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The short-term regulation of foraging in harvester ants

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In the seed-eating ant *Pogonomyrmex barbatus*, the return of successful foragers stimulates inactive foragers to leave the nest. The rate at which successful foragers return to the nest depends on food availability; the more food available, the more quickly foragers will find it and bring it back. Field experiments examined how quickly a colony can adjust to a decline in the rate of forager return, and thus to a decline in food availability, by slowing down foraging activity. In response to a brief, 3- to 5-min reduction in the forager return rate, foraging activity usually decreased within 2–3 min and then recovered within 5 min. This indicates that whether an inactive forager leaves the nest on its next trip depends on its very recent experience of the rate of forager return. On some days, colonies responded more to a change in forager return rate. The rapid colony response to fluctuations in forager return rate, enabling colonies to act as risk-averse foragers, may arise from the limited interval over which an ant can track its encounters with returning foragers. *Key words:* foraging dynamics, interaction network, risk sensitivity. *[Behav Ecol]*

A substantial body of theory has explored how foragers ought to respond to environments that change in space and time (Kacelnik and Bateson 1996). A social insect colony provides interesting solutions to the problem of foraging in patchy and variable environments. Although a colony consists of separate individuals, each worker does not consume the food it collects, and so the colony is not a group of independent social foragers (Giraldeau and Caraco 2000). Instead, a colony can be considered as a single forager, in which individuals bring in food that contributes to the reproductive success of the colony as a whole. How the colony manages its foraging decisions collectively is an intriguing question because the colony operates without central control. In patchy and variable environments, foragers perform patch sampling (Valone and Giraldeau 1993), calibrating foraging effort to the quality of food they discover in a particular patch. Here we examine how an ant colony accomplishes collective patch sampling.

A social insect colony's foraging decisions result from the way that individuals, using local information, decide whether to forage at any moment. In many social insect species, whether a forager is stimulated to leave the nest depends on its 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). Whether a honeybee forager leaves the nest for its next foraging trip is influenced by a variety of interactions with other foragers, including antennal contact (Fernandez et al. 2003), assessment of waggle dances (Von Frisch 1993), and food exchange. However, little is known about how interactions between individual workers produce adjustments in the overall foraging intensity of a social insect colony as conditions change (Fernandez et al. 2003).

The red harvester ant, *Pogonomyrmex barbatus*, lives in the deserts of the southwestern United States and Mexico. Colonies forage for randomly dispersed, long-lasting and partially buried seeds (Gordon 1993), so their food is spatially and temporally heterogenous. Foragers, a distinct group of individuals (Gordon 1989), go back and forth between the nest and foraging area to find and retrieve dispersed seeds and small insects (Gordon 1991). Mass recruitment using pheromone trails is extremely rare. Laboratory observations (Gordon et al. 2005), and observations in the field with a fiber optics microscope, indicate that in these ants, as in many social insects, foraging and food processing are done by different groups of workers. When a forager returns to the nest, it drops its seed just inside the nest entrance. Other, presumably younger workers come up from inside the nest to collect the seeds and take them further down for husking and storage.

The intensity of foraging changes from day to day (Gordon 1986, 1991; Gordon and Kulig 1996). For example, after a rain, foraging activity is high, presumably because the rain exposes seeds buried in the upper layer of the soil. Within a day, foragers inside the nest are stimulated to leave on their next foraging trip by the return of successful foragers (Gordon 2002). The return of foragers without food does not stimulate foraging activity (Gordon 2002; Schafer et al. 2006). Thus, foraging activity is linked to food availability: When more food is available, foragers return more quickly, stimulating more foragers to leave the nest.

