

Polygyny in thief ants responds to competition and nest limitation but not food resources

T. P. McGlynn

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Abstract Colonies of ants often house multiple queens, and variation in polygyny often tracks environmental conditions. Three hypotheses have been proposed to describe how environmental variation may account for the degree of polygyny: competition, food limitation and nest limitation. Here I evaluate these hypotheses with studies on litter-nesting thief ants (*Solenopsis* spp.) throughout a lowland tropical rain forest in Costa Rica. In one component, I measured how polygyny varied across a broad environmental gradient demonstrating substantial variation in resources and competition. In a second component, I manipulated the abundance of food, the spatial presentation of food and the availability of nesting space to assess the effects on queen number. The degree of polygyny increased with nest limitation and competition, but there was no indication that colonies produce queens to capitalize on food availability. The increase in queen number in response to the density of competitors suggests that an increase in queen number enhances exploitative abilities.

Keywords Competition · Colony size · Food limitation · Nest limitation · Polygyny

Introduction

The socioecology of ants is central to understanding environmental pressures that may shape colony structure (Tschinkel, 1991; Robson and Kohout, 2007). Most recent attention to local-scale variation in social organization has

focused on behavioral and genetic mechanisms (e.g., Helms Cahan and Keller, 2003; Smith et al., 2008) with little attention to environmental influences. Nevertheless, the accumulation of findings suggest that environmental forces are a primary force in binding together individuals toward the evolution and maintenance of eusocial groups (Wilson and Hölldobler, 2005; Hunt, 2007). Where social organization is plastic and responds to environmental variation, one may take advantage of plasticity to infer the causes and consequences of environment on the occurrence of multiple queen colonies.

In polygynous societies, queen number is variable among colonies, and this variation can track environmental conditions (Hölldobler and Wilson, 1977; Herbers, 1993; Bourke and Franks, 1995). In the leaf litter of tropical rain forests in Central America, thief ants of the genus *Solenopsis* are the second most abundant genus (second only to *Pheidole*) and are the only common polygynous members of the litter-nesting community (McGlynn, 2006; pers. obs.). Many hypotheses have been generated to account for variation in queen number (Keller, 1995), including three mechanisms to account for environmental influences on the variation in queen number. The following hypotheses address how external pressures on colonies, which can be spatiotemporally variable, may cause colonies to demonstrate variation in queen number.

The competition hypothesis is based on observations that polygyny is positively associated with the degree of local competition (Rosengren and Pamilo, 1983; Seppä et al., 1996). The rationale for this hypothesis is that competition decreases the establishment rate of new colonies, and staying at home results in greater fitness than a risky dispersal event (Rosengren and Pamilo, 1983). A secondary rationale for this hypothesis is that polygyny increases genetic diversity within the colony (Evans,

T. P. McGlynn (✉)
Department of Biology, California State University Dominguez
Hills, 1000 E. Victoria St., Carson, CA 90747, USA
e-mail: terry.mcglynn@gmail.com

1995), which in turn can result in enhanced foraging efficiency (Julian and Fewell, 2004; Wiernasz et al., 2008). This hypothesis will be supported if increases in competitors are coupled with increases in polygyny.

Under the nest limitation hypothesis, new queens stay at home if opportunities to nest away from the natal nest are not available. In a temperate forest, litter-nesting *Temnothorax* ants became more polygynous under conditions of nest limitation (Herbers, 1986; Herbers and Grieco, 1994). In tropical rain forests, nests may also be limiting for litter ants (Kaspari, 1996a; McGlynn, 2006). On the other hand, nest limitation did not account for queen number in the facultatively polygynous rain forest ant *Petalomyrmex phylax* (Dalecky et al., 2005). This hypothesis will be supported if polygyny is enhanced in response to the destruction of potential nest sites, or if measures of nest availability (such as the biomass or depth of leaf litter) are negatively associated with the degree of polygyny.

Under the food availability hypothesis, polygyny occurs to increase the reproductive capacity of the colony (Keller and Vargo, 1993). This hypothesis will be supported if food supplementation increases the degree of polygyny, or if measures of food availability are correlated with the degree of polygyny.

Here I present two approaches to evaluate the response of queen number to environmental conditions—an observational component and a manipulative component—with colonies of thief ants (*Solenopsis* spp.) in the leaf litter of a Costa Rican tropical rain forest. Colonies reproduce through budding (McGlynn, 2006), and cooperative founding is rare and unlikely in this circumstance (Kellner et al., 2007), so it is assumed that polygyny is caused by the retention of daughter queens within colonies (Peeters and Ito, 2001). In each of the two components, I explicitly tested the predictions associated with the competition, nest limitation and food limitation hypotheses (Table 1). As the function of polygyny is elusive, knowledge of the causes and correlates of polygyny may contribute insights into an adaptive role in insect societies.

