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How site fidelity leads to individual differences in the foraging activity of harvester ants

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We examined how differences in activity among individual foragers of the red harvester ant, *Pogonomyrmex barbatus*, could arise from site fidelity. Using observations of individually marked foragers, we found that each day most foragers made a few foraging trips, whereas only a few foragers made many trips. To determine whether only particular individuals are capable of high foraging activity, we removed the foragers that made the most foraging trips on 1 day and examined the frequency distribution of foraging the subsequent day. The most active foragers were replaced by other individuals. We then examined site fidelity of foragers. Though foraging trails extend up to 20 m from the nest, observations of marked individuals showed that on successive trips, a forager returns to sites within about 0.5 m. Foraging trip duration depended on search time and not on the distance from the nest of the final destination. Thus, the more food available, the shorter the search time and the shorter the trip. Because foragers return to the same site over and over within a day, a forager making many short trips to a high-quality patch can make more foraging trips per day. Thus, variation in patch quality, rather than individual variation in foraging ability, could produce the observed distribution of trip number. These results show that regulation of foraging in harvester ants does not require any individuals to show others a particular location with abundant food. Instead, a decentralized system of interactions tunes the numbers foraging to current food availability. *Key words:* individual foraging behavior, patch quality, *Pogonomyrmex barbatus*, search time, site fidelity. *[Behav Ecol]*

Site fidelity of foragers is well known in social insects, including bees (Heinrich 1976; Ackerman et al. 1982) and ants (Fresneau 1985; Rosengren and Fortelius 1986). Site fidelity of foragers may influence both how a colony finds food and how it allocates workers to retrieve it. For example, consider how an ant colony, operating without any central control, finds a nearby picnic and allocates foragers to retrieve food from it. The extent to which ants spread out in space and consequently the chance that a particular picnic will be discovered depends on how thoroughly individuals and cover the ground (Adler and Gordon 1992). If each ant merely visits a particular spot over and over, the chance that a picnic will be discovered depends on whether an ant happens to be dedicated to visiting the picnic site. Site fidelity also affects how the colony responds once the picnic is discovered. In many ant species, certain individuals tend to be more active than others (Jaisson et al. 1988). One possibility is that intense foraging to the picnic occurs because inactive ants are recruited to it. Another possibility is that the ants displaying site fidelity to the picnic site make extra trips.

Here we examine the relation of foraging activity and site fidelity in the red harvester ant, *Pogonomyrmex barbatus*. Foragers search for seeds in an area of about 30 m^2 around the nest (Gordon 1995). Foragers travel from the nest in streams, or trails, and then fan out to search individually for seeds (Gordon 1995). The foraging directions used by a colony vary from day to day; each day, the colony chooses from among a set of up to 8 foraging trails (Gordon 1991). The choice of foraging directions is made early each morning by a distinct group of workers, the patrollers, who search the foraging area before the foragers are active (Gordon 1991; Greene and Gordon 2007b). It is rare for a forager to return to the nest without a seed (Gordon 1991). The rate at which successful foragers return sets the rate at which more foragers go out (Schafer et al. 2006; Gordon et al. 2008).

Previous work showed that individual foragers of *P. barbatus* (Hölldobler 1976; Gordon 1991), *Pogonomyrmex rugosus* (Hölldobler 1976), and *Pogonomyrmex occidentalis* (Fewell 1990) repeatedly travel in the same direction from day to day. Other work on *P. occidentalis* (Crist and MacMahon 1991) and on *P. barbatus* (Wu 1989) suggested that foragers return to the same location on successive foraging trips on a given day.

Variation among individual foragers in the number of foraging trips per day might arise from site fidelity to patches that vary in food availability. To investigate this possibility, we first examined the variation among foragers in the number of trips a forager takes per day, and used removal experiments to learn whether only certain individuals are capable of making many trips. We observed that a few foragers make many trips, whereas most make only a few. We reasoned that this skewed distribution of forager trip number could arise if 3 conditions are met: sites vary in food availability, an individual keeps visiting the same site throughout the day, and search time determines trip duration. If so, then on a given day, the foragers that visit sites with abundant food, requiring little search time, would make more, shorter trips. Previous work showed that sites vary in food availability (Gordon 1993). To test whether the other 2 conditions are met, we examined whether a forager shows site fidelity within a day, returning consistently to the same site on successive trips, and whether search time determines the total duration of a foraging trip.

