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PATTERNS OF ENERGY ALLOCATION WITHIN FORAGERS OF *FORMICA PLANIPILIS* AND *POGONOMYRMEX SALINUS*

Peter Nonacs¹

ABSTRACT.—Foraging workers of *Formica planipilis* and *Pogonomyrmex salinus* were collected at various distances from their colony by pitfall traps in the former species and by catching workers recruited to food at known locations in the latter. In *F. planipilis* the number of larger workers increased in proportional representation to distance from the nest. Larger workers also weighed relatively less with distance from the nest, indicating that energy or water allocated for maintaining all foragers is patterned such that resource loss with forager mortality is minimized. However, the smallest size class involved in foraging shows the opposite pattern, with heavier individuals being found farther from the nest. Thus, it is possible that smaller size classes function as mobile reserves of energy or water to maintain foraging activity of larger classes at a distance from the colony. In *P. salinus* all sizes of workers were equally likely to be found at any distance. Foragers weighed significantly less than mound workers of the same head size, again suggesting resource conservation in provisioning foraging workers. Differences in patterns of energy allocation to foragers are discussed relative to the species' ecologies.

Key words: foraging, ants, *Formica*, *Pogonomyrmex*, body weight.

Ant colonies forage upon a potentially enormous array of food items that can have significant mortality risks in their collection. Thus, natural selection may favor those diets that best balance between collecting food and exposure to mortality risks. At a community level this may lead to species partitioning their habitat by prey size (Kaspari 1996) or activity patterns (Savolainen and Vepsäläinen 1988, 1989). Within a species, combinations of morphological and behavioral responses are possible. Many species have polymorphic worker castes that are distinctly different in size (Hölldobler and Wilson 1991). Worker polymorphism can allow foragers to specialize on particular types of foraging tasks, but such task specialization according to caste is not universally observed (Traniello 1989, McIver and Loomis 1993, Ferster and Traniello 1995).

In conjunction with morphology, behavioral adaptations can also increase the net benefits from foraging. One such behavior is to preferentially forage in those areas that maximize net gain (as measured by colony growth minus worker mortality; Nonacs and Dill 1990, 1991). A 2nd adaptation is for foragers to maintain lower reserves of valued resources, such as food reserves (carbohydrates, proteins, or lipids) and water in arid habitats. Two benefits

would follow from such a strategy. First, more resources could be directly invested in colony growth or sexual production. Second, fewer resources would be lost with the death of any forager.

The evidence suggests that foragers do, on average, carry lower resource reserves than do nonforaging workers. Porter and Jorgensen (1981) found a consistent decline in body weight of *Pogonomyrmex owyheeii* workers from the interior of nests, to those working on the nest surface, and then to foragers. In *Leptothorax albipennis* lipid reserves closely correlate with behavioral roles such that foragers are almost inevitably "lean" (Blanchard et al. 2000). Similarly suggesting that they carry less food, *Myrmica rubra* foragers kept without food died faster than nonforagers (Weir 1958), and old foragers in *Formica rufa* died faster than young ones (Rosengren 1977).

If it is adaptive for foragers to carry fewer reserves than interior workers, it may also be adaptive to have a finer-scale subdivision of resources across foragers in relation to their expected level of mortality risk. As an example, risk could positively correlate with distance traveled from the nest. Although no relationship should be expected to be invariant, on average, it is probable that the farther an ant

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travels, the more likely it is to encounter predators or aggressive competitors and the greater is its exposure to the elements. Also, the farther an ant is from its nest entrance, the more chances it will have of becoming lost and unable to return quickly to the nest if environmental conditions deteriorate. In addition to differing levels of risk, the type of risk may also affect patterns of resource distribution in the forage caste. If the preponderance of forager deaths is likely to result from starvation or dehydration, a "worker-conservative" strategy might be favored. In such a scenario, workers traveling the farthest may carry relatively more food and water as insurance against getting lost or otherwise delayed in replenishing their resources. However, if predation risk or stochastic environmental events cause the preponderance of mortality, then colonies may employ a "resource-conservative" strategy in which those foragers most at risk carry the least reserves.