Methods

All studies were conducted in old-growth lowland tropical rain forest at the La Selva Biological Station, Costa Rica (10°26' N, 84°00' W; elevation 37–150 m, mean annual rainfall 4 m; (McDade et al., 1994). The first component was a set of observations across a broad resource gradient to evaluate the relative significance of competition and resources, and the second was a manipulation of food and nest site availability.

Component 1: environmental gradient

I sampled litter ants, arthropod densities and litter biomass at eighteen 0.5-ha sites (the CARBONO Plots; Clark and Clark, 2000), each site represented by 10 intensive ant samples evenly distributed along a 100-m transect immediately adjacent to the respective CARBONO plot (McGlynn et al., 2009). The CARBONO plots were selected as a sampling template in order to fully encompass the soil-fertility gradient across the old-growth landscape. The litter collected from each 1-m² sampling plot was weighed for fresh mass, and a representative subsample was dried to constant mass at 65°C to estimate total dry mass. Arthropod density was estimated from a series of pitfall trap samples; these data have already been published (McGlynn et al., 2007). As the diet of litter *Solenopsis* is not established, I use the density of all non-ant litter arthropods; note that the densities of all non-ant arthropods and individual taxa (such as Oribatidae and Collembola) are highly correlated across these plots.

Component 2: food and litter manipulation

The second experiment was conducted at La Selva in a 4-ha site centered 100-m East of the intersection of the Camino Circular Cercano and Sendero Suroeste. Plots subjected to manipulation were 1 m² in size, large enough to include several colonies, but small enough that any individual plot

Table 1 Predictions for three hypotheses for variation in polygyny in litter *Solenopsis*

Hypothesis	Predictions for component 1: environmental gradient	Predictions for component 2: nest and food manipulation
Competition	The density of litter ant nests predicts queen number; <i>The density of litter ants predicts queen number</i>	Clumped food supplementation (with more interference competition) increases queen number
Food availability	Queen number decreases with arthropod density	All food supplementation increases queen number; All food supplementation increases the production of new workers
Nest limitation	Queen number decreases with litter biomass; Queen number decreases with litter depth	<i>Destruction of potential nest sites by trampling enhances increases queen number</i>

Predictions supported by results are indicated in italics

sampled only a small proportion of the species pool. I created four treatments in which I altered resource availability (i.e., food or nesting conditions). Plots were randomly assigned in equal proportions among the control and four treatment categories. Two treatments contained supplemental food, about 5 g of dead *Nasutitermes corniger* termites lightly coated in vegetable oil, in “clumped food” and “diffuse food” spatial presentations. Clumped food triggers more interference behavior than diffuse food presentations (McGlynn and Kirksey, 2000). The former received a single pile of food every 48 h in the center of the plot, and the latter received an equivalent quantity of food at the same frequency spread evenly throughout the plot. The first litter manipulation consisted of a litter removal treatment, which was applied once at the beginning of the experiment; approximately 3/4 of the leaf litter was removed without removing any colonies. I only removed leaf matter, without removing any twigs, sticks, nuts, seeds or seed pods. The second litter manipulation consisted of trampling, applied weekly by stepping throughout the plot firmly 10 times in rubber boots. The effect of the trampling treatment was to crush available nest sites, as well as limiting access to resources by the compaction of litter, without the removal of biomass. One week elapsed after the initiation of treatments prior to destructive sampling (without replacement) over a time period of 4 months. As the colony demographic response to treatments was rapid (McGlynn, 2006), and each sample was independent, time after treatment was not included as a variable. Sample sizes for control and treatments ranged from 48 to 55 plots; sample sizes were unequal because of traumatic field events (such as tree or branch falls), and the absence of nesting ants from some plots.

Ant sampling protocol

Litter ant nests were exhaustively sampled using the “intensive sampling” protocol described by Bestelmeyer et al. (2000) and used in prior studies at La Selva (e.g., Kaspari, 1996b; McGlynn and Owen, 2002; McGlynn, 2006). In June 2004 at each plot I removed all standing litter from ten 1 m² quadrats, spaced at 10-m intervals. Ant nests were intact at collection, consequently the total number and the total number of individuals and nests per plot were measured. All ant colonies in the litter inside the quadrat were preserved in 95% ethanol and were sorted and identified to species or morphospecies according to Longino (www.evergreen.edu/ants), and Longino and Cover (www.evergreen.edu/ants).