MATERIALS AND METHODS

The study was performed with a population of harvester ant colonies near Rodeo, NM. Colony ages are known from data collected in a long-term demographic study (census methods

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described in Gordon and Kulig 1996). On a hot summer day, foraging begins at about half an hour after sunrise, reaches a peak 3–4 h later, and gradually declines, ending at midday (Gordon 1984), when soil temperature reaches 52 °C (DeVita 1979). The ants stay inside the nest during the afternoon, sometimes emerging to forage again in the evening.

Individual variation in foraging activity

To measure variation among foragers in the number of foraging trips made per day, foragers were collected for marking from 4 mature colonies (older than 5 years) during July to August 2004. Foragers were collected when returning on a trail at the end of the morning activity period. About 200 ants in each colony were given a unique mark, using colors on head, thorax, and abdomen, made with Uni-Paint markers. Previous work shows that marking does not influence the subsequent foraging behavior of ants (Brown and Gordon 1997). Marked ants were returned to their nest in the afternoon of the day they were collected. Observations began the next day. For one colony (575), ants were observed for 3 consecutive days; for the other 3 colonies, ants were observed for 2 consecutive days. The total numbers of marked ants observed, with all 3 color marks intact so the ant could be identified uniquely, were the following: 186 (colony 575), 187 (colony 872), 192 (colony 306), and 198 (colony 919).

Throughout the morning period of foraging activity, from about 0600 to 1100 h, observers noted the time that a marked ant passed a point on a foraging trail within about 1 m of the nest entrance, either on its way out on the foraging trail or on its way back to the nest. Some ants that we followed individually made trips as short as 3 min. Not every ant was seen entering and leaving the nest on each trip. To count the number of foraging trips an ant made, we assumed that 2 sightings of the same ant were different trips if they were 3 min apart, regardless of the direction the ant was heading. This assumption should lead to an overestimate of the number of trips because a meandering ant may go back and forth past the observation point in the same trip. Using this assumption, the number of trips per ant per day ranged from 1 to 25. To estimate how much this assumption led us to overestimate our measure of trip number, we also counted trips defined more stringently, using only the data in which an ant was seen on its way out onto the foraging trail and then on its way into the nest, with the 2 sightings at least 3 min apart. This led to a somewhat lower count; trip number per ant per day ranged from 1 to 15. The 2 measures gave very similar results because so few ants made many trips (see below); here we report results using the first measure.

We measured the durations of trips in which an ant was seen on the way out and next seen on the way in. If 2 consecutive observations of the same ant were both on the way out, presumably because the ant was missed once on the way in, then the first sighting on the way out was ignored. The same method was used for measuring the duration of the time the forager spent inside the nest: we considered only observations of the ant on the way in that were followed by observations of the ant on the way out. We rarely observed very long trips or very long stays inside the nest, suggesting that we rarely missed seeing the ant for an entire trip.

Individuals differ in numbers of foraging trips. For each colony and day, we found the frequency distribution of foraging trips per forager. To test how much individual differences in foraging activity influenced this frequency distribution of foraging trip number, we performed a 2-day experiment. On day 2, we removed the individuals that had made the most foraging trips on day 1. By inspecting the frequency distribution of trip number (see Figure 1), we chose to focus on the 20 ants that made the most trips. We chose 20 as the smallest number of ants that account for the upper end of the distribution on day 1 but is still a large enough target number to yield a sufficient sample for the removal experiment. On day 2, we removed any of these 20 ants when they were first observed. Not all the 20 ants were seen on day 2, so we removed a total of 12–15 ants in each of 4 trials with 4 colonies.

