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Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*

Jennifer H. Fewell*, Jon F. Harrison, Tammy M. Stiller, and Michael D. Breed**

Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder,
CO 80309–0334, USA

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Summary. We examine how cost and benefit components of resource profitability affect recruitment in the giant tropical ant, *Paraponera clavata*. To vary resource profitability, we changed the quantity of artificial nectar baits presented to foragers and the distance of nectar baits from the nest. Both distance to and amount of resource affected quantitative aspects of recruitment. At increased distances foragers were less likely to recruit, and fewer workers were recruited to the resource area. The amount of nectar affected the tendency of foragers to recruit, but had no effect on the number of ants recruited. Variation in resource distance was also associated with qualitative changes in recruitment strategy. Foragers at distant sites recruited from the canopy rather than from the nest, and often transferred nectar to other workers for transport to the nest. Nectar transfer and extra-nidal recruitment significantly reduced the time required for resource collection. It may also have increased the ability of workers to specialize in specific foraging tasks. A portion of the colony's foraging force specialized spatially by remaining in distant foraging areas without returning to the nest. The flexible recruitment system of *P. clavata* increases colonial net energetic gain rates by concentrating foraging effort on resources yielding the highest net energetic rewards, and increases the competitive abilities of individual colonies at resource sites by decreasing collection times.

Key words: Foraging – Ants – *Paraponera clavata* – Recruitment

Social insects that recruit to resources have an advantage as central place foragers, because colonies can allocate foragers among food sites in ways that match resource profitability (Taylor 1978; Oster and Wilson 1978; Stephens and Krebs 1986; Seeley 1986; Breed et al. 1987; Seeley and Visscher 1988). However, relatively little is known of how social insects integrate information on variation in resource benefit and collection costs, or of the relative importance of foraging cost in determining recruitment strategy. In this study, we examine how foragers of the giant tropical ant, *Paraponera clavata*, integrate information on foraging costs and benefits, and test whether they vary recruitment in response to changes in resource profitability.

A number of studies have demonstrated that social insects, including ants, are able to assess food rewards. Many ant species adjust recruitment of nestmates to food resources in response to variation in food type, quantity and quality (Hölldobler 1976; Taylor 1977; Crawford and Rissing 1983; Breed et al. 1987; Traniello 1989). The mechanisms by which they do so include: (1) variation in the number of pheromone trails or recruitment events (Wilson 1962; Verhaeghe 1982; Breed et al. 1987), and (2) variation in the intensity of motor displays or in pheromonal deposition within individual recruitment events (Szlep and Jacobi 1967; Hangartner 1969; Szlep-Fessel 1970; Cammaerts 1977; Traniello 1977; Jaffe and Howse 1979; Verhaeghe 1982).

In contrast, little is known about how foraging costs affect recruitment systems. In an experimental context, ant colonies varied collection effort based on both caloric value of the resource and predation risk (Nonacs and Dill 1990). There is also limited evidence that time and/or energetic costs affect foraging decisions (Hölldobler 1976; Taylor 1978; Fewell 1988). The foraging intensity of *Pogonomyrmex* colonies seems to decrease at food resources more distant from the nest (Hölldobler 1976; Taylor 1978), but how ants achieve this response is still unclear. The ability to assess foraging costs is expected to benefit colonies if it allows foragers to preferentially recruit to resources that are highest in profitability, rather than only to resources that are highest in reward. We determine the mechanisms by which *P. clavata* vary recruitment in response to changing resource profitability, by presenting foragers with artificial nectar resources

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*, ** *Current address:* Dept. of Zoology, Arizona State University, Tempe, AZ 85287–1501, USA

Correspondence to: J.H. Fewell

that vary both in caloric value and in distance from the nest.

Methods

We studied colonies of *P. clavata* in the arboretum of the La Selva Biological Station of the Organization for Tropical Studies, Heredia Province, Costa Rica. Studies were performed over a two week period in January, 1988. To examine recruitment response, we baited a total of 42 ants from 12 colonies to artificial nectar sources containing 1 M sucrose solutions. We presented foragers with either 40 or 80 µl (approximately 2 or 4 times a forager's maximal capacity) drops of sucrose solution dyed with red food coloring. To facilitate collection by ants, we placed the drops on leaves pinned to tree bases. Baiting stations were located either close to (X = 1.2 m, range = 0.6–1.9) or distant from (X = 40.8 m, range 20.5–60.5 m) nest entrances. All bait stations were well within the foraging range of the colonies being tested. Ants traveled between the nest and distant feeding sites via the forest canopy. We used surveying equipment to measure the distances of the feeding stations from the nest along the routes taken by foragers.

