

Foraging in Social Wasps: *Agelaia* Lacks Recruitment to Food (Hymenoptera: Vespidae)

ROBERT L. JEANNE

Departments of Entomology and Zoology, University of Wisconsin,
Madison, WI 53706, U.S.A.

JAMES H. HUNT

Department of Biology, University of Missouri,
St. Louis, MO 63121, U.S.A.

MALCOLM G. KEEPING*

Zoology Department, University of Durban-Westville,
Private Bag X54001, Durban 4000, South Africa

ABSTRACT: Experimental tests on *Agelaia multipicta* in Venezuela and *A. hamiltoni* in Peru failed to demonstrate recruitment of nestmates to carrion. Foraging ranges of neighboring colonies overlap and foragers occasionally showed aggression when they encountered one another on the baits. These species appear to engage in scramble competition with congeners and non-congeneric scavenging wasps, ants, and bees. A possible reason for the failure of these wasps to evolve nest-based communication of food location is the unfavorable benefit/cost ratio due either to inadequate colony size or to the behavior of inter-specific competitors at carrion.

Many species of termites, ants, and social bees have evolved the ability to recruit nestmates to food resources. When solitary foragers discover an item they cannot handle alone, they communicate its presence to other foragers in the nest. Some ant and higher termite species lay chemical trails that provide distance and direction information about the food resource (Wilson, 1971; Hölldobler and Wilson, 1990). Honey bees (*Apis* spp.) communicate distance and direction information via the round and waggle dances (Frisch, 1967; Gould et al., 1985) and some of the stingless bees (Meliponinae) lay trails of scent marks to sources of nectar or carrion (Lindauer and Kerr, 1958; Roubik, 1989). Based on what is known of ants and bees, the existence of a recruitment mechanism appears to be correlated with large colony size and the utilization of rich, localized, ephemeral food resources (Taylor, 1978; Johnson, 1983; Beckers et al., 1989; Hölldobler and Wilson, 1990).

Some species of social wasps achieve colony sizes of 10^4 or more (Jeanne, 1991), comparable to those of ants, bees and termites that recruit to food. Many also forage on rich, ephemeral food resources such as carrion (O'Donnell, 1995). Yet the social wasps (Vespidae) remain the only group of eusocial insects for which nest-based recruitment to a food source has not been clearly documented. There is evidence for weak recruitment to concentrated food sources in some vespines. When foragers of *Vespula germanica* (Fab.) and *V. vulgaris* (L.) were trained to dishes of scented honey, more nestmates arrived at dishes with the same scent

* Present address: Department of Entomology, South African Sugar Association Experiment Station, Mt. Edgecombe 4300, South Africa.

Accepted for publication 16 December 1994.

than to nearby control dishes scented differently (Maschwitz et al., 1974). When the Japanese hornet, *Vespa mandarinia* Smith, raids a colony of honey bees (*Apis mellifera* L.) the number of attacking hornets increases rapidly during the slaughter phase from two or three to dozens, suggesting some form of recruitment (Matsuura and Yamane, 1990). There is no evidence in either case, however, that distance or directional information is communicated within the nest or that odor trails are utilized.

Within the Polistinae, the species that reproduce by swarms have evolved a system of chemical communication to recruit swarm-mates from the natal nest site to a new nest site selected by scouts (Jeanne, 1981, 1991). This mechanism is similar to that used by stingless bees (Meliponinae) to recruit to food (Lindauer, 1961) and could be used in the context of food recruitment. *Polybia scutellaris* White is said to have a primitive recruitment system lacking communication of distance and direction (Lindauer, 1961). In contrast, Forsyth (1978) asserted that he tested 10 species in 6 genera (*Metapolybia*, *Polybia*, *Parachartergus*, *Synoeca*, *Brachygastra*, *Agelaia*) and found no evidence of recruitment. Neither Lindauer nor Forsyth, however, described the type of bait or methods they used or provided any quantitative data to support their conclusions.

Because food recruitment may be poorly developed in the wasps and therefore difficult to detect, it would be careless to conclude on the basis of the preliminary studies done so far that social wasps lack this ability. Yet the question of recruitment to food among wasps is important for a full understanding of the conditions under which such communication systems evolved in the social insects. If the social wasps lack recruitment, it raises the question of why.

