Foraging Behavior in Two Species of *Ectatomma* (Formicidae: Ponerinae): Individual Learning of Orientation and Timing

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The foraging behavior of marked individuals of Ectatomma ruidum *and* E. tuberculatum *(Formicidae: Ponerinae) was observed on Barro Colorado Island, Panama, in order to determine whether learning of orientation and timing is involved when foraging on patchy resources on the forest floor. Foraging experiments under seminatural conditions were designed to control for the spatiotemporal distribution of resources at one or two preying sites. Using both single- and multi–event past experience, individual foragers of* E. ruidum *and (although less significantly)* E. tuberculatum *made directional and temporal adjustments to their behavior in response to previous differential foraging success. In spite of considerable individual variation in foraging efficiency, it is hypothesized that the observed differences in cognitive abilities can be invoked to explain ecological differences among both species.*

INTRODUCTION

Recent studies in behavioral ecology have attempted to integrate functional explanations of behavior with insights from the cognitive sciences, leading to the emergence of the interdisciplinary field of cognitive ecology (see,

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e.g., Real, 1993; Dukas, 1998; Healy and Braithwaite, 2000). An important focus within this field is the relation between the learning capabilities of animals and their behavioral plasticity in nature. Speaking in the most general terms—What are the benefits of learning? Much research in cognitive ecology has been directed to foraging behavior and to the question of how learning and memory increase foraging efficiency (Bateson and Kacelnik, 1996). Another important question addresses the time span used by animals to assess the food resources in variable environments (Real, 1991). Arguably, more rigorous testing of the adaptiveness and evolution of learning can be achieved by comparing closely related species that differ in their biologies and learning capabilities (see, e.g., Coddington, 1988, Krebs *et al.*, 1990, Wenzel, 1992). In this context, Neotropical *Ectatomma* ants (Hymenoptera: Formicidae: Ponerinae: Ectatommini), especially *E. ruidum* Roger and *E. tuberculatum* (Olivier), have received attention during the past decade as study organisms in the field and in the laboratory. This attention is due in part to the fact that the workers of *Ectatomma* display an impressive diversity of specialized foraging behaviors, rivaling that of vertebrates such as the Cocos finch (Werner and Sherry, 1987). Individual foragers have been observed in the field gathering secretions from treehoppers and from extrafloral nectaries, collecting capituli from the eggs of walkingsticks, ambushing sweat bees at nest entrances, stealing food from conspecific nests, stalking smaller insects, and scavenging arthropod corpses (e.g., Breed *et al.*, 1990; Schatz *et al.*, 1995; Del-Claro and Oliveira, 1996; Windsor *et al.*, 1996; Schatz and Wcislo, 1999). Furthermore, laboratory experiments confirm that they have well-developed cognitive abilities (Schatz *et al.*, 1994), indicating that at least some parts of the foraging repertoire are mediated by social ontogeny (Champalbert and Lachaud, 1990; Schatz *et al.*, 1995). However, presently it remains uncertain if and how these learning capabilities of *Ectatomma* are deployed when foraging under more general conditions.

In this study we attempt to reduce the evidential gap between field observations and laboratory experiments with respect to the presumable adaptiveness of individual learning in *Ectatomma*. Specifically, we ask whether learning of place and time is deployed by individual workers in arguably the most general context of foraging on patchy resources on the forest floor. We also ask if they use single- or multievent past experience in order to adjust their foraging behavior to the distribution of resources in the environment. Field observations on marked foragers of *E. ruidum* and *E. tuberculatum* were conducted under natural conditions on Barro Colorado Island, Republic of Panama, with particular attention to the directional orientation, sampling of space, timing, and the temporal sequence of site revisitation. Subsequently, these observations were corroborated with experimental trials on intact colonies under controlled, seminatural conditions (see

details below). During the experiments, marked foragers of *E. ruidum* and *E. tuberculatum* were exposed to two contrasting situations, involving spatial and temporal variation of foraging success at one or two foraging sites. Our results suggest that there are differences in learning that can be invoked to explain the ecological differences among the two species.

MATERIALS AND METHODS

Natural History of *E. ruidum* and *E. tuberculatum*

Both ponerine species have medium-sized foragers, with body lengths of ±8 mm in *E. ruidum* and ±11 mm in *E. tuberculatum* (for descriptions see Brown, 1958; Kugler and Brown, 1982). They are abundant throughout the Neotropics, occurring in both disturbed and undisturbed habitats (Levings and Franks, 1982). Their small nests are inserted into the forest soil, with densities as high as 11,200 nests/ha (Lachaud *et al.*, 1984; Schatz *et al.*, 1996). The monogynous colonies have 50–150 individuals and only one entrance in most cases.

Individual foraging while using predominantly visual cues is rare in most ant taxa (Hölldobler and Wilson, 1990), yet it is present in *Ectatomma* (Jaffé *et al.*, 1990). The foragers are omnivorous and typically forage individually during the daylight (see, e.g., Weber, 1946; Perfecto and Vandermeer, 1993; Schatz and Wcislo, 1999). Recruitment behavior among several foragers can be observed when especially valuable resources—such as larger arthropod corpses—are discovered (Pratt, 1989; Schatz *et al.*, 1996). Some foragers continue to be active during the night (Wheeler, 1986; W. T. Wcislo, personal observation). Weber (1946) considered *E. ruidum* to forage predominantly on the ground, whereas *E. tuberculatum* appeared to prefer vegetation.

Field Observations

All field observations were made on Barro Colorado Island (9°09′N, 79°51′W; for details on the ecology see Leigh [1999]), from May to August 1999. For each species two colonies were observed for 3 days, between 0730 and 1800, resulting in a total of 25 h per colony (only 15 h for the second colony of *E. tuberculatum*). These four colonies were located either in the laboratory clearing or in the forest understory. In each colony seven foragers received individual marks on the day before the observations (only five foragers for the second colony of *E. tuberculatum*). Those foragers that returned to the focal nest with prey were presumed to belong to the observed

colony. Initially they were aspirated into Eppendorf vials, then placed into an ice-filled styrofoam cooler for several minutes, and, finally, restrained to an even surface with copper wire. There they received marks on the head, thorax, and gaster, using different color combinations of opaque marker or enamel paint. After 15 min they were released near the nest entrance to rejoin their colony. The process of marking foragers had no discernible effects on their subsequent behavior.

The following characteristics of the foraging behavior of the focal individuals were observed: trip time, nest time, trip distance, outbound direction, inbound direction, foraging success, prey size, and additional miscellaneous observations. The time measurements were made to the nearest minute. All trips began and ended when the focal individual exited and entered the nest entrance, respectively. The maximum distance from the nest entrance was measured to the nearest 0.25 m, using small metal flags as markers on the ground during the period of observation and measuring the distance afterward. The direction while leaving from and returning to the nest was measured to the nearest 30° at 0.25 m from the nest entrance. The direction of 0° was arbitrary but constant for each colony throughout the observation period. The foraging success was calculated as the number of successful trips divided by the total number of trips. The prey size was classified into four broad categories: (1) smaller than mandible size, (2) smaller than head size, (3) smaller than body size, and (4) larger than body size. These categorizations were made while observing the focal individual during the inbound trip at ± 10 cm from the nest entrance. At the same time the prey items were classified as protein (e.g., arthropods corpses) or carbohydrate (e.g., nectar droplets that could be observed glistening between the mandibles). All measurements were combined to compute an overall profile for each forager. The statistical analyses were performed with MINITAB 12.23 (for linear measurements) and with Oriana 1.05 (for circular measurements).

