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Forager activation and food availability in harvester ants

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We investigated how foragers are activated in colonies of the red harvester ant, *Pogonomyrmex barbatus*. Each day, a harvester ant forager makes many trips out of the nest to gather seeds and bring them back to the nest. The rate at which foragers return to the nest is linked to food availability: when food is easy to find, foragers return more quickly. We examined how the return of successful and unsuccessful foragers influences the rate at which inactive foragers are stimulated to leave the nest on subsequent trips. In field experiments, successful or unsuccessful returning foragers were removed before they reached the nest. Foraging activity in response to removals was compared to that in computer simulations modelling the effect of returning foragers on departure rate. Field experiments showed that forager departure rates were not affected by the return of unsuccessful foragers, but depended strongly on the return of successful foragers. The results corresponded to the model in which inactive foragers were instantaneously stimulated to leave the nest by the return of each successful forager, and not to three other models that required inactive foragers to remember elapsed time or events. The results of field experiments were thus consistent with a simple behavioural rule that is sufficient to adjust foraging intensity to current food availability.

Social insects have diverse foraging systems that reflect the enormous range of ecological conditions in which they operate. Colonies continually adjust foraging effort to changing conditions. This process is organized without central control. Individuals use local information in foraging decisions and, in the aggregate, colonies can tune foraging effort to the location, quality and abundance of food.

In many social insect taxa, the activation of foragers depends on interaction with other workers. For example, in *Polybia* wasps, the probability that a wasp will leave the nest to forage is increased when it experiences a higher rate of mandibular contact, or 'biting', from other wasps near the nest entrance (O'Donnell 2001). In stingless bees (*Melipona*), foragers are stimulated to leave the nest by the return of other foragers (Biesmeijer et al. 1998). Honeybees adjust foraging rapidly to changes in food availability and quality. A honeybee forager leaves the nest for its next foraging trip in response to a variety of interactions, including contact with other foragers (Fernandez et al. 2003), the waggle dances of other foragers (Von Frisch 1993), its food exchange with other foragers and how long it waits to pass on its nectar load to a nectar storer (Seeley & Tovey 1994). Honeybees have been used in agriculture to pollinate crops for 10 000 years; perhaps this long history of artificial selection has helped to favour foraging behaviour that targets food in time and space.

The ants are a large taxon of about 10 000 species, living across an enormous range of ecological conditions. This ecological variety is reflected in their foraging behaviour. Some ant species that use reliable food sources such as nectar can learn to forage at particular times and places (Schatz et al. 1994). Most ant species, however, must search for food and then bring it back to the nest. How colonies organize foraging depends on whether food sources are ephemeral or long-lasting, and whether food can be retrieved by a single ant. When many ants are required to retrieve a food source, recruitment is mediated by trail pheromones (Hölldobler & Wilson 1990). In some species, recruitment trails are stronger for more abundant food, allowing the colony to adjust the number of foragers to the richness of the food source (Detrain et al. 1999). However, not all species rely on recruitment trails. In many ant species, solitary foragers find and retrieve dispersed food sources, without mass recruitment. When food is long-lasting, the speed of retrieval may not be as important as thorough searching. For such ant species, little is known about how

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the colony's foraging effort, measured by rate of forager activation, is matched to food supply.

We examined how foraging activity is regulated in the red harvester ant, *Pogonomyrmex barbatus*. This species of harvester ant lives in the deserts of the southwestern U.S. and Mexico. It forages for dispersed and partially buried seeds, which are distributed mostly at random by wind and flooding (Gordon 1993). Food availability increases after rainfall has led to seed production (Kemp 1989), in weather conditions that promote the transport of seeds or after flooding has exposed seeds buried in the soil.

The cost of foraging is related to desiccation: harvester ants obtain most of their water from metabolizing the fats in seeds, so foraging ants use water to obtain more water (MacKay 1985). Seeds are stored inside the nest for months and possibly years (Gordon 1993). When little food is available, the cost of water loss by foragers may be too high to offset the benefit of the food that foragers collect. By adjusting foraging effort to food availability, harvester ants may minimize water loss.