The rate at which a colony adjusts to food availability depends on its risk sensitivity or the balance between the costs of foraging and the value of the food it brings in (McNamara 1982). The colony's estimate of the quality of the foraging area, that day's foraging patch, is proportional to the number of food items brought back to the nest per unit time. One general theoretical prediction is that if variance in the environment is high, patch estimates will be sensitive to the rate at which resources are found (Valone 1989). Previous work examined the response of foragers to changes in food availability from hour to hour (Gordon 1991, 2002) and over a 10- to 30-min interval (Schafer et al. 2006). Here we investigate the

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extremely short-term, minute-to-minute regulation of foraging in response to current food availability. We ask how quickly overall foraging activity responds to short-term declines, lasting only 3 min, in the rate at which successful foragers return, and how quickly foraging recovers after the decline has ended.

METHODS

The study was performed in July–August 2004 and 2005 at a long-term study site near Rodeo, NM, with about 300 individually labeled colonies of *P. barbatus* of known age (census methods in Gordon and Kulig [1996]).

Experiment 1. Foragers removed

We measured how quickly colonies respond to short-term changes in the rate at which successful foragers return to the nest. We did this by removing returning successful foragers because previous work showed that the removal of unsuccessful foragers, returning without seeds, had no effect on the rate at which foragers left the nest (Schafer et al. 2006).

Removals were made on 12 days in July and August 2004, with 8 mature colonies (5 years or older), for a total of 21 trials, with each colony observed 1–4 times. Removals were made between 0700 and 0900, around the peak of foraging activity during the morning activity period. Each trial used 3 observers: one person recorded the numbers of foragers leaving the nest at the nest entrance, one recorded the numbers of foragers returning to the nest from foraging trails, and one removed returning successful foragers. Counts of numbers of foragers entering and leaving the nest were made in every 10-s interval during 2 periods, separated by a 3-min wait so observers could rest. The first observation period, before removals, was 5 min long; the second observation period, which began after the 3-min rest, lasted 12–14 min. For 3 min, from min 2 to 5 of the second period, as many as possible successful returning foragers, seen to be carrying a seed, were removed from the most active foraging trail, at least 1 m from the edge of the nest mound, and placed in a box. After the trial was over, these foragers were returned to the nest. Numbers of returning foragers removed in 3 min ranged from 18 to 75 in the 21 trials, depending on the current intensity of foraging, which ranged from a return rate of 0.57–3.35 successful foragers per minute. To estimate the time it would have taken returning foragers to arrive at the nest entrance if they had not been removed, we used the average of the times it took several returning foragers to reach the nest from the place where foragers were collected. These measurements of return time were made when the colony was undisturbed, a few minutes before removals began.

Experiment 2. Effect of colony and day

To investigate the effects of colony and day on response to forager removal, 3 other mature colonies were tested repeatedly, all 3 colonies each day, for 7 days in August 2005, for a total of 21 trials. Methods were as in experiment 1 above. Numbers of returning foragers removed in 3 min ranged from 15 to 76 in the 21 trials, depending on the current intensity of foraging, which ranged from a return rate of 0.55–5.52 ants per minute.

Data analysis

Adjusting for removed foragers

Foraging activity could appear to decrease in response to removals merely because some of the foragers we removed would otherwise have gone out to forage again during our observations. We adjusted for this by adding, to the observed outflow of foragers after removals, the number of removed foragers we estimated would have left the nest during our observations. We estimated what proportion of removed foragers would have been likely to leave the nest to forage again during our observations if they had been allowed to return to the nest, using the following data on marked individuals. In July–August 2004, we observed 4 colonies for 2–3 days. About 250 foragers had been uniquely marked in each colony. The time that each marked forager entered and left the nest was recorded. From data on 6259 foraging trips of 836 marked individuals in the 4 colonies, we found the probability that a forager would leave the nest within 12 min of returning to the nest (Figure 1). We chose 12 min because this is the time that observations continued after removals in our experiments. The probability that a forager left the nest on another trip within 12 min of its return ranged from 0.38 to 0.54, with a mean of 0.47. Using data only from 8 to 10 AM, the time of day when removal experiments were performed, the mean was 0.48. We used 0.47 as the probability that a forager we removed would have gone out to forage again during our observations. Thus, if 36 foragers were removed, in the adjusted data 36 × 0.47 or 17 foragers were added to the observed outflow of foragers leaving the nest. To evaluate the effect of the adjustment factor of 0.47 on the results, we also repeated the analysis twice more with arbitrarily chosen larger values of the adjustment factor, 0.8 and then 1.0 times all removed ants replaced.