Here we report the first controlled experiments designed to test the null hypothesis that nest-based recruitment to food does not exist in polistine wasps. We chose to work with *Agelaia*, a Neotropical genus of 21 species. Members of the genus are potential candidates for the occurrence of food recruitment because some species form colonies in excess of 10^3 adults (10^6 in *A. vicina*) (Jeanne, 1991) and because they forage on vertebrate carrion (O'Donnell, 1995). We conducted our experiments on *A. multipicta* (Haliday) and *A. hamiltoni* Richards because of their availability in our study sites. A colony of *A. multipicta* collected in Brazil contained 5500 adults (Araujo, 1940; Richards, 1978); there are no published records on colony populations of *A. hamiltoni*.

Materials and Methods

Venezuela

Field studies were done on *Agelaia multipicta* October 19–23, 1993 at Hato Piñero, a cattle ranch and biological station in the southern part of the state of Cojedes. The climate is seasonally dry; October is at the end of the wet season. The habitat includes patches of semi-deciduous tropical forest and savanna interspersed with cleared pastureland. Gallery forest borders the waterways. This region of Venezuela is called the llanos (plains); its plant communities are described by Sarmiento (1983). Our experiments were done in a 50×100 m area of grass and low herbaceous vegetation under large shade trees adjacent to ranch buildings (Fig. 1). The area was chosen because of the abundance of foragers of *A. multipicta*, which is the only member of the genus we found at this site. An

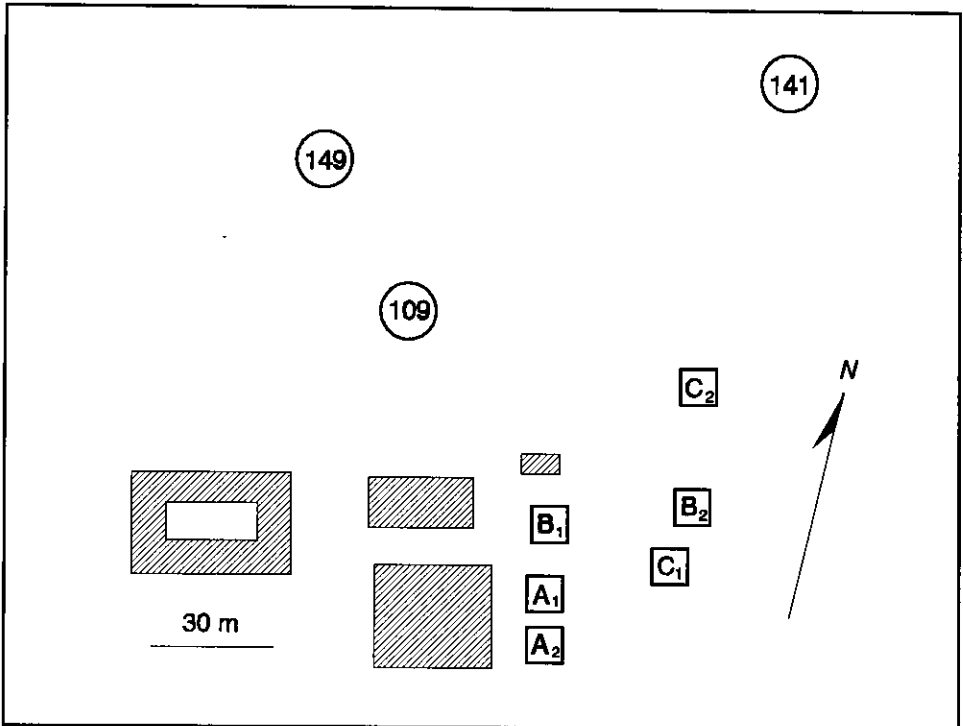


Fig. 1. Positions of bait dishes in relation to sites of known colonies of *Agelaius multipicta* in Venezuela. Circles represent nests, squares indicate bait dishes, and hatched rectangles represent buildings. Dishes belonging to separate replications are labelled with different letters. Subscripts show position of (1) control dish and (2) experimental dish on first trial of each of replications A, B, and C.

A. multipicta colony collected from the nest of a plain-fronted thornbird (*Phacellodomus rufifrons*) contained 1750 adults. Based on comparisons of forager traffic at this colony with that of colonies in our study area, the latter were much larger.

