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Recruitment to food by the German yellowjacket, *Vespula germanica*

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Abstract The hypothesis that *Vespula germanica* foragers can recruit nestmates to food resources was tested using a protocol that controlled for the biasing effects of social factors at the resource, including local enhancement and food-site marking substances. Foragers from an observation colony in the field were trained to visit a dish of scented corn syrup solution 15 m east of the nest. A second feeding station, 22 m northeast of the nest, offered incoming foragers a choice between food with the training scent and food with a control scent. Significantly more naive foragers arriving at that station chose the food with the training scent. We conclude that the German yellowjacket is able to recruit nestmates to carbohydrate food sources, and that recruits use food odor to locate the source of food being brought into the nest.

Key words Communication · Foraging · Recruitment · *Vespula germanica* · Yellowjacket wasps

Introduction

Recruitment is communication that brings nestmates to a place where work is required (Wilson 1971). Among the social insects, it coordinates group efforts in nest defense, colony emigration, and food retrieval. Recruitment in the first two of these contexts occurs in all four major groups of social insects – termites, ants, bees, and wasps (Wilson 1971). In contrast, recruitment to food, while well-documented in the termites, ants, and bees, has not been unequivocally demonstrated in the social wasps (Wilson 1971; Jeanne 1991; Jeanne et al. 1995).

The most important previous work on recruitment to food in wasps is that of Maschwitz et al. (1974) on the yellowjacket species *Vespula germanica* and *V. vulgaris*. Foragers were trained to visit a dish of scented sugar water 60 m from the nest. Once a number of foragers had been marked and were making regular visits to the dish, two more dishes of test-scented sugar water were set out, each 4 m from the training dish. A dish of control-scented sugar water was then placed 0.5 m away from each of these, forming three pairs. While the trained foragers continued to visit the dishes with test-scented sugar water, naive, unmarked foragers arriving at any of the six dishes were captured and the food choice of each recruit was recorded. Later, the captured recruits were marked for individual recognition and released; only recruits seen returning to the experimental colony were included in the analysis. Maschwitz and coworkers found that significantly more recruits chose to feed at the test-scented dishes, and concluded that their recruitment must have been mediated in the nest by food scent.

Weaknesses in the design of this experiment have led some authors (Parrish and Fowler 1983; Reid et al. 1995) to argue that the results of Maschwitz et al. (1974) can be adequately explained by local enhancement, which has since been demonstrated in *V. germanica* (Parrish and Fowler 1983). Local enhancement is a variant of social facilitation in which apparent imitation behavior results from "directing the animal's attention to a particular object or to a particular part of the environment" (Thorpe 1963, p. 134). Indeed, the design of the Maschwitz et al. (1974) experiment allowed naive foragers to arrive at the same dishes that trained foragers were visiting. When a naive wasp landed at a particular dish, trained foragers may already have been present and feeding there. Thus, naive foragers could have arrived at dishes containing the training-scented food not because they had been recruited to food containing that scent, but rather because they were visually

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attracted to the other yellowjackets already feeding there. Although Maschwitz et al. (1974) stated that they controlled for local enhancement by covering the dishes, details were not given.

Even if visual cues were eliminated in the Maschwitz study, odor cues were not, and odor-based cues could have biased their results. We recently demonstrated that *V. germanica* marks its food sites (Overmyer and Jeanne, in press), in contradiction to earlier conclusions (Kalmus 1954; Maschwitz et al. 1974). Foragers entered feeders that had been visited and marked by a number of conspecifics in less time than they took to enter clean feeders; furthermore, they were more likely to refuse to enter unvisited, unmarked feeders than visited, marked feeders. Thus, in the Maschwitz study, odor marks on the food dishes containing the training scent also could have influenced the results, since some of the dishes at which naive recruits were captured had been previously visited by many trained foragers. It is also possible that odors emanating directly from the bodies of feeding foragers could have influenced naive forager choice. Finally, the fact that trained foragers visited the same dishes as naive foragers in the Maschwitz study makes it possible that the naive foragers followed trained foragers to the dishes (tandem flying).

