

## **The Effect of Food Size and Dispersion Pattern on Retrieval Rate by the Argentine Ant, *Linepithema humile* (Hymenoptera: Formicidae)**

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*Food acquisition in central-place foraging animals demands efficient detection and retrieval of resources. Most ant species rely on a mass recruitment foraging strategy, which requires that some potential foragers remain at the nest where they can be recruited to food once resources are found. Because this strategy reduces the number of workers initially looking for food, it may reduce the food detection rate while increasing the postdiscovery food retrieval rate. In previous studies this tradeoff has been analyzed by computer simulation and mathematical models. Both kinds of models show that food acquisition rate is greatly influenced by food distribution and resource patch size: as food is condensed into fewer patches, the maximal acquisition rate is achieved by a shift to fewer initial searchers and more potential recruits. In general, these models show that a mass recruitment strategy is most effective when resources are clumped. We tested this prediction in two experiments by letting laboratory colonies of the Argentine ant (*Linepithema humile*) forage for resources placed in different distributions. When all prey were small, retrieval rate increased with increasing resource patch size, in support of foraging models. When prey were large, however, the mass of prey returned to the colony over time was much lower than when prey were small and widely distributed. As more ants reached a large prey item, the distance the prey item was transported decreased due to a greater emphasis on feeding rather than transport. Because*

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*Argentine ants can transport more biomass externally than they can ingest, food retrieval that depends only on ingestion can depress the biomass retrieval rate. Thus, our results generally support theoretical foraging models, but we show how prey size, through differential prey-handling behavior, can produce an outcome greatly different from that predicted only on the distribution of resources.*

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**KEY WORDS:** foraging; Formicidae; *Linepithema*; food retrieval; Argentine ant.

## INTRODUCTION

Mass recruitment foraging strategies are common in ants, particularly among species with large colonies (Beckers *et al.*, 1989). Mass recruitment requires dividing potential food-gathering workers into two functional groups: (1) workers that move through a foraging area in search of food and return to the nest when food is found (scouts) and (2) workers that wait at the nest until directed by scouts toward discovered food (recruits). A potential drawback of such a system is that it requires keeping a subset of potential foragers either inactive at the nest (Anderson, 2001) or engaged in other functions that may or may not be as limiting to colony growth as food acquisition. Thus, mass recruitment is likely to decrease the rate at which food is discovered relative to a more solitary foraging strategy (e.g., Schmid-Hempel, 1987; Wehner, 1987), which maximizes the number of workers actively searching for food. If food items were always small and widely distributed in time and space, then mass recruitment would likely fail because no scout that found food and immediately retrieved it would be able to communicate the position of additional food to recruits. If food items were large or clumped in space, however, so that a scout that encountered food could carry only a small portion of it, then a mass recruitment system would result in many recruits quickly reaching, defending, and retrieving the food source (e.g., Pasteels *et al.*, 1987; de Biseau *et al.*, 1997). In this case, increased food retrieval rate might compensate for decreased discovery rate and give a selective advantage to the use of mass recruitment over individual foraging.

The tradeoff between resource discovery and resource domination may lead to niche partitioning among competing ant species that rely on either rapid discovery of dispersed resources or effective occupation and transport of clumped resources (Davidson, 1998). Several field studies have shown that many ant species that are quick to discover baits or large prey are eventually displaced by other ant species with superior nestmate recruitment or resource defense behaviors (Fellers, 1987; Cerdá *et al.*, 1998; Traniello, 1983; Holway, 1999). Davidson (1977) showed that seed harvesting ant species with a solitary foraging strategy collected food primarily from dispersed

resources, while seed harvesters with group foraging behavior collected food primarily from clumped resources. The relationship between foraging strategy and distribution of collected resources, however, can be complex. The ant *Aphaenogaster cockerelli* (= *Novomessor cockerelli*), considered by Davidson (1977) to be a solitary forager, does not recruit to clumps of seeds (Sanders and Gordon, in press) but does recruit to large invertebrate prey (Hölldobler *et al.*, 1978) and shifts to a diet richer in invertebrate prey when competing ant species are prevented from foraging (Sanders and Gordon, 2000). When simultaneously presented with different foods in clumped or dispersed distributions, *A. cockerelli* collected more food from the clumped resource when the clumped resource was the preferred food (tuna) and the dispersed resource was seeds (Sanders and Gordon, in press). When the clumped and dispersed foods were the same type, however, more food was collected from dispersed food patches. Thus, interspecific competition and food type, in addition to foraging strategy, can influence the amount of food collected from a given resource distribution.