Resources can be categorized in numerous ways, but relevant to foraging, the important distinction may be the extent to which the particular resource can be rapidly increased or exchanged across individuals. For example, lipids are energy rich but relatively slow in being converted to metabolic needs; also, they cannot be exchanged by trophallaxis between replete and starving foragers. Conversely, aqueous carbohydrates can be relatively quickly metabolized or exchanged between workers when needed. Thus, protein and lipids appear to be shunted into colony growth, while colony respiration and foraging activities are fueled by carbohydrates (Brian 1973, Sudd 1987). Indeed, foragers seem to have minimal fat reserves, which would conserve those particular resources (Porter and Jorgensen 1981, Blanchard et al. 2000). Additionally, in xeric habitats water could be a critical resource for which the above trade-off is important. With more water, desiccation deaths are minimized, but each death results in a greater loss of resources.

Patterns of food reserves among foragers can be set and maintained by trophallaxis between nestmates. Similar patterns could also result without trophallaxis if workers left the colony with energy reserves based on the distance they expected to travel. Site specificity or allegiance in foragers is known from a number of species (Rosengren 1971, Hölldobler

1976, Rosengren and Sundström 1987, Traniello 1989, Fewell 1990, Gordon et al. 1992, McIver and Yandell 1998). Thus, it is possible for a forager to "know" how far it is going and how long it is likely to forage and then to adjust either its initial energy or water reserves. From a colony standpoint of conserving resources or workers, adjusting resource levels throughout the territory or just at colony departure would reflect the same overall goals. The former mechanism might allow finer partitioning in the patterns.

Testing the above scenarios requires measuring weights of unsuccessful foragers so as to avoid confounding food reserves with food to be returned to the colony. With this in mind, I used 2 experimental methods to sample populations of foragers at various distances from their colonies. In the first I set out pitfall traps at specific distances and placed them in areas likely to trap insect-scavenging workers. In the 2nd method I set out food baits at measured distances and collected recruiting workers. The food (cracker bits) was attractive to ants but could not be consumed on the spot. The 2 methodologies differed in that the 1st trapped ants that may have been continuously foraging for some time, and the 2nd generally captured ants that were recently recruited from the colony and probably not foraging immediately prior to recruitment. Wet weights were measured as the best estimator of foraging reserves (water and carbohydrates dissolved therein).

STUDY AREA AND SPECIES

The experiments were conducted in May 1999 at the Sierra Nevada Aquatic Research Laboratory (SNARL) in the Great Basin Desert Province (Franklin and Dyrness 1973). The site is at approximately 2000 m elevation, and the weather during the study was generally warm (daytime highs 20–25°C) and sunny, with no more than trace amounts of rainfall. Vegetation at the site is dominated by sagebrush (*Artemisia tridentata*) and sparse grass cover.

The study species were *Formica planipilis* and *Pogonomyrmex salinus* (keyed from Wheeler and Wheeler 1983). *Formica planipilis* is a thatching ant that builds mounds of plant matter as part of its nests. Colonies often have trunk trails leading to foraging sites where

they collect honeydew. Individual foragers also scavenge arthropods (McIver and Loomis 1993). *Pogonomyrmex salinus* is a seed-harvester that builds low gravel mounds. The species recruits foragers to food sites but does not form well-marked trunk trails like other species of seed-harvesters (personal observation). Both species are very common in the immediate vicinity of SNARL.

For the study I marked out 11 nests of *E. planipilis* and 8 nests of *P. salinus* that were large, actively foraging, and had no conspecific neighboring colony within 15–20 m in at least one direction. None of the *E. planipilis* colonies was within 200 m of a permanent water source. Thus, captured *E. planipilis* workers were not involved in water collection, and differences in wet weight would not reflect encounters with standing water. Several *P. salinus* colonies all were within 20 m of a running stream. However, because only workers recruiting to a food source were collected, wet weight again did not reflect water collection.

METHODS

Pitfall traps were laid out at distances of 1, 4, 7, and 10 m from the center of the mound for each of the 11 *E. planipilis* colonies. The traps were plastic trays with their sides coated with Fluon. Stones were piled in the center of the tray to provide shade from the sun. Ants were collected from the traps in the morning and late afternoon. Pitfall sites were located away from trunk trails and bushes where foragers were actively collecting nectar or honeydew. Hatching ants appear to form strong site allegiances that can be as restrictive as a single bush (McIver and Yandell 1998). Thus, it is likely that most ants trapped were scavenging or otherwise patrolling the territory and not aphid tenders or nectar transporters. On occasion new recruitment trails would form near a trap, and many ants would be found in a sample. I released these ants and moved the trap. When emptying the pitfall traps at 7 and 10 m, I also collected some foragers from the immediate vicinity and placed them on the presumed nest mound. If they were not attacked, I assumed the collected workers in the traps belonged to the marked colony. If attacked, I released any caught ants and moved the traps. Dead *E. planipilis* foragers found in the traps were discarded. Traps were kept in place

around a colony until at least 20 foragers were captured for each distance. However, for one colony (#5), no foragers were collected at 10 m. All collected workers were immediately taken back to the laboratory, killed by freezing for 10 minutes, and then individually weighed.

