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Directional fidelity as a foraging constraint in the western harvester ant, *Pogonomyrmex occidentalis*

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Summary. Understanding the foraging behavior of an animal is critically dependent upon knowledge of the constraints on that animal. In this study, I tested whether fidelity to foraging direction acts as a behavioral constraint to foraging western harvester ants, *Pogonomyrmex occidentalis*. Individual *P. occidentalis* foragers showed strong fidelity to foraging route and direction. Directional fidelity in this population was not related to trunk trail use, food specialization, colony activity levels, or mortality risks. Directional fidelity constrained individual foraging decisions; when colonies were offered seeds of different quality in 2 directions, individuals did not switch directions to obtain the energetically more rewarding seeds. Colony-level recruitment was increased for energetically more profitable seeds, indicating that colonial responses may compensate for the constraints of directional fidelity on individual foragers.

Key words: Route fidelity – Foraging constraints – *Pogonomyrmex occidentalis*

Most foraging models predict that animals will choose the available foraging strategy that maximizes some measure of energetic gain. However, the number of strategies available to an animal depends in part on constraints on the behavioral capacity of that animal. An important goal of foraging research is to identify the specific constraints on a given animal in a foraging system. In this study I examine limits on foraging flexibility in the harvester ant *Pogonomyrmex occidentalis*, to test whether fidelity to foraging direction or to trunk trail use can act as a constraint to the individual forager.

Strong directional fidelity of individual foragers has been demonstrated in a number of ant species, including *Cataglyphis bicolor* (Wehner et al. 1983; Harkness and Maroudas 1985), *Formica* species (Rosengren 1971), *Neoponera apicalis* (Fresneau 1985), and *Pogonomyrmex* species (Hölldobler 1976; DeVita 1979). Foragers of a number of species also show fidelity to an exact route when traveling to and from distant foraging sites (Rosengren 1971; Hölldobler 1976; Fresneau 1985). Strong directional and/or specific route fidelity is presumably related to limits on memory or orientation abilities (Wehner et al. 1983).

Pogonomyrmex ants use two different foraging patterns to gather resources. Individuals may forage independently of other ants in the colony, or may forage on trunk trails. When using trunk trails, multiple foragers travel on an organized, pheromonally marked trail to and from resources (Hölldobler 1974, 1976; Davidson 1977a, b; Whitford 1978). Thus, in *Pogonomyrmex*, directional fidelity could be partly or completely due to fidelity to foraging pattern.

Pogonomyrmex occidentalis workers are capable of responding to variation in environmental structure and food availability in a manner which increases colonial net energetic gain rate (Fewell 1988a). Fidelity to direction or foraging pattern would be considered a foraging constraint on individuals if it prevented them from switching to new foraging areas when doing so could result in a greater energetic gain by the individual. In this study, I determine whether directional fidelity is maintained when changing direction would result in a higher net gain rate.

Social insect colonies represent a unique situation in foraging research, because behavior can be measured at the level of the individual and the colony. Colony-level foraging strategy is not necessarily an extension of the behavior of individuals (Oster and Wilson 1978; Herbers 1981; Rissing and Pollack 1984; Pasteels et al. 1987). It is possible, therefore, for the colony to use strategies which compensate for limits on individual response. I also examine colonial response to resource variation to determine whether strategies of the colony as a whole can compensate for lack of plasticity by individual workers.

Methods

All experiments were conducted at Legion Park, an area of shortgrass prairie located just east of Boulder, Colorado. Data were collected from May through October, 1987. A total of 25 nests were used in the study; no nest was used for more than one experiment. Ants were marked either individually or according to foraging area with small dots of Testor's enamel paint or Pactra hot fuel proof dope placed on the thorax and front and hind legs. Colors were rotated so that each treatment group received all colors that were used within a set of experiments. Some experiments used piles of seeds. All seed piles were pre-measured to contain equal numbers of seeds. Seed piles were replenished during experiments to maintain constant volumes.