Nestmate recruitment system (i.e., proportion of scouts to recruits) and colony size are inversely related: species with small colonies (<100 workers) tend to use a more solitary foraging strategy, while species with larger colonies are more likely to use mass recruitment, trunk-trail, or group hunting strategies (Beckers *et al.*, 1989). Because mass recruiting societies are larger, their lower scout-to-recruit ratio does not necessarily result in their having fewer scouts than a smaller colony with a higher scout-to-recruit ratio. Prey discovery time should reflect the number of scouts (and the search behavior of each scout) in an area (Adler and Gordon, 1992); thus, mass recruitment should suffer a tradeoff in resource discovery relative to resource retrieval only if the optimal scout-to-recruit ratio for resource retrieval is so low that it depresses the total number of scouts in the foraging area relative to other species.

Several researchers (Johnson *et al.*, 1987; Jaffe and Deneubourg, 1992; Anderson, 2001) have shown through mathematical modeling and computer simulation that the optimal scout-to-recruit ratio varies with resource distribution. In their models, as resources become increasingly clumped, the optimal scout-to-recruit ratio decreases. For example, when resource patches required 125 forager visits for depletion in the Jaffe and Deneubourg model, an ant society retrieved the most resources per unit time when scouts accounted for 20% of all foragers. When each resource patch required only 25 forager visits for depletion, however, a colony with 20% scouts did poorly retrieving resources compared to a colony with 40% scouts. Thus, their models provide a numerical framework under which coexistence between resource discovering species and resource dominating species may be viewed as a series of interactions among colony size, foraging behavior, and resource distribution.

To our knowledge, the predicted tradeoff of the model under controlled conditions has not been tested empirically. In this study, our goal was to create a laboratory environment similar to the conditions of the Jaffe and Deneubourg (1992) model (a two-dimensional square grid with ants foraging from the center) and compare resource patch discovery times and resource retrieval rates at different resource distributions. We conducted two experiments: first, to compare resource retrieval while varying only resource distribution, we used only small resources, which were easily transported by single ants; and, Second, to determine if individual resource size influenced resource retrieval rate, we used large individual prey as clumped resources and small prey as dispersed resources.

## METHODS

We used the Argentine ant [*Linepithema humile*, formerly *Iridomyrmex humilis* (Shattuck, 1992)] for our experiments. The Argentine ant is a worldwide invasive species that disrupts biological control programs in agriculture (Markin, 1970), displaces native arthropods (Human and Gordon, 1997), and infests human residences (Klotz *et al.*, 2000). It is polydomous and polygynous in the field but can be made readily into monodomous, monogynous colonies for laboratory studies (Keller, 1988). Argentine ants use a mass-recruitment foraging strategy (Beckers *et al.*, 1988) and seem to forage normally in laboratory studies (e.g., Goss *et al.*, 1990; Gordon, 1995).

The Argentine ants used in this study were obtained from a single large field colony in northern California by the soil-free method of Silverman and Nsimba (2000). Laboratory colonies were fed ad libitum on a diet of 25% sucrose solution, cockroaches (*Blattella germanica*), and a gel-based artificial diet composed of sucrose, casein, cholesterol, potassium phosphate, magnesium chloride, salt, water, and a multivitamin tablet (Nonacs and Dill, 1988, modified by the addition of carrageenan). For details of rearing conditions, see Silverman and Roulston (2001).

Sixteen experimental colonies of 300 workers and three queens were aspirated from the nestbox of the main laboratory colony (after uncovering individual nest containers) 3 days before each set of experiments began. Experimental colonies were housed in 10-cm-square, ca. 2.5-mm-deep plexiglass nests that were kept continually moist by the intrusion of a saturated dental wick from a sealed, water-filled jar. These nests were kept inside 22 × 17.5-cm plastic trays coated with fluon. Colonies were starved for 16 h, then connected via a 1-m-cotton string to the center of a foraging arena that contained no food. The arena comprised a 1.2 × 1.2-m square of wood with 5-cm-high, fluon-coated walls. The floor of the arena was overlaid with a

