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The allocation of foragers in red wood ants

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Abstract. 1. We studied how colonies of the red wood ant, *Formica polyctena*, adjust the numbers of foragers allocated to different foraging trails. In a series of field experiments, foragers were marked and transferred from one nest to another, related nest, where they joined the foraging force. Transferred workers acted as a reserve of uncommitted, available foragers.

2. Previous work shows that each individual forager habitually uses one trail. We found that for an uncommitted forager, the influence of recruitment initially is stronger than that of directional fidelity. Transferred workers were likely to use trails leading to new food sources. When transferred to a new nest, foragers were not likely to use a trail in the same direction as their original trail in the donor nest.

3. After a week, transferred foragers tended to develop route fidelity. Even after bait was no longer present, they continued to use the trail that had formerly led to a bait source.

4. We examined how colonies adjust numbers on a trail by experimentally depleting some trails. Colonies usually did not compensate for depletion: foragers were not recruited to depleted trails.

5. In general, the dynamics of foraging in this species facilitate a consistent foraging effort rather than rapid adjustments of forager allocation.

Key words. Red wood ants, foraging, allocation of foragers, recruitment, directional fidelity.

Introduction

An ant colony obtains food through the foraging behaviour of its workers. A mature red wood ant colony, which may contain nearly 1 million workers and survive for at least 50 years, sends out about 300,000 foragers each day on cleared, permanent trunk trails. Foragers bring in food which is then distributed to the rest of the colony. *Formica polyctena* eats arthropods, both live and dead, but most trails lead directly into trees, where ants travel to collect honeydew secreted from aphids. The study of foraging in red wood ants has been concerned with the quality and amount of food collected (Horstmann, 1974, 1982; Cherix, 1987; Sorensen & Schmidt, 1987), recruitment mechanisms (Horstmann, 1975, 1976; Rosengren & Fortelius, 1987), and the partitioning of foraging grounds among individual workers (Dobrzanska, 1958; Rosengren, 1971; Cosens & Toussaint, 1985; Rosengren & Fortelius, 1986).

An important component of foraging theory deals with the relation between variation in food resources and an animal's capacity to alter its foraging response (Schoener, 1971; Houston *et al.*, 1988). The present study does not directly test optimal foraging theory. Instead we investigate how an ant colony responds to changing food resources, by studying some of the factors affecting the plasticity of individual foragers. A red wood ant worker lives 1–2 years, and individual workers are likely to use a particular foraging trail, a phenomenon known as 'route fidelity' (Rosengren, 1971). Many questions remain about the dynamics of forager allocation; for example, which foragers are recruited to new food sources, whether route fidelity develops in response to food, and whether colonies act to maintain a stable allocation of foragers when food sources are stable.

The design of experiments to approach such questions raises some interesting problems. To follow individuals, they must be marked, and some sampling scheme determines which individuals will be marked. One can identify a pool of individuals *after* a recruitment episode (by mark-

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ing ants recruited to bait), but it is more difficult to follow a pool of individuals of known foraging history *before* and *during* recruitment. For example, if a pool of ants are selected from the foragers on a particular trail, it is impossible to ascertain what combination of recent recruitment or long-standing route fidelity had caused each forager to use that trail. Here we employ a method based on the use of marked ants that were transferred from one nest to another. In this way it is possible to obtain a pool of marked foragers that all begin from the same starting point. As all transferred foragers are equally unfamiliar with any of the trails of the recipient colony, all are equally uncommitted to any trail. Ants of *F.polyctena* can be transferred because colonies may reproduce by budding. As a result, neighbouring nests may contain related individuals. Previous work showed that if two nests are related, such that one budded from the other or both budded from a third, workers transferred from one nest to the other will be accepted into the recipient nest without any aggressive interactions (Rosengren, 1985).