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Fidelity to direction and to foraging pattern

To determine the degree of fidelity shown to both foraging pattern and direction, I divided the foraging space around each of 7 colonies into areas within which the majority of ants either foraged individually or used trunk trails. Foragers were marked according to the area in which they foraged, and according to the foraging pattern being used. All areas in which ants were marked were separated from each other by a distance of at least 20 cm, measured at 0.5 m from the nest center. Three areas were marked for five nests: two trunk trails and one individual foraging area. Two areas were marked for one nest: one individual foraging area and one trunk trail area. The final nest was divided into four areas: two with trunk trails, and two individual areas. The angular sector encompassed by individual areas was approximately 60°, and was generally larger than that encompassed by trunk trail areas. However, the total number of ants foraging in trunk trail areas was similar to or larger than that of the individual areas. Ants from 2 nests were also monitored to determine whether ants within an area switched foraging pattern. Observations were made each day from 2 to 6 days after marking.

Each day, I recorded the area in which marked ants were foraging. Observations were made for a period of 20 min in each area; this is slightly longer than the length of time for an individual foraging trip (Fewell 1988a). Because it is unlikely that an ant would make two trips during this period, data on individual observations were assumed to be on different ants, and thus to be independent within a day. A X^2 test was used to determine whether ants were foraging in random directions or were returning preferentially to the original foraging area. Ants were considered to be choosing foraging areas randomly if the ants marked in a particular area were observed to forage in all areas in proportion to colonial use of each area.

Route fidelity

To determine whether individuals show fidelity to specific routes, six nests were divided into 90° quadrants, beginning at magnetic North. Approximately 20–25 ants from each nest were individually marked, in equal numbers from each section. The nests were then monitored for 5 h for each of 4 successive days. The exact routes of marked foragers were recorded by placing small flags at each turn in the foraging route and then measuring the angle of travel and distances between flags. The quadrant of travel was recorded for marked ants whose specific routes were not followed. Each day I also recorded the foraging activity in each quadrant for 10 min, measured as the number of individuals leaving the nest and traveling more than 0.5 m in each quadrant.

The effect of food quality on directional fidelity

Three seed types were used to test the effect of seed quality on directional fidelity: oats, sesame and millet. Seed quality was determined by weight and by seed energetic content, measured using a Phillipson microbomb calorimeter (Gentry Instruments), and correcting for acid and wire burned (Paine 1976). Seeds were dried and pooled before bombing. Duplicate measures differed by less than 0.1 cal/mg. Choice tests were also conducted to rank seed types by forager preference. In these tests, colonies were presented with seed piles containing equal numbers of two seed types, and the number of ants collecting each seed type within 5 min was recorded. Choice tests were conducted on a minimum of three colonies for each possible seed pairing.

To examine the effect of variation in food quality on directional fidelity, ants from a nest were simultaneously baited to two seed piles. The two piles were located 2 m from the nest entrance, and were angled at least 120° from each other. In three experiments, one pile contained sesame seeds and the other contained oats. In two experiments, millet and sesame were offered, and the final two nests were given piles of the same seed type (sesame or oats) as a control.

During these experiments, approximately 20 ants traveling to each pile were individually marked with two colors. Data were recorded from 1 to 3 h after marking on the day of marking, and then for 1 h each day for four consecutive days. Seed piles were removed at times when foraging was not monitored and seed piles were presented at approximately the same time each day. Individual ants were scored for the direction of travel, the time they arrived at seed piles, and whether a seed was taken. A 1 min count of the total number of ants arriving at each seed pile was taken every 15 min to monitor colony foraging levels. To determine whether directional fidelity is enhanced by fidelity to seed type, the locations of millet and sesame seeds were reversed on the 2nd day in the experiments involving these seeds.

Colony-level response to seed quality

To determine how the colony responds to seeds of different quality, I again simultaneously baited ants to two seed piles containing different types of seeds (oats and sesame). Seed piles were located 2.1 m from the nest entrance, and were angled at least 120° from one another. The number of ants crossing a marker located 10 cm before the pile was recorded for 2 min for both directions simultaneously. Two measures of initial foraging activity were taken at 15 min intervals before seeds were placed on routes; measures were then taken at 10 min intervals for 90 min. In two control experiments the same procedure was followed, but the same seed type (oats or sesame) was given in each direction.