We designed our experiments explicitly to test whether communication of food location occurs at the nest. We baited foragers with lumps of raw ground beef, approximately 2 cm in diameter, placed in petri dishes and set on benches approximately 0.5 m off the ground. The use of benches effectively excluded ants. Baits were refreshed every half hour, either by turning them over, breaking them apart to expose moist surfaces, or by replacing them with fresh pieces. Each of the three replicates consisted of two trials run at the same times on two successive days. Each trial employed one control dish and one experimental dish (treatments) spaced 11–48 m apart. The locations of the dishes for the three replicates were selected so as to sample different parts of the 50 × 100 m area (Fig. 1). On the first day of a replication one of the two dishes was arbitrarily designated the control (location 1), the other experimental (location 2). On the second day the dishes were placed in the same locations at the same hour, but their treatments were switched to control for location effects. This experimental design tests for

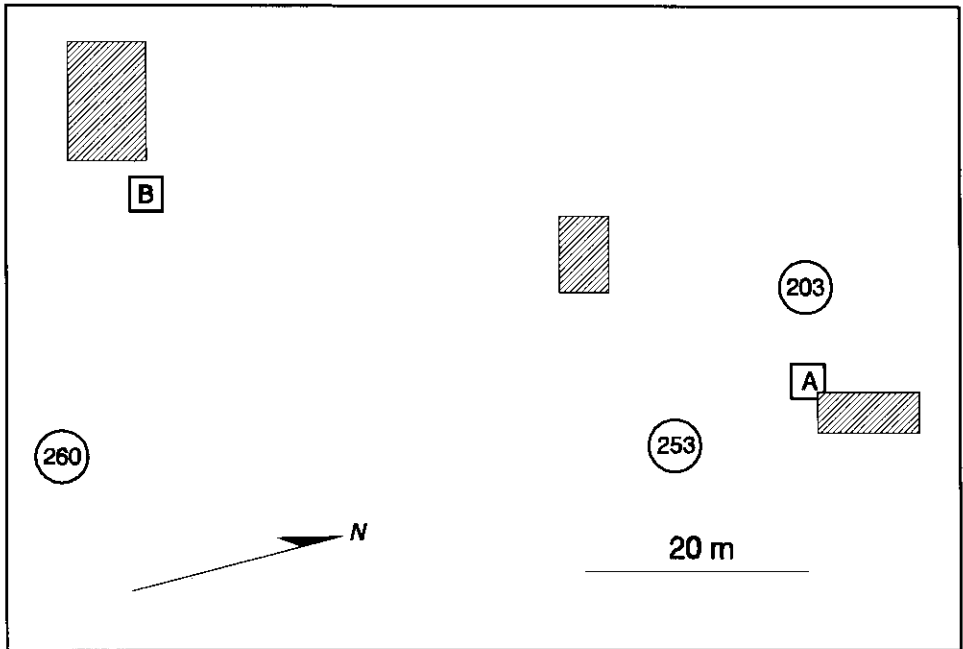


Fig. 2. Positions of bait dishes in relation to sites of known colonies of *Agelaiia hamiltoni* in Peru. Circles represent nests, squares indicate bait dishes, and hatched rectangles represent buildings. Dishes belonging to separate replicates are labelled with different letters.

any kind of communication of the location of a specific resource, but does not test for a general alerting at the nest to all resources with the same odor.

A trial was begun with the simultaneous placing of baits in the control and experimental dishes. All foragers arriving at the control dishes were captured with forceps and killed in a killing jar to prevent them from recruiting or attracting nestmates. Foragers arriving at the experimental dishes were carefully captured with forceps, marked with paint (DecoColor® opaque paint markers), and released. The number of new foragers arriving at each dish during each half-hour interval was recorded. Each of the 6 trials lasted 2 hours.

Peru

Experiments were conducted December 13–17, 1993, at Explorama Lodge, 80 km down the Amazon River from Iquitos, Peru, in an area of disturbed second growth vegetation adjacent to tropical wet evergreen forest. *Agelaiia hamiltoni* was the most common member of its genus in this habitat. This wasp nests in cavities in the carton nests of ants of the genus *Azteca* (Richards, 1978). Colony sizes are unreported for this species, but appear to be large. When we disturbed colony #253 following these experiments, several thousand (estimated) adults emerged from the nest to defend it.

As in Venezuela, bait (approximately 3×3 cm piece of raw beef [replicate 1] or fish [replicate 2]) was placed in a petri dish and set on a stool (approximately 0.5 m above ground) to exclude ants. Two modifications of the Venezuela protocol were made. First, in order to control for the possibility that a general alerting at

the nest to the odor of the bait may bring recruits to both the experimental and the control dishes, the control was put out on one day, followed by the experimental bait in the same position at the same time on the following day. The control was run first to avoid biasing the results. If the experimental trial were run first, it would train a cohort of foragers that could artificially elevate the numbers recorded during the control trial on the second day.

