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The emergence of collective foraging in the arboreal *Gnamptogenys menadensis* (Hymenoptera: Formicidae)

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Abstract *Gnamptogenys menadensis* is an arboreal nester that forages opportunistically almost exclusively on vegetation, sometimes recruiting others to participate in prey retrieval. The three-dimensional characteristics of vegetation suggest that functions describing recruitment decision thresholds or the pattern of recruitment in arboreal species may differ from those predicted by optimal foraging theory. To examine the effects of prey abundance and distance on the recruitment dynamics of *G. menadensis*, we baited nests with one termite, five termites or a number of termites between 20 and 40 either near to or far from the entrance and observed the ensuing behaviors. *G. menadensis* recruited others when encountering multiple termites regardless of the termite pile's distance from the nest, although a few individuals remained at the site and defended the resource. The pattern of arrivals at the site indicates that the majority and sometimes all arrivals were recruited from the branch trails. In combination, these results suggest that the architecture of the foraging habitat, which limits available return routes to the nest and thus increases encounter probabilities with potential recruits, shaped the process of information transfer and generated a collective pattern of foraging and prey retrieval.

Introduction

Social insects exploit a wide range of niches and, consequently, display an enormous variety of foraging strategies (Hölldobler and Wilson 1990). The particular foraging method adopted by a given species is shaped by

such pressures as resource needs and its distribution (Traniello et al. 1992; Sundström 1993) and mortality risks due to encounters with competitors (Nonacs and Dill 1988; Schatz et al. 1997) or predators (Hunt 1983). Because of the constantly changing characteristics of the food resource [e.g., quality (Roces 1993), quantity (Mailleux et al. 2000), retrievability (Detrain and Deneubourg 1997; Robson and Traniello 1998), or size (Schatz et al 1997) of prey], the foraging strategy needs to be flexible, with foragers adhering to systematic decision rules (Hölldobler and Wilson 1990) that take into account the current information about the relevant variables (Detrain and Deneubourg 2002). By modulating recruiting behavior accordingly, individual foragers can generate collective foraging patterns (Detrain et al. 2001) that may enhance prey retrieval efficiency.

Although studies on solitary and collective foraging patterns and prey retrieval mechanisms and efficiencies by termitic foragers abound, only a few studies have examined the foraging strategies of arboreal species (see, e.g., Wojtusiak et al. 1995; Mercier and Lenoir 1999; Richard et al. 2001). The three-dimensional characteristics of vegetation (Weseloh 2001) as well as the relatively limited actual surface area yet greater travel distance needed to search these areas due to the nature of plant architecture (Ganeshiah and Veena 1988) may, however, solicit a different set of contingencies for arboreal foragers. As the general abundance of predators in a tropical forest renders many proteinaceous food sources ephemeral, appropriate coordination of cooperative prey retrieval relatively quickly may facilitate domination of an abundant food find. Consequently the value of a food find and the functions describing recruitment decision thresholds or the pattern of recruitment may vary accordingly.

We studied recruitment patterns in the Indo-Malayan ponerine ant *Gnamptogenys menadensis*, an arboreal nester that forages opportunistically almost exclusively on vegetation (Gobin et al. 1998a, 1998b). Like a few other ponerine species in diverse tribes (see Peeters and Crewe 1987 for review; Breed et al 1987; Schatz et al.

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1997; Daly-Schveitzer et al. 2001), *G. menadensis* sometimes deviates from its usual solitary hunting strategy and recruits others to cooperate in prey retrieval (Gobin et al. 1998a, 1998b). Our aim was to examine the effects of prey abundance and distance on the recruitment dynamics in a tropical arboreal ant species that forages primarily alone but will also collectively exploit abundant food finds. We found that *G. menadensis* recruited others when the food supply contained multiple termites, regardless of distance. The swift amassing of foragers suggests that most or all the others were recruited from branch trails, the pattern reflecting a system of directional signpost orientation with contact/motor recruitment. In conjunction with prey guarding, *G. menadensis* was able to procure an ephemeral resource.