Results

The first set of experiments examined fidelity to both direction and foraging pattern (individual or trunk trail forag-

Table 1. Chi-square values for tests of the hypothesis that foragers tend to return to the same area. Values are given for each of six days after marking. Data are pooled for five nests on days 1–3, and for four nests on days 4–6. The total number of marked individuals observed is given in parentheses. All X^2 values given are significant at $P<0.001$

Day	Trunk trail 1	Trunk trail 2	Individual foraging area
1	103.7 (83)	45.4 (47)	132.8 (38)
2–3	108.6 (129)	130.5 (67)	73.2 (44)
4	29.7 (49)	39.1 (23)	44.7 (25)
5	33.1 (51)	71.1 (43)	116.5 (36)
6	24.3 (47)	20.9 (25)	43.7 (24)

ing). Data were pooled among nests. The trunk trail with the highest foraging population from each colony was designated as trunk trail 1 and the smaller trunk trail designated as trunk trail 2. Ants from all areas tended to forage in the area in which they were originally marked. This tendency remained highly significant for all six days of the study ($P<0.001$ in each area, each day; Table 1), and was consistent among colonies. The relative fidelity of ants in each area (measured as the proportion of ants of a given color seen in the original area of marking) is graphed for the six days of observation in Fig. 1. Average fidelity was approximately 92% for each area on the first day after marking, and approximately 78% on day 6.

A subset of each population did change foraging direction. Ants switching from trunk trails did not show a significant tendency to switch to another trunk trail rather than to an equidistant individual area ($X^2=1.3$; $N=44$). Individuals switching from the more heavily used trunk trail were more likely to switch to individual foraging than to the less heavily used trunk trail ($P<0.005$; $X^2=8.6$; $N=32$). In order to obtain large enough sample sizes to test these hypotheses, data were pooled over the six days, potentially violating the assumption of independence required for the X^2 test (Lewis and Burke 1949). It is unlikely, however, that any ant was monitored for more than five trips, so the data are unlikely to be skewed by the behavior of one or a few ants.

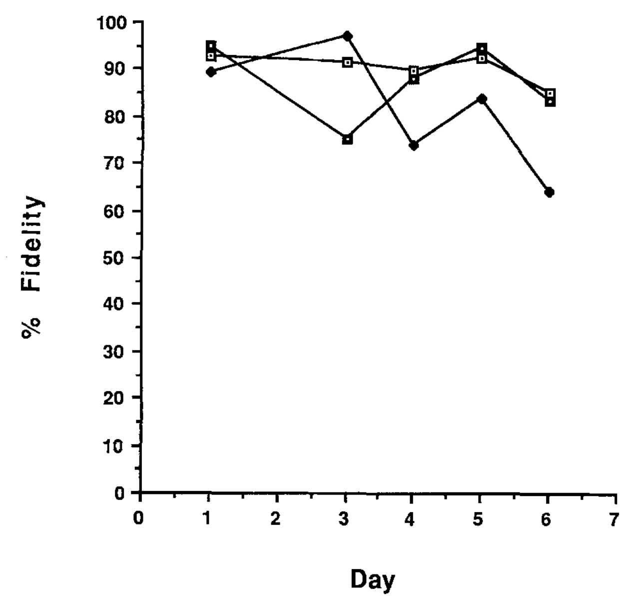

Fig. 1. Fidelity to area by ants foraging on trunk trails and in individual foraging areas. Data are pooled for 5 nests. Percent fidelity is measured as the percent of ants originally marked in an area that were seen in that area in a 20 min period. —⊡— Trunk trail 1; —◆— trunk trail 2; —□— individual area

To test whether individual or trunk trail areas had higher mortality risk, I monitored the proportion of ants originally painted in each area that were seen again in any area on successive days. Ants originally marked in the individual foraging area were resighted at a rate intermediate between that of ants marked on trunk trail 1 and trunk trail 2 (Table 2). When the data from the two trunk trails were pooled, there was no significant effect of foraging pattern on the proportion of marked ants resighted over six days (Paired t-test, $t=1.93$, $N=5$).