To determine whether the ants that made the most trips on day 1 were replaced by other ants that made many trips on day 2, we tested whether the overall frequency distributions of trip number differed on days 1 and 2, using a Kolmogorov–Smirnov test. We also used a *t*-test to compare the mean counts of trip number on days 1 and 2 for the *R* ants with the most trips, where *R* is the number of ants removed on day 2.

To evaluate day-to-day trends in the behavior of particular foragers, we compared the following values for each marked

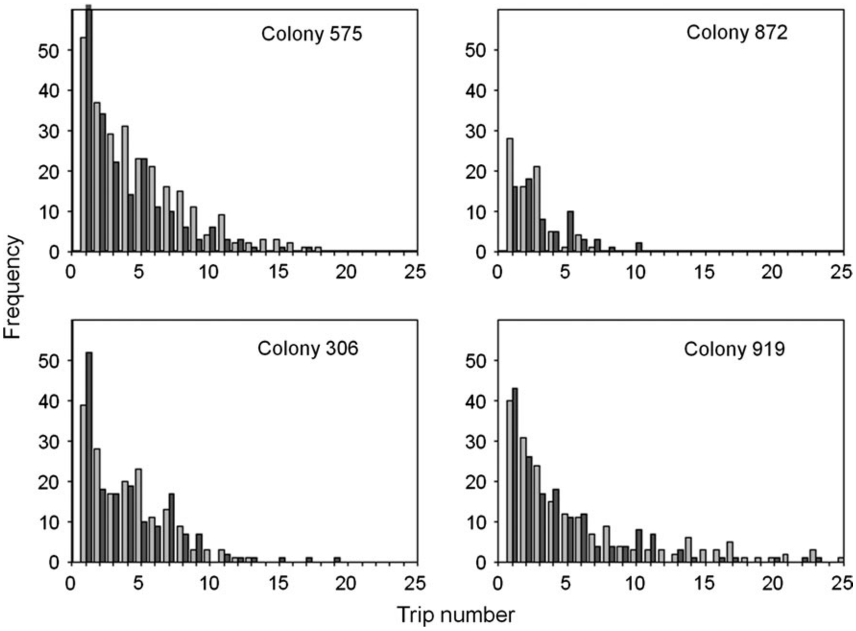

Figure 1
Frequency distributions of trip number on 2 consecutive days in colonies 575 (A), 872 (B), 306 (C), and 919 (D). Light bars represent day 1; dark bars represent day 2. The foragers that made most trips on day 1 were removed on day 2, but there were no significant differences between the frequency distributions of trip number on day 1 and day 2.

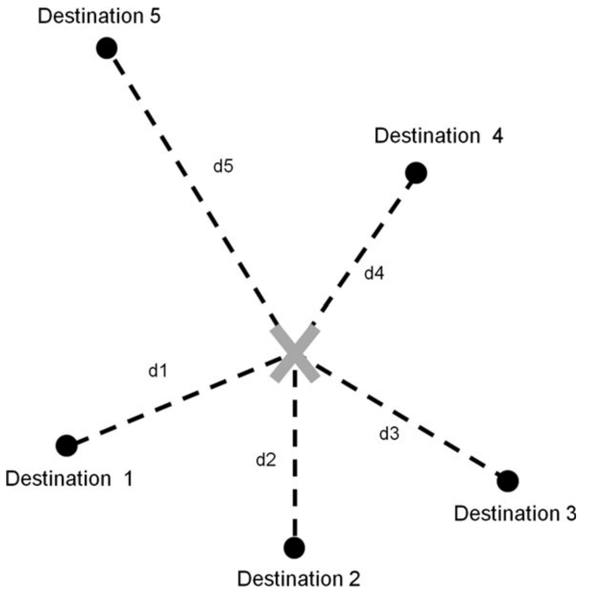

Figure 2
Five hypothetical destinations for a single ant. The "*x*" marks the calculated average of the 5 destinations. The dashed lines indicate the distance from each destination to the average destination. The mean dispersal index of the ant's destinations is $(d1 + d2 + d3 + d4 + d5)/5$.

ant that was seen on 2 consecutive days: number of trips, average trip duration, and time of day the ant was first seen. We tested for significant correlation between day 1 and day 2 for each of these measures for each of the 4 colonies, and for colony 575, which was observed for 3 days, we also compared day 2 and day 3. The removals of the 12–15 most active foragers were performed on day 2, and data for these foragers were not used in calculations of correlations. Two-tailed P values were calculated using Fisher's z transform and then Bonferroni adjusted.