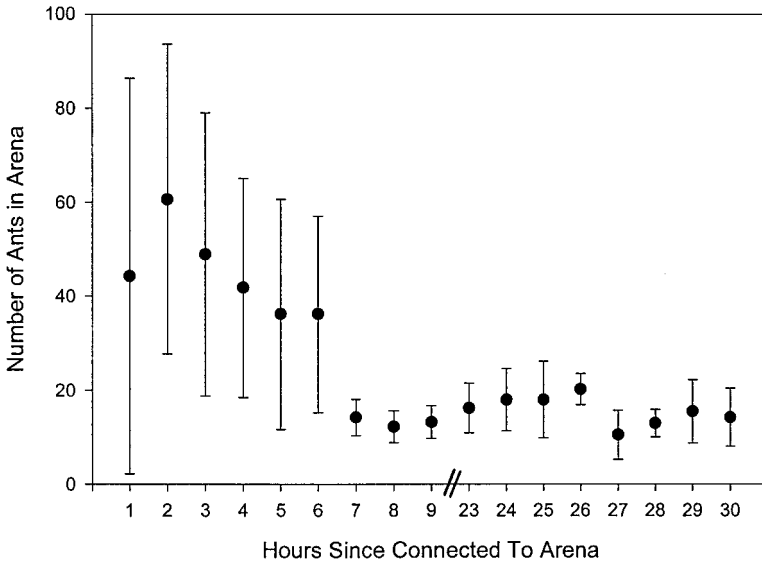


Fig. 1. Number of ants in foraging arena (mean  $\pm$  SD) for eight 300-worker colonies of Argentine ants over time.

paper grid that had been divided into 3600  $2 \times 2$ -cm numbered squares. The grid was covered with clear plastic, which was wiped off with 70% ethanol between trials. At least 24 h elapsed between trials in any arena. Experiments began after an additional 24 h of starvation (total = 40 h starvation) during which the ants explored the arena. A 24-h acclimatization period in the arena prior to taking data was necessary because Argentine ants readily recruit to novel space in laboratory settings (Aron *et al.*, 1989), often flooding the arena with 20% of the entire colony within an hour of introduction (Fig. 1). The number of foragers declined steadily after an initial peak, generally stabilizing within 24 h. We were interested in examining food location and retrieval by colonies after they had reached a steady state.

### Small Prey Experiment

Eight ant colonies were given 16 freeze-killed cockroach nymphs (*Blattella germanica*) as prey in one of three dispersion patterns: one prey in each of 16 arena locations, four prey in each of four locations, and eight prey in each of two locations. The prey ranged from 4 to 9 mg each, a size easily transported by a single Argentine ant. Food locations for both the small prey experiment and the small versus large prey experiment (below) were chosen at random for each trial using a random number generator and

the marked grid squares in the arena. The position and number of ants in the arena and the number of food items remaining in the arena were recorded every 5 min for 3 h. Food items were considered to be in the arena until they were transported to the arena's center, at which point they were transported via an aerial string to the ant colony. Each nest received each treatment once in random order. This experiment was carried out June–August 2000.

### Small Versus Large Prey Experiment

Eight ant colonies were offered 100 mg of freeze-killed cockroaches (*Blattella germanica*) for 3 h in one of two dispersion patterns: 2 adult male cockroaches (ca. 50 mg each) placed at two arena locations or 16 cockroach nymphs (4–9 mg each) placed individually at 16 arena locations. After 3 h, the mass of food returned to the center of the arena was determined. This comprised the total weight of any food item that was transported to the center of the arena and the mass of food ingested (beginning mass of prey–end mass of prey–average water loss in 3 h) for any food item that was fed upon but not transported to the center of the arena. During this experiment we recorded the position and number of ants in the arena as well as the route of transport taken by each prey item until it reached the center of the colony. This experiment was carried out April–May 2000.