Individual route fidelity

A total of 50 individually marked ants were observed on successive foraging trips. The mean number of trips made per ant was 3.2 (SE=0.27; $N=50$). Of the 50 individuals observed, 33 made all trips in the quadrant where they were originally marked, and 17 made one or more trips in another quadrant. All of the ants observed made at least one trip in the quadrant where they were originally marked (Table 3). Marked individuals were more likely to return to the area where they were marked than to forage in other areas ($X^2=75.8$; $P<0.001$; $N=76$). Individuals that switched quadrants for 1 or more trip tended to go to all other quadrants in relatively equal numbers, so that there was not a higher tendency to switch to adjacent versus far quadrants ($X^2=0.35$; $N=32$).

The relative fidelity (measured as number of trips in area of marking/total trips) for 37 individuals making two or more trips was compared to total foraging activity in the different quadrants, to determine whether fidelity is correlated with colonial foraging activity. There was no significant correlation (Pearson Product Moment Correlation

Table 2. Resightings of ants originally marked either on trunk trails or in individual foraging areas. The number resighted in any area is expressed as a proportion of the total originally marked in that area. The actual number of foragers observed is given in parentheses. Data are pooled from a total of five nests for days 1–3, and from four nests for days 4–6. The data indicate that the use of trunk trails versus individual foraging did not significantly affect mortality risks of foragers in this study

Day	Proportion resighted:		
	Trunk trail 1	Trunk trail 2	Individual area
1	0.49 (80)	0.27 (45)	0.37 (40)
2–3	0.72 (116)	0.31 (52)	0.39 (43)
4	0.34 (49)	0.18 (26)	0.27 (28)
5	0.32 (46)	0.30 (44)	0.22 (22)
6	0.41 (54)	0.11 (15)	0.22 (18)
Mean % resighted:	45.6	23.4	29.4

Table 3. Number of individually marked ants seen one or more times in the quadrant where they were originally marked, and in other quadrants around nests. Each quadrant took 90° of space around the nest, starting at magnetic north. Data are pooled for six nests, and were collected over a 4-day period for each nest. The data indicate that individually marked foragers were more likely to be observed in the quadrant in which they were marked than in other quadrants

	Area where ants were originally marked:			
	NE	NW	SE	SW
Quadrants sighted in:				
NE	17	1	1	0
NW	1	8	2	2
SE	4	1	16	2
SW	3	0	5	9
Total ants marked:	17	8	16	9

Coeff. = 0.139; $N = 37$; data arc-sin transformed before analysis). It should be noted that because the mean number of trips made by each individual was low (mean = 3.1; SE = 0.27; range = 2–9; $N = 37$), the fidelity values must be considered rough estimates. However, these data are reflective of the total foraging activity of individuals in a 4 day period (20 h).

Individual foraging routes of 18 ants were followed for two or more trips. For 7 of the 18 ants followed, all trips were made within 2° (measured relative to the nest entrance) of the original trip for more than 50% of the trip. The other 11 ants had 1 or more trip which deviated by more than 2° in any direction. Of 54 trips followed, 36 followed the route of other trips by the same ant, and 18 deviated by 2° or more on either side. These data are difficult to analyze statistically, because the number of possible alternate routes is high and difficult to define. As a conservative test, I compared these data to a null hypothesis that equal numbers of ants remained faithful, deviated to the right or deviated to the left. Significantly more trips were made along the same route than expected ($X^2 = 27$; $P < 0.001$; $N = 54$). These data are not independent (Lewis and Burke

Table 4. Preference ranking, seed weights and seed caloric contents for three seed types presented to *Pogonomyrmex occidentalis* foragers. Preference rankings were determined by the number of ants choosing a seed type during pairwise choice tests. A minimum of three nests were used for each seed pair. Caloric content values were determined using a Phillipson microbomb calorimeter, correcting for acid and wire burned. Two replicates were performed for each seed type. Fresh seed weights are based on samples of 40 individually weighed seeds