Colony and day effects

To test whether colonies and days differed in response to forager removal, we performed an analysis of variance (ANOVA) with A/B as the variate and colony and day as main effects, using the adjustment described above. The analysis was performed for the 21 trials from experiment 2 in 2005 in which 3 colonies were each tested on the same 7 days (Table 1). The method for calculating A/B, the ratio of foraging outflow after removals to outflow before removals, is explained in the following section.

Evaluating the effect of removals

We examined the magnitude of a colony's response to removals. To characterize the magnitude of the response, we used the average rate of outflow of foragers divided into 2 phases,

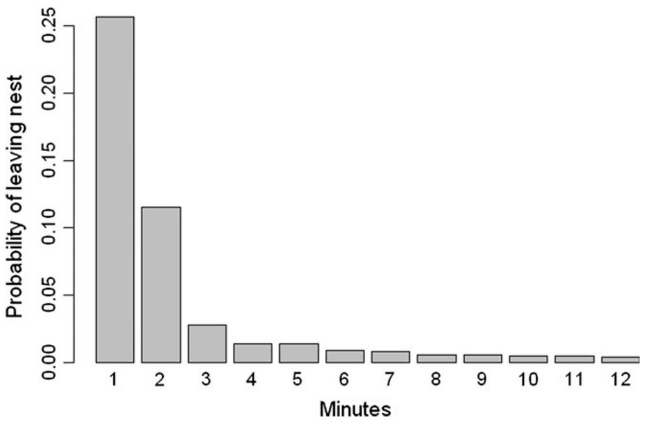

Figure 1
Probability that a forager leaves the nest for another trip within the indicated interval. Data from 6259 trips by 836 uniquely marked foragers.

before and after removals. The "before" or undisturbed phase began at the start of observations. The "after" phase began at (T0) the time the first forager was removed plus the time needed for that ant to return to the nest (estimated as the average of the times it took several ants to return from the site where ants were collected).

As a measure of the response to removals, we used the ratio of the adjusted mean outflow after removals to the mean outflow before removals. This ratio, A/B, was the adjusted ratio of the 10-s counts of foragers leaving the nest averaged over all observations after T0 to the 10-s counts of foragers leaving the nest averaged over observations before T0 (omitting the 3 min when observers rested). We used this ratio A/B to ask:

1. Does foraging activity change when the rate of returning foragers decreases? We considered outflow to decrease when A/B was less than 1 (Table 1). We examined whether foraging decreased after removals, using a *t*-test to evaluate the null hypothesis that the mean ratio A/B for all 11 colonies was 1. In addition, because there was no significant effect of colony, we considered all 42 trials from all colonies and days as independent replicates and used a *t*-test to evaluate the null hypothesis that the mean ratio A/B was 1.
2. What predicts the magnitude of the response? It might be that removals have more effect the larger the proportion of returning foragers removed or that removals have more effect if the rate of returning foragers is low. To examine this, we considered whether the proportion of successful foragers removed or the intensity of foraging determined how much a colony reacts to a decline in the rate of return of successful foragers. We first performed a regression for the 42 trials in experiments 1 and 2 with A/B as the variate, and the number removed and the average inflow before removals (until T0) as main effects.
3. How quickly does a colony respond to a decrease in the rate at which foragers return, and how long does the response last? As above the data for each trial were divided into 2 phases, before and after removals. The before or undisturbed phase began as above at the start of observations and ended as above at T0, the start of removals. The after phase was then further divided to find the interval from the time T0 that we began removals until the time T1 that ants decreased foraging activity; the interval while foraging activity was decreased, from T1 to T2; and the final period when foraging activity had recovered, from T2 until the end of observations (Figure 3). In many trials, recovery did not appear to be complete; though rates of foraging outflow increased after an initial decrease in response to removals, the rates were never as high as they were before removals.