### Terminology

Biesmeijer and de Vries (2001) have criticized the use of the terms scouts and recruits to characterize all workers that participate in foraging. They point out that some researchers differ in their definitions of the terms (e.g., Is a recruit that strays from the recruitment path still a recruit or does it become a scout?) and propose an alternate, seven-category forager taxonomy that incorporates each worker's foraging history, present position, and source of information regarding foraging direction and motivation. While such a system may better represent the transitional phases of forager behavior, it requires detailed information about individual workers and goes beyond the scope of the present research, which is to test whether resource dispersion influences resource retrieval rate. In describing the distribution of ants in the foraging area, we use the term "scout" only for ants that are roaming the foraging area before any food has been detected. This is similar to the use of the term by Jaffe and Deneubourg (1992). After a scout has detected food and recruited nestmates to the foraging area, we distinguish foragers on the basis of their foraging pathways. Foragers that move independently along an apparently random (e.g., Gordon, 1995) or correlated random (Kareiva and

Shigesada, 1983) pathway, we refer to as “searchers.” As we use it, the term searchers may include initial scouts as well as recruited workers that departed from established scent trails. Searchers represent the workers whose pathway may lead them to as yet undiscovered food. All other ants in the foraging area (those at prey and those following recruitment paths) are noted but not named. Their behavior may facilitate the retrieval of discovered prey but does not contribute to new discoveries.

### Statistics

All statistical analyses were carried out using MINITAB version 13 or SAS version 8 statistical software. All count data in both experiments were transformed using the square root (Sokal and Rohlf, 1981) before analyses. These data include minutes to discovery and minutes to removal of first prey, number of ants initially in the arena, maximum number of ants in the arena, maximum number of searching ants, and number of small prey moved from their original position and removed from the arena. For comparing the proportion of discovered prey taken to the center of the arena in 2 h across resource distributions (small prey experiment), proportions were transformed using the arcsin. For comparing the percentage of prey moved within 10 min of discovery (small versus large prey experiment), percentages were transformed using the arcsin. For all of the above comparisons, treatment effects were tested using a general linear model ANOVA (GLM) with prey distribution and ant colony as main effects. No interaction term was included in the model because each colony received each treatment only once. For comparing the distance that large prey were moved with the number of ants at the prey, we performed a repeated-measures analysis using proc mixed in SAS version 8. This was done to control for repeated observations on the same ants at the prey on sequential 5-min sampling times. Our model was square root of number of ants = distance moved and included nest and prey number (first or second) as class variables.

## RESULTS

### Small Prey Experiment

Prey were returned more rapidly to the center of the arena as prey distributions were increasingly clumped (Fig. 2, Table I). Discovery times of first prey were similar among resource distributions, but subsequent prey discovery increased more rapidly when prey were clumped rather than dispersed (Fig. 3). Once prey were discovered they were removed quickly from

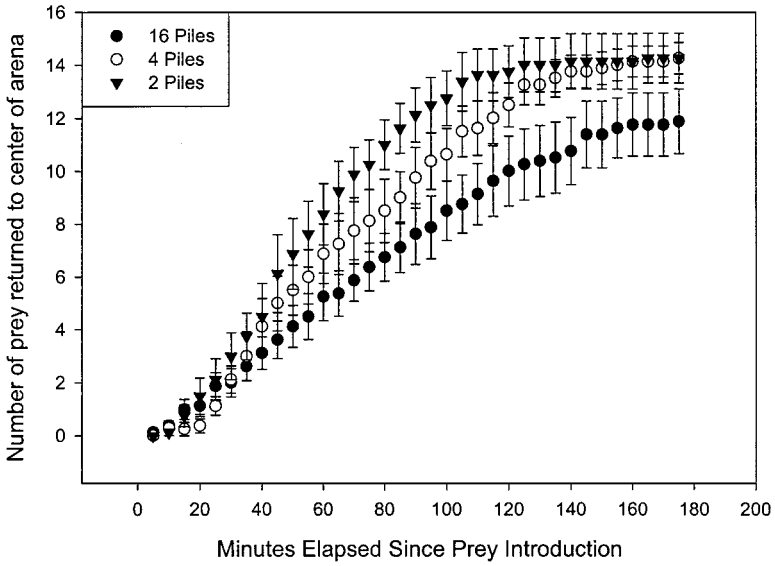


Fig. 2. Number of prey (mean  $\pm$  SE) returned to the center of the arena over time for three prey dispersion patterns.