Each morning foraging is begun in response to stimulation by the patrollers, the first ants to leave the nest each morning. They search the nest mound and foraging area, and choose the day's foraging directions (Gordon 1991). Foraging begins each morning after the patrollers return to the nest (Gordon 1986). Experiments with ant mimics coated with cuticular hydrocarbon extracts show that contact with the cuticular hydrocarbons characteristic of patrollers is sufficient to stimulate the first foragers to leave the nest (Greene & Gordon 2003). Once a forager leaves the nest, it travels in a stream of foragers (a 'foraging trail') and then stops to search the ground for food. As soon as it has picked up a seed or other bit of food, it goes directly back to the foraging trail and returns to the nest.

Harvester ant foragers are stimulated to leave the nest to search for dispersed seeds, not to collect food at a specific location. The streams of foragers can be very broad, spanning more than a metre, and often occupy a fan-shaped region of many square metres (illustrated in Gordon 1995). Because individuals meander around on their own in a large area, it appears that, perhaps like other harvester ant species (Lopez et al. 1994), the *P. barbatus* foragers do not ordinarily follow a chemical trail recently created by another ant. In response to experimental baits, patrollers (but not foragers; Gordon 1984) clearly lay a pheromone trail and recruit foragers to an abundant food source (e.g. Gordon 1991); however, such behaviour is not normally observed except on rare occasions when the ants manage to surround an insect not claimed by a competing ant species. Throughout a foraging season, a colony uses the same habitual set of foraging directions, sometimes cleared of vegetation (Gordon 1991). These directions change from year to year (Gordon 1995). It has been suggested that the foraging directions are marked by some long-lasting chemical, resembling a permanent scent mark rather than an ephemeral recruitment trail (Hölldobler et al. 2001). However, foraging directions persist even the morning after severe flooding has removed the top layer of the soil, so it seems likely that foraging directions involve some visual cue, as in other myrmicine desert species (Collett et al. 1992), rather than chemical ones.

Most foragers do not return to the nest until they have found food; about 90% of returning foragers are successful (Gordon 1991). This means that the rate of return of foragers is linked to food availability: when food is easy to find, foragers return more quickly. Previous work indicated that once foraging has begun, the rate at which inactive foragers leave the nest is related to the rate at which the current foragers return. In one experiment, food was collected from successful foragers and the foragers returned to the nest without any food. This caused foraging to slow down (Gordon 1991). In another experiment, all returning foragers were removed. After about an hour, foraging stopped completely (Gordon 2002). These results show that the activity of foragers inside the nest is influenced by the return of foragers. Foragers, like patrollers, have task-specific cuticular hydrocarbon profiles (Wagner et al. 2001), and it is likely that contact with hydrocarbons of returning foragers stimulates inactive foragers to leave the nest.

It is not known how the rate or number of returning foragers influences foraging activity. Inactive foragers could be stimulated by the return of successful foragers, unsuccessful foragers or both. To investigate this, we developed computer simulations based on different behavioural rules that determine forager activation. In the simulations, we compared response to successful or unsuccessful foragers, or both, and investigated several possibilities for forager memory: the inactive foragers remember numbers returning, elapsed time since foragers returned or a gradient in the activity of returning foragers. The four forager activation rules we modelled were (1) each successful and unsuccessful forager influences forager activation immediately upon return, (2) forager activation depends on the ratios of the average elapsed times since the returns of successful and unsuccessful foragers, (3) forager activation depends on the ratio of numbers of successful and unsuccessful foragers to return per unit time, and (4) inactive foragers are instantaneously stimulated to leave the nest by the return of each successful forager. Next, we performed experiments in the field in which successful or unsuccessful foragers were removed before they returned to the nest and examined the effects on further foraging activity. We then compared the results of simulations and field experiments to determine which of the modelled behavioural rules was most consistent with the foraging activity of harvester ants.

METHODS

Field Experiments

Removal experiments were conducted in July and August 2003 at the study site near Rodeo, New Mexico, U.S.A., that has been used in previous work (e.g. Gordon 1987, 2002).