Nine of the twelve colonies were tested at least once for each of the four possible treatments. We tested two of the colonies only for trials near the nest, and one only for the distant trials. The maximum number of trials for any individual colony was five. We used a given resource location only once, varying the location of the resource bait among trials by changing either the tree or the buttress (for near trials) on which ants were fed. We marked the ant first finding the nectar bait with Tempra or Pactra paint on the abdomen while she fed on the sugar solution. If an ant responded to the painting by pausing from feeding or by grooming the abdomen, we disqualified that trial. Each marked ant was used in only one trial. We quantified recruitment as previously described (Breed and Bennett 1985; Breed et al. 1987), by comparing the number of ants arriving at the resource to baseline activity levels in the resource area before baiting. Baits were placed in areas where we had observed foragers, but away from any trunk trails. Therefore, baseline foraging activity levels near baits were low (a maximum of 2 ants over a 1 h period).

Paraponera clavata carry nectar externally in the mandibles; therefore, we could record the arrival of the dyed solution at the nest even when it was carried by a different, unmarked ant. We observed the nest entrance and the feeding site simultaneously. In each trial, we recorded the time until the droplet and/or the discovering ant arrived at the nest entrance, the time until the ant discovering the resource returned to the resource leaf, the time until the first recruit reached the leaf, and the total number of recruits arriving at the resource. A trial was terminated when any ant left the resource area with a second droplet, or a second ant laid a trail. This allowed us to observe single recruitment events.

During the distant trials, a number of marked ants seemed to forage for several hours without returning to the nest. Therefore, we tested the hypothesis that a subset of workers remain outside of the nest in distant foraging areas for long periods of time. In these experiments individual ants from a single nest were marked on two tree buttresses over 30 m distant (through the canopy) from the nest. The buttresses and the nest entrance were observed continuously from 0730 to 1700 h. Small (< 5 µl) dyed sucrose solution rewards were placed around the tree buttresses at intermittent periods throughout the day to encourage ants to forage in the area, but individual ants were not fed sugar droplets directly.

Results

Effect of nectar quantity and resource distance on recruitment

The proportional number of ants recruiting to the sucrose solutions generally increased with increasing resource quantity and decreased with increasing distance of the resource from the nest (Table 1). Significantly more ants recruited to 80 µl amounts than to 40 µl resources at the distant feeding sites ($\chi^2 = 10.1$, N = 26, $P < 0.01$). However, the effect of resource quantity on the number of ants recruiting was not significant at the near feeding sites ($\chi^2 = 1.80$, N = 26, $P > 0.05$). The effect of distance on the number of ants recruiting was significant with 40 µl rewards ($\chi^2 = 7.77$, N = 34, $P < 0.01$), but not with 80 µl resources ($\chi^2 = 0$, N = 18, $P > 0.05$); all ants encountering 80 µl rewards recruited.

Table 1. The effect of quantity (µl) of 1.0 M sucrose solutions and of distance from the nest on the tendency of foragers to recruit to the resource and the number of ants recruited (mean ± S.E.). Near sites averaged 1.2 m from the nest entrance; far sites averaged 40.8 m from the nest

Distance	Amount	# Recruiting	# Not Recruiting	# Ants Recruited
Near	40 µl	14	3	7.7 ± 1.26
Near	80 µl	9	0	12.4 ± 3.81
Far	40 µl	6	11	3.8 ± 0.56
Far	80 µl	9	0	5.2 ± 1.34

In the cases in which recruitment occurred, the number of ants arriving at the resource sites differed significantly between near and far trials. The mean number of recruits arriving at near resources was 8.3, significantly higher than the mean of 3.5 observed at far resources (*t*-test, 40 µl and 80 µl data pooled, $t = 2.80$, N = 38, $P < 0.01$, data log transformed before analysis). This result remained consistent when 40 and 80 µl data were analyzed separately (*t*-tests on log transformed data, $P < 0.05$). However, there was no effect of the quantity of sucrose solution on the number of recruits whether the data were pooled or analyzed separately for the near and far feeding stations (40 µl: X = 5.9, N = 20; 80 µl: X = 6.0, N = 18; *t*-tests on log transformed data, $P > 0.05$).

Extra-nidal recruitment

We also found that the distance of the resource from the nest affected the location at which recruitment occurred. When the food site was close to the nest, recruitment occurred within the nest itself. In cases of recruitment near the nest, entry of the ant carrying the sucrose solution into the nest was followed within one minute by exit of one to 10 ants that approached the resource (N = 23). In trials involving recruitment to distant resources there was no change in the number of ants leaving the nest after entry of the ant carrying the sugar solution (N = 21). Instead, all recruitment to distant sites occurred in the forest canopy. Within the set of trials in which canopy recruitment occurred, there was no correlation between the distance of the resource from the nest and the number of ants recruited (Pearson's $R = 0.25$, N = 10, $P > 0.1$).