Forager site fidelity

We observed marked foragers to determine whether ants return to the same site in successive trips. In each of 5 colonies, 50–60 foragers were uniquely marked, using the methods described above, in July to August 2005. Colonies were all mature (5–10 years old). All had several trails or foragers spread out in all directions with no distinct trails at all; none were nests with a single trail leading all foragers to the same place. Of the ants that were marked, 5 ants per colony or a total of 25 were observed.

Each observation began when a marked ant, not previously observed, left the nest. During each trip, a coin-sized marker labeled with the ant's identification code and trip number was left on the ground at the point where the ant first left the edge of the nest mound, to indicate its original departure site, and another marker was placed at its final destination. For all trips observed except one, the forager's final destination was the point on the ground where the ant found a food item. In the one exceptional case, the destination was the place from which the ant began to return to the nest, although the observer could not see anything in the ant's mandibles. An *x*–*y* axis consisting of 2 tape measures laid perpendicularly to each other was used to measure to the nearest centimeter the location of the nest entrance and all markers.

We used the statistical analysis package "R" (Verzani 2004) to produce a permutation test to determine the likelihood that the mean dispersal index (Figure 2) for all 25 ants could occur by chance. For each colony, we randomly shuffled the sequence of the observed destination 10 000 times, each destination associated with the location of the focal ant's nest. We divided each randomly ordered sequence into groups corresponding to the number of trips we observed for the ants of that colony and calculated a mean dispersal index for 25 groups (18 groups of 5, 5 groups of 4, and 2 groups of 3). For each colony, we generated a distribution of these 10 000 simulated mean dispersal indices and, using a permutation test, compared the observed mean dispersal index with this randomly generated distribution.

To determine how much search time contributes to trip duration, in each of the 5 colonies, 5 foragers were observed during the morning foraging period between 600 and 1100 h. Each ant was followed for 3–5 foraging trips, for a total of 116 trips from foragers of all 5 colonies. The observer stayed behind the ant and did not cast a shadow on it. For each trip, we noted the time the ant left the nest, the duration of time it spent traveling, the time at which it found a food item and began to return to the nest, and the time at which it reentered the nest. An ant was considered to be traveling when it was moving quickly in a straight line, without making periodic stops along the way, and to be searching when it was moving slowly, making erratic changes in its course, and stopping often to investigate the ground with its antennae. Search time was calculated as the total time from when the ant left the nest until it found food minus travel time. We tested for Spearman rank correlation between search time and the destination's distance from the nest entrance and between trip duration and the destination's distance from the nest entrance.

RESULTS

Individual variation in foraging activity

On all days and in all colonies, most ants made few foraging trips and a few ants made many trips. This cannot be attributed solely to differences among individuals because removing the individuals that had made the most trips the previous day did not change the colony's overall distribution of trip number (Figure 1). There were no significant differences between the frequency distributions of trip number on day 1 and day 2 (Kolmogorov–Smirnov test, colony 872, $P = 0.07$; colony 306, $P = 0.50$; colony 919, $P = 0.26$; colony 575 $P = 0.07$).

There was no consistent trend in the changes after removals in the numbers of trips made by the most active foragers. In 2 colonies, the foragers with the most trips on day 2 made more trips than those from day 1 that were removed (colony 872, $n = 16$, mean for day 1, 4.4 trips, mean day 2, 6.4, $t = -3.54$, $P < 0.001$; colony 306, $n = 13$, mean day 1, 10.1, mean day 2, 11.7, $t = -1.56$, $P = 0.14$), whereas in the other 2 colonies, the most active foragers on day 2 made fewer trips than the ones on day 1 that were removed (colony 575, $n = 14$, mean day 1, 14.6, mean day 2, 11.7, $t = 3.88$, $P < 0.001$; colony 919, $n = 15$, mean day 1, 19.6, mean day 2, 14.5, $t = 3.89$, $P < 0.001$).