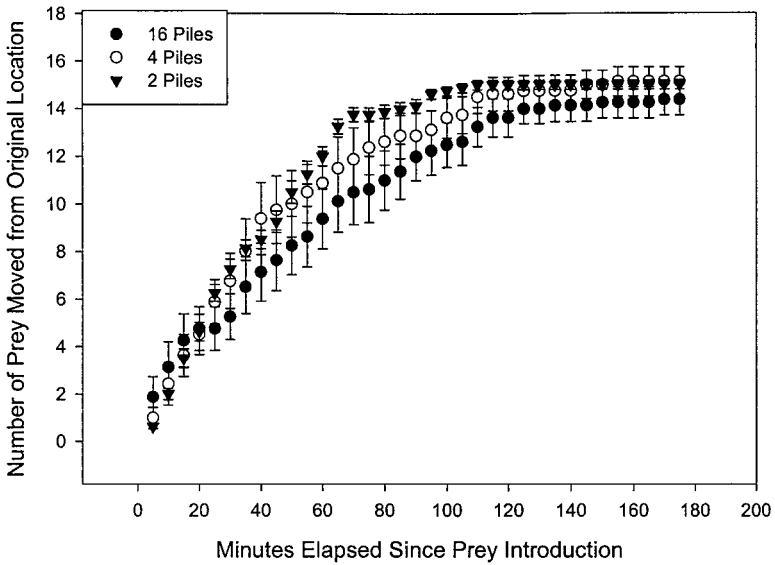


Fig. 3. Number of prey (mean  $\pm$  SE) moved from original location over time for three dispersion patterns.

**Table I.** Comparison of Foraging Behavior/Efficiency for 300-Worker Colonies of *Linepithema humile* Presented with Small Prey in Different Distributions<sup>a</sup> (Eight Colonies)

	Dispersion pattern of 16 dead cockroaches			F	P
	2 piles of 8	4 piles of 4	16 individuals		
Minutes to first prey moved <sup>b</sup>	10.0 ± 1.9	8.1 ± 1.3	8.1 ± 1.6	0.61	0.556
Minutes to first prey removed <sup>c</sup>	20.6 ± 3.1	24.4 ± 2.6	17.5 ± 3.5	1.14	0.347
Number of initial ants in arena	11.0 ± 2.7	9.6 ± 2.7	9.9 ± 1.6	0.09	0.917
Maximum No. of ants in arena	46.1 ± 6.4	43.2 ± 4.8	43.1 ± 4.8	0.15	0.863
Maximum No. of searching <sup>d</sup> ants	19.4 ± 2.4	18.6 ± 3.3	14.9 ± 1.2	1.62	0.232
Prey removed in 1 h	7.6 ± 1.2	6.0 ± 1.0	4.5 ± 0.9	1.83	0.197
Prey removed in 2 h	14.0 ± 0.9	11.7 ± 0.9	9.5 ± 1.3	5.50	0.017

<sup>a</sup>Each nest given each treatment. Mean ± SE. Statistics based on a general linear model with prey distribution and colony as main effects.

<sup>b</sup>Time until first prey moved off original 2 × 2-em grid square.

<sup>c</sup>Time until first prey brought to the center of the arena, where a string connects the arena to the nesting tray.

<sup>d</sup>Searching ants defined as those roaming the arena, neither feeding on prey nor moving along recruitment trails.

the arena when they were clumped: after 2 h, 91.0% of discovered prey were removed from the arena when the prey were in two piles, while only 86.4 and 72.1% of previously discovered prey were removed from the 4-pile and 16-pile treatments, respectively ( $F_{2,14} = 5.63, P < 0.05$ ). The treatments did not differ significantly in the time to first prey moved or removed, initial and maximum number of ants in the arena, or maximum number of ants in the arena that were not on prey or following recruitment trails (Table I). The number of initial scouts was negatively correlated with the time elapsed until the first prey was removed from the arena ( $r = -0.434, N = 24, P < 0.05$ ) but was not correlated with subsequent measures of prey retrieval.