Greenhouse Experiments: General Design

In order to control for the foraging success of the focal individuals, one entire colony per species was transferred to a greenhouse stand. There the colonies of *E. ruidum* and *E. tuberculatum* were observed from May 24 to June 22 (for a total of 33 days) and from July 1 to August 1 (for a total of 31 days), respectively. Initially, both colonies were located in the laboratory clearing. In each case, the nest entrance was sealed with cotton during the night before the transfer procedure. On the subsequent morning, a circular ditch (± 1.0-m diameter and ± 0.5-m depth) was excavated around the nest, leaving the central column with the intact colony. The lower one-third of this
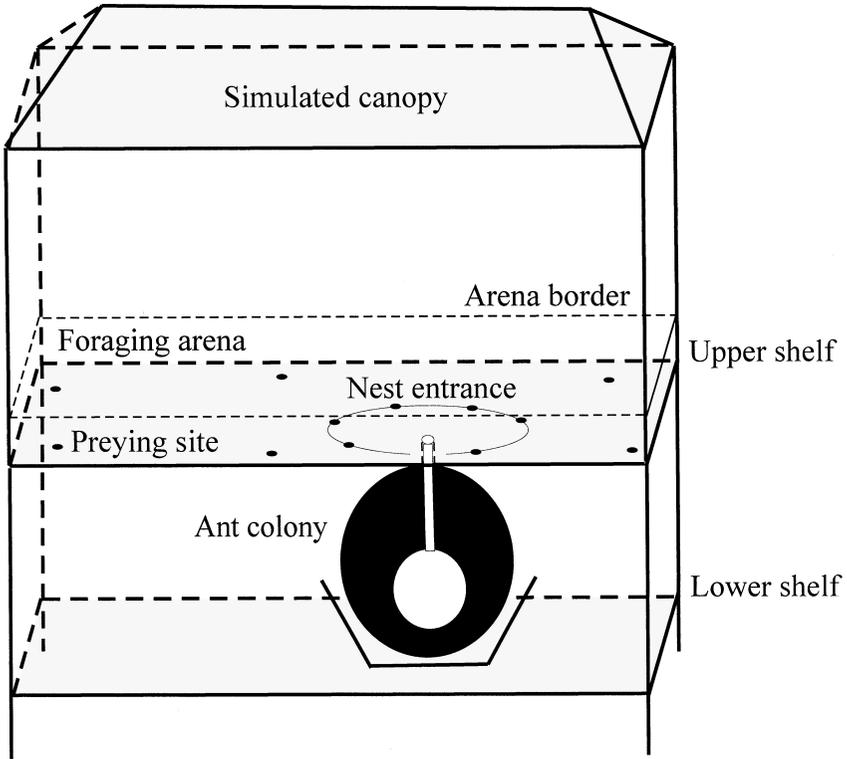
Fig. 1. Schematic representation of greenhouse stand used for foraging experiments with colonies of *E. ruidum* and *E. tuberculatum*.

column was removed, and the remaining upper two-thirds were transferred into a plastic bucket with matching diameter. Subsequently, the nest-bearing bucket was placed on the lower shelf of the greenhouse stand (Fig. 1). At this time, the cotton was removed and replaced with a twig. An extended entrance tunnel was formed around the twig, using damp soil in order to provide access to the foraging arena on the upper shelf of the greenhouse stand. After removing the twig, the foragers were able to explore their new environment for three days before the first experiment began. During this period, all foragers were marked as described above. The transfer procedure was designed to exert minimal stress on the colonies.

The foraging arena consisted of a rectangular area of 2.8 m² (Fig. 1). Its boundaries were covered with aluminum foil, and the upper borders were smeared with Tanglefoot glue to prevent the foragers from escaping. Every effort was made to simulate a natural environment. The floor was covered

with soil, leaf litter, twigs, and rocks. A canopy was constructed with a transparent plastic sheet that was suspended over the foraging arena and covered with several larger branches. The preying sites for the first experiment were situated along the borders of the foraging arena, at a distance of 0.80–1.45 m from the nest entrance. These sites consisted of cutoff bases of Eppendorf vials ($\pm$1-cm length) that were inserted into the soil and flush with its surface. The preying sites for the second experiment were situated at a distance of 0.25 m from each other and at 0.5 m from the nest entrance—corresponding to a difference of $\pm 30°$ with respect to the outbound angle.

Each day during the period of experimentation, the entire colonies—including the focal individuals—were provided with 25–50 large, unarmed *Nasutitermes* sp. nymphs (Isoptera: Termitidae; average nymphal weight, 1.6 ± 0.5 mg; $N = 25$). These nymphs were common prey for colonies in the field and accepted by all individuals. In order to achieve nutritional balance, diluted honey was offered twice per week for one hour at different locations. Both colonies were starved for 3 days before initiating the second experiment. Their general condition, including the foraging behavior of nonfocal individuals, was checked each day. After concluding all experiments, both colonies were collected into ethanol at 70%. Voucher specimens were mounted, labeled, and deposited in the Insect Collection of the Smithsonian Tropical Research Institute (STRI) and in the Cornell University Insect Collection (CUIC). The *E. ruidum* colony yielded 125 adults (with 10 alates), 60 pupae, 112 larvae, and 94 eggs, whereas the *E. tuberculatum* colony yielded 110 adults (with 8 alates), 25 pupae, 0 larvae, and 0 eggs.

First Experiment: Foraging Behavior at One Site

The first experiment was designed to quantify the presumed benefits of learning in *Ectatomma* while foraging with variable success at one preying site. The individual trials were conducted with 18 different foragers per colony, 1 forager at a time and usually 2 per day, between 0730 and 1800. These experiments were completed from May 27 to June 6 for *E. ruidum* and from July 5 to July 17 for *E. tuberculatum*. During each trial, the focal individual was able to forage at one of six possible sites (Fig. 2A), where a series of 15 termites was provided and preyed upon during 15 individual trips. After each catch one termite was placed into the Eppendorf vial, using smooth forceps. Therefore, the focal individual encountered individual items of live prey at only one site. The termites were replaced while the focal individual was either inside the nest or searching for prey at a distance from the actual preying site. Consequently, the focal individuals did not notice the replacement procedure.
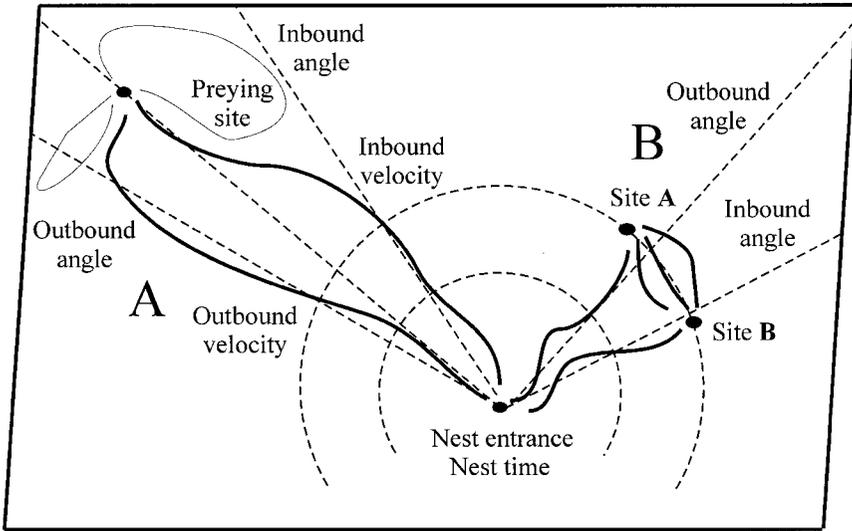
Fig. 2. Schematic representation of foraging arena used for experiments with individual foragers of *E. ruidum* and *E. tuberculatum*. Thick lines depict movements from nest entrance to preying sites, thin lines depict movements during intermediate search trip, and dashed lines illustrate how the foraging characteristics were measured for statistical analyses. (A) First experiment. (B) Second experiment.

During trips 1–5 and trips 11–15, the termites were replaced before the focal individual was able to return to the preying site for the *first time—immediate replacement.* Contrastingly, during trips 6–10, the empty preying site had to be checked twice before the termite was replaced. Therefore, the focal individual was denied success until returning to the preying site for the *third time—delayed replacement.* The checking of sites was considered to be an independent event if separated from previous checking by minimally one minute. Typically, the focal individuals departed for more than 10 cm from the preying site during their intermediate searches for prey. Trips 1–5 are referred to as the *training period*; trips 6–10, as the *manipulation period*; and trips 11–15, as the *recovery period.*

The direction while leaving from and returning to the nest (i.e., outbound and inbound angles, respectively) was measured during each trip at a distance of 0.5 m from the nest entrance (Fig. 2). To facilitate the measurements, an imaginary line was drawn from the nest entrance to the actual position of the focal individual and then to the border of the foraging arena which was labeled with angular measurements. This procedure yielded results with a precision of 5°.

For the purpose of computing the statistical analyses, all angles were re-calculated as absolute deviations from the optimal angle (i.e., straight line) to the preying sites. The individual averages for the angular deviations from the optimal angle were calculated for each of the three trial periods with five trips (i.e., training, manipulation, and recovery period). The outbound velocity was computed as the distance (measured in cm) divided by the time (measured in s) that passed while the focal individual moved from the nest entrance to the preying site (i.e., contact with the vial). The inbound velocity was measured as the period from leaving the preying site to entering the nest. Finally, the nest time was calculated as the period between entering and exiting the nest. The statistical analyses were performed as among-period comparisons for each individual and as among-trip comparisons for all individuals.

Four additional measurements were made with respect to the 10 intermediate searches (i.e., two searches times five trips) in the vicinity of the preying site during the manipulation period (i.e., trips 6–10; Fig. 2A). The search angle was measured to the nearest 30°, with 0° as the optimal angle for the outbound direction. The search distance was measured to the nearest 5 cm as the maximum distance from the preying site. The search time was measured to the nearest second. Finally, the search pattern (i.e., angular range covered during the search) was classified as a line if inside 45°, as a triangle if inside 180°, and as a circle if outside 180°. The average values of these additional measurements were calculated for each individual.