Not surprisingly, the ants that made the most trips tended to make short trips: the correlation between the number of trips taken by an ant 1 day and the average duration of its trips the same day was always negative and was statistically significant in 3 of 4 colony–day pairs (colony 872, $r = -0.16$, $N = 68$, $P = 0.20$; colony 306, $r = -0.17$, $N = 143$, $P = 0.04$; colony 919, $r = -0.21$, $N = 171$, $P < 0.02$; colony 575 (days 1–2), $r = -0.31$, $N = 183$, $P < 0.02$).

Individual foragers showed slight but significant day-to-day correlations in trip number in 2 of 4 colonies (colony 872, $r = 0.33$, $N = 30$, $P = 0.4$; colony 306, $r = 0.32$, $N = 114$, $P < 0.02$; colony 919, $r = 0.21$, $N = 124$, $P < 0.1$; colony 575 (days 1–2), $r = 0.30$, $N = 130$, $P < 0.02$; colony 575 (days

Table 1

Results of permutation test comparing observed and simulated dispersal indices in meters of the destinations of the same forager on successive trips

	Colony				
	922	987	916	817	881
Ant 1	0.89	0.07	0.33	0.34	0.34
Ant 2	0.95	0.66	1.09	0.06	0.03
Ant 3	0.06	0.55	0.01	2.42	0.35
Ant 4	0.12	0.07	0.97	0.01	0.43
Ant 5	0.15	0.97	0.03	0.37	1.29
Observed mean ± SD	0.43 ± 0.45	0.47 ± 0.39	0.49 ± 0.51	0.64 ± 0.47	0.49 ± 0.47
Minimum simulated mean	1.46	1.43	1.22	1.88	3.42

2–3), $r = 0.57$, $N = 114$, $P < 0.02$). There were significant day-to-day correlations in an individual's average trip duration in some colonies (average $r = 0.23$; correlations significant in 3 out of 5 colony–day pairs). There seems to be little individual day-to-day consistency in the time of day an ant is first observed to forage (average $r = 0.15$ for day-to-day correlations; 1 out of 5 correlations significant).

Forager site fidelity

Foragers show strong site fidelity within a day. Foragers tended to return to the same destination on successive trips. For each colony, the observed mean dispersal value was significantly lower than the lowest mean dispersal value of the 10 000 random permutations (permutation test $P < 0.001$). The mean dispersal index of the observed destinations was 0.47 ± 0.56 m (standard deviation [SD]), $N = 25$ (median = 0.34 m, range = 0.01–2.42 m; Table 1); of the 10 000 random permutations generated from our data, the lowest average dispersal value of 25 ants' destinations was 3.7 m. Foragers also showed strong directional fidelity; every ant used the same initial departure direction from the nest mound that it had used in the most recently observed previous trip.

Trip duration was related to search time ($R_S = 0.96$, $N = 110$, $P < 0.001$; Figure 3) but was not related to the distance from the nest of the final destination ($R_S = 0.168$, $N = 116$, $P = 0.079$; Figure 3) or to travel time ($R_S = 0.447$, $N = 95$, $P = 0.001$). Foragers spent more time searching than traveling. On average, foragers spent 56% of the foraging trip searching (median = 0.57, range = 0.04–0.97, $N = 94$). Of 116 foraging trips observed, 115 were successful. The average destination distance from the nest entrance was $X \pm \mathrm{SD} = 5.36 \pm 2.34$ m, $N = 116$ (median = 4.57 m, range = 1.38–13.01 m, $N = 116$), and the average trip duration was 13.1 ± 10.34 min, $N = 110$ (median = 9.57, range = 1.52–47.37 min, $N = 110$). Sample size differs for measures of trip duration and the destination's distance from the nest entrance because for 5 ants, though the destination's distance from the nest entrance was recorded, trip duration was not.