### Small Versus Large Prey Experiment

More than twice as much prey biomass was removed from the arena in 3 h when the prey comprised 16 randomly placed cockroach nymphs rather than two randomly placed adult male cockroaches (Table II). The first prey item was discovered more quickly when the prey were small and widely scattered (Table II), but ants discovered a greater cumulative prey biomass per unit time when prey were large rather than small at all time intervals between 10 min and 3 h (Fig. 4). Small prey were more likely than large prey to be moved from their original position within 10 min of discovery ( $\bar{X} \pm SD, 31.2 \pm 25.9\%$  for large prey and  $86.83 \pm 10.3\%$  for

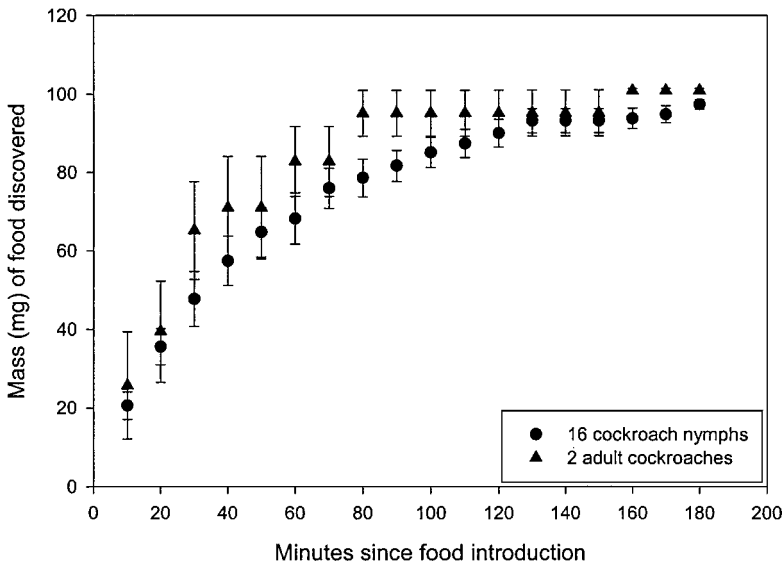
**Table II.** Comparison of Foraging Behavior/Efficiency for 300-Worker Colonies of *Linepithema humile* Given 100 mg of Total Prey (Two 50-mg Adult German Cockroaches or 4–9 mg Nymphal German Cockroaches) Placed Randomly<sup>a</sup>

	Prey type		<i>F</i>	<i>P</i>
	2 adults	16 nymphs		
Minutes to first roach discovered	19.9 ± 1.5	6.5 ± 1.0	6.30	0.040
Number of initial ants in arena	9.3 ± 1.5	10.2 ± 2.5	0.27	0.623
Maximum No. of ants in arena	60.2 ± 5.8	65.7 ± 4.2	0.73	0.421
Maximum No. of searching <sup>b</sup> ants	23.2 ± 3.3	31.2 ± 1.8	7.14	0.032
Mass of material removed	40.4 ± 5.9	86.1 ± 4.4	54.4	<0.001

<sup>a</sup>Each nest given each treatment. Mean ± SE. Statistics based on a general linear model with prey type and colony as main effects.

<sup>b</sup>Searching ants defined as those roaming the arena, neither feeding on prey nor moving along recruitment trails.

small prey;  $F_{1,7} = 24.1$ ,  $P = 0.008$ ). At the end of the observation period,  $12.6 \pm 5.5$  ( $\bar{X} \pm SD$ ) ants were feeding or guarding each large prey item, while  $2.8 \pm 2.4$  ants traveled recruitment paths between the center of the arena and the prey. When large prey items were moved, there was a negative relationship between the number of ants (transformed by the square root) at



**Fig. 4.** Cumulative mass of food (mean ± SE) discovered over time for two dispersion patterns.

the prey and the distance the prey traveled in the previous 5 min (repeated-measures analysis with nest and prey number as class variables,  $F = 6.92$ ,  $P < 0.01$ ), indicating that prey transport slowed down as more ants reached the prey.

Eighty percent (103/128) of small prey were returned to the center of the arena. The transportation time after discovery was positively correlated with the initial distance of the prey from the center of the arena ( $r = 0.476$ ,  $P < 0.001$ ). Ants did not always transport prey by the most direct route. In 77 of 122 transports of small prey, the prey was observed farther from the center of the arena during at least one observation than it had been during the previous observation. The proportion of small prey transports away from the center of the arena was positively correlated with the original distance of the prey to the center ( $r = 0.272$ ,  $P < 0.01$ ). There was no difference in maximum recruitment level between treatments, but more ants became searchers (ants neither on prey nor on recruitment trails) when the prey were dispersed (Table II).