Each removal experiment required two observers and one person to remove ants. Observers sat near the nest mound. One counted numbers of foragers leaving the nest mound on a foraging trail; the second observer, using a multiple counter, tallied numbers of successful foragers returning with seeds and unsuccessful foragers returning without seeds. Some seeds are too small to see, and foragers were not counted as successful unless the seed was clearly visible; our counts thus probably underestimate success and overestimate lack of success. However, we did not attempt to estimate the magnitude of the error in assuming an ant was unsuccessful when in fact it was carrying a small seed. The person removing ants sat alongside the foraging trail, on the far side of the nest from the observers, about 2–3 m from the nest mound.

Forager counts were made for 1 min each, at 2-min intervals. In each trial, during the first 20 min, counts were made of foragers leaving the nest, successful foragers returning and unsuccessful foragers returning to the undisturbed nest. Then either successful or unsuccessful foragers were removed for 10–30 min. During removals, numbers removed were counted in 2-min intervals from the beginning of one forager count to the beginning of the next. In some trials, foraging was again tallied after removals had ceased.

Removal of unsuccessful foragers was done in seven colonies (colony numbers 720, 769, 871, 940, 810, 872 and 691) on 12 days during 19–31 July and 6–7 August 2003. Trials were conducted in the mornings, after foraging activity had begun and before it had diminished due to midday heat. In total, there were two to five trials per colony, and two to five colonies observed per day. Removal of successful foragers was done in all 10 colonies on 10 days, and the removal of unsuccessful foragers was done in five colonies (720, 769, 871, 940 and 810) on 2 days. All colonies used in experiments were mature (>5 years old), based on data on colony age from a yearly census (Gordon & Kulig 1996).

To measure the effect of removals, we found the average rates (in ants/min) of foragers leaving the nest, and of successful foragers and unsuccessful foragers returning to the nest. The average departure rate of foragers in undisturbed colonies was calculated as the forager departure rates during the 20–30 min before removals began. To find the average forager departure rates during removals, we used the forager departure rates beginning with the first count after removal began and ending with the last count during removals. To compare the effects of removing successful and unsuccessful foragers, we analysed average rates using Student's *t* tests. To assess the effects of colony and day on foraging activity, we compared departure rate data from four undisturbed colonies (720, 769, 871 and 940) over five consecutive days (21–25 July 2003) with a nonparametric Kruskal–Wallis test with Scheirer–Ray–Hare extension.

Computer Simulations

The computer simulation of foraging behaviour was written in Matlab (Version 6.5, Mathworks, Natick, Massachusetts, U.S.A.). Each run simulated one morning of foraging, beginning with the first foragers leaving the nest and ending after 5 h of simulated time had elapsed. The foraging area was a square plane, with the focal nest at the centre and reflecting boundaries, which were rarely reached by the foragers, at the edges of the square.

The simulation was restricted to foragers, ignoring ants performing other tasks. Each simulated colony consisted of 2000 potential foragers. When each forager departed from the nest, it travelled for a set distance along a foraging trail, then left the trail and began its search for seeds. After either finding food or giving up, it returned to the trail and then returned to the nest. Interactions between foragers outside the nest were recorded, along with numbers and locations of food items collected. An interaction between foragers outside the nest prolonged each forager's search for food by 120 s.

Environmental parameters in the simulation were set to imitate the observed environment of *P. barbatus*. First, temperature during the simulated morning rose as a sine function based on data (from the Western Regional Climate Center) on temperatures at Rodeo, New Mexico, near the site of the field research. In all simulations, there were two foraging trails, with equal numbers of ants departing on each of the trails. Both trails reached just over 4 m in length, and extended at a rate of 2–6 cm in length per degree Celsius throughout the day, to mimic the observed elongation of trails over the course of the day in the field (Gordon 1995). A forager step length was defined as the distance travelled by a forager in 1 s, and was used to determine ant speed, which increased with temperature as $\text{speed(m/s)} = e^{-2.23+0.018\times T}$, where T is temperature in Celsius (Morehead & Feener 1998). The initial step length was approximately 1.5 cm/s, increasing to about four times this length by 1100 hours in the simulated morning.

An ant colony is more likely to harvest seeds that are close to the nest. The simulated food distribution was modelled to be most sparse around the nest, with food density increasing exponentially with distance from the nest. The number of food items was set to one million seeds in the 1600-m^2 foraging area, corresponding to a food density of 625 seeds/m^2. This number is significantly smaller than estimates of standing seed crops in the Sonoran Desert (Price & Reichman 1987), because only those seeds on or near the surface of the ground can be located and collected by ants.