To eliminate any effect of pseudoreplication, we tested for the same correlations using, for each of the 25 ants, the average values for search time, travel time, trip duration, and the destination's distance from the nest. Results were similar to those above. Trip duration was strongly related to search time ($R_S = 0.93$, $N = 24$, $P < 0.001$), but not the destination's distance from the nest entrance ($R_S = 0.02$, $N = 25$, $P = 0.918$), and was weakly related to travel time ($R_S = 0.43$, $N = 24$, $P = < 0.035$). We were not able to record search and travel time data for 1 of the 25 ants observed, reducing sample sizes for these tests from 25 to 24.

DISCUSSION

Individual foragers differ in the duration and number of foraging trips. Most foragers make a few long trips in a day, whereas a few foragers make many short trips. When the foragers that make many, shorter trips were removed, new foragers stepped in the next day to become the most active foragers. Observations of marked individuals showed that a forager returns to the same place, within about 0.5 m, on successive trips. The duration of the foraging trip is related to how long the ant spends searching, not to how far from the nest the ant travels.

Our results suggest that variation among forager destinations in food abundance, rather than differences among individuals in activity level, accounts for the observed distribution of trip number. Wherever a forager finds a food item on its first trip of the day is the site to which it will return on the rest of its trips that day. The more abundant the food at the site, the less time required for searching and thus the shorter the forager's trips, because search time determines trip duration. Variation among patches in food abundance could produce the observed distribution: the foragers that happen to choose the best patches make more, shorter trips, whereas those visiting patches with less food make fewer, longer trips. It is likely that forager destinations, on the scale of less than 0.5 m, vary in seed abundance because seeds in desert grasslands tend to be patchily distributed on the scale of centimeters (Price and Reichman 1987; Gordon 1993).

It is possible that some ants are better than others at finding the best patches and would thus tend to be the ones that make more, shorter trips. However, we found only small day-to-day correlations in an ant's trip number (average $r = 0.37$; correlations significant in 2 out of 4 colony–day pairs) and trip duration (average $r = 0.23$; correlations significant in 3 out of 5 colony–day pairs). It seems likely that such correlations would be higher if some ants were consistently much more competent than others at finding good patches.

It seems unlikely that a forager often returns to the same place day after day. We did observe 1 ant that returned to the same patch it searched the previous day. However, a harvester ant colony uses different foraging directions from day to day (Gordon 1991, 1995). Further research is necessary to determine whether, if a forager uses the same trail on consecutive days, it also returns to the same site.

We do not know what cues the foragers use to return to the same location on successive trips within a day. Site fidelity has been observed in many ant species, including ponerine ants (Fresneau 1985) and those in the *Formica rufa* group (Rosengren and Fortelius 1986). Individual foragers of *Cataglyphis bicolor* (Harkness and Maroudas 1985) and *Formica*