Second Experiment: Foraging Behavior at Two Sites

The second experiment was designed to explore the adaptiveness of learning in *Ectatomma* in relation to variable foraging success at two preying sites. As in the first experiment, the individual trials were conducted with 18 different foragers per colony, 1 forager at a time and usually 2 per day, between 0730 and 1800. This set was completed from June 13 to June 21 for *E. ruidum* and from July 21 to July 31 for *E. tuberculatum*. During each trial, the focal individual was able to forage at two of eight possible sites (here referred to as site A and site B; Fig. 2B). Before starting the trial, three termites were provided at each of the two preying sites in an alternating sequence. This was achieved by offering the termite as a bait on the forceps while guiding the focal individual from site to site. Presumably, this procedure was appropriate for *training* the focal individual *to check both sites* for potential prey. It was not analyzed any further.

After the training period was concluded, the focal individual was subjected to three manipulations. First, site A yielded one termite on every

second visit, using the same criteria as in the first experiment, whereas site B yielded one termite on every fourth visit. This period was completed as soon as the focal individual caught a total of five termites at site A. As described above, the replacement of termites was performed in secretion i.e., without attracting the focal individual to the preying sites. Second, the rate of replacements was reversed among site A and site B. This period was extended until the focal individual made an immediate check at site B—which was now the more attractive site—after catching the previous termite at that site. Interestingly, this event occurred without additional manipulation in all foragers of *E. ruidum*, whereas the majority of foragers of *E. tuberculatum* had to be baited to site B after having checked site A during 12 consecutive visits (see also below). Third, the same conditions as in the second period were presented until the focal individual caught a total of five termites at site B. The last catch concluded the trial.

The temporal sequence of checking both sites was recorded for each of the three trial periods. Furthermore, the direction while leaving from and returning to the nest (i.e., outbound and inbound angles, respectively) was measured at a distance of 0.25 m from the nest entrance (Fig. 2B), using similar methods as in the first experiment and yielding a precision of 2.5°. For the statistical analyses, all angles were recalculated as absolute deviations from the optimal angle (i.e. straight line) to site A and averaged for each period.

RESULTS

Field Observations

Ectatomma ruidum. The following aspects of the foraging behavior under natural conditions could be quantified (Table I). The 14 foragers made 0.4–1.5 trips per hour (see Fig. 3A for the frequency distribution of trip times), over a distance of 0.7–1.9 m from the nest. In the majority of cases their rates of success were higher than 35%, yielding prey sizes lower than 2.0 (i.e., below head size). Throughout the 3-day period of observations they maintained an individual directionality during their trips, with an angular deviation of 0–65°. Consequently, Raleigh's test of uniform directionality was significant for all foragers in both outbound and inbound directions ($P < 0.01$; $N = 14$ for each direction), suggesting that past experience and present foraging behavior are related.

The qualitative aspects of the foraging behavior of *E. ruidum* varied to some extent, as the following description indicates. Typically, a forager departed toward her "preferred" direction during previous trips until reaching

Table I. Foraging Characteristics of 14 Individuals from Two Colonies (A and B) of *E. ruidum*, Averaged Over 3 Days of Field Observations with Standard Deviations (for Details See Text)

Colony—individual	No. of trips	Trip time (min)	Nest time (min)	Trip distance (m)	Outbound angle (°)	Inbound angle (°)	Success rate (%)	Prey size
A—1	15	35 ± 28	14 ± 13	1.5 ± 0.6	300 ± 0	302 ± 23	47	1.7
A—2	16	30 ± 28	15 ± 23	1.9 ± 1.9	113 ± 65	108 ± 65	50	1.3
A—3	11	22 ± 16	23 ± 21	1.5 ± 0.6	265 ± 17	265 ± 21	36	1.5
A—4	24	17 ± 12	14 ± 26	0.8 ± 0.4	59 ± 13	63 ± 21	54	1.1
A—5	24	25 ± 19	7 ± 9	1.4 ± 0.5	327 ± 13	316 ± 23	63	1.9
A—6	29	18 ± 13	2 ± 2	0.9 ± 0.2	299 ± 5	295 ± 14	56	1.1
A—7	25	31 ± 27	11 ± 21	1.4 ± 0.4	83 ± 15	84 ± 15	46	1.8
B—1	18	31 ± 23	23 ± 16	0.7 ± 0.4	181 ± 56	201 ± 60	22	1.8
B—2	29	26 ± 18	13 ± 13	0.9 ± 0.2	98 ± 35	91 ± 44	38	1.8
B—3	38	21 ± 15	11 ± 13	0.8 ± 0.3	329 ± 35	336 ± 39	45	1.6
B—4	18	41 ± 34	25 ± 31	1.0 ± 0.5	89 ± 52	85 ± 55	17	2.0
B—5	18	26 ± 21	12 ± 25	0.9 ± 0.4	43 ± 33	43 ± 33	50	2.0
B—6	25	22 ± 18	23 ± 28	0.8 ± 0.3	265 ± 27	254 ± 33	8	2.5
B—7	14	52 ± 35	20 ± 15	1.3 ± 0.6	56 ± 34	44 ± 40	50	3.1

E. ruidum
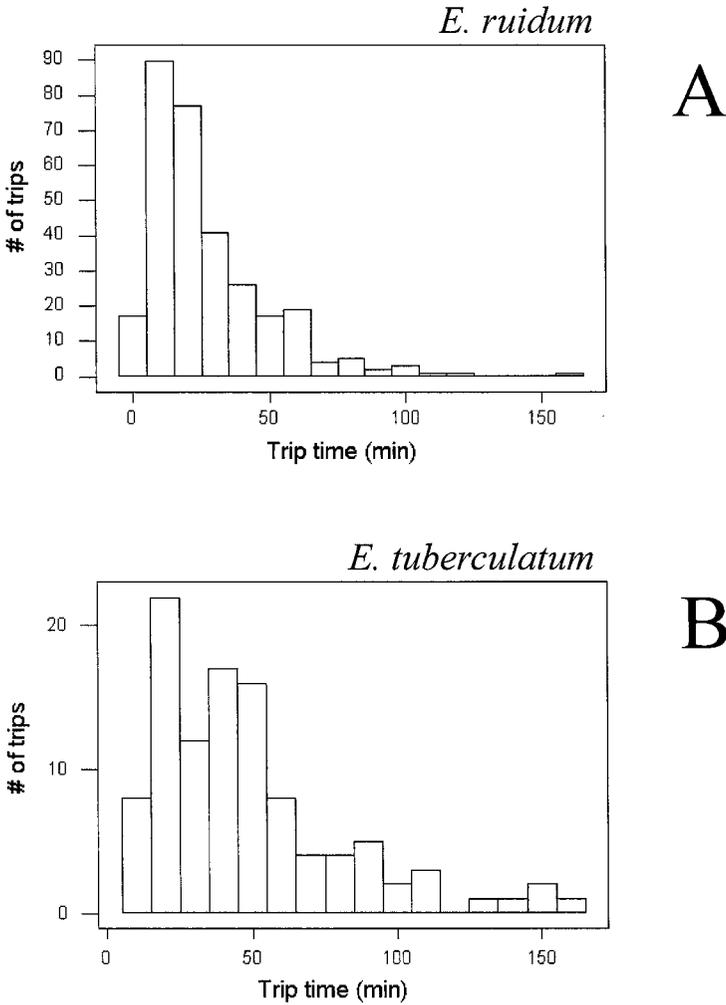
E. tuberculatum

Fig. 3. Frequency distribution of trip times during field observations on focal foragers of (A) *E. ruidum* (*N* = 304) and (B) *E. tuberculatum* (*N* = 106) (for details see text).

the maximum distance from the nest entrance. Subsequently, three general scenarios were observed. First, if prey was caught during her outbound trip, she returned it to the nest with a high velocity. Only moments later, she departed to the same location along a more "streamlined" path and with increased velocity in comparison to the previous trip. Another success at the same location elicited an even stronger attraction. Second, if no prey

item was caught while moving away from the nest, a forager initiated several circular trips of increasing diameter in the same area. Moving constantly during these searches within an extended corridor of her "preferred" direction, she was able to sample the area along the corridor extensively. Third, if prey was caught during these search trips, it would be returned as described above. However, if no prey item was caught, a forager would eventually return to the nest without prey, sometimes after over an hour and many circles of searching (Fig. 3A). Her subsequent trip would be delayed and not as "streamlined" with respect to directionality and velocity.