We defined these intervals using a maximum likelihood model to choose, from all possible pairs of times T1 and T2 (with T1 greater than T0), the T1 and T2 that resulted in the intervals over which outflow varies the least. We modeled 10-s counts of the number of foragers leaving the nest as independent Poisson random variables having constant mean over each of 3 intervals: 1) until response, from the beginning of observations, past the time that removals began at T0, up until response to removals began at T1, about 5–10 min (ignoring the observers' rest in experiments 1 and 2); 2) response to removals from T1 until T2; and 3) recovery from removals from T2 until the end of observations.

We used these maximum likelihood estimates of T1 and T2 to measure the interval between the onset of removals and a decrease in foraging activity (T0–T1) and the time until the colony recovered (T1–T2).

Table 1

Response to forager removals

	Date		Colony	Outflow before removals	Outflow after removals	After/ before
2004	July	29	621	4.05	3.09	0.76
		29	729	11.73	10.38	0.89
		30	576	5.67	4.82	0.85
		30	908	4.37	5.29	1.21
		02	306	7.00	6.07	0.87
	August	02	452	1.75	1.18	0.67
		02	615	4.16	1.42	0.34
		02	686	2.66	1.50	0.56
		03	576	7.71	1.84	0.24
		03	621	2.94	1.99	0.68
		04	306	5.06	2.86	0.57
		04	621	3.65	4.11	1.13
		06	908	1.61	0.72	0.45
		07	615	1.62	1.79	1.11
		09	729	0.50	0.97	1.93
		10	306	5.59	3.25	0.58
		10	621	1.60	0.73	0.46
		11	576	1.19	1.07	0.90
		11	615	1.54	1.04	0.67
		12	729	4.32	3.01	0.70
		17	908	4.53	4.33	0.96
2005	August	01	927	2.93	4.48	1.53
		02	927	4.38	2.28	0.52
		03	927	5.16	3.94	0.76
		04	927	6.98	2.09	0.30
		05	927	4.20	5.00	1.19
		09	927	3.83	2.08	0.54
		13	927	1.93	2.50	1.29
		01	947	1.00	1.48	1.48
		02	947	0.67	1.27	1.89
		03	947	1.57	0.90	0.57
		04	947	1.37	1.09	0.79
		05	947	1.49	1.41	0.9
		09	947	1.07	0.97	0.91
		13	947	0.98	0.79	0.80
		01	964	3.59	4.98	1.39
		02	964	2.79	1.71	0.61
		03	964	2.77	1.65	0.60
		04	964	2.91	0.76	0.26
		05	964	3.13	3.10	0.99
		09	964	2.70	0.63	0.23
		13	964	2.61	2.65	1.02

Outflow after removals was adjusted for missing foragers (see text for adjustment methods; adjustment factor 0.47).

RESULTS

Colony and day effects

When the same colonies were repeatedly tested on 7 days in 21 trials in 2005 (Table 1), there were significant differences among days in response to forager removal but no significant differences among colonies (ANOVA for 21 trials in experiment 2, day SS 2.3, df 6, $F = 3.2$, $P < 0.04$; colony SS 0.4, df 2, $F = 1.6$, $P < 0.2$). For example, though all colonies usually decreased foraging in response to removals, all 3 increased foraging after removals on 1 August 2005 (Table 1).

Magnitude of response

When the rate at which foragers return was diminished, the rate at which foragers go out usually decreased (Table 1, Figure 2). Foraging decreased after removals in 17 of 21 trials in 2004 and in 14 of 21 trials in 2005. Of 8 colonies tested in