Second, to control for the possibility that killing foragers at the control dish may deplete the local foraging population and result in a downward bias of the numbers finding the experimental dish on the next day, each new arrival at the control dish was aspirated from the control bait, marked, held for the duration of the trial, then released. In other words, wasps discovering the control dishes were not allowed to return to their nests with food, but they were returned to the foraging population prior to the next day's experiment. Foragers reaching the experimental dish were captured with forceps, marked, and immediately released, as before. The number of new foragers arriving in each half hour interval at each dish was recorded. The position of the dish in each trial in relation to known nests of *A. hamiltoni* is shown in Fig. 2. Each of the two control and two experimental trials lasted 2.5 hours.

Analysis

Analysis of variance on square-root-transformed data was used to test the null hypothesis that the numbers of new foragers arriving at the experimental and control baits did not differ (Systat for Windows, 1992).

Results

Venezuela

Handling and marking new arrivals at the experimental dishes did not appear to have any lasting effect on the behavior of foragers. Most returned within a few minutes after their release and went on to make regular trips for the duration of the trial.

Analysis of variance on half-hourly intervals (Fig. 3) showed no effect of time ($P = 0.122$) or treatment ($P = 0.120$) (split-plot ANOVA model in which the whole plot consisted of 3 replicated 2×2 Latin squares, subplot treatment = time). Because data for half-hourly intervals were sparse, we reanalyzed the results using data summed for the entire 2 hours of each trial (Latin square design with 3 replicates, with location and trial used as blocking factors; Table 1). There was no effect of treatment or location (Table 2). While the effect of treatment was close to significant, control dishes had more arrivals than experimental, the opposite of what would be expected if recruitment occurred. There was a significant trial effect: control dishes yielded more than experimental at location 1 in two out of three replicates.

By searching in the directions indicated by the bearings of foragers departing from the food dishes, we were able to discover the nests shown in Fig. 1. At most of our dishes, foragers arrived from at least two of these colonies. Departures to nests #109 and #149 could not be distinguished because they lay in approximately the same direction from the experimental area. Foragers departing from the baits could be tracked visually for up to 20 m. In most cases departing foragers flew directly and without stopping toward the nest at heights of 2–4 m. On one occasion