We performed several experiments which, in combination, address three questions about how foragers respond to changes of colony environment. (1) For an uncommitted forager, are the influences of recruitment and directional fidelity equally strong? In one experiment we considered whether transferred foragers were susceptible to recruitment by observing their response to bait. In another experiment we examined the influence of route fidelity by observing whether transferred foragers continued to forage in the direction they originally took in the donor nest. (2) Does the development of route fidelity require sustained recruitment to food? Previous work showed that route fidelity develops quickly in young foragers recruited on a trail to a sustained food source (Rosengren, 1971). We examined whether workers recruited to a bait trail maintain route fidelity after the food is no longer present. (3) How often does a colony adjust numbers on a trail? We tested whether more workers are recruited to a trail that has suffered a sudden depletion.

Methods

Experiments were conducted in late May and early June 1989, in a pine forest in the rural district of Sjundea, about 40 km west of Helsinki in southern Finland. The habitat, and the morphological characteristics of the ants used to identify them as *F.polyctena*, have been described previously (Rosengren, 1977).

The choice of colonies to be used in transfer experiments was based on previous records of budding in a polydomous population under observation for 15 years (R. Rosengren, unpublished data). Nine recipient nests were observed, three in each of three experiments involving transferred ants. Some donor nests were used to transfer ants to more than one of the recipient nests (Table 1). Most donor–recipient pairs of nests were known to be descended by budding from the same nest, because the budding had been observed during the past 15 years. The other pairs had been used before in similar transfer experiments in which no hostility was observed; these were probably related by budding that occurred more than 15 years ago. In the experiments reported here, no hostility was ever observed between transferred ants and those of the recipient colony. When transferred ants were released on the recipient nest, they remained on the nest mound for some hours, where they were apparently ignored, and never harrassed, by the ants of the recipient colony. After that they appeared to act as normal foragers in all recipient nests, travelling on the foraging trails, carrying nest material and prey to the recipient nest, and visiting aphids. There were no trails shared by any donor and recipient colonies. Most trails led directly from the nest into trees containing aphids, so it seems unlikely that variation in transferred ants' familiarity with the terrain surrounding the trails affected the results.

Table 1. Trail differences in numbers of transferred ants.

Recipient colony	(Donor)	Week	df	SS	F	P
Bait						
*4	(12)	1	4	1179.5	3.8	0.02
5	(3)	1	1	52.1	2.7	0.13
6	(1)	1	4	382.7	0.7	0.60
4		2	4	292.8	1.4	0.26
*5		2	2	44	5.1	0.02
*6		2	4	590.5	2.9	0.04
Directional fidelity						
*7	(13)	1	3	1810.5	6.4	0.003
*8	(11)	1	4	229.0	4.2	0.01
*9	(3)	1	3	173.8	5.1	0.004
*7		2	3	581.5	8.9	0.0006
8		2	3	828.2	2.8	0.06
*9		2	4	335.1	9.1	0.0001
Depleted trail plus transferred ants						
*1	(2)	1	3	1883.5	17.6	0.0001
2	(1)	1	4	110.7	0.3	0.89
3	(10)	1	3	18.1	0.5	0.71
*1		2	3	609.8	6.5	0.003
2		2	4	37.5	0.4	0.83
3		2	3	30.1	0.2	0.88

Each line of the table shows the results of an ANOVA comparing the numbers of transferred ants on all trails of one colony. No distinction was made between the experimental and any other trail. * indicates colonies for which numbers of transferred ants varied significantly across trails ($P < 0.05$). The number in parentheses identifies the colony used as a donor for each of the observed, recipient colonies.

All experiments used the same procedure for collecting and marking ants. Ants were collected using a pitfall trap, consisting of a plastic tray coated with Fluon (which produces a slippery surface so that trapped ants cannot climb out) buried in the foraging trail at least 5 m from the nest. About 5000–20,000 ants were collected per colony, marked with spray paint (techniques as in Rosengren, 1971) and placed on the nest of the second, experimental colony. We estimate that about half the transferred ants survived the marking process; numbers of surviving transferred ants ranged from 3000 to 10,000. Mortality was due to the high concentration of formic acid produced by the ants when they were crowded together during the marking procedure, and while being carried to the recipient nest. To reduce mortality we attempted to spread out the ants and to release them as soon as possible after marking.