Resource specialization was not observed in *E. ruidum*. The focal foragers caught an impressive range of prey items, including arthropod corpses, arthropod larvae, parts of lichens, small flies, and termite nymphs. The majority of trips were completed on the forest floor (as described by Weber, 1946). In some cases, the differences in efficiency among foragers were related to the patchy distribution of resources on the forest floor, e.g., the temporary exposure of termite trails or the corpse of an isopod. Such abundant resources were returned to over several subsequent trips, and sometimes even triggered recruitment behavior (Pratt, 1989). Among the additional factors that appeared to influence the foraging efficiency were prey theft by ants of other colonies (Breed *et al.*, 1999) and disturbances by predators that resulted in hiding behavior.

Ectatomma tuberculatum. The foraging behavior under natural conditions (Table II; see Fig. 3B for the frequency distribution of trip times) was similar to that of *E. ruidum*, with the following differences. Fewer trips were made by the 12 foragers (i.e., 0.1–0.9 trip per hour), yet often they extended over longer distances (i.e., 0.9–6.3 m). The foraging success, prey size, and presence of an individually "preferred" direction were similar, with an angular deviation of 4–56° throughout the 3-day period of observations. Raleigh's test of uniform directionality was significant for all foragers in both outbound and inbound directions ($P < 0.05$; $N = 12$ for each direction). One qualitative difference among the two species was apparent in the fact that most foragers of *E. tuberculatum* moved toward one destination after departing from the nest, often to particular locations on shrubby vegetation. There they displayed "sit-and-wait" ambush behavior until prey was caught (as observed by Schatz and Wcislo, 1999; W. T. Wcislo, personal observation). This behavior resulted in comparatively longer trip times (Fig. 3B) and less sampling effort in relatively smaller areas. All foraging trips were made on shrubby vegetation (as observed by Weber, 1946), and typical sites for ambushing prey were open flowers and extrafloral nectaries that attracted other arthropods. Interestingly, two-thirds of the focal foragers caught protein resources and gathered nectar droplets during consecutive trips, as opposed to specializing on particular resources.

Table II. Foraging Characteristics of 12 Individuals from Two Colonies (A and B) of *E. tuberculatum*, Averaged Over 3 Days of Field Observations with Standard Deviations (for Details See Text)

| Colony—individual	No. of trips	Trip time (min)	Nest time (min)	Trip distance (m)	Outbound angle (°)	Inbound angle (°)	Success rate (%)	Prey size
A—1	11	43 ± 27	35 ± 29	1.7 ± 0.5	155 ± 13	165 ± 38	27	2.0
A—2	22	34 ± 16	19 ± 22	1.8 ± 0.3	269 ± 6	266 ± 10	41	2.0
A—3	10	63 ± 31	27 ± 49	1.5 ± 0.4	264 ± 12	245 ± 40	40	1.5
A—4	13	36 ± 27	31 ± 34	1.2 ± 0.6	269 ± 49	243 ± 56	31	2.5
A—5	11	35 ± 19	40 ± 36	1.6 ± 0.6	164 ± 29	176 ± 52	18	2.0
A—6	8	48 ± 27	17 ± 10	1.0 ± 0.5	30 ± 15	69 ± 61	0	—
A—7	11	59 ± 44	43 ± 34	1.0 ± 0.3	31 ± 26	55 ± 17	18	1.5
B—1	2	86 ± 7	—	1.3 ± 0.0	105 ± 15	105 ± 15	50	1.0
B—2	3	97 ± 26	—	3.9 ± 0.8	260 ± 14	260 ± 14	0	—
B—3	7	48 ± 46	27 ± 24	2.1 ± 0.6	116 ± 11	112 ± 4	29	1.5
B—4	3	97 ± 53	—	6.3 ± 0.7	290 ± 14	29 ± 14	0	—
B—5	5	60 ± 48	20 ± 9	0.9 ± 0.1	12 ± 15	12 ± 15	60	2.0

Table III. Average Deviations from Optimal Angle (i.e., 0°) to Preying Site in 18 Individuals of *E. ruidum* and *E. tuberculatum*, Calculated for Both Outbound and Inbound Directions for Three Periods of First Experiment: Combined Period Averages with Standard Deviations

| Species	Direction	Training period (trips 1–5; °)	Manipulation period (trips 6–10: °)	Recovery period (trips 11–15; °)
E. ruidum (N = 18)	Outbound	6.7 ± 5.8	11.8 ± 6.6	5.5 ± 4.9
	Inbound	7.7 ± 7.2	7.9 ± 7.9	7.2 ± 7.7
E. tuberculatum (N = 18)	Outbound	9.1 ± 7.4	9.0 ± 7.2	8.5 ± 6.4
	Inbound	8.7 ± 7.2	8.5 ± 6.7	8.8 ± 7.3

First Experiment: Foraging Behavior at One Site

The average trial duration for the first set of experiments was 122 ± 43 min for *E. ruidum* ($N = 18$) and, thus, significantly longer than for *E. tuberculatum* (88 ± 16 min; $N = 18$; $t = 3.2$, df = 21, $P < 0.01$). During the three periods of each trial (i.e., training, manipulation, and recovery), the individual deviations from the optimal angle did not vary significantly with respect to the inbound direction in *E. ruidum* and for both directions in *E. tuberculatum* (Table III). However, there was significant variation in the outbound direction of the 18 foragers of *E. ruidum*. Watson's f-test for circular means (with Bonferroni correction) indicated an increase in the angular deviation during the manipulation period in comparison to the training period ($f = 5.7$, df = 34, $P < 0.01$) and the recovery period ($f = 10.1$, df = 34, $P < 0.01$). Thus, their outbound trips were significantly more "streamlined" during the periods of immediate foraging success.

In accordance with the previous findings, the outbound velocity decreased significantly during the manipulation period in 15 foragers of *E. ruidum* (Fig. 4A) and in 6 foragers of *E. tuberculatum* (Fig. 4B; $N = 18$ for each species; Kruskal–Wallis, df = 2, $P < 0.05$; the same statistic was used for the following two among-period comparisons). The inbound velocity decreased significantly in four foragers of the former species (Fig. 5A) and in three foragers of the latter species (Fig. 5B). The nest time increased significantly in 12 foragers (Fig. 6A) and in 3 foragers (Fig. 6B), respectively. Considering the among-trip comparisons, the foragers of *E. ruidum* made significant adjustments when experiencing immediate or delayed foraging success in 9 of 18 selected pairs of comparisons (Table IV; paired t with Bonferroni correction, df = 17, $P < 0.05$), whereas those of *E. tuberculatum* responded significantly in only four comparisons. However, the foragers of both species decreased their outbound velocity by 45 and 20% from trip 5 to trip 6—i.e., the transition from the training period to the manipulation
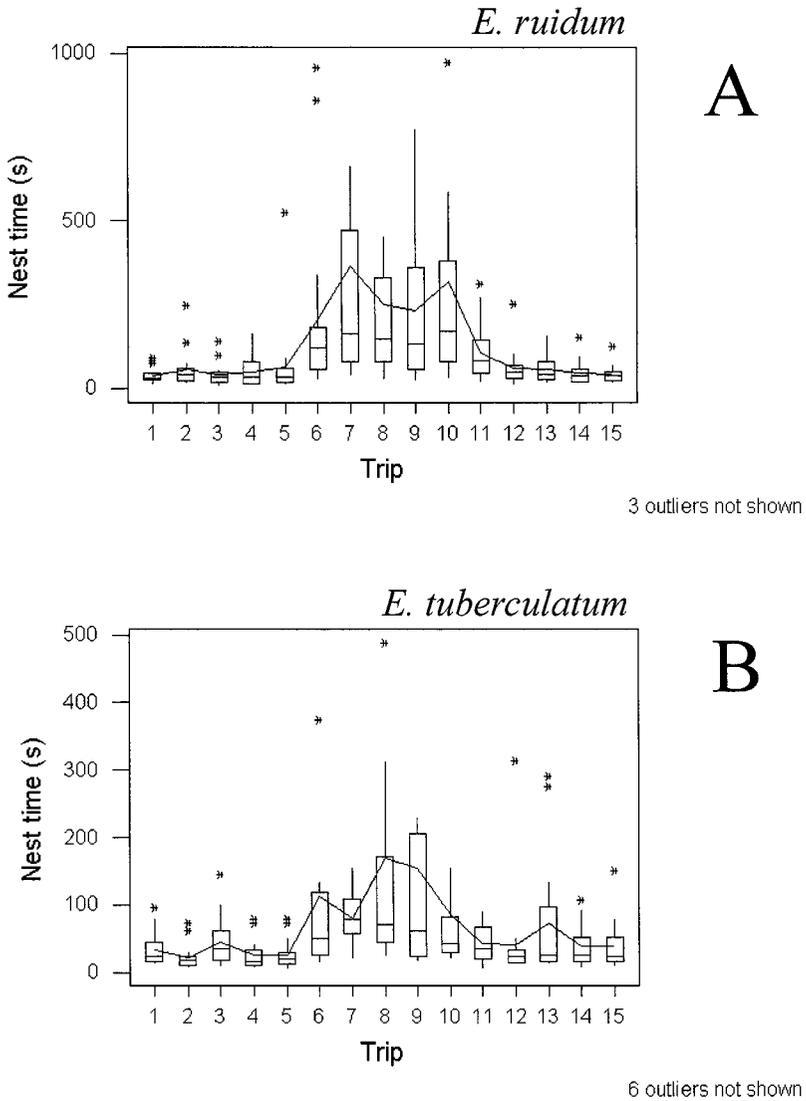
E. ruidum
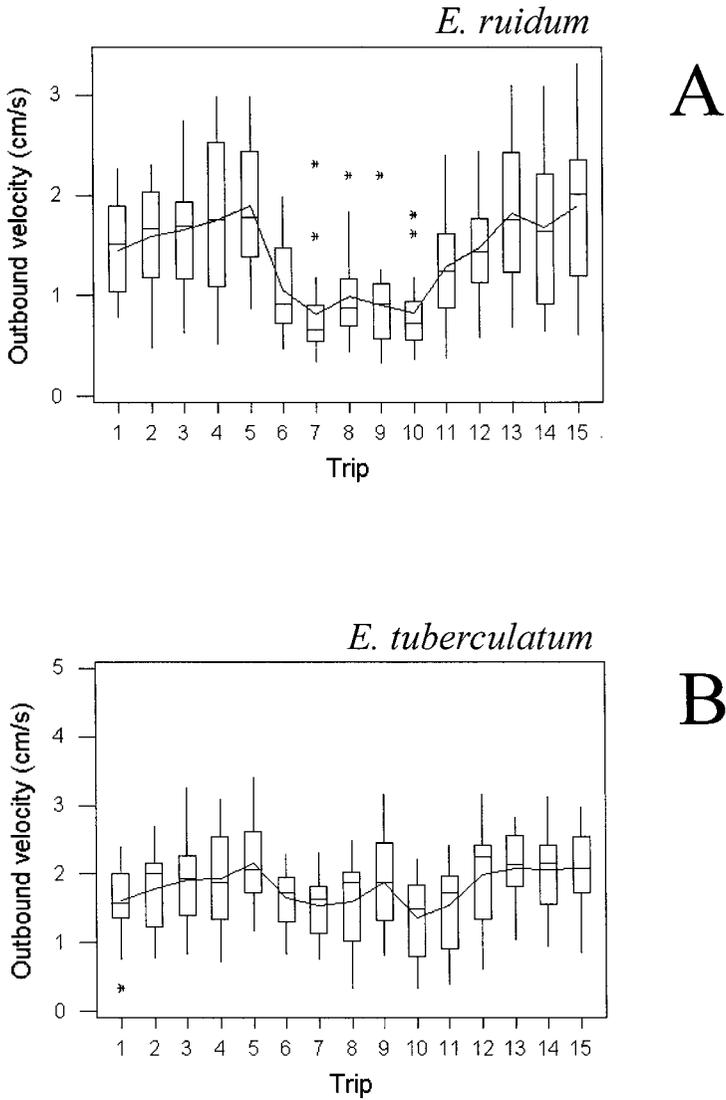
E. tuberculatum

