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Caste allocation in litter *Pheidole*: lessons from plant defense theory

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Abstract The allocation to growth, defense and reproduction varies in social insects within a species' life cycle and between species. A life cycle model (Oster and Wilson 1978) generally failed to predict caste allocation in small litter-nesting colonies of Neotropical *Pheidole*. Two of its assumptions were often invalid: food was unlikely to be limiting in four of five populations, and sexual biomass production accelerated, not decelerated, with colony size in three of five populations. One of five *Pheidole* populations studied had higher caste ratios (soldiers/workers) in reproductive colonies as predicted, and in no species did caste functions conform to predictions. We also adapted three models from plant defense theory to study between-species patterns of caste allocation. Among 12 litter *Pheidole* the amount of sterile biomass devoted to soldiers varied from 18 to 62%. Queen size, growth rate, and soldier investment positively covaried. Only one model, the cost of replacement hypothesis (McKey 1979), correctly predicted that species with costly female alates invest more in defense. The two hypotheses linking apparency to defense may also be valid if fast-growing colonies are more likely to attract the attention of predators.

Key words Caste · Life history · Ant · *Pheidole* · Defense

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Introduction

Caste allocation

All organisms must decide how to allocate resources to growth, defense and reproduction. In the ants (family Formicidae) these decisions reflect investment to different castes. Most ant species have at least three castes, two sexual castes and a sterile female caste that itself may vary in size and shape (Wheeler 1991; Wilson 1953). In the genus *Pheidole*, the sterile caste is dimorphic. The larger caste (henceforth soldiers) have large heads and limited behavioral repertoires that include nest defense. The smaller caste (henceforth workers) have larger repertoires that include brood care and foraging (Creighton 1966; Wilson 1976, 1984; Feener 1986). The proportion of worker, soldier, and sexual forms varies between ant species (Wilson 1984), between colonies (Johnston and Wilson 1985), and over time within colonies (Tschinkel 1993; Walker and Stamps 1986). Yet the functional significance, if any, of this caste variation is still unclear (Schmid-Hempel 1992).

Much of what we know about caste allocation comes from species with large colonies (e.g., *Solenopsis invicta*) that may have over 100,000 workers (Porter and Tschinkel 1985; Tschinkel 1993; Vargo and Fletcher 1987). *Pheidole* colonies from the tropical litter are much smaller (as are colony sizes of the majority of ant species, Kaspari and Vargo 1995) often becoming sexually mature with less than 100 workers. Further, litter ant colonies never appear to achieve the permanence of many large soil nesting species. Nests of twigs and leaves are fragile and temporary, subject to predation and disturbance (Yamaguchi 1992), forcing litter colonies to move periodically (Byrne 1994; Herbers 1986; Ward 1981). Life for a litter ant colony may be more unpredictable than for their large soil nesting counterparts.

The problem of allocation to soldiers, workers and sexuals has been studied at two time scales. Life cycle models (e.g., Oster and Wilson 1978) explore allocation through the birth, growth, and senescence of individual colonies. Oster and Wilson use optimal control theory to study how colonies maximizing sexual production should allocate resources to workers, soldiers and sexuals. Their model has a number of key assumptions. Workers are assumed to be best able to harvest resources and turn them into new workers, soldiers, and sexuals. Soldiers are assumed to be best able to protect colony members. The model assumes sexual production increases sigmoidally with resources harvested and number of workers. Oster and Wilson's life cycle model yields two predictions. Generally, reproductive colonies should invest more in soldiers. More specifically, the caste function (a plot of soldier number against worker number) should be positive and concave in growing colonies. The caste function of reproductive colonies, in contrast, should be steeper, positive, and convex (Oster and Wilson 1978; Walker and Stamps 1986).

Using plant defense theory to explore caste allocation patterns between species

Social insect species differ in their allocation to soldiers (Haverty 1977; Wilson 1984) yet little is known about the causes of this interspecific variation and it has provoked little theoretical interest. One relatively untapped source of ideas comes from the plant literature (Andersen 1991). Botanists have produced three models predicting how plant species should apportion resources to growth, defense and reproduction (Herms and Mattson 1992; McKey 1979). They assume defenses divert resources from reproduction.