## DISCUSSION

Our results using equally sized prey distributed at different resource patch sizes support the predictions of prior mathematical and computer simulation models (Jaffe and Deneubourg, 1992; Johnson *et al.*, 1987). When resource patches were large but rare, resources were collected at a faster rate than when resource patches were common but small (Fig. 2). This result may be due to at least three separate factors. First, there was no evidence of a lag in discovering the first small resource patch (Table I). Because small dispersed objects have a greater surface area than tightly packed objects, we might expect that a randomly moving ant would encounter one dispersed object, on average, more quickly than it would encounter a rare clump of objects. If clumped resources, however, are substantially easier to perceive at a distance than sparse resources, due to increased odor or increased visual detection range, then their perceptibility might increase faster than their surface area would predict. Kaspari (1993) compared the rate of discovery of seeds in bird droppings to the circumference of bird droppings. He found that seed caches were discovered more quickly as patch size increased but that discovery rate did not increase as rapidly as patch circumference increased. Thus, the increase in perceptibility of the larger patch did not wholly compensate for the smaller surface area of the larger patch relative to small patches. Second, in the present study, after the first prey in a large resource patch was detected, the number of prey subsequently discovered increased dramatically (Fig. 3). This indicates that prey detection facilitated

subsequent prey detection. It appears that when resources were small and scattered, initial detection of resources had a lesser effect on subsequent detection of resources. Third, when clumped resources were found, they were efficiently returned to the colony. When a recruitment trail was established between a clumped resource and the nest, discovered prey were efficiently retrieved. When an ant encountered a dispersed resource, however, no clear trail led it back to the colony. This interpretation is supported by the second experiment, involving small versus large prey retrieval. In that experiment, the pathway taken by each prey item to the center of the arena was recorded. Dispersed prey were more often moved away from the center of the arena when they were initially distant (presumably because no clear trail marked the route to the nest) than when they were initially close to the center. Thus, ants collecting dispersed resources may be far less efficient at returning to the colony after resource discovery than ants collecting clumped resources.

The number of scouts at the time of food introduction was  $9.9 \pm 6.4$  ( $\bar{X} \pm \text{SD}$ ), for all treatments combined. This number corresponds to 3.3% of the original colony size and, if taken as the percentage of scouts in the total forager pool, is predicted to be most efficient when resource patches are extremely large (Fig. 1 of Jaffe and Deneubourg, 1992). This percentage, however, likely underestimates the scout-to-recruit ratio because many workers may be engaged in other tasks, such as queen tending and nest cleaning, and may not participate in foraging during a given foraging period (e.g., Gordon, 1996). The percentage of initial scouts to maximum number of foragers observed during a trial was  $23.7 \pm 12.1\%$  ( $\bar{X} \pm \text{SD}$ ). This number probably underestimates the total number of ants that participated in food retrieval because it excludes any ants that were in the nest at the time of maximum foraging. This figure does provide an upper bound to the percentage of initial scouts, however. For the whole range of 3.3–23.7% scouts, the Jaffe and Deneubourg model predicts maximal retrieval efficiency when resource patches are quite large. When prey size and resource patch size differed, more resources were returned to the colony from small prey than from large prey. This indicates that food handling behavior can predominate over retrieval advantages predicted by patch size alone. In this experiment, individual ant behavior upon reaching large prey included dragging the prey toward the center of the arena, feeding for a short time before recruiting nestmates, and feeding for an extended time while nestmates discovered the prey on their own. Because many ants remained on the prey at the end of the observation period, their slow retrieval did not result from a lack of interest in the prey after extended feeding. On occasion, several ants stood on the prey and fed while other ants attempted to drag the prey toward the nest. Often, two or more ants pulled the prey from opposite ends, apparently

canceling out each other's efforts to move the prey. Sudd (1965) observed similar transport deadlocks when either *Myrmica rubra* or *Formica lugubris* workers were presented with large prey. Traniello (1989) observed that some recruited workers of *Formica schaufussi* climbed on top of prey while others pulled the prey in opposite directions, thus reducing the loading capacity of retrieval groups compared with individual workers. Although Argentine ants were observed cooperatively dragging both large and small prey, it was not clear what determined whether ants fed on or transported prey. As in the present experiment, Sudd (1965) and Rabaud (cited by Sudd, 1965) also found that prey transport decreased with an increase in the number of ants at prey.