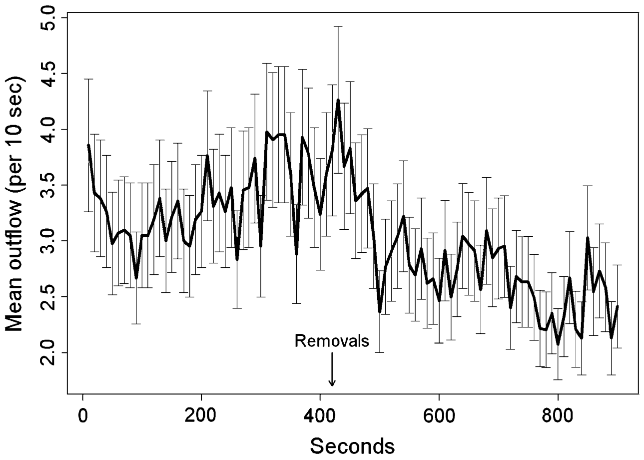

Figure 2
Mean outflow in response to removals. Each point shows the average outflow for 42 trials, adjusted for the removed foragers. Error bars show the standard error of the mean. Foragers were removed beginning at 420 s and ending at 600 s. Foraging activity fluctuates before removals, when colonies were undisturbed, and then decreases after removals.

2004, 2 colonies decreased foraging in response to removals in 3 of 3 trials, 1 decreased in 3 of 4, 3 decreased in 2 of 3, and 2 decreased in 1 of 1. Of 3 colonies tested in 2005, 2 decreased foraging in response to removals in 5 of 7 trials and 1 in 4 of 7. The mean ratio A/B was significantly different from 1 (11 colonies, $t = -3.689$, $P = 0.004$). Considering results from both years or all 42 trials together, forager outflow decreased in 31 of 42 trials, or 74% (Table 1, Figure 3). Both the mean and median ratio of outflow after to before removals (A/B) were 0.84 for the 42 trials, with a range from 0.24 to 1.93. The mean ratio A/B was significantly less than 1 (*t*-test, $t = -2.59$, $n = 42$, 1-sided $P = 0.01$). This trend persisted even with unrealistically large adjustment factors for the proportion of removed foragers replaced (0.8, decrease in 29 of 42 trials, and 1, decrease in 26 of 42 trials). However, in the other 11 trials, outflow increased after removals, usually only slightly (e.g., Figure 3B).

The magnitude of response to forager removal did not depend on the number of foragers removed or on the rate at which foragers were returning before removals began (multiple regression for all 42 trials in experiments 1 and 2, number removed, coefficient -0.05, $P < 0.5$, inflow when undisturbed coefficient -0.0, $P < 0.9$). The number of foragers removed ranged from 18 to 76; the average rate of returning foragers per 10 s before removals ranged from 0.42 to 5.52.

Timing of response

Colony response to a decrease in the rate of returning foragers occurs very quickly (Figure 2). In the 31 of 42 trials in which foraging decreased in response to removals, the decrease occurred within an average of 2–3 min (mean interval between removals at T0 and onset of decreased foraging rate at T1, 188 ± 172 s, median 110 s).

The reduction in foraging activity in response to removals lasted about as long as the removals did. In the 31 of 42 trials in which foraging decreased in response to removals lasting 3 min, the response lasted about 5 min (mean interval between onset of decreased foraging at T1 and recovery at T2, 320 ± 225 s, median 320 s).