I also collected 12 *E. planipilis* workers from each of the nest mounds in the morning between 0800 and 0900 hours. These were not random samples, as I tried to represent equally a wide range of worker sizes. The ants were immediately taken to the laboratory and weighed. Thereafter, they were placed in plastic containers (2 ants per container) and put outside in the shade for the day. In the late afternoon (between 1600 and 1700 hours), the ants were killed by quick freezing and weighed again to measure weight loss over the length of a foraging day.

The pitfall trap method could not work for the *P. salinus* colonies because of higher colony densities (i.e., at 10 m traps were likely to contain foragers from more than a single colony) and lower aggression levels (i.e., known foreign workers transferred to another mound were not always obviously attacked). Instead, I placed bright orange cracker crumbs at distances of 5 or 10 m. Only one distance was presented to a colony at a time. All colonies located the crumbs at 5 m within 20–30 minutes and foragers were actively recruited. Six of 8 colonies also quickly found the crumbs at 10 m, but in 2 colonies the crumbs were always removed by other ant species before *P. salinus* could recruit in numbers. Thus, for 2 colonies there are data only for 5 m. After allowing the recruitment process to begin, I collected between 18 and 30 foragers returning with crumbs at each distance. Thus, it is likely that most ants collected were inside the colony prior to collection rather than outside foraging.

For *P. salinus* colonies I also collected 20–30 workers per nest that were working at the mound (either moving pebbles from the nest or patrolling the entrance). These samples probably accurately reflect the population of mound workers, as I would collect the ants in the order they exited the nest. All collected ants were immediately placed in 95% alcohol. Although this may affect water and lipid content to some extent, I assumed the effects were unbiased across ant sizes. (Note that since ant

size was eventually found not to vary across distance, the results are robust even if the assumption does not hold.) Later the ants were briefly dried from the alcohol and then individually weighed. For both species morphometric size for each individual was estimated as its widest headwidth, which was measured with a calibrated dissecting microscope to the nearest 0.04 mm.

For the majority of the statistical analyses, I combined headwidths into discrete size classes based primarily on where the mean mass increased more rapidly with headwidth. In *E. planipilis*, I categorized the distribution into 5 size classes that are in approximate agreement with McIver and Loomis's (1993) 7 size classes, the difference being that I collected very few individuals in their 2 smallest size classes. In *P. salinus*, I categorized the ants into 4 size classes. Where needed, I ln-transformed body weight as weight increases cubically with linear increases in headwidth.

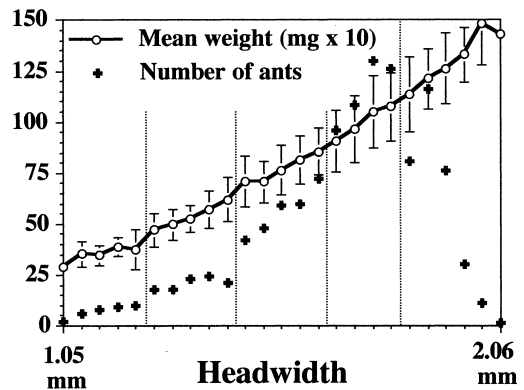
RESULTS

For both species there is a strong positive correlation between headwidth and body weight (Fig. 1). In *E. planipilis* there is a skewed size distribution toward larger body size in foragers. In *P. salinus* intermediate body sizes are the most common.

For both species I did ANOVAs on the percentage of ants, with factors of size class and distance from nest. In *E. planipilis* there is a significant effect of size class ($F = 124.1$; $df = 4,195$; $P < 0.0001$), which reflects the relationship in Figure 1A of larger ants being more abundant in pitfall traps than smaller ants. There is no effect of distance of pitfall traps, but there is a significant interaction between size class and distance from nest ($F = 3.199$; $df = 12,195$; $P = 0.0003$). This results from the smallest size class being rarely trapped far from the colony and larger size classes becoming relatively more common (Fig. 2A). For *P. salinus* there is a significant effect only of size class ($F = 4.441$; $df = 3,76$; $P = 0.0063$). Distance does not have a significant effect, and all size classes are equally likely to work around the nest entrance or forage at distance (Fig. 2B).