As ant abundance increases at prey in the field, the ability of nestmates to defend the prey against competing ants should also increase, lessening the need to transport it quickly to the colony (Human and Gordon, 1999). For ant species that are good at finding, but poor at defending resources (e.g., Fellers, 1987; Traniello, 1983), quick transport of prey is essential. For species that commonly commandeer and retain large resources, however, such as *Monomorium minimum* [Adams and Traniello (1981) = *M. emarginatum sensu* Dubois (1986)], *Monomorium eratogyna* (Holway, 1999), *Camponotus ferrugineus* (Fellers, 1987), and *Pheidole pallidula* (Cerdá *et al.*, 1998), rapid transport may be less important than rapid recruitment and defense. Some species, such as *M. minimum* (Adams and Traniello, 1981) and *P. pallidula* (Cerdá *et al.*, 1998) do not cooperatively transport large prey, but rely on defending large prey until their workers can dissect and individually transport it. Argentine ants excel at both discovering and defending large resources (Holway, 1999). Thus, slow transport of large resources may not reduce their resource retrieval rate as greatly as it would for other species. Because Argentine ants can individually drag at least 50 mg, yet ingest less than 1 mg (Silverman and Roulston, 2001), a retrieval process that relies on ingestion will be much slower than one that relies on external transport.

In both experiments, there was no difference in maximum number of ants in the foraging arena among treatments. When prey were small and scattered, so that no ant that found and retrieved prey could direct nestmates to additional prey, recruitment was as high as when foraging ants discovered large resources. Argentine ants produce trail pheromone in the Pavan's gland (Wilson and Pavan, 1959) and deposit it on the substrate during trips away from and to the nest, even when resources have not been discovered (Deneubourg *et al.*, 1990). They deposit trail pheromone in greatest abundance while exploring novel space or returning to the nest after discovering food (Aron *et al.*, 1989). Because our experimental design included a fixed 1-m string connecting the nest to the foraging arena, any ant marking a return

route to the nest, regardless of the position of food discovery, would mark the same path along the string. Thus, a well-marked scent trail could lead ants from the nest, even though it could not lead them directly to food. As ants reached the end of the trail, they would then search until encountering other areas of pheromone (e.g., Deneubourg *et al.*, 1990). As some of these wandering ants encountered new food and returned to the nest while laying trail pheromone, they would perpetuate the recruitment process. This is similar to “a strategy of errors” (Deneubourg *et al.*, 1983, 1987). Trail-following fidelity or ability is apparently a species-specific trait (Deneubourg *et al.*, 1983) that may lead to differential success at exploiting resources of different distribution patterns. When food is dispersed, recruited but wandering ants may find new resources, but when food is highly clumped wandering ants may only reduce the retrieval rate of discovered resources. Thus, trail-following “error” can increase resource acquisition in some circumstances. Weidenmüller and Seeley (1999) suggest that the ability of recruited honey bees to reach a particular destination is limited by the imprecision of the waggle dance in indicating direction. When scouts from a honey bee swarm locate a potential nesting site, which is typically small, their dance is more precise than when they locate a food resource at the same distance (Weidenmüller and Seeley, 1999). The authors suggest that this imprecision may be adaptive because floral resources typically occur in broad patches, in which case bees that reach the general area are likely to find rewarding flowers, but bees that do not immediately reach a nesting area (typically a tree cavity) will delay colony establishment.

In our experiments with Argentine ants, pheromone trails leading into the arena but not leading directly to prey (because the discovered prey was already moved), could act as an imprecise cue that promotes area searching. When we offered Argentine ant colonies 16 small, scattered prey or 2 large prey, we found no difference in the maximum number of ants in the arena at one time. There were more ants moving through the arena on unestablished routes (referred to as “searchers” in Tables I and II), when the prey were small and scattered. Thus, the discovery of small, scattered prey could lead to a colony foraging behavior (increased random searching) that increases the discovery of more scattered prey. In the first experiment, however, when all prey were small and readily moved, there was no difference in the maximum number of searchers among treatments.

Resource distribution, abundance, and composition influence the resource acquisition rate for a given foraging strategy. Our results support theoretical models that predict increased resource retrieval efficiencies at larger resource patch sizes but show that size-specific handling of prey may greatly alter the rate of resource acquisition. Thus, theoretical models may be most accurate when considering homogeneous resources that can be transported only through ingestion (e.g., liquid foods).

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