Seed type	Preference rank	Fresh seed weight		Caloric density (cal/mg dry wt)	Caloric content (cal/fresh seed)
		mean (mg)	SE		
oats	1	6.7	0.69	4.30	26.91
millet	2	5.3	0.23	4.29	21.10
sesame	3	3.0	0.14	6.66	19.62

Table 5. The number of individually marked ants switching direction in experiments with (1) sesame and millet added in different directions, (2) sesame and oats added in different directions, and (3) in control experiments, with the same seed type in two directions from the nest. Data are pooled for two nests for the sesame/millet and for the control experiments. Data are pooled for three nests for the sesame/oat experiments

	Number of ants changing direction	Total ants observed	Proportion changing direction
Sesame/millet	5	28	0.18
Sesame/oat	20	87	0.23
Control	13	53	0.24

Table 6. Number of ants switching from a given seed type in experiments with (1) sesame and millet baits, and (2) sesame and oat baits. Data are pooled for a total of two nests in the sesame/millet experiments, and for three nests in the sesame/oat experiments

	Experiment			
	Sesame/millet[a]		Sesame/oat[b]	
	Sesame	Millet	Sesame	Oat
No. ants seen:	13	17	48	39
No. ants switching:	2	3	12	7

[a] Difference in number switching not significant, $X^2 = 0.2$.

[b] Difference in number switching not significant, $X^2 = 0.043$

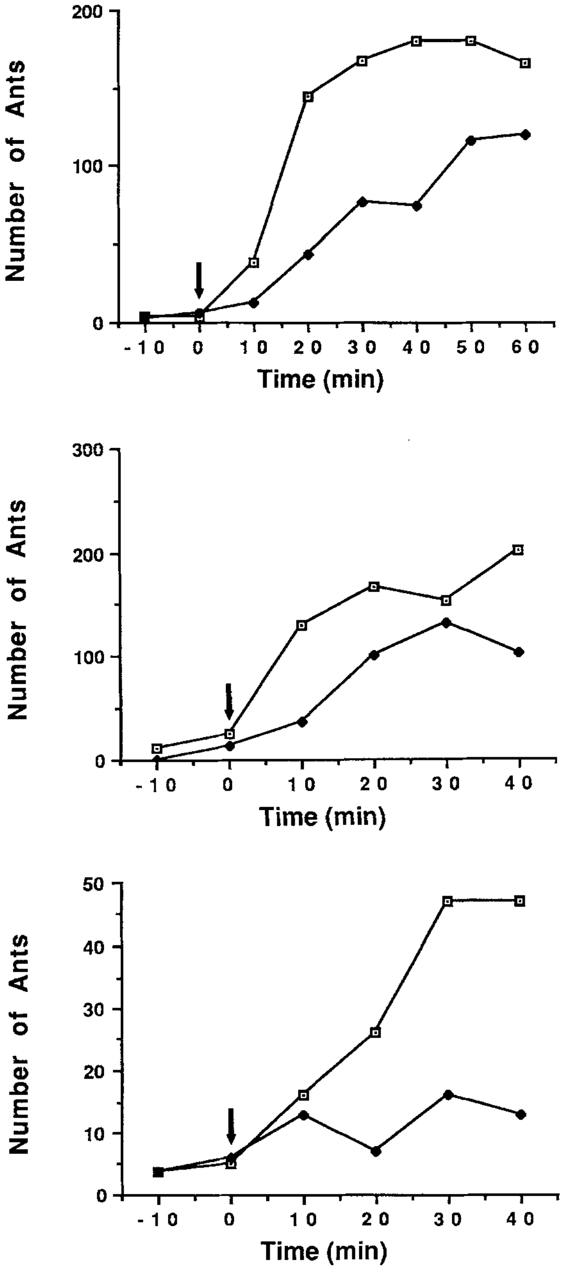

Fig. 2. Activity levels at two seed piles located equal distances, but in opposite directions from each of three nests. Seed piles were located approximately 2 m from the nest. Oats were placed in one direction, and sesame seeds in the other direction. Activity measures were taken before and after seeds were added; activity was measured as the number of ants leaving the nest and crossing a mark located 10 cm before each seed pile. Arrows indicate the time at which seeds were added. —▫— Oat pile; —◆— sesame pile

1949), because they include more than one data point per individual. However, they were not skewed by a large number of trips made by one individual (mean No. trips = 3.1; SE = 0.27; range = 2–5; $N=18$).