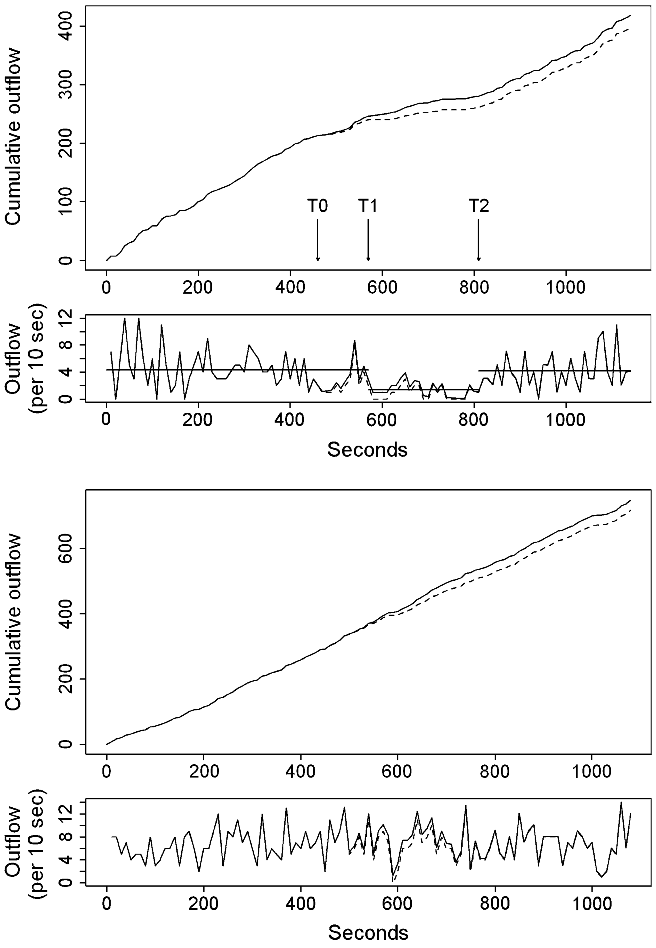

Figure 3
(A) Cumulative number of foragers leaving the nest (above) and outflow (below) in one trial. Removals began at 420 s and ended at 600 s. T0, time the first forager was removed plus the average time for foragers to return to the nest from the site of collection; T1, onset of decreased foraging, estimated by maximum likelihood model; and T2, onset of recovery from decreased foraging, estimated by maximum likelihood model. In the upper graph, the solid line shows cumulative number of foragers leaving the nest adjusted for the removed foragers; dashed line shows the cumulative number of foragers observed. In the lower graph, the solid line shows adjusted forager outflow per 10 s and the dashed line shows the observed forager outflow. The solid horizontal lines show the means for 3 intervals: 1) from beginning of observations until response to removals begins at T1, 2) response to removals: T1–T2, and 3) foraging recovered: T2 until end of observations. (B) Same as in (A), for a trial in which there was no decrease in foraging in response to removals. In the lower graph, there are no means shown because no response to removals was detected.

DISCUSSION

Foraging activity is tuned with remarkable speed to the rate at which foragers return (Figures 2 and 3). Within about 2–3 min, colonies responded to a decrease in the rate at which successful foragers return. When foraging slowed or ceased, it did so for about 5 min, about as long as the diminished rate of forager return had lasted.

Previous work showed that inactive foragers are stimulated to leave the nest by the return of other foragers. When foragers returning to the nest were removed, the foragers inside the nest did not come out to forage (Gordon 2002). Further experiments showed that this is not an effect of the removal itself and that only successful foragers, bringing back food, stimulate further foraging. The removal of unsuccessful foragers, ants returning without seeds, did not affect the rate at which foragers leave the nest (Schafer et al. 2006). Inactive foragers may respond to the rate of brief antennal contact, when they can detect the task-specific hydrocarbon profile of returning ants; this is how foragers are stimulated early in the morning by the return of patrollers (Wagner et al. 1998; Greene and Gordon 2003, 2007). Further work is needed to determine how inactive foragers distinguish successful and unsuccessful foragers and how the food carried by returning foragers affects the response of inactive foragers.

The results here show how quickly foraging rate responds to a decline in the rate of forager return. These results indicate that a forager's decision whether to leave the nest depends on its very recent interactions with incoming, successful foragers. Because the decline in forager outflow, which reflects the aggregate response of many individual foragers, occurred only 2–3 min after removals began, the interval over which an inactive forager evaluates the rate of returning foragers must be 3 min or less. Similarly, because foraging activity recovers only a few minutes after the decline in return rate has ended, foragers must evaluate the end of the decline quite rapidly. This is consistent with other work showing that at the onset of foraging, encounters between patrollers and foragers must occur at intervals of about 10 s to stimulate forager activity (Greene and Gordon 2007).