Because there is no size class:distance relationship in *P. salinus*, I analyzed forager weights directly. An ANOVA of ln-transformed body weight found a significant effect of size

A. *F. planipilis*



B. *P. salinus*

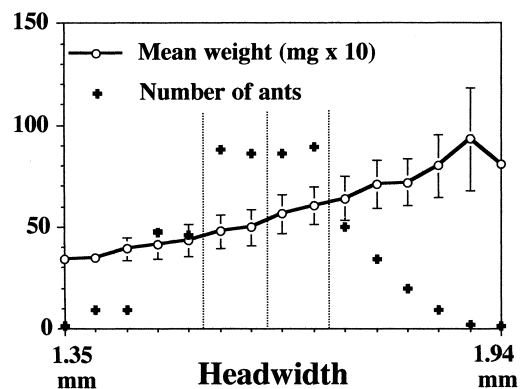


Fig. 1. Mean weight (\pm s) of each headwidth class and number of ants collected in each class for *Formica planipilis* (A) and *Pogonomyrmex salinus* (B). Data for *F. planipilis* are those only for ants collected foraging and not at the nest mound. Dashed lines indicate where size class breaks were added for ANOVA analyses.

class (i.e., physically larger ants weigh more: $F = 188.7$; $df = 3,565$; $P < 0.0001$) and distance ($F = 8.834$; $df = 2,565$; $P = 0.0002$). The latter result comes from ants of all size classes weighing less when foraging than when working around the nest (Fig. 3). There was, however, no significant interaction between the 2 factors, which indicates that all size classes behave similarly regarding their body weight. A Scheffé-S post hoc test found body weights of ants at 5 and 10 m are significantly less than at 0 m ($P < 0.012$ for both comparisons). On average ants weighed more at 5 than at 10 m, but the trend was not significant. The difference in weights between ants at the nest and foragers is unlikely to be due to foraging activity

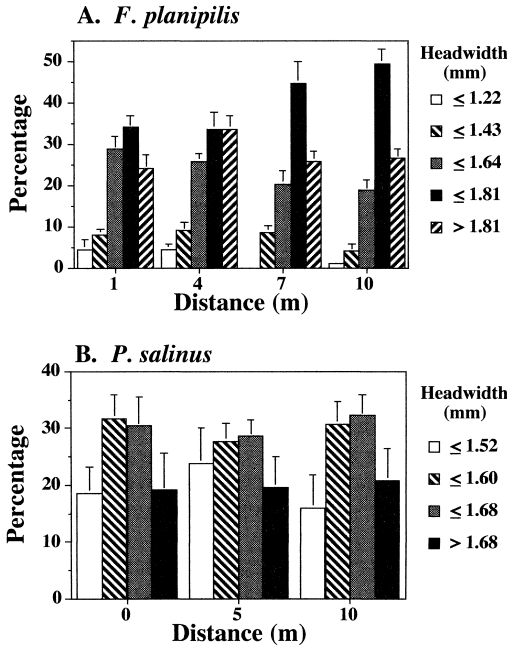


Fig. 2. Percentage of ants (\pm SE) in each headwidth class collected at set distances from the nest entrance for *Formica planipilis* (A) and *Pogonomyrmex salinus* (B).

alone. Fewell (1988) estimated that a foraging trip of approximately 12 m in *P. occidentalis* costs 0.088 J. If foragers use a liquid equivalent of 20% sugar water as their energy source, this would translate into an estimated biomass loss of 0.03 mg (using a value of 3.2 J of energy per mg of sugar water) to travel 10 m. In comparison, the mean weight differential between ants at 0 m and those collected at 5 and 10 m is 0.33 and 0.43 mg, respectively.