Methods

Our field experiment was conducted at the Ulu Gombak Field Studies Center of the University of Malaya during August 2002, using two relatively large log-nesting colonies in two valleys of the primarily dipterocarp forest (Putz 1978) alongside the road. *G. menadensis* foragers wander a connected network of stems, branches, associated leaves, twigs and lianas that sometimes reaches up to 10 m from the nest in search of food. We therefore placed 1, 5 or 20–40 slightly marred termites (to limit mobility) of a local species on a leaf or a branch (to facilitate observation) either near to (~190 cm) or far from (~640 cm) the nest entrance ($n=25$). Termites can be considered neutral prey and the numbers reflect those of other arthropod larvae that foragers occasionally encounter in branch crevices (B. Gobin, personal observation). Three trials were aborted due to termite predation by other ant species before the arrival of *G. menadensis* or the approach of dusk. We waited for the termite(s) to be discovered by a *G. menadensis* forager and recorded the following data: time to termite discovery, behaviors of the discoverer, time the discoverer exited the feeding site, time to subsequent arrivals (from discoverer exit time) and their exits and behaviors, and time to reaching the nest with a termite. We noted whether a forager treaded, made antennal contact with, strung or grabbed the termites upon encountering them at the baited site, and whether the forager then stayed on the leaf clasping a termite or fighting with other ant species, or left with or without a termite. We also recorded our observations of forager gaster-tapping upon leaving a food site and, when possible, whether a forager interacted (made antennal contact) with other foragers encountered on the return trip home. From this information and information about inter-individual arrival intervals (the interval between one arrival and the next) and number of individuals arriving after the discoverer's departure, we could determine whether the discoverer had recruited other individuals to the site and from where (the branch trails or nest). We subtracted recruit arrival time (R-AT) from the discoverer return-trip duration (D-RTD) plus the recruit

return-trip duration (R-RTD). If R-AT at a site exceeded the combined D-RTD and R-RTD times, we surmised that the individual was recruited from the nest. The possibility that the individual was another forager arriving on the trail, however, was not discounted. This information was strengthened with counts of individuals exiting the nest for 10 min after the first termite-carrying individual entered the nest for each trial ($n=25$) and with counts of exiting individuals when termites were not available approximately 1 h before or after testing ($n=3$). The experiment was conducted over several days to minimize termite satiation, which might influence the decision to recruit, and the order of the different trial conditions was counterbalanced (Zar 1999).

Because our recruitment data followed a contagious or overdispersed distribution, we used a negative binomial generalized linear model (McCullagh and Nelder 1989) to analyze the number of individuals recruited to the food source site with respect to number of termites provided and termite-pile distance from the nest. We used non-parametric Mann-Whitney U tests to compare discoverer return-trip durations with the latencies to the food site of the first recruit, and to compare the number of individuals exiting the nest with number of individuals arriving at the food site when termites were still present. An equality of variances F -test ($F_{41,73}=0.518$, $P=0.019$) revealed that the variances differed significantly between groups; data were therefore log-transformed and a two-factor ANOVA was used to compare the inter-arrival intervals of recruit numbers 2–6, when termites were present, and recruit numbers 1–5, after termites had been appropriated, in order to assess 'recruitment signal strength'.

Results

Numbers recruited

There was a main effect of the termite pile number on the number of individuals arriving at a food site. The distance at which termites were placed from the nest did not have an effect (Table 1). A post hoc comparison indicated a significantly different number of individuals arriving at the site with 20–40 termites than at the site with five termites ($z=6.028$, $P<0.0001$) or one termite, and a significantly different number at the site with five termites than the site with one termite ($z=-2.058$, $P=0.0396$) (see Fig. 1a).

There was also a main effect of termite pile number but no effect of distance on the number of individuals arriving at a food site after the termites had been depleted (Table 1). The post hoc comparison indicated that 5-termite trials and 20–40-termite trials did not differ from each other ($z=0.23$, $P=0.818$), but differed significantly from the 1-termite trials ($z=-2.554$, $P=0.011$) (Fig. 1b).

Table 1 Generalized linear model results (analysis of deviance) of the number of recruits arriving at a food provisioning site

	<i>df</i>	Deviance residual	Chi-squared probability
Termites present at site			
Distance	1	0.303	0.582
Termites	2	166.628	<0.0001*
Distance×Termites	2	0.308	0.857
Termites depleted from site			
Distance	1	0.001	0.974
Termites	2	10.999	0.004*
Distance×Termites	2	2.145	0.342

