig. 1), so a mean of these first four 5-min intervals was taken for each trial. Additional contrasts were then used to compare each 5-min interval that occurred after the manipulation to the average baseline departure rate. To compare between treatments we conducted contrasts to compare departure rates within each 5-min interval. These contrasts were performed only if the overall ANOVA (in particular the nest-by-treatment interaction) was significant, and were thus viewed as “protected” from type-I errors (Carmer and Swanson, 1973). Thus, no alpha-level adjustments were made. PROC MIXED in SAS[®] software, Version 9.1.3 for UNIX (SAS Institute Inc., Cary, NC) was used for all analyses.

Results

Within minutes after the sucrose was applied, wasps that imbibed the solution from droplets on the nest envelope were sometimes observed running rapidly over the surface of the nest envelope. These runs were not accompanied by wing-buzzing. The running individuals most frequently made straight-line runs toward the nest entrance, but often stopped before entering the nest if they encountered a nestmate. During these stops, the running individual would usually make a short (~1 s) trophallactic contact with a nestmate before continuing toward the nest entrance. In

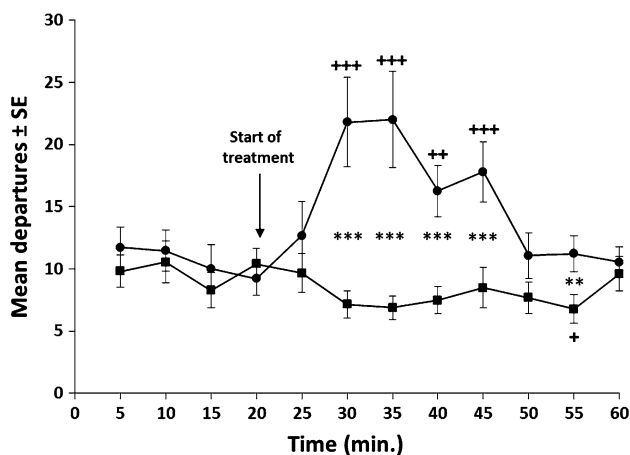


Fig. 1 The departure rate of the sucrose experimental treatment and water control treatment over time. Each *point* represents the average number of departures \pm SE during the previous 5-min interval. The *asterisks* represent a significant difference between the sucrose and water treatments for the indicated time interval ($***P < 0.001$, $**P < 0.01$, $*P < 0.05$). The *crosses above and below the lines* represent significant differences between the average baseline rate (minutes 0–20) and the indicated 5-min interval for the sucrose and water treatments, respectively ($+++P < 0.001$, $++P < 0.01$, $+P < 0.05$)

contrast, after the addition of water, wasps were observed imbibing the water then leaning out of the nest entrance or over the side of the nest and regurgitating it. No such behavior was observed following the introduction of sucrose solution. When the nests were later dissected, we found large amounts of honey stored as droplets in the cells. This liquid was clear and watery rather than yellow and viscous, suggesting that it had not had time to lose water to evaporation, and therefore was likely the sugar solution added during the experiment.

The mixed-model ANOVA revealed significant effects for treatment ($F_{1,13.7} = 27.52$, $p < 0.001$), time ($F_{11,256} = 2.14$, $p = 0.018$), and the time-by-treatment interaction ($F_{11,256} = 4.60$, $p < 0.001$). Departure rates were significantly higher for the sucrose treatment than for the water treatment in all but one 5-min interval between 25 and 55 min (Fig. 1). Departure rates increased to a peak of approximately double the baseline rate in the sucrose treatment, and were significantly higher than the mean baseline rate of 11 departures/5-min interval for all intervals between minutes 25 and 45, after which departures returned to the baseline rate (Fig. 1). The droplets of sucrose solution on the nest envelope were often completely imbibed within 10–15 min after the solution was added, meaning that increased departure rates continued for approximately 10–15 min after the sucrose was depleted. Based on the mean departure rates per interval, there were approximately 36 additional departures, that is, over the baseline rate, during the 20 min that the departure rate was higher than the baseline rate. This amounts to an

average of 13 extra departures per g of added sucrose during those 20 min.

In contrast to sucrose, departure rates for the water treatment declined slightly, yet not significantly, immediately after water was introduced, but were significantly lower than the baseline during the 50- to 55- min interval. This suggests that the significant difference found between the sucrose and water treatment during this interval was due more to a decrease in departure rates in the water treatment than to a higher departure rate in the sucrose treatment.