Fidelity to seeds of varying quality

In choice tests involving single seed piles with two seed types, oats were collected 2.1 times as often as sesame ($X^2=50.9$, $P<0.001$, $N=396$), and 1.8 times as often as millet ($X^2=50.7$; $P<0.001$; $N=661$). Millet was taken 1.5 times as often as sesame ($X^2=24.6$; $P<0.001$; $N=635$). The differences in preference ranking correlated with differences in measures of seed quality. Oats ranked higher than millet, and millet ranked higher than sesame in seed weight and total caloric content (Table 4). Despite a two-fold difference in seed weights, transport times to the nest were not significantly different for sesame and oats (ANOVA; NS, $F=2.85$, $N=32$).

When sesame seeds and oats were placed in different directions from a nest, the total number of ants switching foraging direction was not significantly different than the number of ants switching per nest in controls where the same seed type was offered in each direction ($X^2=0.626$; Table 5). The number of individual ants switching from sesame to oats within 5 days was not significantly different than the number switching in the opposite direction ($X^2=0.043$; Table 6). Similar results were obtained in the sesame/millet experiments (Tables 5 and 6). The directions of seed piles were switched in the sesame/millet experiments, without an observed effect of food fidelity on these results.

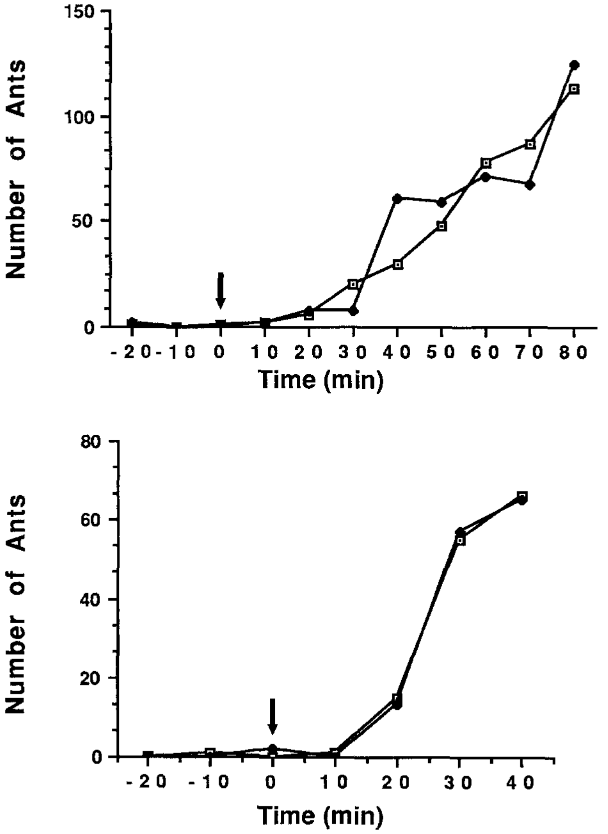

Fig. 3. Activity levels at two equidistant seed piles, located in opposite directions, approximately 2 m from each of two nests. The same seed type was given in each direction for each of the experiments. Activity was measured as the number of ants leaving the nest and crossing a mark located 10 cm before each seed pile. Arrows indicate the time that seeds were added. —□— Sesame pile 1; —◆— sesame pile 2

In all experiments involving seed piles of different types, colonies responded by increasing foraging activity in the direction of the higher quality seeds. When colonies were offered oats and sesame seeds in opposite directions, the rate of recruitment to oats was higher than to sesame (Fig. 2). In these experiments, although initial foraging activity did not differ significantly between the two directions (t-test, $t=0.64$, $N=5$; data pooled for five nests), activity counts after the placement of seeds were significantly higher for the oat direction than for the sesame direction for each nest (Paired t-test; Nest 1, $t=2.95$, $P<0.05$; Nest 2, $t=4.99$, $P<0.01$; Nest 3, $t=7.14$, $P<0.001$). In two control experiments where the same seed type was placed in each direction, activity levels were similar in both directions after the addition of seeds (Nest 1, $t=0.406$, $N=7$; Nest 2, $t=0.580$, $N=4$; Fig. 3).