Because there is a size class:distance relationship in *F. planipilis*, forager weights cannot be analyzed directly. An effect of distance can come from either larger workers going different distances or workers within any size class carrying different amounts of food depending on the distance they forage. Therefore, I calculated a mean body weight for each measurable headwidth gradation. Subtracting these means from each individual ant's weight gives a residual value that can be statistically analyzed. (Note that the smallest size class had to be dropped from this analysis because such ants were absent or rarely collected at 7 and 10 m.) The residuals are not significantly affected by headwidth ($F = 0.003$; NS), which removes the effect of morphologically larger

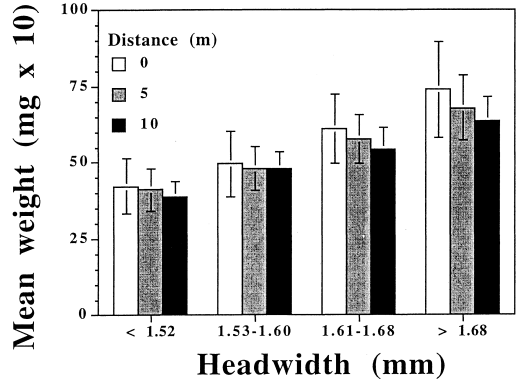


Fig. 3. Mean weight (\pm SE) of each headwidth class collected at 0, 5, or 10 m from the nest mound in *Pogonomyrmex salinus*. Ants collected at 0 m were not foraging, and those at 5 or 10 m were foraging.

workers being relatively more abundant at greater distances. The ANOVA of residuals found a significant effect of distance ($F = 2.469$; $df = 4,1139$; $P = 0.0432$), no effect of size class ($F = 0.232$; NS), and a significant interaction between size class and distance ($F = 2.124$; $df = 2,1139$; $P = 0.0134$). Thus, workers are overall likely to weigh less farther from the nest, but this relationship is not the same for all size classes. As can be seen in Figure 4A, individuals in the smaller size class (1.23–1.43 mm) tend to weigh more farther from the nest, while the larger size classes show the opposite relationship.

The basis of the distance effect on *F. planipilis* worker weights can be estimated by adjusting observed body weights with the weight loss measured in the control series. When kept the entire day in a container without access to food or water, the average ant loses 6.31% (± 1.5 s) of its body mass. A regression of weight loss against headwidth was not significant ($F = 0.092$; NS), indicating that ants of different sizes do not lose relatively different proportions of their body weight over time. Therefore, I adjusted upward the weights of all ants proportional to the distance they were trapped from the colony. Ants trapped at 1 m and 10 m had their weights increased by 0.631% ($= 6.31 \times 0.1$) or by 6.31% ($= 6.31 \times 1$), respectively. Ants caught at intermediate distances were similarly adjusted proportionally. The underlying assumption for these adjustments is that, on average, ants caught farther

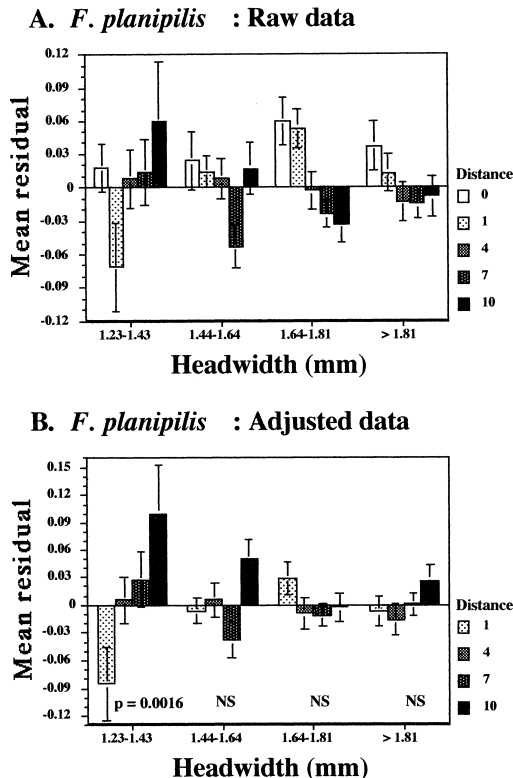


Fig. 4. Mean residuals ($\pm s_{\bar{y}}$) of *Formica planipilis* headwidth classes collected on the nest mound or 1–10 m distant pitfall traps. In (A) recorded weights are given. In (B) weights from pitfall traps have been adjusted upward as might be expected if foragers at more distant sites had spent more time traveling (see text). Only the smallest headwidth had a significant regression of residual values with distance from nest mound.

from the colony have been foraging longer and thus may have lost more weight. The magnitude of the adjustment is an approximation. Under natural conditions, ants probably move more than they do in containers, which would lead to underestimating weight loss. However, this is likely to be balanced in the field by the fact that foraging workers could get food from others or return to the colony for more food.