During its search for seeds, each forager followed a biased random walk. The direction of a forager's step was equal to its previous direction, plus a normally chosen element with standard deviation 0.6 radians, and a 0.01-radian bias away from the nest. These parameters yielded results that agree with observations that suggest that a forager's search for food is stochastic, but with a characteristic drift of 0.25 cm/s away from the nest. The number of steps that an ant took while searching, before quitting if unsuccessful, was normally distributed ($\overline{X} \pm \text{SD} = 200 \pm 40$ steps).

We simulated four different rules that determine forager activation, and thus the rate of departure of foragers. Each of the rules used a departure parameter, λ_t, that represented the instantaneous rate of foragers leaving the nest at any given time. This parameter was used as the mean for a Poisson random number generator, and was capped at 1.5 ants/s to approximate the physical constraint imposed by the nest entrance on the rate at which foragers can leave the nest.

At the beginning of every simulation, for all four forager activation rules, a static departure rate of 0.3 ants/s was assigned. This initial interval lasted for 800 s, during which no forager had time to complete a foraging run and return to the nest. After the initial interval, the simulated colonies diverged in the strategy used to establish λ_t.

(1) Tracks successful and unsuccessful foragers (TSU)

$$\lambda_{t+1} = d\lambda_t + bF_t - pf_t \tag{1}$$

The instantaneous departure rate, λ_t, was changed at each time interval in response to incoming successful foragers F_t, and incoming unsuccessful foragers f_t. The return of each successful forager added to the departure rate a constant b (in ants/s); each unsuccessful forager subtracted a constant p. This rule included an exponential decay over time, d, so that in the absence of returning foragers, the departure rate would eventually dwindle to zero, as observed in the field (Gordon 2002). The values of b, p and d were adjusted by trial and error so that λ_t was similar to the average departure rates of natural colonies: b was 0.01, p was 0.021, and the decay rate, d, was 0.999.

(2) Ratio of return times of successful and unsuccessful foragers (RRT)

$$\lambda_t = c\,\frac{\bar{t}_r(f_{1:A})}{\bar{t}_r(F_{1:A})} \tag{2}$$

The instantaneous departure rate, λ_t, was calculated using the time since return (t_r) of successful and unsuccessful returning foragers (F and f, respectively). It tracked the average elapsed time since the return of the A most recent unsuccessful foragers ($\bar{t}_r(f_{1:A})$), and of the A most recent successful foragers that returned to the nest. The departure rate was the ratio of these two averages, multiplied by a constant to reproduce observed rates.

When the mean return time of unsuccessful foragers was small, the numerator was small, slowing the departure rate. Similarly, when the mean time since successful foragers returned was small, the denominator was small, increasing the departure rate. In all simulations, A was set to 10 ants, corresponding to an average memory interval of 1–2 min. The constant c was set to 0.067 to mimic observed values for the magnitude of change in the departure rate.

(3) Ratio of numbers (RN)

$$\lambda_t = c\,\frac{\sum_{j=t-\tau}^{t} F_j}{\sum_{j=t-\tau}^{t} f_j} \tag{3}$$

The instantaneous departure rate, λ_t, was determined by tracking the numbers of returning foragers during a set time interval. The returns of successful and unsuccessful foragers (F and f, respectively) were counted during the time interval beginning τ seconds before the present, and ending at the present (from $t-\tau$ until t). The number of successful foragers that returned in that interval was divided by the number of unsuccessful foragers that returned in that interval. The time interval of the forager count was set at 2 min to include many foragers and, as in rule 1 (TSU), to limit the time that ants track the returns of foragers. The greater the number of successful foragers that returned, the larger the numerator and the greater the departure rate. The greater the number of unsuccessful foragers that returned, the larger the denominator and the smaller the departure rate. The normalizing constant was set to 0.056 to mimic observed departure rates.