Each experiment was repeated two or three times, at intervals of 1 week. When experiments were repeated, a different colour of paint was used each time that another group of ants were marked and transferred to a given nest. In each weekly trial of an experiment, nests were observed for 3 days. On each foraging trail of each nest, counts were made of the numbers of marked and unmarked foragers passing an imaginary line that crossed the trail, in 2 min. The endpoints of this line were labelled so that all counts were made from the same place and encompassed the same width of trail. Two counts were made per colony each day, one in the morning and one in the afternoon. In week 1, counts were made from 07.00 to 11.00 hours and from 17.00 to 20.00 hours; in weeks 2 and 3, from 10.00 to 12.00 hours and from 16.00 to 18.00 hours. In week 3, one count on one day was missing for all colonies due to rain. Each nest had three to six foraging trails.

1. *Bait*

This experiment used three undisturbed recipient nests and was conducted in weeks 1, 2 and 3. The bait (sugar syrup poured over several sponge cloths) was placed in a new location each time the experiment was made, alongside the currently weakest foraging trail of each recipient nest. Baits were put down at least 2 h before the first foraging count was made. Sugar syrup was renewed each day if it appeared to be depleted. Each nest received marked, transferred ants from another nest, as above. Bait was never placed in the direction of the trail from which transferred ants were taken, so recruitment was independent of directional fidelity.

2. *Directional fidelity*

This experiment used three undisturbed recipient nests, and was conducted in weeks 1 and 2. Each recipient nest had one foraging trail running in a direction similar (within 20°) to the trail from which transferred ants were taken in the donor nest. Ants were taken from the same trail of each donor nest in both weeks 1 and 2.

3. *Depleted trails*

(a) *With transferred ants.* This experiment used three nests, and was conducted in weeks 1 and 2. Foragers were removed from one trail of each recipient nest using the pitfall traps described above. In addition, about the same number of ants were collected from another nest, marked, and placed on each recipient nest. In each experimental nest, the same trail was depleted in both weeks 1 and 2.

(b) *Depletions without transferred ants.* This experiment used three nests, and was conducted in weeks 1 and 2. Methods were exactly as above, except that no ants were added from other nests. In all nests the trail chosen for depletion was clearly the trail with the largest number of foragers. Data analysis for this experiment was based on the previous result that the rank ordering of foraging intensity on various trails does not change from one week to the next (Rosengren, 1971). If after depletion the depleted trail was no longer the strongest, it would mean that colonies did not compensate for depletion by recruiting more ants to the depleted trail. We tested whether the mean number of foragers observed on the depleted trail was greater than the mean of the numbers on the strongest of the remaining trails, using a paired *t*-test that compared the depleted and remaining trails observed in one colony at the same time. To be as conservative as possible in detecting any difference between the means, a two-tailed hypothesis was used in estimating significance levels.

To examine whether transferred ants acted independently of the recipient nest, we compared the numbers of transferred ants on each trail using a one-way ANOVA. An ANOVA was performed separately for each nest and each week, which consisted of a 3-day bout of observation (six counts per trail in each nest). To provide similar numbers of replicates for all three experiments, data from the third week of bait experiments were not included (see Table 1). This first part of the analysis led to the conclusion that transferred ants were affected by factors in the recipient nest that influence the allocation of different numbers of workers to different trails. Thus in subsequent analysis, the null hypothesis was that transferred workers were found on foraging trails in the same proportions as the workers of the recipient colony. Deviation from this null hypothesis, in response to some experimental treatment, confirms that transferred workers were influenced by the experiment.