Reanalyzing the data after adjustment leads to several possible outcomes, each of which would imply something about the foraging process. If distance has a negative effect on body weight both without and with the adjustment, it would imply that foragers going farther from the nest begin their trips with less energy reserves than those foraging at closer distances. If distance has a negative effect

without the adjustment, but no effect with the adjustment, this would leave open the possibility that all foragers leave with about the same energy reserves and that the distance effect is due to differential energy expenditure. Finally, if after adjustment the distance effect is positive, this would imply that foragers going farther leave the colony with proportionally more energy reserves.

The data of unadjusted body weights in *F. planipilis* suggest that different size classes of foragers carry different levels of energy resources (Fig. 4A). Therefore, I regressed adjusted residual weights against distance foraged (1–10 m) separately for each size class. Only the smallest size class shows a significant effect of distance: workers are more likely to weigh more farther from the colony (Fig. 4B). For all other size classes, once weight was adjusted upward, there was no significant effect of distance from colony.

The previous analyses of *F. planipilis* data viewed individual ants as independent data points, although they were all members of only 11 colonies. To rule out any problems with pseudoreplication, I also correlated the residuals with distance at the colony level for each of the 4 largest size classes. If there is no weight-distance relationship, then the overall mean of the correlation coefficients should not be significantly different from zero. With the unadjusted data, the 3 largest size classes all show a significantly negative relationship between body weight and distance from colony (Table 1). The smallest size class shows a positive relationship that approaches significance ($P = 0.0621$). When weight is adjusted upward, there is a significant positive relationship between weight and distance for the smallest size class considered, but no significant relationships in the 3 largest size classes (Table 1). Therefore, when the *F. planipilis* data are analyzed at the colony level, results are consistent with the analysis at the individual level.

DISCUSSION

Foraging is a relatively dangerous activity for ants, and foragers can be considered expendable or even disposable (Porter and Jorgensen 1981). Estimates of mean life spans for *Pogonomyrmex* foragers are about 14 days (Porter and Jorgensen 1981), and few foragers of the thatching ant, *F. obscuripes*, were

TABLE 1. One-sample t tests of correlation coefficients of residual value versus distance from colony across 11 colonies of *F. planipilis*. Nonadjusted tests have original data, and adjusted tests have data corrected for possible loss of weight due to activity (see text).

Size class	Nonadjusted			Adjusted		
	Mean	t -value (df)	P	Mean	t -value (df)	P
1.23–1.43	0.261	2.100 (10)	0.0621	0.413	2.509 (9)	0.0334
1.44–1.64	-0.125	-2.843 (10)	0.0174	0.035	1.105 (10)	NS
1.65–1.81	-0.211	-4.588 (10)	0.0010	-0.064	-1.110 (10)	NS
>1.81	-0.161	-2.524 (10)	0.0302	0.015	0.200 (10)	NS

observed for longer than 20 days (McIver and Yandell 1998). Given an expected high loss rate of foragers, it is adaptive for colonies to minimize the resources lost with each worker. For foragers in xeric habitats, resources may equate to some combination of water and dissolved carbohydrates (Brian 1973, Sudd 1987, Lighton et al. 1994). Porter and Jorgensen (1981) found that *P. owyheeii* foragers weighed less than those doing mound work, which correlates with their task-related mortality rates. Data from *P. salinus* show a similar pattern: foragers weigh less than mound workers. In *P. salinus* there is weak evidence for further conservation of resources in that the mean weight of foragers traveling 10 m is less than for those traveling 5 m (Fig. 3). However, this effect is not statistically significant.

There is stronger evidence for distance-related foraging in *F. planipilis*. Overall, larger workers formed a larger fraction of the work force farther from the nest (Fig. 2A). This result differs from McIver and Loomis (1993), who found a relationship of worker size with distance from colony in nectar-collecting workers, but not scavenging workers. Differences between the studies may result from differences in behavior across species (*F. planipilis* vs. *F. obscuripes*) or in collection techniques (pitfall traps vs. collection by sight). A 2nd distance effect in *F. planipilis* is that body weights of the 3 largest size classes of workers decline significantly with distance from the nest. This pattern could result from workers either maintaining lower reserves at greater distances or losing proportionately more weight on longer foraging trips. Both possible scenarios are consistent with minimizing resource loss rather than worker loss. There is no support for large foragers increasing food or water reserves, which would be expected if forager deaths were due mostly to starvation or dehydration.