Statistical analyses

All analyses were conducted using JMP 5.1.2 (SAS Institute, Cary, NC, 2004). I conducted Spearman’s nonparametric

correlation and ordinal logistic regression separately on samples from both experiments to determine the extent to which queen number was explained by colony size, separately for each experiment. The metric of polygyny is queen number, defined as the number of dealate queens per nest. Species of *Solenopsis* were compared for heterogeneity with respect to the number of workers per nest using an ANOVA test, and for heterogeneity in queen number by Kruskal–Wallis test. After these tests showed no significant differences, all species were pooled in subsequent analyses. In the gradient experiment, I evaluated each prediction using linear correlation and regression analysis or, in the cases in which distributions did not meet assumptions of parametric tests, Spearman’s rank correlation. In the food and litter treatment experiment, I compared the response of treatments relative to control with ANOVA and the Dunnett’s post-hoc test, except in instances in which the data did not meet assumptions of parametric tests, in which I conducted logistic regression.

Results

Component 1: environmental gradient

A total of 374 nests were collected representing 69 ant species (McGlynn et al., 2009). Among these, 73 nests of *Solenopsis* were collected, representing 16 species. *Solenopsis* nests were not sampled at 4 of the 18 sites, all in alluvial soils, and were only represented by one or two nests in two other sites; these six sites have been excluded from analyses. There were no significant differences in colony size ($F_{14,57} = 1.22$, $P = 0.27$) or queen number ($\chi^2_{10} = 7.69$, $P = 0.66$) among species. Queen number was only very weakly associated with colony size (Component 1: $r^2 = 0.096$, $\chi^2_6 = 13.56$; $N = 42$, $P = 0.035$; Fig. 1).

The number of queens did not significantly increase with the density of ant nests (queens = $1.63 + 0.035$ nests; $F_{1,12} = 1.45$, $P = 0.25$), though did significantly increase with the total density of ants (queens = $1.12 + 0.0019$ ants; $F_{1,12} = 1.45$, $P = 0.047$; $r^2 = 0.30$; Fig. 2). There was no association between arthropod density and queen number ($r_s = -0.22$, $P = 0.52$). Queen number demonstrated no association with either litter biomass (queens = $-1.98 + 1.68 \log$ litter mass; $F_{1,12} = 0.18$, $P = 0.67$; $r^2 = 0.02$) or litter depth (queens = $3.12 - 0.03$, litter depth; $F_{1,12} = 0.34$, $P = 0.57$; $r^2 = 0.03$).

Component 2: food and litter manipulation

A total of 1,375 nests were collected, including 290 *Solenopsis* nests (McGlynn, 2006). Less than 1% of these nests were excluded from analysis, because they were most

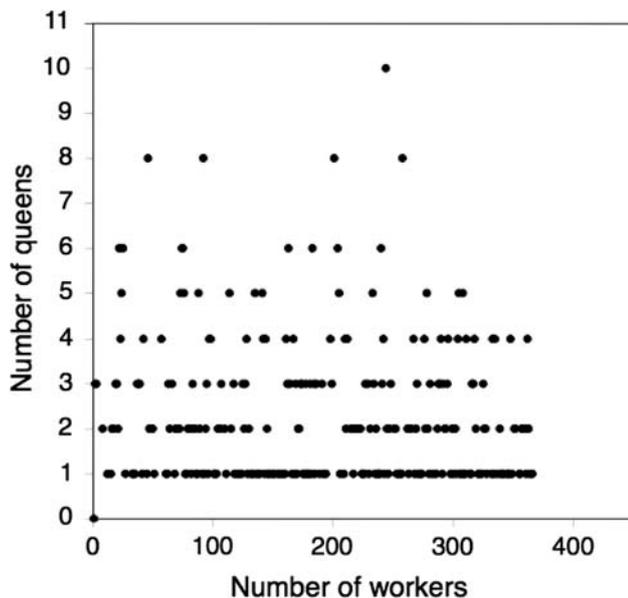


Fig. 1 The relationship between queen number and nest size per sampling unit (1 m^2). Logistic regression statistics are in text; all variates are pooled from experiments 1 and 2

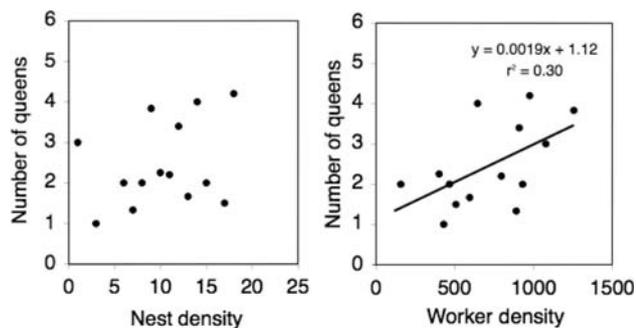


Fig. 2 The relationship between mean queen number and the local density of ant nests and ant workers per site (10 m^2). Statistics are presented in the “Results” section

likely not fully collected as they lacked adult workers or queens. As in experiment 1, queen number was significantly, though very weakly, associated with nest size ($r^2 = 0.028$, $\chi^2_7 = 18.48$; $N = 218$, $P = 0.01$; Fig. 1). Queen number was significantly different among control and treatment plots, with Dunnett’s post-hoc indicating higher queen number in diffuse food and trampling treatments relative to the control (Table 2). There were no significant differences among plots with respect to the production of new workers (Table 3).