Fig. 4. Outbound velocity of focal foragers during the first experiment. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$). Lines across boxes are medians (connected by line), lower and upper boundaries are first and third quartiles (i.e., Q1 and Q3), adjacent whiskers are lowest and highest values that fulfill Q1 − 1.5 (Q3–Q1) and Q3 + 1.5 (Q3–Q1), and asterisks are outliers.

E. ruidum

A

E. tuberculatum

B
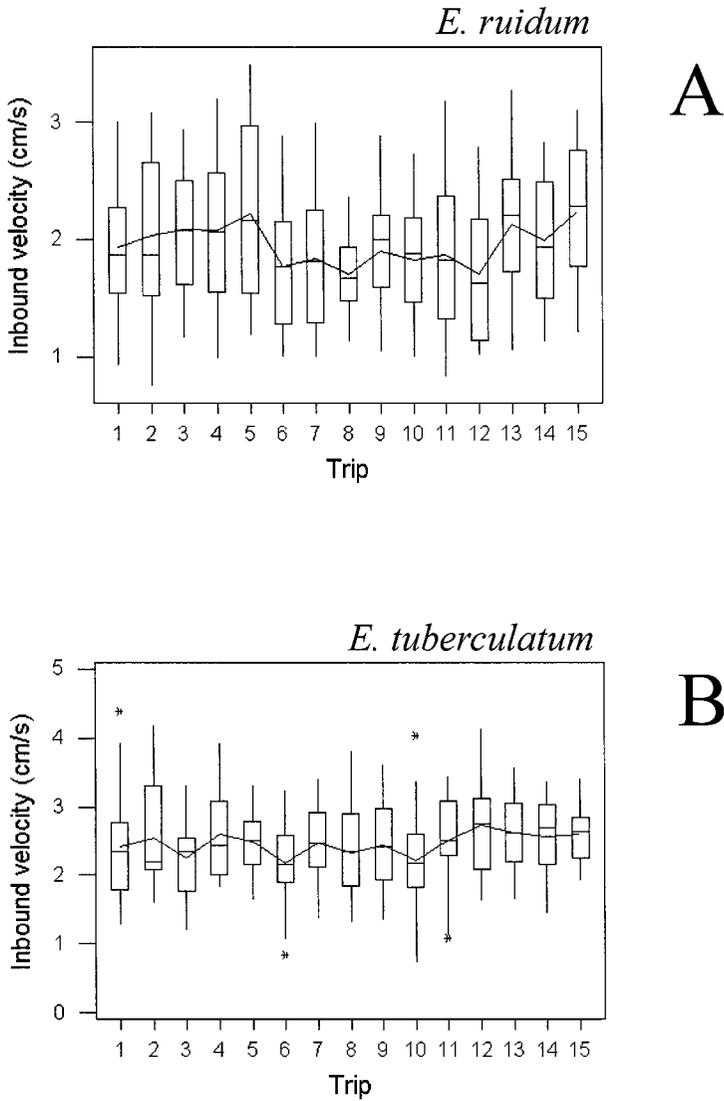
Fig. 5. Inbound velocity of focal foragers during the first experiment. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$).

period—indicating that single-event past experience is sufficient to cause an adjustment in the foraging behavior of *Ectatomma*. An accumulative effect of multiple immediate foraging success within both the training period and the recovery period was evident as well.
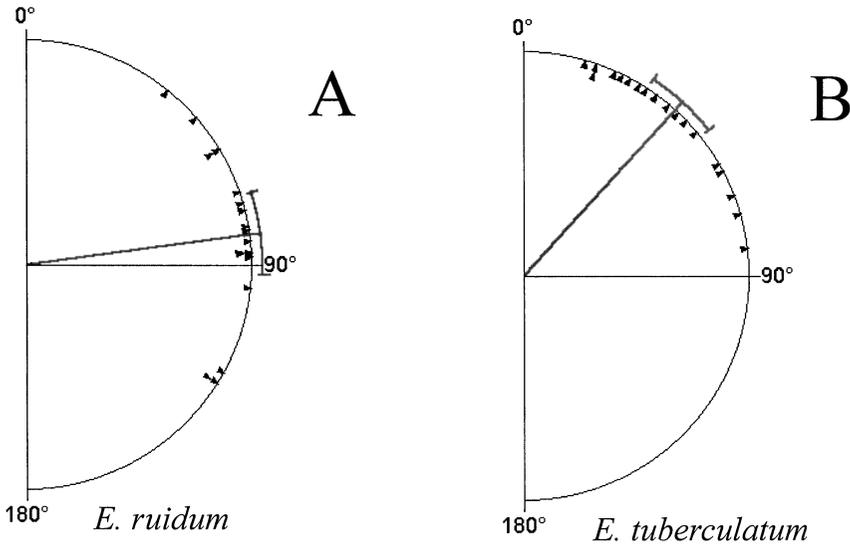
E. ruidum

A

3 outliers not shown

E. tuberculatum

B

6 outliers not shown

Fig. 6. Nest time of focal foragers during the first experiment. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$).