Ants that recruited to baits laid pheromonal trails as they left the area (see Breed and Bennett 1985 for a more detailed description of this behavior). The behavior of

Table 2. Comparison between trials at distant resources in which cooperative food transfer occurred and trials at distant resources in which the ant discovering the resource transported nectar to the nest. Time until arrival of recruits at resources is given only for those trials in which recruitment occurred

	No Nectar Transfer			Nectar Transfer		
	Mean	S.E.	N	Mean	S.E.	N
Distance of resource from nest (m)*	26.8	2.40	10	42.8	1.90	11
Time for first drop to reach nest (min)*	11.4	1.38	10	34.4	6.61	11
Speed of travel, drop to nest (m/min)	2.6	0.38	10	1.9	0.35	11
Time until return of discovering ant to resource (min)	25.1	3.10	9	24.4	5.77	10
Time until arrival of recruits (min)	20.4	4.32	4	15.3	4.50	9

* Difference significant at $P<0.001$ (see text)

recruited ants was qualitatively similar for ants arriving at both the near and distant resource sites. Recruits arriving at the bait stations behaved differently than the foragers that were first baited to resources. They moved along pheromonal trails directly to the resource area, instead of showing general searching activity. They tended to arrive in groups, rather than being solitary, and were often accompanied by the original ant. These behaviors collectively provide evidence that ants arriving at bait stations were actively recruited to the resources, rather than independently following pheromonal trails. This is supported also by the results of Breed and Harrison (1988a) demonstrating that ants recruited from the nest do not follow the pheromonal trails of other workers unless actively recruited to those trails.

Cooperative transfer of sucrose solutions

Ponerine ants generally have been considered to transport food individually (Wilson 1971). However, Baird (1986) reported that *P. clavata* foragers may transfer nectar at flowers. We examined the hypothesis that distance from the nest affects the tendency for cooperative transport of resources. In all trials at close distances (N = 26), the collecting ant carried the food to the nest. The ant carrying the resource into the nest was identified in 21 of the trials using distant feeding stations. In 10 of the distant resource trials, the ant which originally collected the resource carried it into the nest. In those trials involving recruitment, the collecting ant recruited from the canopy on her return trip, arriving back at the food site with recruits (Table 2).

In 11 cases, the ant finding the resource site passed her nectar load on to an unmarked ant in the canopy for transport to the nest. This transfer was observed in one instance, when it occurred on the trunk of the resource tree. In 10 of the instances in which food transfer occurred, the ant that originally found the nectar reward returned to the resource area without having visited the nest. In the subset of these trials involving recruitment, the ant finding the resource returned to the resource area at the same time as, or slightly later than recruited ants (Table 2).

The tendency of ants to transfer nectar solutions for transport was related to the distance of the resource from the nest, but not to resource quantity. The distance to resources was significantly greater for trials in which ants transferred their sucrose solutions than for those in which the ant finding the resource transported the droplet to the nest (t-test; $t=5.3$, $P<0.001$; Table 2). However, there was no difference in tendency to transfer resources between the 40 µl and 80 µl trials (Table 3). Although there was no relationship between resource quantity and drop transfer, there was an association between drop transfer and the tendency to recruit. Significantly more ants recruited in the trials in which transfer occurred than in the trials where the discovering ant transported the droplet to the nest ($\chi^2=3.88$, N = 21, $P<0.05$; Table 3).

Table 3. Number of trials at distant resource sites involving: (1) nectar transfer from the ant collecting the resource to another ant for transport to the nest, and (2) recruitment from the canopy to the resource site

	Recruitment		No Recruitment		Row Total
	40 µl	80 µl	40 µl	80 µl	
Nectar transferred	4	5	2	0	11
Nectar not transferred	1	3	6	0	10
Column total	5	8	8	0	21

The amount of time that it took the resource to reach the nest was significantly longer in the trials in which drop transfer occurred (Mann-Whitney $U=97$, N = 21, $P<0.001$; Table 2). This was primarily due to the greater distance to the nest, as the actual speed at which the resource proceeded to the nest was not significantly slower when drop transfer occurred (t-test, $t=1.33$, $P>0.2$; Table 2). Despite the increased distance to the resource for trials involving drop transfer, there was no significant increase in the time until arrival of recruits, or the time for the discovering ant to return to the resource (Table 2).