Discussion

Directional and route fidelity

Ants in all experiments showed strong directional fidelity. Directional fidelity remained high for all areas for at least a 6 day period (Fig. 1). Because *Pogonomyrmex* forager longevity is about 14 days (Porter and Jorgensen 1981), this study sampled a significant portion of the total foraging lifetime. These results are consistent with other studies on ant species showing strong directional fidelity (Rosengren 1971; Wehner et al. 1983; Fresneau 1985). Also, levels of fidelity to specific areas were independent of foraging activity (Fig. 2). This result is similar to the situation seen in *Formica* (Rosengren 1971), and suggests that, once established, directional fidelity is not influenced strongly by recruitment.

The experience gained about a route through fidelity may reduce total time costs by enabling ants either to orient to food resources more quickly, or to return faster to the nest. *Cataglyphis bicolor* ants in familiar areas orient to the nest faster than ants in unfamiliar areas (Wehner et al. 1983). *Paraponera clavata* ants returning to familiar food areas along the same route travel more than twice as fast as naive ants travelling along the same route (Harrison et al. 1989). Therefore, food availability could be reduced 50% in a foraging patch, and directional fidelity would still be energetically favorable for *P. clavata*.

In *Pogonomyrmex occidentalis*, time is the most important cost factor in determining energetic decisions during foraging (Fewell 1988a), and most food items are evenly distributed (Fewell 1988b). Thus a decrease in time costs during foraging could also be a significant energetic advantage. In the extreme case, route familiarity also reduces mortality risks, because ants in unfamiliar areas are more likely to become lost (Wehner et al. 1983). Finally, if food resources are evenly distributed around the nest over time, directional fidelity may also speed up the discovery of new resources in old foraging areas.

Individually marked ants also showed strong fidelity to the specific route taken within a general direction, suggesting that fidelity is related to specific orientation cues. *Pogonomyrmex* foragers use pheromonal cues to orient

(Hölldobler and Wilson 1970; Hölldobler 1976). Route fidelity may be particularly advantageous when using pheromonal trails, as the range of such cues is limited.

Fidelity to foraging pattern

Foraging area fidelity did not differ for ants on trunk trails or individual routes (Fig. 1). This is consistent with studies on other *Pogonomyrmex* species (Hölldobler 1976; DeVita 1979) and on *Formica* species (Rosengren 1971), where both species that are primarily trunk trail foragers and species that are primarily individual foragers show directional fidelity.

Ants which switched from trunk trails did not forage preferentially on another trunk trail, suggesting that fidelity to foraging pattern does not occur independently of fidelity to foraging direction. In fact, ants from more heavily used trunk trails tended to go to individual areas rather than to the smaller trunk trails. This is probably a result of a drop in the intensity of use in some of the smaller trunk trails, one of which disappeared completely by the end of the experiment.

A few individuals within each area also switched foraging pattern to form temporary trunk trails, or to forage individually. These data suggest that the fidelity observed here is mainly to foraging direction, while foraging pattern may be based on resources or vegetational structure in the area to which the forager is returning. Both *Pogonomyrmex* and other ant species have been shown to change foraging pattern in response to changes in the distribution of preferred resources (Bernstein 1975; Hahn and Maschwitz 1985; Fewell 1988a, b), and to changes in vegetational density along a route (Fewell 1988b). If use of alternate foraging patterns does help ants collect resources efficiently under different environmental conditions, then a relatively weak fidelity to foraging pattern would be advantageous in an environment where resources and vegetational structure are variable.