(4) Instant response to successful foragers (IRS)

$$\lambda_t = \Lambda\mathbb{1}\{a_t > 0\}, a_t = c(a_{t-1} + i_{t-1}) \text{ per successful forager} \tag{4}$$

In the instant response to successful foragers method, IRS, the rate-determining step was the activation of an inactive forager by a returning successful forager. Upon the return of a successful forager, a fraction c of the inactive foragers (i) instantaneously became activated (a) and entered a queue to leave the nest. The return of an unsuccessful forager had no effect on the inactive foragers. In equation (4) above, $\mathbb{1}$ represents the indicator function, which returned a value of 1 whenever a queue was present (when $a_t > 0$), and a zero otherwise. When there was a queue of activated foragers, foragers left with the mean departure rate of 0.3 ants/s (Λ in equation 4). The departure of the queued foragers from the nest was gradual. The proportion, c, of inactive foragers stimulated to leave the nest by each returning successful forager was set to 0.0035, to mimic observed departure rates.

Simulated Removal Experiments

To investigate the differences between these four forager activation rules, two removal experiments were simulated. First, returning unsuccessful foragers were removed from the trail before entering the nest. Second, only successful returning foragers were removed. Removals lasted for 22 min between 1 and 3 h after the onset of foraging, and departure rates were recorded during the 20-min interval beginning 2 min after removals began.

To mimic the ants that are probably missed when ants are removed in field experiments, 10% of the simulated foragers in the targeted group (unsuccessful foragers in experiment 1, and successful foragers in experiment 2) were allowed to return to the nest.

RESULTS

Field Experiment Results

We removed a mean ± SD of 130.38 ± 73.51 foragers per trial ($N = 33$ trials). Using the mean ± SD baseline departure rate of 30.38 ± 13.43 ants/min ($N = 33$ trials) and an estimated foraging trip duration of 20 min (Gordon & Kulig 1996), we estimated that colonies had a mean ± SD of 607.7 ± 268.7 foragers active in the field at the

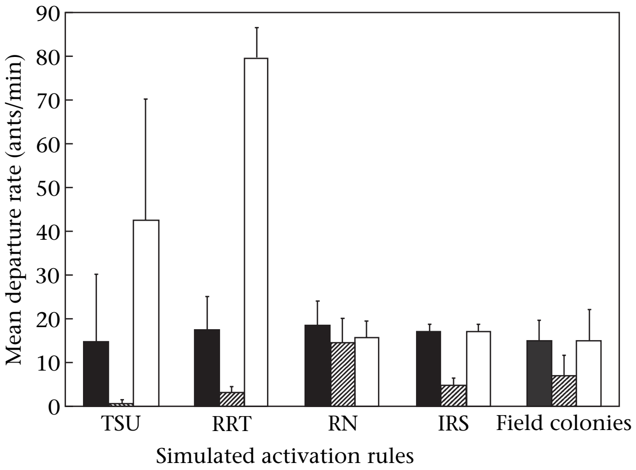

Figure 1. Mean ± SD departure rates of foragers (ants/min) in simulated and field colonies of the red harvester ant. Simulated forager activation rules: (1) TSU: tracks successful and unsuccessful foragers; (2) RRT: ratio of return times; (3) RN: ratio of numbers; (4) IRS: immediate response to successful foragers. ■: undisturbed colonies; ▨: successful foragers removed; □: unsuccessful foragers removed.

beginning of each trial. We thus removed an average of 24.3% of the active foragers per trial.

Removal of returning successful foragers immediately reduced the rate at which foragers left the nest. The removal of returning unsuccessful foragers had no effect on departure rate (Fig. 1). There was no significant difference between the departure rates of foragers in undisturbed colonies ($\overline{X} \pm \text{SD} = 15.2 \pm 6.6$ ants/min, $N = 34$ trials) and the rates of foragers in colonies with unsuccessful returning foragers removed (14.5 ± 6.3 ants/min, $N = 9$; Student's t test: $t_{41} = 0.26$, $P = 0.7935$). The departure rates of foragers were significantly lower when returning successful foragers were removed (6.7 ± 5.4 ants/min, $N = 24$; Student's t test: $t_{56} = 5.2$, $P < 0.001$).