Extra-nidal specialists

To examine the possibility that some foragers remain outside the nest for extended time periods, we simultaneously observed the nest entrance of a single colony and two distant foraging areas for workers from that colony. The foraging areas were located around two tree trunks located approximately 35 and 40 m (traveling distance for a forager) from the nest entrance. We observed a total of 13 marked workers from the colony. The marked ants were known to be affiliated with the observed nest, because dyed sucrose droplets were observed being transported from the sites into the nest, and because no other colony was located in the area. The majority of the marked ants made frequent trips to, and spent a large portion of their time visible in the distant foraging area. Foragers made an average of 6 trips to the foraging area (S.E. = 0.99) However, all marked foragers returned at least once to the foraging area within the 9.5 h observation period. In contrast, only three of the 13 ants returned to the nest, and they did so a maximum of 2 times. The 13 foragers spent a mean of 98.2% (S.E. = 3.68) of the observation time outside of the nest. The amount of time individual workers spent actually in the foraging area averaged 30% of the observation period (S.E. = 4.2), and ranged between 1% and 51% of total observation time.

Discussion

Paraponera clavata workers use a foraging system that adjusts the number of individuals recruited in response to costs of collection as well as to the caloric value of the resource. The increased foraging costs incurred at distant foraging sites can significantly decrease the net profitability of resources (energetic benefit – cost). Foragers matched foraging effort to increases in costs at longer distances via two mechanisms: (1) a reduction in the relative number of foragers that recruit to resources requiring higher time and energetic costs, and (2) extra-nidal recruitment (rather than nest recruitment) to distant resources, with a corresponding reduction in the number of workers recruited. The strategy of extra-nidal recruitment to more distant resources reduces the time between discovery of a food resource and the arrival of recruits. Foraging at distant sites may also be enhanced by groups of workers that concentrate their foraging at distant resources, rarely returning to the colony.

Resource distance and energetic cost

Increased resource distance can elevate both time and energy costs to foragers, significantly reducing resource profitability (Stephens and Krebs 1986). However, in harvester ants, (*Pogonomyrmex occidentalis;* the only ant species for which comparative data are available), the energetic costs of foraging are so low relative to the energetic value of collected seeds that the metabolic costs of foraging become negligible (Fewell 1988). Ants vary considerably in size, distances travelled, and in the type of resource collected, making them an ideal group in which to make comparative measures of energetic costs. Therefore, we estimated the magnitude of the increase in energetic costs at varying resource distances for *Paraponera clavata.*

Metabolic rate as a function of walking speed for *P. clavata* has been measured by J.R.B. Lighton, from oxygen consumption rates for ants running on a treadmill (minimum cost of transport = 213 joules kg^{-1} m^{-1}, Lighton, unpublished data). We calculated the energetic cost/trip for ants collecting from the different resource sites, using Lighton's measures of metabolic rate, average trip speed (3.24 m min^{-1}), and distances to and from the sites. Ants in the canopy travel longer distances than are measured by the linear distances between connecting trees. In a separate data set, (Fewell et al. unpublished data) we found that the distance actually travelled by an ant through the canopy is on average 1.3 times the measured linear distance. We corrected our measures of canopy distances for ants travelling to the far sites accordingly.

Resource distance had strong effects on the energetic costs of foraging for *P. clavata.* We estimated the energetic cost of travelling from the nest to the resource and back to be 0.1 j for near sites and 3.2 j for distant sites. Field measures of individual load sizes collected by unmanipulated foragers averaged 7.5 μl (S.E. = 1.21, N = 15). Artificial nectar rewards consisted of 1 M sucrose, yielding an energetic reward of 15.5 j for a 7.5 μl nectar load. The estimated energetic costs of foraging in this population were approximately 1% of energetic reward at near sites, and 21% at distant sites. In contrast, total energetic costs for western seed harvester ants are estimated to be less than 0.1% of energetic gain (Fewell 1988).

Effect of resource profitability on recruitment

Paraponera clavata foragers integrated information on both costs and rewards in making recruitment decisions. We found a graded recruitment response over a range of nectar quantities (see also Breed et al. 1987). There was also a clear effect of distance on reward assessment; foragers required larger reward quantities to recruit at longer distances. These findings fit the predictions of central place foraging theory that animals should choose resources of higher quality as distance from the nest increases (Schoener 1971; Stephens and Krebs 1986). Although they did not measure caloric reward directly, Taylor (1977), and Davidson (1978) found similar responses by seed harvester ants, which chose larger seeds at longer distances from the nest.