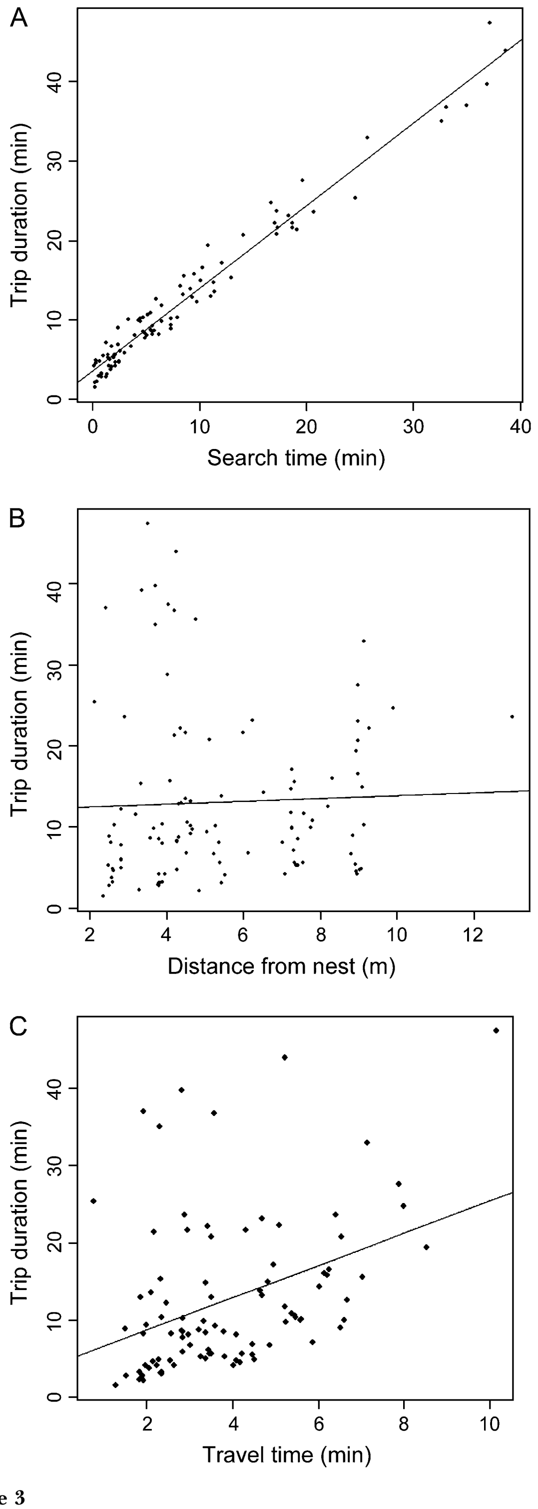

Figure 3
Trip duration versus search time for 110 foragers (A) and the destination's distance from the nest (B) for 116 foragers.

schaufussi (Fourcassié and Traniello 1993) repeatedly use the same route to arrive near the same final destination. The initial direction *P. barbatus* foragers take is determined by chemical cues on the nest mound deposited by patrollers (Greene and Gordon 2007a); once on the trail, foragers may use the direction of polarized sunlight (Hölldobler 1976; Wu 1989). Our results here help to explain the puzzling observation that foragers will ignore seed baits, even walk right over piles of seeds, unless the bait is offered early enough to be found by the patrollers (Gordon 1983). Once foraging has begun, a forager returns repeatedly to the day's destination and apparently cannot be distracted by food in a different location.

The result that the duration of a foraging trip depends mostly on how long the forager has to search means that the rate at which foragers bring back food to the nest is tightly linked to the availability of food that day. Less food means a longer search and a delay in the forager's return. This is crucial in the regulation of foraging. The number of ants that are out foraging at any time is regulated by interactions between foragers. Inactive foragers are stimulated to leave the nest to forage by the return of successful foragers bringing in food (Schafer et al. 2006). The rate of forager return, which depends on search time and on food availability, translates within minutes to a change in the rate at which more foragers go out (Gordon et al. 2008).

Recruitment of foragers to a specific location is well known in social insects, for example, by means of trail pheromones in ants and the waggle dance in honey bees. The result that foragers return to the same place in successive trips implies that harvester ants, by contrast, use a recruitment system that ignores location. Foragers are stimulated to leave the nest by the return of successful foragers. The success of a forager in a particular place, returning quickly to the nest with a seed, stimulates another forager to travel to a different place.

The regulation of foraging activity without specific information on location would be appropriate in an environment in which food availability in a particular location is correlated with its availability elsewhere. In such an environment, if search time is high for forager A on its patch, search time will also be high for forager B on its patch in a different location. Comparisons of the foraging behavior of many colonies on the same day suggest that food availability is similar for all colonies on a given day (Gordon 1991), and differences among days, for all colonies, in the intensity of foraging are consistently stronger than differences among colonies (Gordon 1984, 1987; Schafer et al. 2006; Gordon et al. 2008). For example, on the day after heavy rainfall, foraging intensity is high, presumably because the rain has exposed seeds in the upper layer of the soil. Seeds are distributed mostly by wind and flooding (Gordon 1993), factors that vary consistently over a large area. Thus, regulation of foraging in harvester ants does not require any individuals to show others a particular location with abundant food. Instead, a decentralized system of interactions tunes the numbers foraging to current food availability. A similar process may regulate recruitment in other social foragers.

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