In view of these shortcomings of the Maschwitz et al. (1974) study, we revisited the question of whether yellowjackets recruit to food. Here we report the results of an experiment on *V. germanica* designed to test for recruitment to a scented food source in the absence of both local enhancement and chemical marking at the food site. These factors were eliminated by recording the preferences of recruits at food dishes distant from the dish frequented by the trained foragers. We conclude that *V. germanica* is indeed able to recruit naive nestmates to a food source, and apparently does so by means of odor cues present in the food.

Methods

The colony and field site

On 27 July 1995 a queenright colony of *V. germanica* containing approximately 600 workers was excavated from a lawn in Madison, Dane County, Wisconsin. The nest envelope was removed and the pedicellate connections between the horizontal combs were cut, separating the combs from one another. The combs were then glued by their pedicels next to one another onto the ceiling of a wooden nest box (40 × 36 × 4 cm inside dimensions) with a glass bottom (design after Akre et al. 1976). At 0800 hours the next morning the nest box containing the colony was placed inside a nylon screen house (1.7 × 3 × 1.7 m) at the University of Wisconsin's Charmany Farm in Madison, which was 12 km from its original site. The screen house was situated in the shade of a stand of poplars (*Populus grandidentata*) surrounded by meadowland. Foragers could exit via a 65-cm length of 2.0 cm (inside diameter) clear Tygon tubing connecting the nest box to a hole in the screen house wall. Workers were allowed to forage freely outside within 1 h after the nest box was put in place. During the remainder of the season the colony population increased, exceeding an estimated 1000 workers at its peak.

Forager training

Because German yellowjackets often forage on fruit juices and soda beverages containing corn syrup (S. Overmyer, personal observations), we used consumer grade corn syrup (a mixture of glucose, maltose, and glucose oligomers; BeMiller and Whistler 1996) diluted 3:1 corn syrup:water as the food source throughout this experiment, instead of the more familiar sucrose solution.

A 0.7-m-high tripod was set up 15 m east of the nest (Fig. 1). Atop the tripod we placed a 10-cm-diameter plastic petri dish ("training dish") containing corn syrup solution scented with vanilla extract (45% alcohol; extract = approximately 1% of the final solution by volume; final solution colored pale brown). Foragers were trained to visit this "training station" during the latter part of August 1995. The wasps were captured in vials as they exited the experimental colony, numbered by means of a color + position code of paint spots applied with Decocolor paint pens to the thorax, and released at the training dish. Twenty-four foragers were trained to visit the training station; at the beginning of the first experimental trial on 1 September, only these marked foragers were visiting the training station.

Experimental setup

A second 0.7-m-high tripod was set up approximately 22 m northeast of the nest and 18 m from the training station (Fig. 1). On this tripod we placed two 5-cm-diameter food cups, each containing corn syrup solution from the same batch as used to fill the training dish. The corn syrup in one of these (the "test cup") was scented with vanilla extract in the same concentration as used in the training dish, while the syrup in the other (the "control cup") was scented with imitation strawberry extract (30% alcohol; extract = 1% of the final solution by volume; final solution pale pink). The cups were positioned approximately 10 cm apart along a line perpendicular to the wind direction (Fig. 1). For each experimental trial the positions (i.e., to the right or left of the observer as she faced upwind) of the vanilla and strawberry cups were decided arbitrarily by blind shuffling. No foragers were trained to this "experimental station."

To ensure that biologically significant amounts of the food site marking substance did not accumulate on the cups at the experimental station and thus bias the choice of naive foragers, new cups were used for each trial. Our previous work had shown that dishes

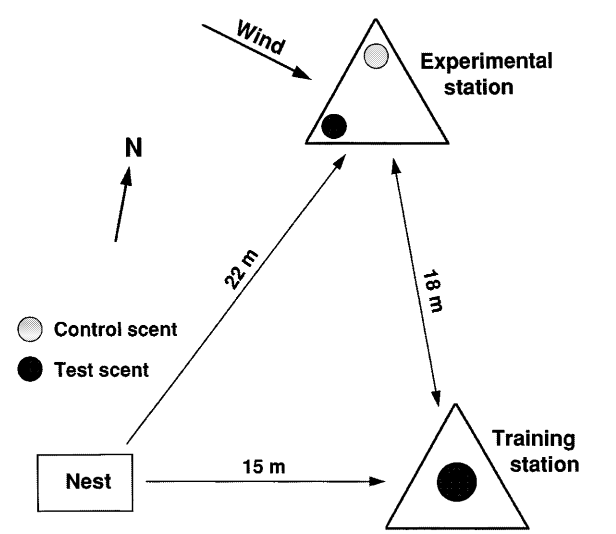

Fig. 1 Experimental design for field test of recruitment to food in *Vespula germanica*. The two cups on the experimental station were maintained across wind to one another through changes in wind direction from trial to trial

with ten or fewer previous visits are treated in the same way as new dishes by foraging *V. germanica* (Overmyer and Jeanne, in press). Foragers that arrived after more than ten foragers had visited either of the dishes during a single trial were not included in the data set.