* Statistically significant

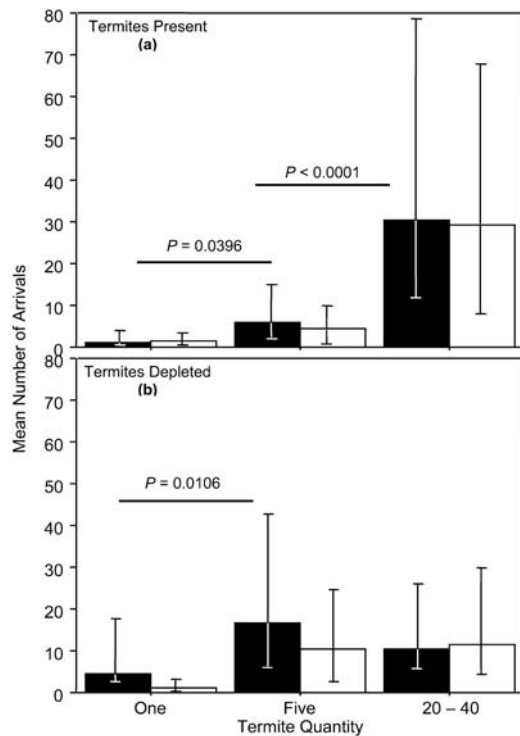


Fig. 1 Mean number of arrivals at the provisioning site, **a** within 30 min after the first termite had been discovered, and **b** within 30 min after the last termite had been taken from the site. *White bars* are trials in which the termite supply was placed near the nest and *black bars* are trials in which the termite supply was placed far from the nest. *Extension bars* represent the upper and lower estimates of the standard error of the mean

Recruitment location

Regardless of whether multiple termites were being retrieved from locations near to or far from the nest, the discoverer's mean return-trip duration [Near: (min:s) 03:50, $\pm 01:56$ SD, $n=6$; Far: 10:05, $\pm 05:51$ SD, $n=5$] significantly exceeded the average time it took for the second individual to arrive at the site (Near: 01:56, $\pm 00:50$ SD, $n=8$; Far: 03:58, $\pm 02:15$ SD, $n=5$) (Near: Mann-Whitney $U=7$, $P=0.0282$; Far: Mann-Whitney $U=2$, $P=0.0282$). This is a clear indication that at least the first forager was recruited to the food site from the trail. This is further supported by significantly fewer mean numbers of individuals exiting the nest (12.31 ± 5.74 SD, $n=13$) than the mean number of individuals arriving at the food site (28.083 ± 17.08 SD, $n=12$) when termites were still present (Mann-Whitney $U=35.5$, $P=0.0208$). The average number of individuals exiting the nest during a 10-min period approximately 1 h before or after testing was 10 ± 6.08 SD. In three 'near' trials and one 'far' trial in which 20–40 termites were offered, the arrival times of later arrivers eventually exceeded the total D-RTD and R-RTD times, indicating that some individuals may have been recruited from within the nest.

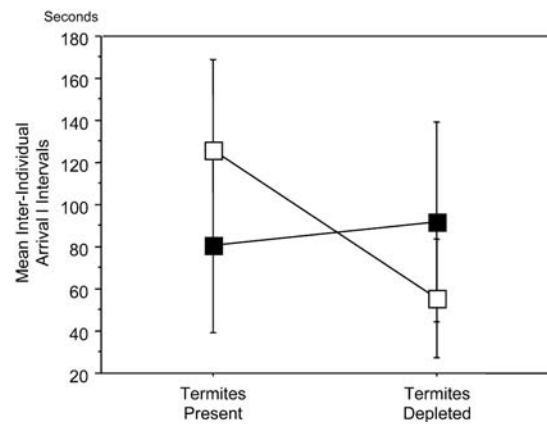


Fig. 2 Average inter-arriver intervals of Recruits 2 – 6 before and of Recruits 1 – 5 after termite depletion in trials baited with a pile of 5 (*black squares*) or 20–40 (*white squares*) termites. *Extension bars* represent 95% confidence intervals

Recruitment 'signal strength'

The rate at which the first five individuals arrived at the baited site before and after termite depletion (Fig. 2) did not differ with respect to the number of termites provided ($F_{1, 112}=2.704$, $P=0.102$) or whether the termites were present or had been depleted ($F_{1, 112}=0.865$, $P=0.354$). There was also no interaction ($F_{1, 112}=1.681$, $P=0.197$).

Observations on general foraging behaviors

The searching by foragers on stems with leaves or pinnae appeared to be systematic. Instead of exploring all leaves of a plant or all pinnae of a compound leaf, the forager probed one, returned to the stem, bypassed several leaves or pinnae, and turned onto another for inspection. This sometimes led the forager to skip the leaf or pinna on which we had placed the termites, and the latency to termite discovery was in some cases several hours. Recruits, on the other hand, rarely missed a food site. Instead, if a termite-holding leaf was bypassed, the recruit backtracked the few centimeters overshoot and made the correct turn. When exiting a leaf containing multiple termites, discoverers and recruits were observed tapping their gaster-tip on both the leaf and a portion of the associated branch as well as executing prolonged contact (3–5 s) with other foragers encountered on the return trip. The obvious tapping of the gaster against the substrate strongly suggests the laying of a chemical trail. Gobin et al. (1998b) previously reported that a product associated with sting-tapping originates from the Dufour's gland and presumably has recruitment as well as orientation properties.

In most instances, a forager immediately grabbed a termite and, with it, returned to the nest. On several occasions in trials with 20–40 termites, however, the discoverer ($n=2$) or a relatively early recruit ($n=9$)

inspected and promptly left the termite pile without taking a termite.