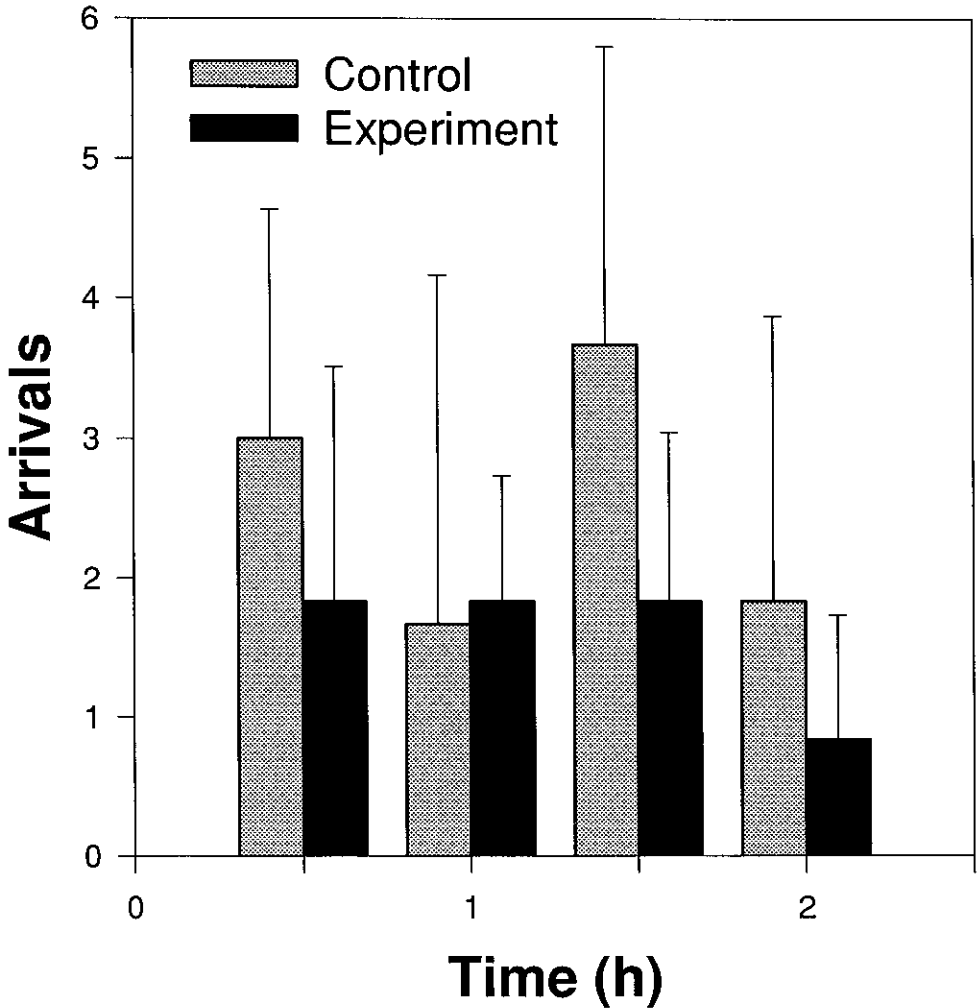


Fig. 3. Numbers of new foragers of *Agelais multipicta* arriving on the experimental and control dishes during each half hour. Error bars = standard error.

a departing forager landed for a few seconds on a leaf several meters from the bait, apparently to adjust her load. There was no evidence of any behavior suggesting that she scent-marked the leaf. Likewise, there was no evidence that foragers returning to the baits landed on nearby vegetation to scent-mark.

The first forager arrived on average 11.2 minutes after the baits were placed out ($SD = \pm 10.6$; $n = 12$). As the numbers of individual foragers exploiting the experimental dish increased, the likelihood that two or more found themselves together on the bait also increased. In some cases, when two foragers encountered one another on the bait they displayed aggression, with one chasing the other from that part of the meat. On other occasions foragers encountered each other without displaying such aggression. Because foragers arrived from two or more colonies, these attacks may have been on non-nestmates.

Table 1. Results of baiting experiments with *Agelais multipicta* (Venezuela). Each row represents a single bait dish. Replication: 1 set of 2 paired control and experimental baits, set out on successive days. Treatment: 1 = control dish; 2 = experimental dish. Location: 1 = dish serving as control on day 1; 2 = dish serving as experimental on day 1 (see Fig. 1). Trial: 1 = day 1; 2 = day 2. Arrivals = number of new foragers arriving at each dish during two hours.

Replication	Trial	Treatment	Location	Arrivals
A	1	1	1	16
A	1	2	2	10
A	2	1	2	5
A	2	2	1	4
B	1	1	1	22
B	1	2	2	6
B	2	1	2	5
B	2	2	1	8
C	1	1	1	6
C	1	2	2	4
C	2	1	2	7
C	2	2	1	6

Peru

Capturing and marking did not appear to disturb foragers arriving at the baits. Many of those marked on the control dishes and released at the end of the trial showed up at the experimental dishes the next day. New arrivals at the experimental dishes often returned within minutes after their release and most made many trips during the course of the trials.

Most of the arrivals came in the early time intervals (Fig. 4), yet the time effect was only marginally significant ($P = 0.051$) (split-plot ANOVA, time nested within day). If recruitment were going on, we would expect the numbers of arrivals to increase with time. Analysis of lumped data (Table 3) showed no effect of treatment or replication (randomized complete block design, blocked on pairs of days) (Table 4).

Our baits were exploited by at least four colonies of *Agelais hamiltoni*, as determined by the bearings taken by foragers departing from the dishes. The locations of three of these were known colonies in the vicinity of our experiment (Fig. 2). The fourth, which we could not find, lay to the NW of dish location A. As was the case in Venezuela, foragers sometimes showed aggression when they encountered each other on the baits. As in *A. multipicta*, there was no evidence of anything other than direct, non-stop flights by foragers to and from the baits.

Table 2. Results of ANOVA on square root transformed data for Venezuela. Squared multiple $R = 0.983$.