Discussion

The competition and nest site limitation hypotheses were supported (Table 1). In short, shifts in the density of

Table 2 Response of queen number to food and nest manipulations

Plot treatment	<i>N</i>	Mean queen number	<i>SE</i>	Dunnett’s test <i>P</i>
Control	38	1.68	0.15	1
Clumped food	29	2.34	0.29	0.249
Diffuse food	55	2.56	0.25	0.028
Trampling	53	2.51	0.24	0.045
Litter removal	34	1.94	0.21	0.889

ANOVA results indicate significant differences among treatment categories ($F_{4,204} = 2.55$, $P = 0.041$)

Table 3 Response of worker pupae to food and nest manipulation

Plot treatment	<i>N</i>	Mean number of worker pupae	<i>SE</i>
Control	38	11.66	1.96
Clumped food	29	13.49	2.19
Diffuse food	55	13.15	1.70
Trampling	53	13.86	1.70
Litter removal	34	12.11	2.16

ANOVA indicates no significant differences among treatment categories ($F_{4,226} = 0.24$, $P = 0.918$)

competing ants are associated with increases in queen number, and the destruction of nest sites increased the degree of polygyny.

The competition hypothesis posits that the density of other ant species results in an increase in queen number. Across the environmental gradient, there was great variance in the density of competing ants that was positively associated with queen number. In addition, we also found that experimental diffuse food supplementation increased queen number.

The most parsimonious explanation for the increases in queen number in the diffuse food supplementation is coupled with the association between queen number and total ant density. These results must be interpreted in concert, as a principal consequence of diffuse food supplementation is a marked increase in ant densities (McGlynn, 2006). If behavioral interactions with ants competing for food resources enhanced queen number, then we would have observed an increase in polygyny in the clumped food supplementations. It is unlikely that the food itself enhanced polygyny which was unassociated with prey densities and the supplementation of food did not increase the production of new workers.

What, then, is the consequence of ant densities on polygyny if not through increased behavioral interactions? It is clear in this instance that an increase in queens does not translate to greater production of workers. Colonies with higher queen number will have more genetic diversity in the workforce (Herbers, 1982; Herbers and Stuart,

1996), which is likely to increase competitive abilities. However, some studies have shown that lower relatedness (one consequence of polygyny) reduces colony efficiency (Linksvayer, 2008). While genetic diversity in thief ants may result in intracolony conflict, research has shown that colonies with greater genetic diversity may excel at exploitative competition by foraging for longer periods throughout the day, perhaps with greater diet breadth and more efficient division of labor (Cole and Wiernasz, 1999; Wiernasz et al., 2008).

Nest limitation apparently affects polygyny in thief ants. The destruction of actual and potential nest sites—through the trampling of litter—caused an increase in polygyny. This result was not mirrored in correlative findings across the productivity gradient, however, this is not surprising as the nest destruction treatment was more extreme than ambient variance in nest availability. I conservatively estimate that the difference in potential nest density in components 1 and 2 was an order of magnitude. To illustrate the severity of nest limitation, in the trampling treatment colonies often occupied non-twig items, such as leaves or seedpods, which were rarely occupied in control plots, even those with very little leaf litter (McGlynn, 2006).

The results suggest that competition increases polygyny in thief ants, even though not through interference interactions at large clumped food items (which is not typical of the diet of these ants, Byrne, 1994). Supplemental food, in both diffuse and clumped spatial presentations, doubled the density of ant colonies in the area (McGlynn, 2006), and the sample size in the clumped food treatments was much smaller than control and other treatments. *Solenopsis* nests apparently emigrated from the clumped food treatment plots, perhaps in response to behavioral interactions at the supplemental food items. My finding may be compared with the results of a study of the temperate forest-dwelling *Temnothorax longispinosus* (Foitzik et al., 2004); supplemental food and nests had no effect on queen number, however, in concert they resulted in a reduction in queen number in one of three sites.

In summary, I found that queen number may increase as a result of environmental constraint (nest limitation), and also adjusts to the competitive environment. The latter finding reinforces the notion that ant colonies adjust their social organization in response to the competitive environment (Linksvayer and Janssen, 2008). As the change in queen number does not increase worker production, attention should be focused on other consequences of polygyny, such as increased genetic diversity of the workforce and the consequences for competition and efficiency. Further experiments may test the working hypothesis that colonies with greater diversity are superior competitors.

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