During the 10 intermediate trips of the manipulation period, the foragers of *E. ruidum* (Fig. 7A) searched for prey in more extended areas than those of *E. tuberculatum* (Fig. 7B), as reflected in comparatively higher deviations from the optimal angle of the outbound direction (Watson's *f*-tests,

Table IV. Percentage Adjustment of Outbound Velocity, Inbound Velocity, and Nest Time in 18 Foragers of *E. ruidum* and *E. tuberculatum*, Calculated by Comparing Values for Selected Pairs of Trips During the First Experiment: Combined Trip Averages with Standard Deviations

| Species	Variable	Adjustment among pairs of trips (%)					
		1 to 5	5 to 6	6 to 10	10 to 11	11 to 15	1 to 15
E. ruidum (N = 18)	Outbound velocity	+39 ± 55*	−45 ± 14*	−13 ± 41	+68 ± 66*	+53 ± 42*	+34 ± 49*
	Inbound velocity	+17 ± 27*	−19 ± 12*	+7 ± 22	+3 ± 27	+26 ± 30*	+21 ± 30
	Nest time	+50 ± 40	+495 ± 850	+212 ± 459	−20 ± 92	−45 ± 40*	+26 ± 80
E. tuberculatum (N=18)	Outbound velocity	+56 ± 91*	−20 ± 27*	−17 ± 35	+30 ± 61	+60 ± 109*	+40 ± 59*
	Inbound velocity	+9 ± 32	−11 ± 25	+13 ± 66	+29 ± 65	+11 ± 33	+16 ± 36
	Nest time	+8 ± 18	+439 ± 710	+56 ± 166	−6 ± 80	+57 ± 205	+71 ± 175

* $P < 0.05$ (paired *t* with Bonferroni correction).

Fig. 7. Individual deviations from optimal angle by focal foragers during 10 intermediate trips (i.e., manipulation period) in the first experiment. Solid lines depict the average angle with standard deviation for all individuals. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$).

$f = 29.4$, df = 34, $P < 0.01$). The average search distance was also significantly longer in the former species than in the latter species (Figs. 8A and B; $t = 8.7$, df = 21, $P < 0.0001$), contrasting with similar durations of search time (Figs. 9A and B; $t = 0.6$, df = 29, $P > 0.5$). Finally, the angular range covered during the search trips was significantly more "complex" in *E. ruidum* than in *E. tuberculatum* ($N = 18$; $t = 6.2$, df = 23, $P < 0.0001$), with combined averages of 1.9 ± 0.4 (i.e., "triangular") and 1.4 ± 0.2 (i.e., "linear"), respectively. Considering the intermediate search trips by all foragers as a total ($N = 180$ per species), the percentage distribution of patterns for *E. ruidum* was 38% lines, 30% triangles, and 32% circles, whereas *E. tuberculatum* had 70% lines, 25% triangles, and 5% circles. These results indicate that the foragers of *E. ruidum* made an extensive effort to sample the area adjacent to the site of recently experienced foraging success. Contrastingly, the majority of foragers of *E. tuberculatum* adopted the typical "sit-and-wait" behavior in the vicinity of the preying site.

Additional observations outside of the trials were congruent with the previous findings. Before initiating the trials each day, it was common to locate 5–15 foragers of *E. ruidum* in the arena. However, only three or fewer foragers of *E. tuberculatum* were present, usually "waiting" next to the preying sites of the last trials. New prey items at other preying sites were

E. ruidum

A

E. tuberculatum

B
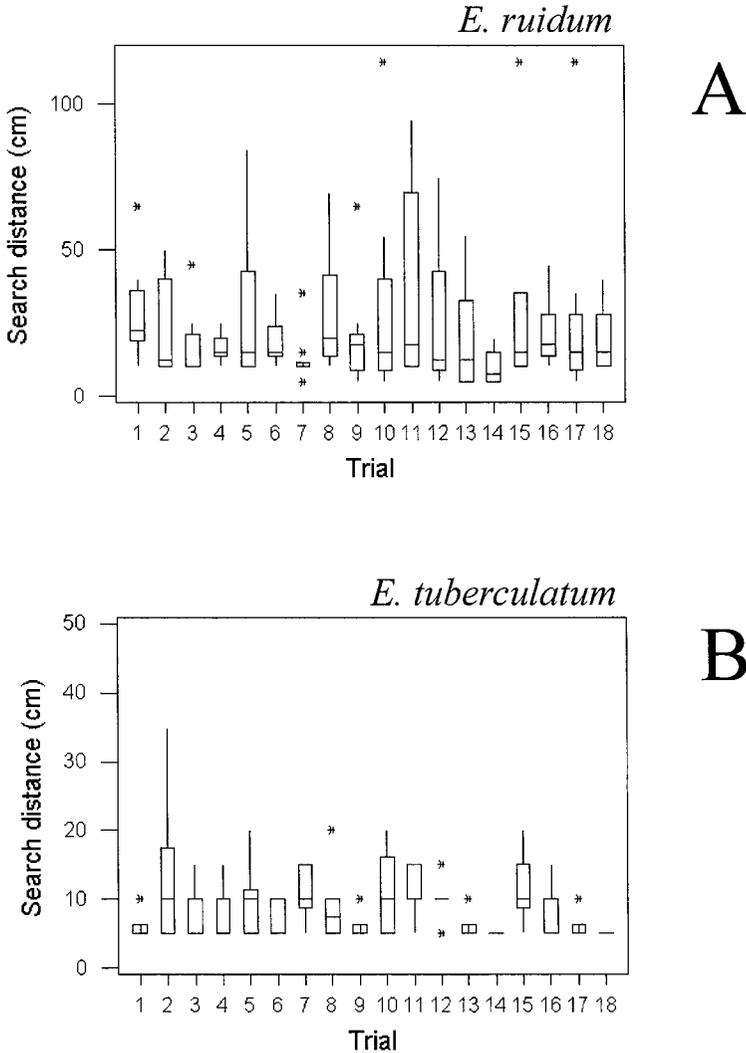
Fig. 8. Search distance of focal foragers during 10 intermediate trips (i.e., manipulation period) in the first experiment. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$).

discovered within minutes by *E. ruidum*, yet only after hours or even days by *E. tuberculatum*. Furthermore, the foragers of *E. tuberculatum* appeared to recheck the former preying sites with a higher frequency and for longer time periods—in one case for 5 days.

E. ruidum

A

3 outliers not shown

E. tuberculatum

B

2 outliers not shown
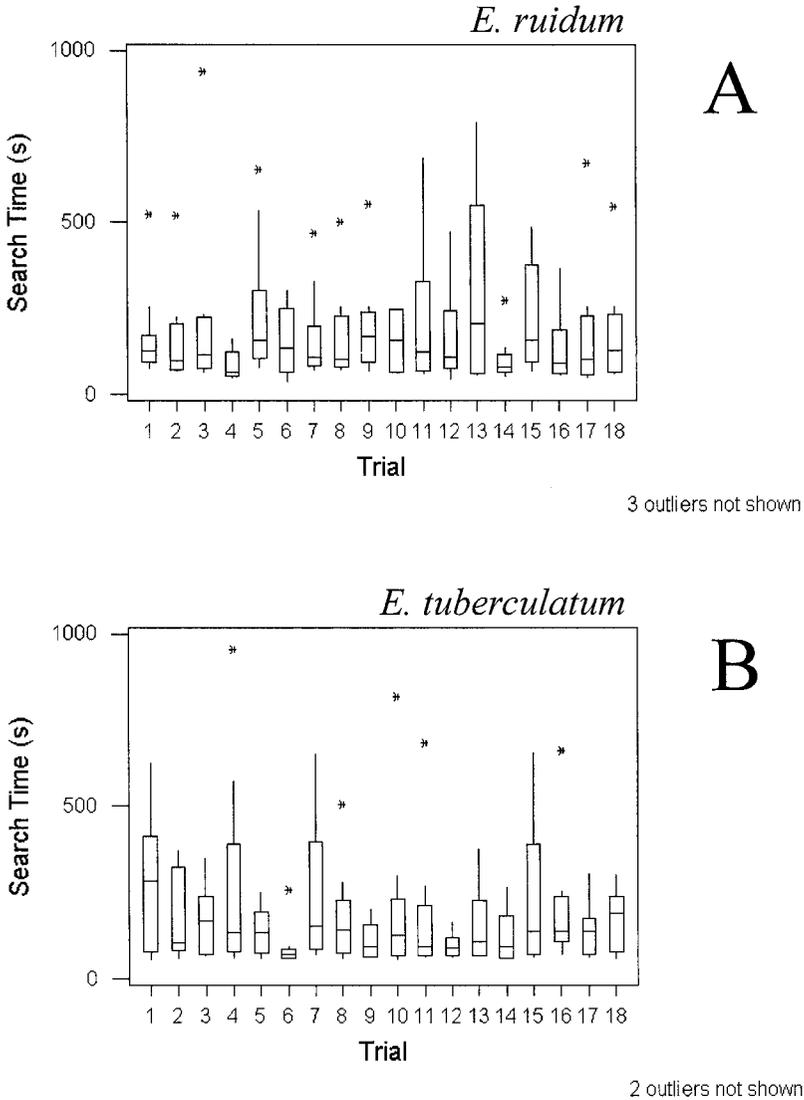
Fig. 9. Search time of focal foragers during 10 intermediate trips (i.e., manipulation period) in the first experiment. (A) *E. ruidum* ($N = 18$). (B) *E. tuberculatum* ($N = 18$).