Source	Sum-of-squares	DF	Mean-square	F-Ratio	P
Replication	0.930	2	0.465	7.345	0.120
Treatment	0.945	1	0.945	14.934	0.061
Location (rep)	2.113	3	0.704	11.129	0.084
Trial	1.581	1	1.581	24.978	0.038
Replication•Trial	1.741	2	0.870	13.749	0.068
Error	0.127	2	0.063		

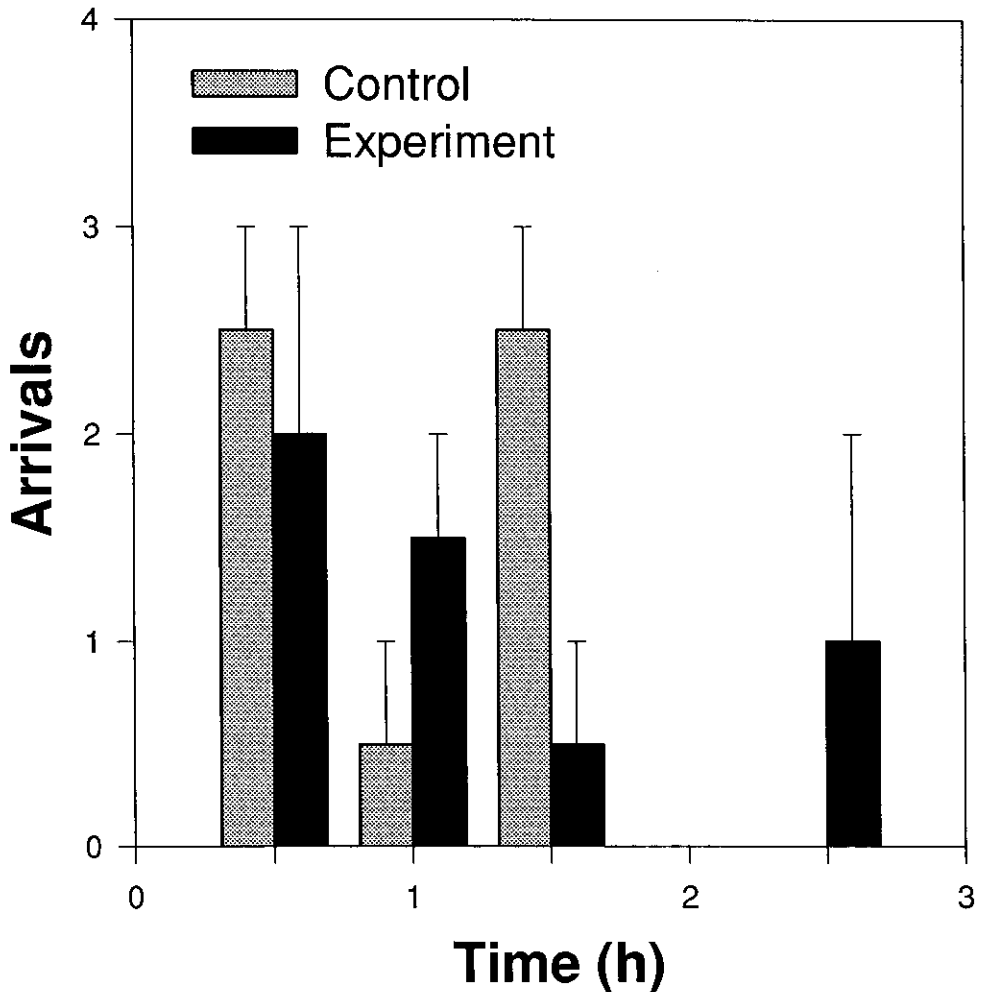


Fig. 4. Numbers of new foragers of *Agelaiia hamiltoni* arriving on the experimental and control dishes during each half hour. Error bars = standard error.

The first *A. hamiltoni* forager arrived on average 2.8 minutes after the bait was exposed ($SD = \pm 3.7$; $n = 4$). In addition to *A. hamiltoni*, similar numbers of *Angiopolybia pallens* were attracted to the baits. These wasps are smaller than *A. hamiltoni* and were often chased by the latter but they never attempted to chase *A. hamiltoni*.

Discussion

Our results failed to reject the null hypothesis that *Agelaiia multipicta* and *A. hamiltoni* do not recruit nestmates to concentrated protein resources. In Venezuela, although our experiments were not designed to rule out the possibility of a general alerting at the nest to a food resource, for example via food odor carried to the nest, the fact that total numbers (experimental and control dishes) of new foragers arriving did not increase over time suggests that this was not going on.

Table 3. Results of baiting experiment with *Agelaia hamiltoni* (Peru). Each row represents one trial at one dish. Replicates positioned as in Fig. 2. Treatment: 1 = control dish; 2 = experimental dish. Arrivals = total number of new foragers arriving during two and a half hours.