The "apparency hypothesis" assumes that larger, long-lived species are more conspicuous to predators. It predicts that larger species should invest more in defense (Feeny 1976). Ant colonies range in size from fewer than ten to more than 100 million workers (Kaspari and Vargo 1995) with colonies of some larger species living over 30 years and building nests that are conspicuous parts of the habitat (Hölldobler and Wilson 1990). Large colony species may also be subject to more genera of parasites (M. Kaspari, unpublished work). We thus predict a positive correlation between colony size in *Pheidole* species and investment in soldiers.

The "growth rate hypothesis" (Coley et al. 1985) extends the apparency hypothesis. It assumes that herbivores are more likely to find slow-growing plants than weedy plant species, which grow and reproduce quickly. Extended to social insects, it predicts an inverse correlation between soldier investment and colony growth rate.

In the "cost of replacement hypothesis", different parts of the plant are harder to replace and thus more worthy of defense (e.g., young leaves vs. old leaves, McKey 1979). In the ants, female sexuals represent the colony's reproductive future and are typically the largest, most expensive caste. We predict that colonies with more massive female sexuals will invest more in soldiers to defend them.

In this paper we examine how litter *Pheidole* allocate resources to growth, defense, and reproduction. We first ask if the life cycles of five populations of litter *Pheidole* vary as predicted by Oster and Wilson (1978). We then explore between-species variation in 12 species using the three plant defense models.

Methods

Pheidole colonies were collected in 1990 and 1991 at the Estacion Biológica La Selva in Costa Rica. La Selva, a lowland tropical wet forest with yearly rainfall of 3,991 mm (Holdridge et al. 1971; Sanford et al. 1994), is located on the Caribbean slope of Costa Rica. Nests were sampled in February, March, and May 1990 by MB, and in May and August 1991 by M.K. February and March make up part of La Selva's mild dry season; May and August are in the early to mid-wet season.

Additional *Pheidole* colonies were sampled by M.K. on Barro Colorado Island (BCI), Panama, a 1500-ha hill in Lake Gatun created by the construction of the Panama canal. BCI is a lowland tropical moist forest averaging 2,600 mm rainfall yearly (Dietrich et al. 1985; Holdridge et al. 1971), with 90% of the rain coming during the May-December wet season. M.K. sampled BCI habitats June-July and September-November 1991.

Colonies were collected from 1-m^2 plots by searching the litter, piece by piece (Byrne 1994; Kaspari 1993). Nests were bagged, brought back to the lab, and the adults and brood were stored in 70% ethanol. Later, colonies were sorted, counting numbers of queens, workers, soldiers and sexuals. M.K. additionally tallied the pupae for each group, and separated sexuals into male and female. For the life cycle model, we focused on the three most common *Pheidole* (by nest number) in both sites. For the plant defense models, we used mean values of variables derived from at least three nests. We evaluated cost of different castes by weighing up to 30 individuals of each caste from each species on a Mettler HK-60 balance, sensitive to 0.00001 g.

Pheidole species were identified by Stefan Cover at the Museum of Comparative Zoology, Harvard University. Vouchers were deposited there. They are referred to by their code names here (e.g., PCCC). The ants mentioned in this study are to be described in a forthcoming revision of the New World *Pheidole* by Edward O. Wilson and William L. Brown Jr. We list each species' code name followed by its future name. As such, this does not constitute a species description according to the International Code of Zoological Nomenclature. PNIT = *Pheidole "nitella"*, PINT = *Pheidole "annectans"*, PNGA = *Pheidole "nigricula"*, PCCC = *Pheidole* sp. nov. 2 (no name), PNIG = PRUG-L and PPEBB = PRUG-B, PRUG-B and PRUG-L = *Pheidole "rugiceps"*, PPOC = *Pheidole "specularis"*, PBIC = *Pheidole "dasypyx"*, PCHO = *Pheidole "multispina"*. PNEB, PHFB, PEYE, PMIC have yet to be identified.

Results

The common tropical litter *Pheidole*

We recorded a total of 24 species of *Pheidole* at La Selva, Costa Rica and 16 at BCI, Panama. The three commonest species at each site included one shared species (henceforth referred to as PRUG-B and PRUG-L). Colonies of five of the six populations yielded 1 queenright nest for every 1.5 to 1.1 nests. Since queens are often the first to abandon a nest at collection, we conclude the standard condition for these populations was a queen in every nest (i.e., "monodomy"). The other species, PCCC, was clearly polydomous, with one queened nest for every ten sampled. In four populations all nests had no more than one queen. In two species, one-queen nests were the norm (96% of PNGA and 93% of PCHO).