In five of the trials containing multiple termites, several individuals arrived at the baited area and remained there until nearly all the food was taken, leaving eventually without prey. During some of these trials, three other ant species (*Polyrhachis rufipes*, *Myrmica* sp., *Pheidole* sp.) approached the termite supply. In each instance, between one and five *G. menadensis* succeeded in keeping the competition at bay while other *G. menadensis* foragers retrieved the termites.

G. menadensis often maintains a significant proportion of its colony members outside the nest (Gobin et al. 1998a; B. Gobin, personal observation). Many individuals were often observed on the primary branch trails leading to/from the nest. These individuals might be considered as belonging to a 'reserve' foraging subset which is awaiting mobilization.

Discussion

According to optimal foraging theory for central-place foraging societies, the net energy intake of a colony is maximized by the selection of an appropriate foraging strategy that effectively balances the costs and benefits. It implies a complex, integrative cost-benefit assessment of factors such as food quality, quantity, and distance from the nest, relative to colony needs and forager risks (Taylor 1978; Pyke 1984). Indeed, resource characteristics have been shown to affect recruitment in both ground-foraging (Daly-Schweitzer et al. 2001) and arboreal-foraging species (Breed et al 1987; Mercier and Lenoir 1999). The proximate mechanisms by which a foraging event is shaped, however, are often neglected pressures of foraging strategy or recruitment decisions (Detrain and Deneubourg 1997, 2002). The pattern of collective behavior that emerged when the arboreal *G. menadensis* was confronted with different food quantities at two distances from the nest suggests that the particular foraging environment may exert strong influence on the recruitment decision in the foraging process. Optimal foraging theory predicts that recruitment will decrease for central-place foragers as foraging distances increase (Taylor 1978; Pyke 1984). *G. menadensis* nonetheless recruited termite piles far from the nest even when only five termites were discovered. This may be explained by a lowered recruitment threshold in response to typical high probabilities of encountering another forager on the return trip, due to the limited number of primary branch routes leading to the nest. Indeed, in only one instance was there evidence of individuals being recruited from the nest in addition to branch trails when the termite pile was far from the nest. When multiple termite piles were near the nest, on the other hand, individuals were recruited from both the branch trail and nest, especially when 20–40 termites were available.

Typically, opportunistic ant species that forage for clumped, ephemeral resources tend to favor a 'directional

recruitment' system (Rosengren and Fortelius 1987), in which the recruiter lays a chemical trail from the food source to the nest that alerts and orients other foragers (Dobrzanska 1958). Orientation trails spanning the distance between food source and nest are likely to be common in species that have limited other means for orientation but many directional foraging options; for example, the ground-dwelling, arthropod predator *Gnamptogenys horni* (Pratt 1994). The usefulness of the orientation trail doubling as a recruitment signal is also likely to depend on the probability of encountering the chemical trail. Conversely, high encounter rates with recruits resulting from limited foraging direction options may select for directed recruitment with chemical orientation signposts, as this may enhance the efficiency in modulating recruit numbers, be pheromonally conservative, and provide immediate directional information. In *G. menadensis*, each individual leaving the termite supply has the potential to recruit others either by adding to the recruitment/orientation trail or by soliciting other foragers via contact. Foragers were undoubtedly depositing chemicals when gaster-tapping the branch as they left the site. However, the precipitous drop in *G. menadensis* arrival numbers while maintaining consistent interarrival intervals after termite depletion suggests that foragers mediated recruitment via motor contact.

Information about *Gnamptogenys* foraging behaviors and recruitment methods is primarily anecdotal, with few experimental investigations. However, they appear to traverse the continuum from solitary to group raiding and from tandem running to group or possibly mass recruitment, respectively (Pratt 1994; Latke 1995). For many species, control over a resource depends on who gets there first (e.g., *Myrmica sabuleti*; de Biseau et al. 1997). The swift organization of *G. menadensis* to cooperate in quantitatively abundant prey retrieval accompanied by prey guarding probably facilitates domination of a food source and may be considered similar to that found in higher ants. This similarity, however, is likely to reflect their ecology (Rosengren and Fortelius 1987; Peeters 1997) rather than Ponerinae phylogeny (Peeters and Crewe 1987). Our results suggest that an environmental factor, in this case habitat architecture, may have shaped the dynamics of simple information transfer, ultimately generating a unique collective pattern of foraging and prey retrieval (see Camazine et al. 2001 and Detrain and Deneubourg 2002 for reviews). With further comparative investigations, we may uncover a more intimate association between foraging environment and foraging patterns and recruitment decisions by social insect societies.

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