Experimental trials

One experimental trial was conducted per day, weather permitting. A trial began when all three food sources were placed atop the two tripods. An observer sat 1–2 m from each station and recorded the arrival of each forager to the nearest minute. Because the food dishes were set out only when the observers were present, we knew that each unmarked forager arriving at either station was visiting it for the first time and had no previous experience with either station. We refer to these as "naive" foragers. At both stations all naive foragers were captured and chilled to immobility on ice. Trials lasted on average 2.3 h (range 1–3 h); if few trained foragers were visiting the training station, we ended a trial early.

At the end of each trial, the captured foragers were individually marked and then released at the training station so that they would begin visiting the training station regularly, instead of returning to the experimental station on their next foraging trip. Each newly marked forager was confirmed to belong to the experimental colony by observing her as she entered the nest through the clear entrance tube. Only foragers from the experimental colony were included in the data set. Each naive forager had her food choice at the experimental station scored only on her first visit; thereafter she was regarded as a "trained" forager. These new additions to the training cohort approximately balanced the numbers lost to attrition during the course of the study. The occasional trained (marked) forager that attempted to feed at the experimental station was immediately captured and released at the training dish.

We conducted food choice tests in two series of trials on the same colony. Series I began 1 September 1995 and lasted until 12 September. During this series, vanilla was the training and test scent, while strawberry was the control scent. In series II, run from 15 September to 11 October, the scents were reversed, i.e., strawberry became the training and test scent and vanilla became the control scent. This paired design controlled for any inherent preference *V. germanica* foragers may have for corn syrup solution scented with either vanilla or strawberry. On 13 September, prior to the beginning of series II, the trained foragers were retrained during a single 4-h period to forage on strawberry-scented, instead of vanilla-scented, solution at the training dish. By the end of the retraining session, the newly retrained foragers approached the training dish containing the strawberry-scented food without any hesitation, just as they had when approaching the vanilla-scented food in the dish during series I.

Data analysis

The food scent choices of naive foragers at the experimental station were analyzed with a binomial test of the null hypothesis of no preference for either test scent. We tested both the lumped data from series I and II and, because lumping gives more weight to the larger of the two data sets (series II in this case), we also tested data from each series separately.

As a further test for the effects of inherent forager preferences and training, we used the model

$$P(\mathrm{A}|\mathrm{A}) = P_\mathrm{A} + P_\mathrm{R}(P_\mathrm{B}) \text{ and } P(\mathrm{B}|\mathrm{B}) = P_\mathrm{B} + P_\mathrm{R}(P_\mathrm{A}),$$

where

$P(\mathrm{A}|\mathrm{A})$ = probability that a recruit will choose to feed at food scented with A, given that the trained foragers fed on food scented with A (i.e., A was the test scent),

$P(\mathrm{B}|\mathrm{B})$ = probability that a recruit will choose to feed at food scented with B, given that the trained foragers fed on food scented with B (i.e., B was the test scent),

P_A = probability that a forager inherently prefers food scented with A over food scented with B,

P_B = probability that a forager inherently prefers food scented with B over food scented with A (P of 0.5 = no preference; $P_\mathrm{A} + P_\mathrm{B} = 1$), and

P_R = probability that trained foragers returning with food scented with B could cause a recruit to choose food B despite its inherent preference for A (or vice versa).

We tested two hypotheses:

H_0: $P_\mathrm{R} = 0$, i.e., a recruit's food choice is influenced only by its inherent preferences [$P(\mathrm{A}|\mathrm{A}) = P_\mathrm{A}$ and $P(\mathrm{B}|\mathrm{B}) = P_\mathrm{B}$], and

H_A: $P_\mathrm{R} > 0$, i.e., a recruit's choice is biased toward the type of food brought back to the nest by trained foragers.