There was considerable variation among colonies in departure rates, ranging from 6.2 ants/min (colony 720, 24 July 2003) to 28.6 ants/min (colony 871, 22 July 2003). There was a significant effect of colony on departure rate (Kruskal–Wallis test with Scheirer–Ray–Hare extension: $\chi^2_3 = 11.4$, $P < 0.01$), and no significant effect of the day of observation ($\chi^2_4 = 2.7$, $P = 0.6092$).

Simulation Results

In the simulations, parameters were set to mimic the observed departure rates of undisturbed colonies. As a result, there were no significant differences between forager activation rules in the average departure rates of undisturbed simulated colonies (ANOVA comparing departure rates of colonies in each of four simulations, and the results of field colonies: $F_{4,97} = 0.54$, $P = 0.7067$).

Simulated removal experiments had different effects on foraging activity, depending on the forager activation rules. The simulated removal of unsuccessful foragers led to significant increases in departure rates for rule 1, tracks successful and unsuccessful foragers (TSU), and for rule 2, ratio of return times (RRT). Departure rates increased from a mean ± SD of 14.2 ± 14.9 ants/min ($N = 24$) to 41.2 ± 26.8 ants/min ($N = 11$; Student's t test: $t_{33} = 3.71$, $P < 0.001$) for rule 1 (TSU), and from 16.9 ± 4.2 ($N = 18$) to 76.8 ± 6.6 ants/min ($N = 12$; $t_{28} = 29.55$, $P < 0.001$) for rule 2 (RRT). This change is because in both rules the return of unsuccessful foragers diminished departure rate, so their removal prevented the departure rate from being suppressed. For rule 1, TSU, the return of each unsuccessful forager simply acted to diminish departure rates by a constant, p. The magnitude of the increase in departure rate when unsuccessful foragers were removed was thus proportional to the magnitude of p. For rule 2, RRT, when the rate of return of unsuccessful foragers slowed down drastically with removal, the numerator of equation (2) became very large, leading to an increase in departure rate.

Simulated removal of unsuccessful foragers had little effect on departure rate for rules 3 and 4. In simulations using rule 3, ratio of numbers (RN), the mean departure rate without removals was 17.8 ± 5.3 ants/min ($N = 17$); during removals it was 15.4 ± 2.7 ants/min ($N = 16$; Student's t test: $t_{31} = 1.59$, $P = 0.1216$). Here the tracking of forager returns was constrained to a time window of 2 min, and the effect of an unsuccessful forager's return was not weighted by time. If there were weighting by time, so that a short interval since the last return strongly increased the departure rate, as in rule 2 (RRT), the results of rules 2 and 3 would have been similar.

For rule 4, instant response to successful foragers (IRS), departure rate was 16.6 ± 0.4 ants/min ($N = 9$) without removals and 16.4 ± 1.1 ants/min ($N = 18$; Student's t test: $t_{25} = 0.54$, $P = 0.703$) with removals. Here the return of an unsuccessful forager had no effect on departure rate.

The simulated removal of successful foragers decreased departure rates in three of the four forager activation rules. The exception was rule 3, ratio of numbers (RN). For simulations using rule 1 (TSU) and rule 2 (RRT), the simulated removal of successful foragers drastically slowed departure rate (rule 1, TSU: $\overline{X} \pm \text{SD} = 14.2 \pm 14.9$ ants/min without removals, $N = 24$; 0.49 ± 1.0 ants/min during removals, $N = 25$; Student's t test: $t_{47} = 4.51$, $P < 0.001$; rule 2, RRT: 16.9 ± 4.2 ants/min without removals, $N = 18$; 1.6 ± 0.5 ants/min during removals, $N = 14$; Student's t test: $t_{30} = 13.14$, $P < 0.001$). For rule 1 (TSU), the magnitude of response to the removal of successful foragers was proportional to b, the rate at which a successful forager increases departure rate. For rule 2 (RRT), a decrease in the rate of return of successful foragers increased the average elapsed time since successful foragers returned, thus decreasing the numerator and decreasing the departure rate.

Rule 3 (RN) showed the least response to the removal of successful foragers as they approached the nest. There was no difference between the baseline simulated departure rate of 17.8 ± 5.3 ants/min ($N = 17$) and the rate during removals, 14.0 ± 3.6 ants/min ($N = 25$; Student's t test: $t_{40} = 2.76$, $P < 0.01$). Because the time window over which foragers were counted was short, and forager returns were not weighted by return time, the 10% of successful foragers that leaked back to the nest was enough to maintain the departure rate.