For bait, directional fidelity and depleted trail experiments involving transferred ants, we analysed the data using the proportions, not numbers, of transferred ants, to determine whether the proportion of transferred (and marked) to unmarked ants on a foraging trail was affected by each experimental treatment. The proportion of marked to unmarked ants was derived for each count of each foraging trail. In each nest, one trail was considered the experimental trail. In experiment 1, it was the trail to the bait. In experiment 2, using undisturbed nests, the experimental trail was the trail in the same direction as the one from which transferred ants were taken. In experiment 3, it was the depleted trail. The data analysis compared proportions of transferred ants on the experimental trail, with these proportions on all other trails (summed for each observation). The proportions were not subjected to an arcsin transformation because the analysis appeared to be robust without it, and because the assumptions of the transformation were not met (e.g. its assumption that proportions are based on a binomial distribution is dubious in this case because numbers of marked and unmarked ants may not be independent).

A three-way, full-factorial ANOVA was performed using the proportions of marked ants with colony (three colonies), observation (six observations per experiment, i.e. two counts per day for 3 days), and trail (2: experimental or sum of the others) as main effects (see Table 2). (We use the term 'colony' instead of 'nest' here because, with the exception of nests 1 and 2 which were related, the three nests observed in each experiment were unrelated.) The error term was the trail × observation × colony effect. We were especially interested in the trail effect, which if significant would show that the proportion of marked ants on the experimental trail (i.e. the bait trail, depleted trail, or trail in the same direction as the one from which transferred ants originated) differed from that on other trails. A significant colony effect would indicate differences among colonies in relative proportions of transferred ants on experimental and other trails. A significant observation effect, or interactions involving the observation effect, would indicate that the proportions of transferred ants over experimental and other trails were subject to significant fluctuation or change in the course of the 3 days of observation.

An ANOVA using proportions was performed for each weekly trial of each experiment. In addition, we examined whether the effect of each experiment persisted from one week to the next. To test this for the data of a given week, the ANOVA used the proportions of the ants transferred the previous week observed on the experimental trail of the previous week. This tests whether, in a given week, ants that had been transferred in the previous week still continued to use the trail that had received experimental treatment when they were first transferred. In the directional fidelity experiments, and in the depleted trail plus transferred ants experiments, the experimental trail remained the same in both weeks. In the bait experiments, the bait was moved each week so the experimental, or bait trail, changed each week.

Results

Transferred ants respond to cues in the recipient nest that affect the allocation of different numbers of foragers to different trails. This conclusion is supported by the observation that transferred ants used the recipient colony's trails, rather than wandering at random all around the recipient nest. If transferred ants recognized foraging trails as such but were unaffected by factors determining foraging allocation, they might be expected to disperse on the trails at random. In this case, they would be equally likely to forage on any trail, and would be expected to appear in equal numbers on all foraging trails. Table 1 shows the results of the ANOVA testing for an effect of trail using numbers (not proportions) of transferred ants on each trail. (Full ANOVA tables are available from the senior author.) In this analysis, no distinction was made between the experimental trail and any of the others, though data from all three experiments are included. The results show that in ten of eighteen tests, numbers of transferred ants differed significantly among foraging trails of a colony

Table 2. Summary of results of ANOVA using proportions of transferred ants on each trail.

Data from week	Ants transferred in week	Col	Obs	Col × Obs	Trail	Col × Trail	Obs × Trail
Bait plus transferred ants							
1	1	–	–	–	*	**	–
2	2	–	*	–	–	–	–
3	3	*	–	–	*	–	–
2	1	**	–	–	**	**	–
3	2	–	–	–	*	–	–
Directional fidelity of transferred ants							
1	1	–	–	–	–	–	–
2	2	**	–	–	**	*	–
2	1	*	–	–	–	–	–
Depleted trail plus transferred ants							
1	1	–	–	–	–	–	–
2	2	**	*	–	**	*	–
2	1	**	*	*	–	**	–

Each line of the table shows the results of one ANOVA. Each ANOVA compared the proportion of transferred, marked ants (out of the total number of transferred ants plus unmarked ants from the recipient colony) on the experimental trail, with the proportion on other trails. In experiment 1 the experimental trail was the bait trail. In experiment 2 the experimental trail was the one in the same direction as the trail in the donor nest from which transferred ants were taken. In experiment 3 the experimental trail was the depleted trail. Main effects were colony, observation and trail; effects tested are listed across the top of the table. – = not significant, * $P<0.05$, ** $P<0.01$.