The probability of recruitment by foragers of this species clearly varies with resource profitability. However, it is not clear that foragers match recruitment to profitability by varying the intensity of individual recruitment events. Significantly fewer workers were recruited from the canopy than from the nest, but we found no relationship between resource distance and the number of ants recruited within the set of trials involving extra-nidal recruitment. It is possible that the difference in recruitment intensity between near and far trials occurs because fewer workers are available for recruitment from the canopy than from the nest.

Resource quantity also did not influence the number of ants recruited within a single recruitment event. Similarly, Breed et al. (1987) found no relation between nectar quality and size of the recruitment population. These results indicate that, in this population, an individual recruitment event is an all-or-none behavior.

However, variation in total recruitment clearly occurs in this species (Breed et al. 1987). We predict that this variation occurs as a result of changes in the number of times recruitment occurs, rather than in the intensity of a single recruitment event.

Cooperative food transfer

At the most distant sites, the discovering ant transferred nectar to another ant for transport to the nest. Food transfer substantially reduced the time before the discovering ant returned to the resource site with recruits. Ants which transferred drops arrived back at resource areas 1.5 to 3 times faster than would be possible if they had returned to the nest (calculated from measured resource distances and walking speeds). In this population colonies engage in scramble competition at resource sites (Breed et al. 1991), in which colonies that recruit most rapidly to a food site obtain most of the resource. Therefore, requirements for speed in nectar collection may provide a strong selective force for foraging behaviors, such as food transfer and canopy recruitment, which reduce the time between discovery and removal of a resource.

Food transfer during foraging has been reported in the more behaviorally derived leaf-cutting ants (Jaffe and Howse 1979; Hubbell et al. 1980), but this level of task organization is surprising in *P. clavata,* which is considered to be behaviorally primitive (Wilson 1971). Colonies of *P. clavata* are relatively small (less than 2500 workers; Breed and Harrison 1988b). However, a strongly organized system of food transfer requires that workers along trunk trails are relatively easily encountered. How *P. clavata* foragers accomplish this is yet to be discovered.

Food exchange for the purpose of transport has not been reported in other ponerines. However, food exchange in other contexts is quite common in ants (Wilson 1971; Hölldobler 1985; Hölldobler and Wilson 1990). For example, foragers of another ponerine genus, *Pachycondyla,* routinely distribute water and nectar to other workers within the nest (Hölldobler 1985). It may be a small evolutionary step to utilize this behavior in the context of resource collection.

Extra-nidal recruitment

Recruitment of workers from foraging trails substantially decreased the time for recruits to reach distant resources. Using the time for drops to arrive at the nest as an estimate of travel time in one direction, we estimate that extra-nidal recruitment decreased the time for arrival of recruits to a quarter of that required if recruitment had occurred from the nest (Table 2).

In all trials recruits generally arrived at the food site within minutes, and often seconds, of each other, suggesting that recruitment may occur from a pool of ants which are spatially clustered in the canopy. Extra-nidal recruitment involving spatially clustered foraging groups has been reported for the tropical ant *Proatta butteli,* which forages primarily on insect prey (Moffett 1986). The occurrence of a pool of extra-nidal workers is more likely in the tropical environment of the rain forest than in more temperate areas, where extremes of temperature and humidity limit the amount of time that workers can spend away from the nest (Lighton and Feener 1989).

The qualitative switches in recruitment behavior at long distances from the nest were associated with short-term specialization on specific foraging areas. One advantage of such site fidelity is that both scouts and recruits can orient to and from resources more quickly. Fidelity to foraging area has been reported for a number of ant species (Rosengren 1971; Hölldobler 1976; Hölldobler and Möglich 1980; Wehner et al. 1983; Fresneau 1985; Fewell 1990). Previous experience with a foraging route significantly increased traveling speeds to food resources by *P. clavata* workers (Harrison et al. 1989). Familiarity with a foraging area also can reduce the probability that an ant will become lost (Wehner et al. 1983).

The complex and behaviorally graded system of recruitment and food retrieval in *P. clavata* allows colonies to respond relatively flexibly and efficiently to fluctuations in resource conditions (Breed et al. 1987). However, ecological and life-history characteristics also impose extremely high energetic foraging costs on this species. Foraging is an area in which environmental variation has strong direct effects on colony success. Our data and that of other studies (Heinrich 1975, 1979; Traniello et al. 1984; Schmid-Hempel et al. 1985; Lighton et al. 1987; Fewell 1988; Wolf et al. 1989; Nielsen 1990) suggest that variation in foraging energetics among social insect species is closely linked to the ecological variables experienced by a given population.

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