In colonies using rule 4 (IRS), simulated removal of successful foragers decreased forager departure rate from

16.6 ± 0.4 ants/min without removals ($N = 9$) to 4.5 ± 1.2 ants/min during removals ($N = 19$; Student's t test: $t_{26} = 29.09$, $P < 0.001$). According to this rule, the return of successful foragers was the only way to stimulate the departure of inactive ants. When most successful ants were prevented from returning, the departure rate dropped dramatically.

Comparison of Simulation and Experimental Results

The results for simulations using rule 4 (IRS) were most similar to results from field experiments: there was a decrease in departure rate when successful foragers were removed, and no effect when unsuccessful foragers were removed (Fig. 1). There were no significant differences between departure rates in response to removals in experimental and simulated colonies using rule 4 (Student's t test: successful foragers removed: $t_{42} = 1.75$, $P = 0.880$; unsuccessful foragers removed: $t_{25} = 1.17$, $P = 0.2536$).

DISCUSSION

Our results show that a simple behavioural rule is sufficient to adjust the foraging behaviour of the colony to changes in food availability, and suggest that the regulation of foraging activity does not require memory or the capacity to monitor colony-level activity. Foraging activity is stimulated by the return of successful foragers, while unsuccessful foragers do not affect foraging activity when they return to the nest. This links the rate of foraging activity to food availability. When food availability is low, it takes longer for successful foragers to find food and return, thus slowing the rate at which more foragers leave the nest.

The process described here linking foraging activity to food availability has parallels in honeybee behaviour. Honeybee foragers are stimulated to leave the hive by contact with returning foragers (Farina 1996). Another example from honeybees involves nectar foragers: when a nectar forager arrives at the nest, the delay it experiences in unloading nectar is linked to nectar abundance (Seeley & Tovey 1994). This correlation relies in turn on the connection between nectar foragers and food storers: food storers leave the area when they have received a load, so as more nectar foragers arrive, more food storers leave, and subsequent nectar foragers have to wait longer before meeting a food storer. The process differs in harvester ants because no ants are needed to receive a forager's load; the forager can simply drop its food. Instead, if the returning forager ants mix at random with the inactive foragers inside the nest (as the food storers and nectar foragers are assumed to do in honeybees; Seeley & Tovey 1994), then the more returning foragers arrive, the sooner an inactive forager will meet one and go out to forage. The accuracy with which this system reflects food availability depends in part on the variance in the time it takes foragers to give up if they do not find food: the higher the variance, the less well this system will track food availability.

The system described here links foraging activity to food availability, but there is no evidence that it links foraging activity and food quality. In this way the harvester ant system is simpler than that of honeybees, in which foraging activity is finely tuned to food quality (Fernandez et al. 2003), and that of some ant species, in which recruitment trails reflect food quality (Detrain et al. 1999). In harvester ants, however, any successful forager, no matter how valuable its load, appears to have about the same effect in stimulating further foragers to leave. Another study (Gordon 1993) showed that a surprisingly large proportion of about 15 000 food items brought in by foragers at this site were apparently inedible husks of grass seeds and empty seed cases. Foragers seem to bring whatever they find back into the nest, and the rejected items are taken out to the midden by other workers. The foragers are not being recruited to a localized source, so there may be no advantage of a system that adjusts foraging activity to food quality. Harvester ant foragers work in an environment where all food items, valuable and useless, fluctuate together in availability. For example, the day after rain has washed away the top layer of the soil, both seeds and seed husks are exposed. Thus, the rate at which ants bring in poor food items is probably correlated with the rate at which they bring in good ones. There may be little information to be gained about overall food availability by distinguishing foragers bringing in seeds from those bringing in chaff.