We define a new variable, S, as $P(\mathrm{A}|\mathrm{A}) + P(\mathrm{B}|\mathrm{B})$. S can take values between 1 and 2. If the null hypothesis is true, then $P_\mathrm{R} = 0$ and $S = 1$. The P-value for this model is the likelihood that an equal or more extreme value of S would be obtained by chance alone, if the null hypothesis is true.

We make the assumption that our results will show either that naive recruits have no preference for the training- or the control-scented dish, or that they will choose the training-scented food more often. In other words, we do not expect that if trained foragers are bringing training-scented food into the nest, then this food will become less attractive to recruits than it otherwise would be. Given this assumption, one-tailed tests are appropriate for all three of our tests.

Results

Data in series I were gathered over 8 days (20.15 h), while data in series II were gathered over 18 days (39.25 h). Foraging traffic was lower during series II, probably because of cooler weather and because the worker population was beginning to decline as the end of the season approached.

All foragers approached the dishes of food at the experimental station from downwind, flying in a zig-zag pattern. Each naive forager arrived at least 3 min after the previously arriving forager was captured, so local enhancement or other as yet unknown social factors acting at the food site could not have influenced the food dish choice of any of the recruits. Furthermore, there was no evidence of tandem flying: all foragers arrived singly.

During the course of the entire experiment, 32 naive (unmarked) foragers from the experimental colony arrived at the experimental station. (Four foragers arrived from other nests during the same time period.) Of these 30 arrived when 10 or fewer foragers had previously visited the dishes, and were therefore included in the analyses. In both series of trials, the majority of naive foragers arriving at the experimental station chose the test scent, regardless of whether it was vanilla or

Table 1 Number of naive foragers of *Vespula germanica* choosing test- and control-scented corn syrup solution at the experimental station. *P* values are for one-tailed binomial tests

Series	Number of naive foragers choosing:			
	Training scent	Test scent	Control scent	*P*
I	Vanilla	13	0	< 0.001
II	Strawberry	13	4	0.024
Both		26	4	< 0.001

strawberry (Table 1). A binomial test on the lumped data led to rejection of the null hypothesis of an equal likelihood of choosing the test- and control-scented solutions (Table 1). Separate tests of each data set (series I and II) also rejected the null hypothesis of equal likelihood of choosing each type of food (Table 1). In the analysis based on the model, the null hypothesis, that recruitment does not exist and thus cannot overcome a forager's natural preference for the control scent, was rejected ($S = 1.764$, $P \ll 0.001$). If we relax the assumption made above (that training foragers to a food scent does not make it less likely that recruits will choose that scent) and apply a two-tailed test, the results for all three analyses still reject the null hypothesis of no recruitment at the 0.05 level.

All four arrivals of naive foragers at the control dish (Table 1) occurred on a single day, 20 September. On that day the activity level of the colony was unusually low when we arrived at the field site. No foragers left the nest and few entered during a 10-min observation period. This low level of activity may have been caused by a preceding period of unseasonably cool weather during which few workers could forage. To stimulate foragers to become active so that an experimental trial could be initiated, we placed approximately 0.5 ml of unscented corn syrup solution in the entrance tunnel of the nest. Soon several foragers began feeding on the droplets, and within 1 h several of the previously trained foragers began making regular foraging trips to the training dish. During the experimental trial that immediately followed, eight naive foragers arrived at the test-scented cup (strawberry) and four arrived at the control-scented cup (vanilla). Later it was learned that the corn syrup had been manufactured with a minute amount of vanilla, equal to about 1/20th the amount in the vanilla-scented corn syrup solution used in our feeding dishes.

Discussion

We conclude that *V. germanica* is indeed able to recruit nestmates to carbohydrate food. This is the first unequivocal demonstration that recruitment to food occurs in the social Vespidae. Our result agrees with the earlier conclusion of Maschwitz et al. (1974). Unlike their experimental design, however, ours ensured that naive foragers approached the experimental station and made their food choices there in the absence of any social cues, such as local enhancement or the food site marking substance. Because trained foragers did not visit the experimental station, the possibility that they could have led naive recruits there by tandem flying is also ruled out. Furthermore, the naive foragers could not have discovered the food at the experimental station primarily by searching independently. If they had, they should have chosen the test and control scents with equal frequency, given that they showed no preference for either of the odors we used over the course of the experiment. Rather, the fact that significantly more naive foragers chose the food with the training scent leads us to conclude that the critical cue is food odor.