Discussion

Our results clearly showed a significant increase in departures in response to the addition of scented sucrose, supporting the hypothesis that an influx of carbohydrate food stimulates wasps to leave the nest. The foragers in our experiment could have remained on the nest and treated the food that was added as a resource bonanza on their doorstep and proceeded to collect it on foot and transfer it to nectar receivers within the nest, as per our first hypothesis. In this case, the foraging rates would have remained the same or even decreased, as individuals that were previously engaged in foraging at natural nectar sources were drawn away from that task. This, however, did not occur. It is likely that the increase in departures was due to an increase in numbers of foragers leaving the nest to search for the source of the sucrose in the field, supporting our second hypothesis. As prior studies of wasps have shown, whether food is inserted directly into the nest or brought back by foragers trained to a foraging site, other wasps cue on the scent of the resource to find the source of food in the field (Maschwitz et al., 1974; Overmyer and Jeanne, 1998; Jandt and Jeanne, 2005; Schueller et al., 2010; Taylor et al., 2010). Combined with previous studies, our results suggest that an influx into the nest of a rich resource causes large numbers of newly recruited foragers to leave in search of the resource, but that only a small fraction succeed in finding it.

Although our experimental treatment was scent extract dissolved in a sucrose solution, it is unlikely that the foragers responded to the scent of the food alone and left the nest in search of its source, that is, without associating it with the sucrose reward. Although it has been shown for honey bees that the addition of an olfactory cue alone can stimulate an increase in foraging, that response occurs only among foragers that had previously learned to associate that scent with a food reward (Reinhard et al., 2004; Beekman, 2005), and the response diminishes rapidly if the scent is not paired with a reward (Beekman, 2005). Thus, a response to scent alone would likely require recent previous experience with the scent/reward pairing. In the present study this was unlikely, as no known orange-scented resources were

located in the vicinity of the study area. Our results suggest that the rich sugar solution stimulated foragers to leave the nest and that if we had placed orange-scented sugar solution in the field, some of these foragers would have found it.

Another possible alternative explanation for our result is that the carbohydrates inserted into the nest in plentiful amounts simply provided foragers the necessary extra energy to begin foraging at a higher rate and/or to enable previously inactive foragers to become active. We believe this explanation is unlikely for the following reason. The speed at which social insects are able to utilize ingested sugars to power their flight muscles depends partly on how quickly sugars are moved from the crop to the midgut (Crailsheim, 1988a; Rocés and Blatt, 1999; Blatt and Rocés, 2001, 2002) and partly on how quickly sucrose can be metabolized in the midgut. During digestion in the midgut, sucrose is cleaved into glucose and fructose, which migrate to the fat-body cells, where trehalose, the main haemolymph carbohydrate, is synthesized (Candy, 1989; Wheeler, 1989). In honey bees, haemolymph glucose levels increase within 5 min after ingestion of sugar solution, while trehalose levels take 10 min to increase (Crailsheim, 1988b; Woodring et al., 1993). In our experiment, departures started to rise within 5 min after sucrose introduction and were significantly higher by the 5- to 10- min interval. During this time, we observed high activity on the nest suggesting that potential foragers were not energy-deprived prior to imbibing the liquid. The observation that *P. occidentalis* colonies showed a strong spike in foraging rate when termite alates were abundant (Forsyth, 1978) supports the conclusion that the increased outflow of foragers cannot be explained as a response to ingestion of a quick-energy nutrient. We conclude that the stimulus causing the departures we observed was information, not energy.

The decrease in departure rates after the introduction of water to the nest, although slight, may have been real. The regurgitation of wastewater imbibed from the nest, a behavior called ‘bailing’ has been observed in this and other social wasps following rain showers (Naumann, 1970; Jeanne, 1991). Recruitment of workers to bail may have included some of the active foragers, delaying their subsequent departures, thus depressing the overall departure rate. Bailing was never observed after sucrose introduction, suggesting that all sucrose was treated as a food resource. The large amounts of dilute nectar found stored in our nests upon collection indicate that much of the solution we added to the nest was stored by nest workers.

The results of our study bear comparison with those of similar work on bumble bees (Dornhaus and Chittka, 2001, 2005). Bumble bees do not engage in trophallaxis (Wilson, 1971; Michener, 1974). Instead, returning nectar foragers unload directly into honey pots in the nest. There is evidence that the honey in these stores acts as an information source