Replication	Treatment	Arrivals
A	1	6
A	2	5
B	1	5
B	2	5

There is therefore no evidence, either from our numerical data or our direct observations of the behavior of foragers, that foragers of either species recruit nestmates to carrion. We conclude that foragers of these species do not inform naive nestmates about the location of resources, either by communicating information at the nest, by laying scent trails, or by leading them in flight to the site. Although our experiments were not designed to test for local enhancement, as has been documented for yellowjackets (Parrish & Fowler, 1983; Reid et al., 1995), the fact that the numbers of foragers at the experimental dishes did not increase over time suggests that it is not going on.

The fact that foragers from two or more colonies fed at the same dish in each experimental area indicates that these species do not maintain foraging territories; instead, the foraging ranges of adjacent colonies overlap. Thus, the foraging strategy utilized by these species appears to be scramble competition. Foragers find food quickly in their foraging area and exploit it individually but quickly, rather than recruit nestmates or try to defend a foraging area or a resource against non-nestmate congeners.

The arrival of significantly more foragers at some of the control dishes than at experimental dishes in Venezuela deserves comment. Difference in handling is not a likely explanation: new foragers arriving at both dishes were captured using forceps and so had equal opportunity to release any attractive or repellent substances onto the baits. A second possibility is a reverse local enhancement effect, such that foragers are less likely to land on a resource at which one or more wasps are already present. Our observations of wasps coming into the baits revealed no evidence of this. Third, it is possible that foragers avoid areas of high forager density and move into areas of low density. Trapping foragers out of the area of the control dish may have reduced the density so that new foragers moved in from neighboring areas and discovered the control baits. Further research on the dynamics of foraging in this species will be necessary to determine if this result is anything more than statistical artifact.

Why do these species lack the ability to recruit to rich patches of food such as

Table 4. Results of ANOVA on square-root-transformed data for Peru. Squared multiple $R = 0.667$.

Source	Sum-of-squares	DF	Mean-square	F-ratio	P
Treatment	0.250	1	0.250	1.000	0.500
Replication	0.250	1	0.250	1.000	0.500
Error	0.250	1	0.250		

carrion? One possibility is that during their evolutionary history social wasps lacked the genetic variability to give natural selection appropriate material on which to operate. This seems unlikely, in view of the fact that the swarm-founding species have evolved a system of chemical communication for guiding swarms from the natal nest to a new nest site (Jeanne, 1981, 1991), suggesting that adaptable traits are present.

A second possibility is that there may be a social constraint. Perhaps there is a threshold colony size below which the costs of recruitment exceed the benefits. Numbers of recruitable foragers may be too low, for example, to enable a colony to build up enough numbers at a resource to defend it against competitors. Likewise, recruitment may pay only if colonies are so big that relying on individual foraging would require extremely large areas to be covered to bring in enough food. We have no idea what critical colony sizes would be, except that it appears to be larger than for ants (Beckers et al., 1989).

Third, the apparent lack of ability of wasps to store food of this type in the nest may mean that little fitness gain is to be had by the ability to recruit nestmates to it. Although the larvae could likely absorb protein food at higher rates than the colony is ordinarily able to collect it, the size of this buffer may not be large enough to make recruitment adaptive. Some wasp species collect and store nectar in the nest, sometimes in large amounts (Jeanne, 1991). If lack of storability is the constraint, it would be worth knowing whether such species recruit to carbohydrate sources.

Finally, ecological factors almost certainly have played a role. Perhaps carrion occurs too rarely for this kind of resource to have been a significant selective force on foraging behavior in epiponine wasps. Alternatively, the benefit/cost ratio of recruiting to these resources may be too low for wasps, given the nature of competition that must exist for them. The costs of communicating to nestmates, measured, for example, as the time and energy it would take to lay a chemical trail, may not be repaid unless recruitment can result in effective defense of the resource against competitors of the same or other species. Many species of ants recruit to carrion and are difficult for wasps to counter. In fact, some of the ant species wasps are likely to encounter at carrion may well pose a threat of predation for the wasps. Several species of stingless bee are carrion feeders and recruit quickly (Roubik, 1989). In the face of such competition, the wasps' best strategy may be to be opportunistic solitary foragers, i.e. by being first to discover a newly-available food patch and by exploiting it rapidly until ants and/or bees recruit enough numbers to force the wasps out.