(Table 1). Thus in some experimental conditions, transferred ants are more likely to use particular trails, and to avoid others.

Bait experiments showed that transferred ants were likely to forage toward the bait. In four of five experiments, there was a significant effect of trail (Table 2), showing higher proportions of transferred ants on the bait trails than other trails. In weeks 1 and 3 the ants transferred that week were significantly likely to use the bait trail (Figs 1A, 1C).

There is mixed evidence regarding directional fidelity in transferred ants, relative to their original direction in the donor colony. In the first experiment, transferred ants did not forage in the direction of the trail in their original nest that they were using when collected (week 1, no significant trail effect; Table 2). The ants transferred in week 1 also showed no directional fidelity later on, in week 2 (no significant trail effect). However, results are different for the second group of ants, transferred in week 2. Here there was a significant effect of trail, of colony, and a colony by trail interaction (Table 2).

Route fidelity develops very quickly in uncommitted foragers, and does not require sustained recruitment to food. Once recruited toward a bait, transferred ants continued to forage in that direction for more than a week, even when no food was offered. Ants transferred in week 1 were still significantly likely to forage during week 2 in the direction of week 1's bait, although the bait was no longer present at that site (Table 2; Fig. 1D). Similarly, ants transferred in week 2 were still significantly likely during week 3 to forage toward the former site of week 2's bait (Fig. 1E). The latter result is especially striking