Our results show that ants distinguish successful from unsuccessful foragers. Previous work shows that ants distinguish the task of their nestmates using task-specific cuticular hydrocarbons (Greene & Gordon 2003; Wagner et al. 1998). This would enable an ant to recognize that another ant returning to the nest is a forager, rather than an ant of another task group, such as nest maintenance. Waiting foragers may also evaluate the success of returning foragers using the odour of the food that successful foragers carry. Another possibility is that waiting foragers evaluate the amount of food brought in, rather than the number of successful ants. Observations inside the nest in the field with a fibre optics microscope, and the behaviour of laboratory colonies, both suggest that foragers drop their loads quickly, and the food is retrieved by other ants from lower down in the nest; a 'bucket brigade' (sensu Anderson et al. 2002) of at least two steps. Waiting foragers inside the nest may respond to the amount of food scattered at their feet by returning foragers, not yet collected by the ants from lower down in the nest, rather than to the foragers that bring the food. However, this explanation seems unlikely because the response of outgoing foragers to small changes in numbers of returning foragers appears to be very rapid. Ants would have to evaluate small changes in food supply in a short time, because the spatial distribution of food on the chamber floor is so variable.

In our field experiments, we did not remove enough ants to explain the observed decline in foraging activity. A mature colony has about 2000 foragers (Gordon & Kulig 1996); based on the observed departure rates and an average foraging trip duration of 20 min (Gordon & Kulig 1996), we estimate that more than 600 foragers are actively foraging outside of the nest at any time. In each trial, we removed an average of about 24% of the active foragers, only 6.5% of the total available foragers. In response to the removal of successful foragers, average departure rate dropped by 55%; thus, the 24% of foragers removed was not a large enough proportion to account for the decline in foraging activity. In addition, when unsuccessful foragers were removed, there was no effect on foraging activity, also indicating that the absence of the removed foragers did not account for the decline in foraging activity.

When foragers were removed in the field, there was probably some error in our identification of successful foragers. We were more likely to identify a successful forager as unsuccessful than the reverse: foragers were not considered to be successful unless they were carrying a seed large enough to be clearly visible. Thus we are confident that all the successful foragers removed actually carried seeds. However, some of the ‘unsuccessful’ foragers that we removed may have carried a seed too small to see. If we misidentified successful foragers as unsuccessful often, so that many of the foragers that we removed as unsuccessful were carrying food, then we would expect the removal of the presumed unsuccessful foragers to inhibit forager activation and decrease colony departure rates. This did not occur, indicating that our error in identifying unsuccessful foragers was not significant.

The four simulated forager activation rules modelled various possibilities by which foraging is regulated. The comparison between departure rates from the simulations and the field data suggests that the return of each successful forager has an instantaneous effect, but the return of unsuccessful foragers does not influence foraging activity. This simple rule requires each ant to react only to one other individual at a time, without evaluating global or collective behaviour and without remembering or integrating information over time.

The rate at which foragers leave the nest is due to at least two distinct processes: the activation of inactive ants by successful returning foragers, and the processes that create the pool of ants available to be activated. The pool of available ants comes both from ants deeper inside the nest that move up to the chamber just inside the nest entrance, and from the returning foragers after they drop their loads and become available to be reactivated. In one of our simulations, rule 4 (IRS), we imagined that the return of successful foragers added ants from somewhere inside the nest by adding to the queue of foragers. Little is known about the rate at which new foragers are recruited from inside the nest.

We found that colonies differ significantly in forager departure rates. This may be considered a colony-specific behaviour syndrome (Sih et al. 2004). Although foraging behaviour in all colonies responds to the weather (Gordon 1984, 1986, 1991), colonies also differ in the ways that they regulate foraging activity. A colony does not forage every day. Some colonies forage on more days, and have fewer inactive days, year after year (Gordon 1991). Our results indicate that there is also variation among colonies in the effect of each returning successful forager, which helps to explain intercolony variation in foraging behaviour. If colonies use a forager activation rule like our simulated rule 4 (IRS), instantly responding to successful foragers, then colonies may vary in the magnitude of response to each returning forager, corresponding to the proportion c of waiting foragers in our model that are stimulated by each returning forager. Colonies may also vary in the number of potential foragers waiting inside the nest, corresponding to i in equation (4) of our model. Nests may vary in the topography of their underground chambers in ways that influence how the inactive ants make contact with returning foragers, and thus are stimulated to forage. The features of colony organization that determine the colony’s sensitivity to returning foragers are behavioural traits that, if heritable, may be shaped by natural selection.

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