for foragers, i.e. that the pots provide information about food availability, and that odors associated with the resource are used by subsequent foragers to locate similar resources in the field (Dornhaus and Chittka, 1999, 2001, 2005; Molet et al., 2009). Unlike bumble bees, returning *P. occidentalis* nectar foragers engage in trophallaxis, downloading sugar solution to receivers at the nest (Jeanne, 1991), who further distribute it throughout the colony via trophallaxis with adults and with larvae, with only excess amounts stored as droplets on the walls of open cells in the nest (Hunt et al., 1987, 1998). Because stored sugar solution was found in our nests, it is possible that these stores serve as an additional, indirect source of information about foraging opportunities, similar to the honey pots in a bumble bee nest (Dornhaus and Chittka, 2001, 2005; Molet et al., 2009). Even if so, given the rapid increase in departure rates after introduction of the sucrose solution, we believe it is far more likely that adult–adult trophallaxis is the major mechanism of transfer of information about incoming resources in this wasp, as it is in honey bees (Farina et al., 2007). Wasps will frequently feed on ripe and rotting fruits which are long-lasting resources rich in sugars and marked by characteristic odors (Spradbery, 1973; Edwards, 1980). For such resources, trophallaxis may provide a more efficient mechanism for the transfer of information about a new resource than could food stores. First, it is more direct and therefore potentially faster, and second, it is likely to be more reliable in that the transferred information is about a single source, rather than the mixture of all the sources recently exploited by the colony.

Taken together with the results of prior work, our study strongly suggests that information transfer about foraging opportunities occurs via trophallaxis, as incoming carbohydrate foragers transfer their loads to receiver wasps, and that the mere experience with the gustatory cue obtained during this process can induce a foraging response in nest-mates. The food-associated olfactory cues could increase foraging success per trip by decreasing search time for the resource, and thus decrease the energetic and mortality risks associated with foraging (Hocking, 1953; Kammer and Heinrich, 1974; Schmid-Hempel and Schmid-Hempel, 1984; Schmid-Hempel and Wolf, 1988; O’Donnell and Jeanne, 1992; Biesmeijer and Tóth, 1998).

Our results do not rule out the possible existence of an alerting signal that could increase the number of workers responding to the incoming food, such as excited runs and wing fanning accompanied by pheromone release, as seen in *Bombus* spp. (Dornhaus and Chittka, 2001, 2005; Dornhaus et al., 2003; Molet et al., 2008). The observed increase in rapid running across the nest envelope after the introduction of sucrose is similar to what Naumann (1970) observed in *Protopolybia acutiscutis* (= *pumila*) and described as a “departure dance” performed by returning food foragers.

This behavior may embody an alerting signal. Because these runs were not observed immediately upon adding the sucrose to the nest and were not accompanied by wing-buzzing, they were unlikely to have been an alarm response to the disturbance we caused (Jeanne, 1981). The short trophallactic contacts made by individuals that imbibed the solution we observed on the nest envelope may likewise be a factor that increases foraging. Naumann (1970) also reported similar behavior during swarming as scouts ran through the swarm, buzzing their wings and lifting their abdomens, suggesting the possible release of an airborne pheromone. This activity apparently stimulated nestmates to fly. However, no wing-buzzing or abdomen lifting was observed during our experiment. Still, the bumping of other individuals during these runs could itself be a stimulus to depart from the nest. In the context of swarm emigration in *P. occidentalis*, scout wasps run and bump into wasps in the swarm more frequently in the minutes just prior to swarm lift-off and departure for the new nest site, suggesting that bumping is a stimulus to induce individuals to fly (Sonntag and Jeanne, 2009). However, rigorous tests of the function(s) of this behavior in a foraging context have not been conducted for any species.

Our results quantify the magnitude of the response to information about food resources brought to the nest by foragers. While we showed that the response can be massive, we acknowledge that our stimulation was massive. It is likely that, of those leaving the nest with a just-learned olfactory search image, only a fraction succeed in finding the source of the reward in the field. However, for a persistent resource such as the sugar in a rotting fruit, positive feedback can have a multiplier effect over time. If one forager from a colony discovers such a resource and her return to the nest stimulates a handful of nestmates to depart in search of it, even if only one of these succeeds in finding the resource by homing on the associated odor learned in the nest, the effect is to double the rate of input of that resource into the colony. With two now bringing resource and odor information to the nest, the chance that more recruits will find the resource increases, and so on, until the overall response may be as massive as we observed, or even greater, as Forsyth (1978) reported in the case of the response of *P. occidentalis* to mating swarms of termites.

Even though all 4 ml added to each nest were quickly absorbed by the colony, including as increased stores in cells, the colony was still stimulated to increase foraging rates significantly to exploit the resource at levels beyond current colony demand. The massive response our sucrose treatments generated strongly suggests that supply in the environment, not just demand within the colony, plays a major role in setting foraging rates. In other words, these wasps clearly are opportunistic foragers, able to take advantage of resource bonanzas, and this advantage is

enhanced by their ability to utilize the food-associated olfactory cues to find food in the field.

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