Second Experiment: Foraging Behavior at Two Sites

The average trial duration was 152 ± 30 min for *E. ruidum*, not significantly different from that for *E. tuberculatum* (164 ± 44 min; $N = 18$;

$t = 1.0$, df $= 30$, $P > 0.3$). Throughout all three periods, the focal foragers of *E. ruidum* made 37 ± 4 checks at both preying sites and, therefore, significantly fewer than those of *E. tuberculatum* (51 ± 9 checks; $N = 18$; $t = 6.0$, df $= 22$, $P < 0.0001$). Consequently, more prey times were caught in total by the foragers of the latter species (i.e., 18 ± 3 by *E. ruidum* amd 14 ± 1 by *E. tuberculatum*; $N = 18$; $t = 5.7$, df $= 20$, $P < 0.0001$). However, these results were difficult to interpret because 15 of 18 foragers of *E. tuberculatum* made 12 consecutive checks at site A after completing the first trial period, although prey was presented only on every fourth visit at that site. Apparently, they were "fixed" on site A, i.e., the first site where prey was caught in abundance after the training period. In order to complete the trial, these 15 foragers had to be baited to site B. This procedure provided them with 4 ± 2 extra prey items—corresponding to 8 ± 3 additional site visits— before they made an immediate check at site B. Because of this experimental interference in *E. tuberculatum*, the values were not directly comparable.

As mentioned above, the foragers of *E. tuberculatum* made most of their sampling effort at site A throughout the trial (Table V), although site B yielded prey twice as often as site A during the second and third periods. The sampling effort of *E. ruidum* was more evenly balanced among the two sites (Table V), as the foragers made more checks at the less profitable site B during the first period and fewer checks at the less profitable site A during the second period. Consequently, the overall correspondence of checks and catches was significantly more balanced in *E. ruidum*, reflecting the general observation that the focal foragers of this species responded better to the design of the experiment than those of *E. tuberculatum*.

Table V. Frequency and Proportion of Checks and Catches at Site A and Site B by 18 Foragers of *E. ruidum* and *E. tuberculatum* During Three Periods of the Second Experiment: Combined Averages with Standard Deviations (for Details See Text)

|	Trial period	Less profitable site	*E. ruidum*	*E. tuberculatum*	Significance[a]
No. of checks at less profitable site	1	B	5.1 ± 3.1	1.4 ± 1.6	$P < 0.0005$
	2	A	5.0 ± 2.8	16.1 ± 6.6	$P < 0.0001$
	3	A	4.5 ± 2.1	5.1 ± 3.0	$P > 0.5$
No. of catches at less profitable site	1	B	0.7 ± 0.8	0.1 ± 0.2	$P < 0.005$
	2	A	0.7 ± 0.7	3.5 ± 1.7	$P < 0.0001$
	3	A	1.2 ± 0.7	1.1 ± 0.9	$P > 0.6$
Combined proportion of checks and catches over all periods			1.1 ± 0.1	1.5 ± 0.2	$P < 0.0001$

[a]t-test, df $= 17$.
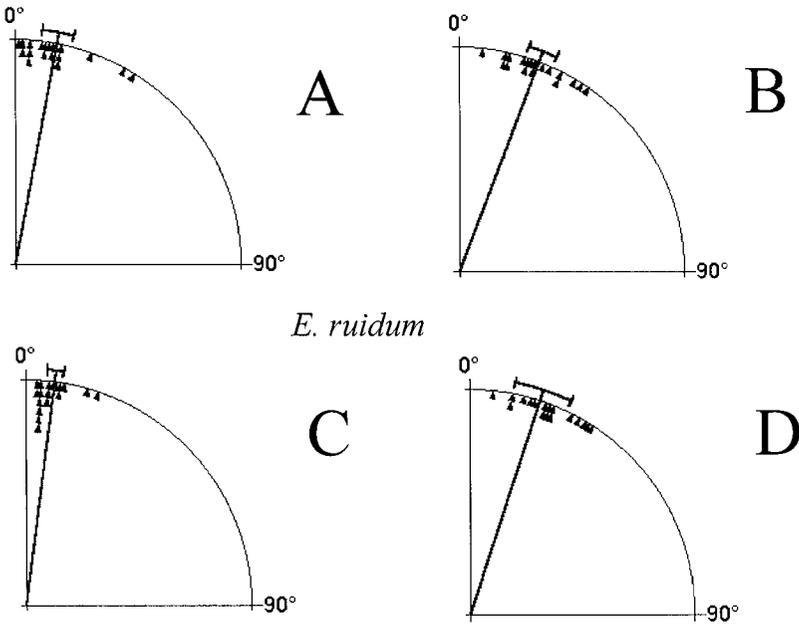
Fig. 10. Individual deviations from optimal angle by focal foragers of *E. ruidum* ($N = 18$) to site A during the second experiment. (A) Outbound trip, first period. (B) Outbound trip, third period. (C) Inbound trip, first period. (D) Inbound trip, third period.

In the course of the trial, the 18 foragers of *E. ruidum* made significant adjustments with respect to the outbound direction, from $10.8 \pm 8.5°$ in the first period to $20.8 \pm 7.6°$ in the third period (Figs. 10A and B; $f = 13.1$, df $= 34$, $P < 0.01$). This indicates that they used the differential experience of foraging at the two sites to modify their behavior. No significant adjustments were observed in *E. tuberculatum*: $14.7 \pm 10.3°$ in the first period and $16.3 \pm 9.9°$ in the third period (Figs. 11A and B; $f = 0.2$, df $= 34$, $P > 0.6$). Therefore, although the focal foragers of *E. tuberculatum* caught more prey at site B, this was not reflected in modifications of their outbound direction. Similar results were obtained for the inbound direction: The 18 foragers of *E. ruidum* made significant adjustments toward site B from the first period to the third period (Figs. 10C and D; from 7.5 ± 4.3 to $18.4 \pm 15.2°$; $f = 8.1$, df $= 34$, $P < 0.05$), whereas those of *E. tuberculatum* did not (Figs. 11C and D; from 11.5 ± 7.9 versus $17.5 \pm 10.1°$; $f = 3.7$, df $= 34$, $P > 0.05$).

Some additional observations during this experiment suggest that its complexity surpassed the cognitive abilities of several foragers. All focal foragers made more or less extensive effort to sample areas distant from the two preying sites, although no prey items were offered there at any
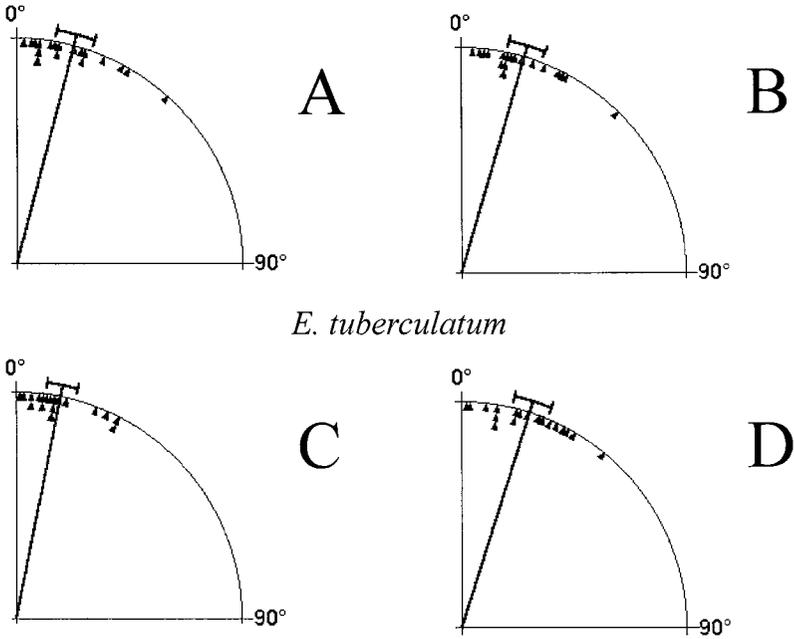
Fig. 11. Individual deviations from optimal angle by focal foragers of *E. tuberculatum* to site A during the second experiment. (A) Outbound trip, first period. (B) Outbound trip, third period. (C) Inbound trip, first period. (D) Inbound trip, third period.

time. The typical sampling behavior of *E. ruidum* and the "sit-and-wait" behavior of *E. tuberculatum* were observed as well, yet the most efficient strategy for this trial would have been to check both sites as frequently as possible. Furthermore, many site checks appeared to be "coincidental," because the forager sampled the area in general or returned to the nest before she "discovered" the site with prey. Two foragers of *E. tuberculatum* departed and/or returned to the nest outside of the imaginary triangle between the two sites and the nest entrance. However, some individuals foraged efficiently during the experiment, making alternating checks among both sites until they caught prey. Interestingly, after catching prey at site A, some foragers immediately checked site B (and vice versa), suggesting that they expected prey at that site.