It is surprising that the ants can assess a change in return rate so quickly because the interval between the return of successive foragers is quite variable on the scale of minutes (Figure 2). Suppose the probability that a forager leaves the nest depended on its calculation of a moving average rate of forager return, on the scale of minutes. When the rate of forager return changes, often the variation in intervals between encounters would exceed the shift in the mean rate, so the ant would fail to detect the change. The rapid colony response we found here suggests that instead of using an average rate of encounter with returning foragers, inactive foragers are stimulated to forage by a threshold number of encounters within a short time.

Colonies usually respond to a decline in the rate at which foragers return by slowing down the rate at which foragers leave the nest (Figure 2). This occurred in about 75% of trials (Table 1, e.g., Figure 3A). However, it is puzzling that in 25% of trials, foraging activity did not slow down when the rate of forager return was diminished (Table 1, e.g., Figure 3B). Whether a colony slowed foraging activity did not depend on the number of ants removed or on the intensity of foraging before removals began. The only variable to predict whether colonies responded to removals was the day. Previous work has repeatedly shown day-to-day variation in foraging activity (Gordon 1984a, 1984b, 1986, 1991; Gordon and Kulig 1996). Variation in foraging activity is presumably linked to variation in food supply (Adler and Gordon 2003): Most foragers continue to search until they find food, and successful foragers stimulate more foraging activity. Thus, on days when foraging activity is high, food availability is presumably high as well. We do not know what explains the effect of day on colony response to removals. Perhaps in some climatic conditions when the cost of foraging is low, or on days when particular seeds are available and the benefits of finding rare seeds are high, foragers are less responsive to a short-term decrease in the rate of forager return that signals low food availability.

Our results here add to the growing number of examples of coordination in social insect colonies based on encounter rate (Gordon 1999; Gordon and Mehdiabadi 1999). The role of encounter rate in forager activation, including encounters between returning and inactive foragers in honeybees (Fernandez et al. 2003), or between biters and foragers in paper wasps (O'Donnell 2001), is reviewed above. A honeybee that encounters another performing a vibration becomes more active (Lewis et al. 2002). The ant *Temnothorax albipennis* uses encounter rate to assess nest mate density and thus the suitability of new nest sites (Pratt 2005). A harvester ant worker is more likely to change tasks to do midden work when its rate of encounter with midden workers is high (Gordon and Mehdiabadi 1999). Intervals between loads of water brought to the nest influence nest construction behavior in wasps (Jeanne and Nordheim 1996). Rates of interaction may be fundamental in many aspects of task partitioning and task allocation in social insects (Gordon 1999; Anderson et al. 2002).

A colony is acting as a risk-averse forager when it decreases foraging activity in response to a decline in food availability indicated by a decline in forager return rate (Nonacs and Soriano 1998). Risk aversion is the optimal strategy when the costs of poor foraging decisions tend to be greater than the rewards of favorable ones (Kacelnik and Bateson 1996). The main risk associated with foraging in *P. barbatus* is water loss. Predation on harvester ants is mostly by the horned lizard, and losses to predation are small (Munger 1984). Seeds are stored inside the nest for months and possibly years (Gordon 1993), providing a buffer when availability is low. However, harvester ants obtain most of their water from metabolizing the fats in seeds (MacKay 1985). Thus, ants foraging in the high temperatures and low humidity of the desert are using water to obtain more. When little food is available, the cost of water loss by foragers searching for a long time could be greater than the benefit of the food that they manage to collect.

A rapid response to a decline in patch quality is predicted when rewards may be low (Valone and Giraldeau 1993; Caraco et al. 1995) and tend to be variable (Shafir 2000). This seems to be characteristic of the environment in which harvester ant colonies forage; the seed supply in desert grasslands is spatially heterogeneous and temporally variable (Reichman 1984; Gordon 1993). The proximate cause of the colony's ability to respond rapidly to a change in forager return rate may be the limited interval over which an ant can track its encounters. Each individual ant need make only a short-term assessment of its encounters with others, and colony foraging activity is closely linked to food availability.

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