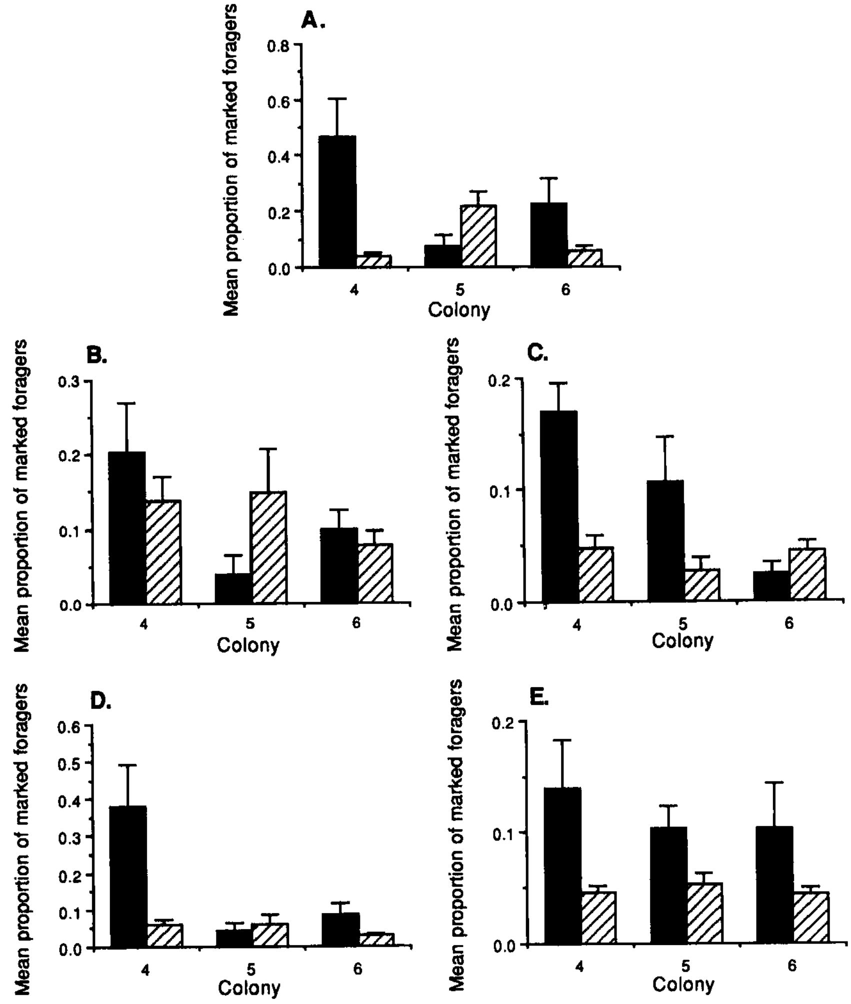

Fig. 1. Mean proportion of transferred ants on the bait trail. Each figure shows data for three colonies, observed for 3 days. Shown are the proportion of marked and transferred to unmarked ants on the trail to the bait (solid bars), and the proportion on all other trails (hatched bars). The bait was moved to a different trail each week. (A) Mean proportions during week 1 of ants transferred in week 1. (B) Mean proportions during week 2 of ants transferred in week 2. (C) Mean proportions during week 3 of ants transferred in week 3. (D) Mean proportions during week 2 of ants transferred in week 1, on the trail on which bait was located in week 1. (E) Mean proportions during week 3 of ants transferred in week 2, on the trail on which bait was located in week 2. Error bars show standard errors of the means for each colony ($n = 6$ observations per colony).

since there was no significant effect for this group during week 2 itself (Fig. 1B): week 2's transferred ants were not likely to forage along the bait trail until after the food was gone.

Experiments with depleted trails show little evidence that colonies recruit more foragers to compensate for ants that were experimentally removed. In experiments in which transferred ants were added to colonies with depleted trails, transferred ants tended to forage on depleted trails in only one of three tests (Table 2). Ants transferred in the first week were not significantly likely to forage on the depleted trail, either in the first or second week (no significant trail effect, Table 2). Ants transferred in the second week were significantly likely to use the depleted trail (Table 2) though in this week, differences among colonies and the colony × trail interaction were statistically significant.

When trails were depleted and no transferred ants were added, there was no evidence that colonies allocated workers to the depleted tail. We compared counts made after removals of the depleted trail (which was the strongest before removals) with counts of the strongest of the remaining trails. After removals, the depleted trail was either not different from, or weaker than, the strongest of the remaining trails. The results of the paired t-tests were: nest 10, week 1, no difference, $\mathrm{df}=5$, $t=2.06$, $P<0.09$ (two-tailed), week 2, no difference, $\mathrm{df}=5$, $t=1.34$, $P>0.24$; nest 11, week 1, depleted trail weaker than trail A, $\mathrm{df}=4$, $t=-6.33$, $P<0.003$, week 2, depleted trail weaker than trail A, $\mathrm{df}=5$, $t=-5.94$, $P<0.002$; nest 12, week 1, no difference, $\mathrm{df}=4$, $t=0.95$, $P<0.39$, week 2, depleted trail weaker than trail A, $\mathrm{df}=5$, $t=-5.25$, $P>0.003$.

Discussion

The results of this study suggest that transferred ants act as a reserve of available foragers. They were likely to use trails leading to a new food source (four of five experiments, Table 2). The high proportions of transferred foragers on bait trails, relative to unmarked ants of the recipient colony, suggest that transferred foragers are especially amenable to recruitment. The method of transferring ants employed here may be useful in future studies of forager allocation. Colonies are most likely to recruit to bait early in the spring, and recruitment to bait diminishes as the season progresses (Horstmann, 1975; Sudd & Sudd, 1985). Seasonal variation in recruitment intensity probably influences the response of transferred ants.

Initially, recruitment to bait has a stronger effect on an uncommitted forager than does route fidelity. In two of three experiments, transferred ants did not maintain directional fidelity in the recipient colony. Previous work shows that red wood ants rely on landmarks to remember trail directions between foraging bouts (Rosengren & Fortelius, 1986), though they depend on the sun and polarized light to persevere in a given direction during a foraging bout (e.g. Jander, 1957). Transferred ants, deprived of the usual landmarks in the home nest, may have been unable to persist in their usual direction.