DISCUSSION

Our results indicate that the foragers of *E. ruidum* and *E. tuberculatum* use their individual cognitive abilities not only when foraging on particular

items (e.g., extrafloral nectaries) or at particular locations (e.g., sweat bee nests), but also under the more general conditions of foraging on various resources with patchy distributions on the forest floor. Both experiments confirm that they are able to make significant adjustments to the directional and temporal aspects of their behavior, in response to previous differential foraging success. Furthermore, we have demonstrated that the foragers of *Ectatomma* use both single- and multi–event past experience in order to increase their foraging efficiency. As a result, it is now more apparent how learning and memory facilitate the presumable transition from more generalist foraging on the forest floor—as observed in this study—to various levels of resource specialization (see, e.g., Wheeler, 1986; McCluskey, 1987; DeVries, 1991; Passera *et al.*, 1994; Schatz *et al.*, 1995, 1996; Schatz and Wcislo, 1999). Exceptionally profitable, long-term resources are likely to elicit specialization in individual foragers. Finally, by reducing the evidential gap from observations in the laboratory (e.g., Champalbert and Lachaud, 1990; Dejean and Lachaud, 1992; Schatz *et al.*, 1994) to those in the field, we provide evidence as to the adaptiveness of learning and memory in *E. ruidum* and *E. tuberculatum*. In this context, our results represent an example of how the ecological dynamics of animals may be contingent upon their cognitive abilities to adjust to variable environments (Wcislo, 1989; West-Eberhard, 1989). However, more behavioral research has to be conducted before addressing the evolution of cognitive abilities in *Ectatomma* critically.

Apparently, the conditions of the first experiment bore closer resemblance to nature than those of the second experiment (especially for the colony of *E. tuberculatum*). The remarkable decrease (by $\pm 5°$; see Table III) in the directional precision of the outbound trip, after recent experiences of delayed success, can be interpreted as an adaptive strategy in *E. ruidum*. In an environment such as the forest floor where the spatiotemporal distribution of resources is presumed to vary within short time intervals, repeated sampling of adjacent areas results in more efficient foraging than focusing exclusively on the location of the most recent successes (Stephens and Krebs, 1986). Congruent with this interpretation are the observed adjustments in the outbound velocity and nest time in both species (Figs. 4 and 6). These adjustments conferred an efficient exploitation of the highly concentrated resources during the training and recovery periods. Similar cognitive abilities, including the use of single-event past experience, have been observed in other ant species that occur in habitats with equally patchy resources (see, e.g., Schmid-Hempel and Schmid-Hempel, 1984; Harrison and Breed, 1987; Traniello, 1988; Johnson, 1991; Dejean *et al.*, 1993). The accumulative effect of multiple immediate successes on the foraging behavior of *Ectatomma* (Table IV) indicates that past experiences can be integrated over longer intervals than single events. This is supported by the observation that foragers

in the field maintain an individual directionality throughout several days (Schatz *et al.*, 1995). In combination with the diversity of specialized behaviors (see references above) and the evidence of spatiotemporal learning (Schatz *et al.*, 1994), our results suggest that the individual cognitive abilities of *Ectatomma* are superior to most ant taxa. Whether they match those of honeybees or even smaller mammals remains to be tested (Bittermann, 1988).

Perhaps as indicative as the successful trials with individual foragers of *E. ruidum* and *E. tuberculatum* are those that "failed" to some extent. Both experiments were designed to demonstrate the effect of learning through comparison of spatiotemporal differences in foraging success. However, such an approach is contingent upon extensive sampling efforts by the foragers under trial (Stephens and Krebs, 1986). As it turns out, the sampling effort was the critical difference among the two species. Because the foragers of *E. tuberculatum* sampled smaller areas during the manipulation period (Figs. 7 and 8), they completed the first experiment as efficiently as those of *E. ruidum* (and in even less time). Furthermore, they did not adjust their foraging behavior as significantly when experiencing immediate versus delayed success. This relative failure of response enabled them to exploit the resources at one site with efficiency. As for the foragers of *E. ruidum*, their extensive sampling of areas where no prey items were caught, and the adaptability to temporal differences in foraging success, decreased the foraging efficiency in the first experiment. One of the more obvious differences among both species was the extent of adjustment in the nest time during the manipulation period (Fig. 6). The observation that several foragers of *E. ruidum* were in the foraging arena at any time during the day—regardless of whether they caught prey or not—is significant as well. Short-term variations in the distribution of resources cannot be learned unless the environment is sampled with a high frequency (Stephens and Krebs, 1986).

The effect of differential sampling effort on the foraging efficiency was amplified in the second experiment where two sites had to be checked. The majority of foragers of *E. tuberculatum* did not sample the second site as intended (i.e., without experimental interference), in spite of the fact that initially they had caught three termites there. Contrary to expectation, there were no significant adjustments in directionality by *E. tuberculatum* throughout the trial periods (Fig. 11). The experimental design was apparently more appropriate for the foragers of *E. ruidum*, which checked both sites as often as necessary to complete the trials, while making directional adjustments toward the more profitable site (Fig. 10). Again, differences in the profitability among two preying sites cannot be learned unless both are sampled throughout all trial periods. From this perspective, the second experiment was inappropriate to address the cognitive abilities of most *E. tuberculatum*

foragers, which appeared to be "fixed" on the first site. At the same time, our experiments have exposed behavioral differences at various levels that should be corroborated in future studies.

Based on the previous conclusions, one might be tempted to relate the behavioral and ecological differences among the two species on Barro Colorado Island. As observed by Weber (1946), *E. ruidum* is concentrated on the ground, whereas *E. tuberculatum* has an apparent preference for vegetation. It is conceivable that the distribution of resources on the ground varies in relatively shorter intervals than on vegetation where resources at most likely associated with flowers, fruits, nectaries, and other herbivorous arthropods. Such a scenario would be congruent with the hypothesis that the strategy of extensive sampling and short-term adjustments in *E. ruidum* is an adaptation to foraging on the ground, whereas the "sit-and-wait" strategy at one long-term location in *E. tuberculatum* is adaptive when foraging on vegetation. Because these contrasting environments pose different cognitive constraints on the foragers, behavioral differences are expected as well (Real, 1991). While we have no observational evidence to reject this hypothesis, our study involves several critical aspects that caution against such evolutionary conclusions. First of all, there was considerable individual variation among foragers of both species, to the extent that none of the observed foraging characteristics could be considered species-specific. To be sure, three foragers of *E. tuberculatum* "anticipated" prey during the second experiment at the less profitable site after catching several prey items at the other site. This indicates that they memorized their previous successes, in accordance with the experimental design. Furthermore, ambush behavior—presumably the preferred foraging strategy of *E. tuberculatum*—can be observed when foragers of *E. ruidum* specialize on sweat bee nests (Schatz and Wcislo, 1999). Variation among individuals is expected in animals with extensive cognitive abilities. The proximate causes for such behavioral differences may be genetic (Chandra *et al.*, 2000), ontogenetic (Champalbert and Lachaud, 1990; Dejean and Lachaud, 1992; Schatz *et al.*, 1995, 1996, 1999), ecological (Pratt, 1989; Passera *et al.*, 1994; Del-Claro and Oliveira, 1996; Windsor *et al.*, 1996; Schatz and Wcislo, 1999), and/or accidental. Evidently, our *E. tuberculatum* colony was queenless at the end of the experimentation period. Both colonies appeared to be satiated with more nutritional resources than typical under natural conditions. The spatial transition from the original habitat to the foraging arena was probably more significant for *E. tuberculatum* whose foragers had been concentrated on vegetation. Because few of these critical aspects could be controlled in our experiments, we are cautious to extend our conclusions beyond observations of individuals of *Ectatomma* to colonies, populations, and species. In order to corroborate the hypothesis that the cognitive abilities in *E. ruidum* and *E.*

tuberculatum reflect adaptations to structurally contrasting environments that differ in their spatiotemporal distributions of resources, it would be necessary to observe representative laboratory colonies over longer time periods. Such an approach confers potential control over ontogenetic, ecological, and accidental causes of behavioral differences among species of *Ectatomma*.

Our understanding of the evolution of learning in *Ectatomma* is likely to increase in the presence of phylogenetic information. Unlike in many other taxa of arthropods, this should be achieved within the near-future, since *Ectatomma* has only 12 species (Kugler and Brown, 1984). Then it will become feasible to propose and test homologies in the foraging behaviors and cognitive abilities of related species (Wenzel, 1992). Interestingly, current phylogenetic hypotheses render Ponerinae paraphyletic with respect to Ecitoninae (Keller, 2000), suggesting that the army ants evolved from the ancestors of behaviorally highly plastic taxa like *Ectatomma* and *Paraponera* (see, e.g., Breed *et al.*, 1996).

ACKNOWLEDGMENTS

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