What is the recruitment mechanism? The simplest hypothesis consistent with our results is that nestmates naive about the location of the resource come into contact with rich food brought into the nest by successful foragers and learn its odor, forming an olfactory search image. They then leave the nest and search for that odor. (Because the corn syrup solution placed in the nest entrance on 20 September contained a small amount of vanilla flavoring, it is likely that the four foragers choosing vanilla-scented corn syrup solution on that date had developed an olfactory search image for vanilla.) Such an odor-based mechanism can be expected to bias exploitation in favor of resources that are upwind of the nest. Indeed, in the two trials during which the wind blew from the experimental station toward the nest, more recruits than usual were captured. Similarly, Gaul (1952), working with *V. maculifrons*, found that foragers discovered honey baits upwind of the nest, while downwind baits went undetected. Because our experimental station was rarely upwind of the nest, our data likely underestimated the actual recruitment rate.

Our results do not exclude the operation of more complex recruitment mechanisms in tandem with the odor-based mechanism. It is possible, for example, that successful foragers in the nest enhance the number of naive foragers that leave to search for the food source by attracting their attention with some sort of signal, or even that they communicate direction and/or distance information about the location of the resource. If communication of location were occurring, one might have expected significantly more recruits to have come to the training station than to the experimental station, and this did not happen (38 vs. 30 recruits, respectively). However, our design accommodated differences between the two stations with regard to wind direction, density of the marking substance, and local enhancement that may have obscured the effects of location communication. Thus, our experiment does not provide any evidence relevant to establishing whether location communication exists. To determine whether any signals are given in the nest to accompany the food-odor-based recruitment mechanism will require further experiments designed explicitly to test for them.

The distribution of recruitment ability among the social wasps remains an open question. Maschwitz et al. (1974) studied recruitment in *V. germanica* and its close relative, *V. vulgaris*, and obtained similar evidence for recruitment in both species. Given that we confirmed their results for *V. germanica*, we suspect that future work will show that *V. vulgaris* also recruits to carbohydrate sources. *V. pensylvanica*, however, a member of the same species group, may lack the behavior: Akre was unable to demonstrate recruitment to fish baits in this wasp (Akre 1982). The species needs to be reexamined, however, because his test was not designed to detect modest rates of recruitment such as we found in *V. ger-*

manica. On the other hand, if Akre (1982) is right, it raises the possibility that yellowjackets are able to recruit to carbohydrate sources but not to protein. Recruitment ability, even if to only one type of food, could well provide a species with an important competitive edge. Unlike other members of their species group, *V. germanica* and *V. vulgaris* have become established in many parts of the world, where they successfully compete with native fauna. For example, since its introduction into North America, *V. germanica* has partially taken over niches occupied by *V. maculifrons* and is able to dominate resources associated with garbage (Keyel 1983). The relative success of these two species may be due in part to their ability to recruit to food.

There is anecdotal evidence for recruitment to food in two genera other than *Vespula*. *Vespa mandarinia* is an Asian hornet that specializes in raiding colonies of other vespines and honey bees. Following initial visits to the victim colony by one or a few *V. mandarinia* foragers, up to several dozen nestmates arrive in a short period of time, initiating the "slaughter phase" of the raid (Matsuura 1991). The dramatic increase in number of foragers suggests that some form of recruitment is in operation, but the mechanism has not yet been worked out. Another instance is the Neotropical polistine wasp *Polybia scutellaris*, for which Lindauer (1961) cited preliminary evidence for recruitment to food. Unfortunately, he gave no details. In contrast, experimental tests on two species of *Agelaia*, another Neotropical polistine, failed to demonstrate strong recruitment to carrion baits (Jeanne et al. 1995).

Improving on our extremely rudimentary understanding of the distribution of recruitment among the social wasps will require carefully designed field experiments. As we learn more about the taxonomic distribution of this behavior, it will be particularly interesting to discover whether recruitment is limited to just a few species, and if so, whether it correlates with ecological dominance.

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