Mortality risks and foraging pattern

Differential mortality for individually foraging versus trunk trail foraging ants may result in preferences for one foraging pattern over another. For example, species of *Pogonomyrmex* which primarily use trunk trails are better able to fend off attacks from horned lizards than species relying on individual foraging patterns, as more foragers are involved in defense (Rissing 1981). The similar proportion of marked foragers that were resighted on trunk trails and in individual areas suggest that mortality risk in this population is similar for the two foraging patterns.

It should be noted, however, that number of resighted foragers is not always an accurate measure of mortality. On a number of occasions I observed ants which had previously been foraging engaged in other activities, such as nest maintainence and refuse removal. If some unsuccessful foragers turn to other nest activities instead of foraging in other directions, this could explain the low proportion of resightings for ants on the less heavily used trunk trails compared to the more heavily used trails (Table 2).

Fidelity as a foraging constraint

The strong directional fidelity seen in this population constrains the foraging choices of individual workers. Ants given piles of mixed seeds choose larger seeds, with higher energetic content (Table 4; see also Taylor 1977; Davidson 1978; Kelrick et al. 1986), suggesting that energetic content is an important factor in the foraging decisions of these ants. If directional fidelity is not a constraint, then foragers should select seeds based on energetic content, independently of direction, as long as ants in the colony have some knowledge of the resources. However, when seeds of differing qualities were placed in different directions from nests, there was no change in the strong directional fidelity of individual foragers. This indicates that directional fidelity limits the responses of foragers.

The verification of constraints is an important component of foraging theory, because accurate foraging models cannot be made without establishing the environmental or intrinsic limitations for an animal (Cheverton et al. 1985; Stephens and Krebs 1986). Studies of foraging constraints often focus on what may be considered fixed biological characteristics, which are unlikely to change over the animal's foraging lifetime. Potential fixed constraints on ants include temperature tolerance (Box 1960; Rogers 1972; Bernstein 1975; Traniello et al. 1984), and maximal load size (Wilson 1978; Rissing and Pollack 1984; Franks 1986). Directional fidelity is not a fixed constraint, because the forager is potentially capable of changing foraging direction in response to environmental variation and resource changes. For example, *P. occidentalis* colonies have been observed to abruptly switch foraging areas in response to the appearance of highly preferred *Eriogonum effusum* blooms (Fewell 1988b). In experiments where *P. occidentalis* colonies were provided with seeds in cleared and vegetated areas, there was a slow but significant trend toward switching by individuals to the cleared area (Fewell 1988a).

When colonies were provided with oats and sesame seeds, the per trip net gain rates for ants collecting sesame seeds were approximately 16.5 cal/min, while net gain rates for ants collecting oats were approximately 22.9 cal/min. In these experiments, directional fidelity persisted despite a potential 1.4-fold increase in net gain rate. Directional fidelity is therefore valuable enough to be retained even when doing so reduces individual foraging net gain rate.

My experiments cannot determine conclusively whether lack of directional plasticity in these ants is due to an intrinsic constraint, such as a learning constraint, or is due to lack of communication during recruitment. Foragers travelling in one direction may have had no knowledge of the availability of the more preferred seed. However, foragers from different directions entered the colony through a common entrance, and the probability of encountering an ant with food from the alternate direction was extremely high. Also, the experiments were conducted over successive days, and foraging was eliminated when seed piles were removed. Simultaneous recruitment events occurred each day, again increasing the probability that ants received information about both seed piles.

Colony-level responses to different seed qualities

When examining the foraging strategies of social insects, it is important to consider behavioral changes both at the level of the individual and the colony. My experiments show that individual foragers were constrained from making some foraging decisions that could increase energetic gain rate. However, the colony as a whole was able to compensate for individual limitations by varying recruitment effort to the different seed types. Because social insect groups are able to respond to environmental conditions both at the level of individual foragers, and at the colonial level, the colony is not acting as the sum of the behaviors of individual ants. These emergent properties of the colony as a whole are a unique and important feature of social insect foraging.

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