In contrast to larger size classes, smaller *F. planipilis* workers have a positive relationship between weight and distance from the nest that is strengthened by weight adjustments for assumed differences in activity. The pattern in these workers is most consistent with minimizing their loss rather than the resources they carry. Thus, colony-level strategy seems diametrically opposite in small versus large size classes of foragers. Four hypotheses may account for this. First, smaller workers may get lost more often because of their relatively poorer orientation abilities (Bernstein and Bernstein 1969, McIver and Loomis 1993). If they are more likely to make navigation errors, this could favor carrying extra resources. Second, because smaller workers have a larger surface-to-volume ratio, they may have to carry more water because of a relatively higher desiccation risk (Lighton et al. 1994). Lighton et al. (1994) found that smaller workers lose water at faster rates than do larger workers in *Messor pergandei*. However, there was no such size-based effect in the control measurements with *F. planipilis*. Smaller workers did not desiccate more rapidly than larger workers. Third, food may move differentially between smaller and larger workers during transport to the colony. McIver and Yandell (1998) found that smaller tending ants transferring honeydew to larger ones, which transport it back to the colony. However, for this to result in the observed patterns in *F. planipilis*, the exchanges would have to occur more frequently on a per capita basis closer to the colony, and it is not obvious why this should be the case. Moreover, pitfall traps were located so as to avoid workers collecting honeydew; thus, it is likely that most workers were not involved in the immediate transport of food back to the colony. Fourth, food may move differentially between smaller and larger workers, but not in the context of transport to

the colony. Instead, small workers may form a resource pool from which larger foragers can draw resources when needed. Smaller workers form a smaller proportion of the work force as distance from the nest increases (Fig. 1A), and if they serve as "gas stations," then the results are consistent with both resource- and worker-conserving strategies. Relatively fewer stations should be found far from the nest where they are most at risk, and each station should have relatively more fuel.

Comparing across *F. planipilis* and *P. salinus*, there are both similarities and differences. In both species foragers as a class weigh less than mound workers. In *F. planipilis* larger workers form an increasingly greater proportion of the work force with distance from the nest, and there appear to be significant differences in the amount of energy workers carry depending on their class size and the distance they expect to travel. In *P. salinus* there is no evidence of the former and only weak support for distance affecting foragers' energy reserves. These differences across the species may result from either differences in the foraging behavior sampled or in the species characteristics. In *F. planipilis* the collected ants were most likely on open-ended foraging trips that might continue for some time until they found prey or returned to the colony. If foragers far from the nest are more at risk per trip, then significant modulation of energy reserves might be expected. In *P. salinus* most collected ants were probably recruited from within the colony. If foragers travel directly to the food patch and back, there may be relatively little difference in energy requirements (Fewell 1988) or exposure time. If the mortality risk for foragers is more a factor of time spent foraging than distance traveled, then the ants recruited to food at 10 m will be only marginally more at risk than ants going 5 m. Thus, in recruited workers there may be only a weak relationship between distance and resource reserve.

Besides differences in sampling, the species have different life history characteristics. *Formica planipilis* has polymorphic workers that show monophasic allometry (Hölldobler and Wilson 1991). There is a significant proportional bias toward the larger size classes in foraging (Fig. 1A) and size-based task specialization (McIver and Loomis 1993). *Pogonomyrmex salinus* is monomorphic, and the size

range in workers could result simply from developmental noise. *Formica planipilis* also specializes in nectar collection, while *P. salinus* forages mostly on seeds. The combination of a larger evolved range of worker sizes and access to an easily divisible food source may favor more fine-scaled adjustments of foraging strategy in *F. planipilis* than in *P. salinus*. It is interesting to note that in the genus *Formica* there is fairly consistent size-based specialization in foraging tasks (Herbers 1979, Rosen-gren and Sundström 1987, Sundström 1987, McIver and Loomis 1993, McIver and Yandell 1998), while in seed-harvesting ants (*Pogonomyrmex* and *Messor*) results are far more mixed and mostly negative (see reviews in Traniello 1989, Ferster and Traniello 1995).

In conclusion, variation in body weight of ants in *F. planipilis* and *P. salinus* at least suggests that all foragers are not equal in their distribution of energy reserves. The mechanisms by which food is moved through and shared by a population of foragers are yet to be elucidated. The efficiency with which an ant colony collects food must depend on how much energy is allocated to each of the disposable elements and how well a colony balances between maximizing worker survival and resource conservation.

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