In the one replicate (one of three experiments) in which transferred ants foraged in the original direction, recruitment, not directional fidelity, may have been responsible for the result. Here there were significant effects of trail, but also significant effects of colony and a trail by colony interaction (Table 2, directional fidelity experiment, week 2). These demonstrate significant differences among colonies in the extent to which transferred workers used the trail in their original direction. In one colony (colony 8) transferred foragers travelled in the original direction. In this colony, the trail in the same direction as the one from which transferred ants were taken led to trees that were a source of aphids. Thus, use of this trail by transferred ants may have been due to recruitment as well as directional fidelity. In the other two colonies used in this experiment, the trails in the direction corresponding to the one originally used by transferred ants did not appear to lead to aphid trees. In these other colonies, it appears that there was strong recruitment to trails in directions other than the one habitual for transferred foragers in their home nest.

Route fidelity develops quickly in foragers recruited to a new trail, and does not require sustained recruitment to food. Transferred ants recruited to bait one week, tended to forage toward it the next, even after the bait was gone. Further work is needed to determine how much longer route fidelity would be maintained on a trail leading to no food source. Like recruitment itself, the rate at which route fidelity develops may have a seasonal component. The age distribution of foragers in a colony changes from month to month. In the spring, a high proportion of a colony's active foragers are young and inexperienced, and young foragers can become committed to a particular trail after a single visit in which food is obtained (Rosengren, 1971). Successive batches of transferred foragers could have contained increasing proportions of younger, inexperienced foragers recruited to take the places of previously removed, older foragers. Young transferred ants may be especially likely to acquire route fidelity on a bait trail.

Colonies appeared not to compensate for the disappearance of workers by recruiting more foragers to a depleted trail. The probability of compensation probably depends on the the ratio of numbers of available foragers to the amount of food to be retrieved. For example, in the early summer, foragers maintaining route fidelity may continue to use trails to the site of the previous year's aphid supply, although all aphids have not yet matured enough to produce honeydew. Then the ratio of forager numbers to food supply would be high, and foragers would be relatively unoccupied. If the trail were depleted, recruitment would not be necessary because the reduced number of foragers could still handle the existing food supply.

It may be that *F.polyctena* colonies act to stabilize numbers on a trail, but not in response to depletion. In this habitat, there is little predation on red wood ants when they are on the foraging trails, so it must be unusual for large numbers of ants to disappear suddenly, as they did in our experiments. Previous experiments with seed-eating ants (*Pogonomyrmex barbatus*) had very different results. When foragers were removed (Gordon, 1986) or obstructed (Gordon, 1987, 1991), the timing and intensity of several tasks changed, including foraging, nest maintenance, and patrolling. *P.barbatus* colonies frequently experience predation: the horned lizard (*Phrynosoma*) waits beside trails and captures foragers as they pass. The present results suggest that a *F.polyctena* colony responds less than a *P.barbatus* colony to a small change in rate of successful foragers returning to the nest. More rapid adjustment of foraging behaviour may be necessary to *P.barbatus* because of frequent predation, more ephemeral food sources (wind-blown seeds), and smaller colony size. Comparative studies are needed to show whether differences among ant species in the dynamics of foraging behaviour reflect differences in ecology.

In some ways, forager allocation in *F.polyctena* seems geared to stability rather than to a rapid response to changes of environment. For example, route fidelity in undisturbed colonies, the continued use of particular trails by particular individuals, clearly acts to stabilize the numbers of individuals on each trail. If numbers of foragers are limited, the timescale on which route fidelity sets in partially determines how soon colonies can respond to new food sources through recruitment to a new trail. The foraging system of *F.polyctena*, though stable, allows it to a take advantage of new food sources. Within hours baits drew large numbers of ants, both transferred and not. It is likely that workers in the recipient nests found the food and recruited the transferred ants to it, but this remains to be investigated. The behaviour observed here seems suited to an ecological situation in which food sources are renewable, and a new food source is as likely to persist as those already in use. Red wood ants utilize food resources that during the warm season do not fluctuate much in time or space: aphids in pine trees. If resources are stable, it may be more important for foraging efforts to be consistent than for adjustments of forager allocation to be rapid.

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