A full understanding of foraging in polistine wasps will require proceeding on two fronts. First, we need to extend behavioral studies such as this one to other species and genera to determine the presence or absence of recruitment to protein and carbohydrate food. Second, we need ecological studies to learn how wasps compete for resources in a variety of habitats against potential competitors, including not only other wasp species, but ants and stingless bees as well.

Acknowledgments

Our thanks go to the Fundacion Branger and to the staff of Hato Piñero and to Expediciones Amazonicas for all their help in making our visits possible. We also thank Dr. Klaus Jaffe for his help in arranging the visit to Venezuela. James

Carpenter kindly determined our specimens. We thank Erik Nordheim for statistical advice. For thoughtful and helpful comments on early drafts of the manuscript we thank Godfrey R. Bourne, Stanton G. Braude, and Zuleyma Tang-Martinez. Research supported by the South African Foundation for Research Development, National Science Foundation grant #IBN-9222108 to RLJ, the College of Agricultural and Life Sciences, University of Wisconsin, Madison, WI 53706, and by the Office of Research and the Department of Biology, University of Missouri–St. Louis, St. Louis, MO 63121.

Literature Cited

- Araujo, R. L. 1940. Contribuição para o conhecimento de "*Gynopolobyia meridionalis* (Iher., 1904)" (Hym.). Arquivos do Instituto Biológico São Paulo 11:11–16.
- Beckers, R., S. Goss, J. L. Deneubourg, and J. M. Pasteels. 1989. Colony size, communication and ant foraging strategy. *Psyche* 96:239–256.
- Forsyth, A. 1978. Studies on the behavioral ecology of polygynous social wasps. Unpublished Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts. 226 pp.
- Frisch, K. v. 1967. The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, Massachusetts.
- Gould, J. L., F. C. Dyer, and W. F. Townes. 1985. Recent progress in the study of the dance language. In B. Hölldobler and M. Lindauer (eds.), *Experimental Behavioral Ecology and Sociobiology*, pp. 141–162. Fischer-Verlag, New York.
- Hölldobler, B., and E. O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge, Massachusetts.
- Jeanne, R. L. 1981. Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier). *Animal Behaviour* 29:102–113.
- Jeanne, R. L. 1991. The swarm-founding Polistinae. In K. G. Ross and R. W. Matthews (eds.), *The Social Biology of Wasps*, pp. 191–231. Comstock Publishing Associates, Ithaca, New York.
- Johnson, L. K. 1983. Foraging strategies and the structure of stingless bee communities in Costa Rica. In P. Jaisson (ed.), *Social Insects in the Tropics*, pp. 31–58. Université Paris-Nord, Paris.
- Lindauer, M. 1961. *Communication Among Social Bees*. Harvard University Press, Cambridge, Massachusetts.
- Lindauer, M., and W. E. Kerr. 1958. Die gegenseitige Verständigung bei den stachellosen Bienen. *Zeitschrift für Vergleichende Physiologie* 41:405–434.
- Maschwitz, U., W. Beier, I. Dietrich, and W. Keidel. 1974. Futtermverständnis bei Wespen der Gattung *Paravespula*. *Naturwissenschaften* 11:506.
- Matsuura, M., and S. Yamane. 1990. *Biology of the Vespine Wasps*. Springer-Verlag, Berlin.
- O'Donnell, S. 1995. Necrophagy by Neotropical swarm-founding wasps (Hymenoptera: Vespidae, Epiponini). *Biotropica* 27:133–136.
- Parrish, M. D., & H. G. Fowler. 1983. Contrasting foraging related behaviours in two sympatric wasps (*Vespula maculifrons* and *V. germanica*). *Ecological Entomology* 8:185–190.
- Reid, B. L., J. F. MacDonald, & D. R. Ross. 1995. Foraging and spatial dispersion in protein-scavenging workers of *Vespula germanica* and *V. maculifrons* (Hymenoptera: Vespidae). *Journal of Insect Behaviour* 8:315–330.
- Richards, O. W. 1978. *The Social Wasps of the Americas Excluding the Vespinae*. British Museum (Natural History), London.
- Roubik, D. W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.
- Sarmiento, G. 1983. The savannas of tropical America. In F. Bourliere (ed.), *Ecosystems of the World*, pp. 245–288. Elsevier, Amsterdam.
- Systat for Windows: Statistics, Version 5 Edition. 1992. Systat, Inc., Evanston, Illinois.
- Taylor, F. 1978. Foraging behavior of ants: theoretical considerations. *Journal of Theoretical Biology* 71:541–565.
- Wilson, E. O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, Massachusetts.