Size at reproductive maturity (i.e., when colonies produce sexuals) for the monodomous species ranged from 69 workers and soldiers for PNGA to 110 for PCHO. The polydomous PCCC, with one queened nest in ten and an average of 85 ants/nest, may have a total colony size of around 850 ants.

In sum, the common litter *Pheidole* at both sites tended to have small colonies with a single queen, and live in one nest. We use these five monodomous populations to test the life cycle model of Oster and Wilson (1978).

Testing the life cycle model

Oster and Wilson (1978) assume that colonies have a limited energy budget from which to grow and that sexual production is a saturating function of colony size. It predicts higher caste ratios in reproductive colonies, and steeper, concave caste functions in the reproductive season.

Assumption 1: litter Pheidole are food limited

If energy limits colony growth, then as colonies grow they should eventually deplete local resources. This should lead to decreasing number of larvae per worker yielding a positive, concave caste function (Michener 1964). In constructing pupae-worker curves, we pooled queened and no-queen nests, since analysis of covariance (ANCOVA) for all five populations yielded the same result: significant regressions of pupae number on worker (all Ps < 0.0001), but no effect of queens and no interactions (all Ps > 0.1).

We evaluated the shape of the pupae-worker curve using stepwise multiple regression with linear and squared worker terms. A variety of pupae-worker curves resulted, but only one was consistent with resource limitation (Fig. 1). Three pupae-worker curves were linear (PRUG-L $F_{1,15} = 145$, $P < 0.001$, PRUG-B, $F_{1,39} = 18$, $P < 0.001$, PPOC, $F_{1,52} = 70$, $P < 0.001$), explaining 58–73% of the variance (Fig. 1). Quadratic terms, when forced into the model, explained only 2–3% more variation. Pupae production efficiency increased with colony size in PNGA ($F_{2,52} = 32$, $P < 0.001$, Fig. 1). Only PCHO yielded diminishing pupae returns with increasing colony size ($F_{1,40} = 84$, $P < 0.001$).

In sum, four of five *Pheidole* populations (and three of four species) tested produced pupae as efficiently when small as at their maximum observed size. By this criterion, only PCHO's colony growth may be limited by food availability.

Assumption 2: sexual production is a sigmoidal function of colony size

There are at least two measures of reproductive success: total number of offspring produced, and total biomass of offspring produced. Since biomass measures avoid the necessity of calibrating the relative fitness contributions of males and females, we focus on alate biomass as a measure of colony reproductive success. Regardless, the correlation between numbers and biomass was high ($r_p = 0.74$–0.96) for the five populations in this study. We pool queened and queenless nests since

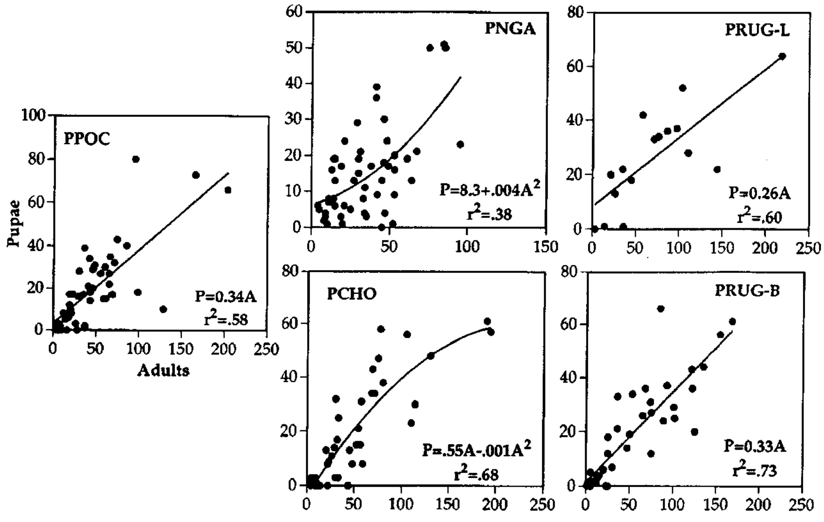

Fig. 1 Allocation to future workers as a function of current worker force in five neotropical litter *Pheidole*. PRUG-L and PRUG-B are two populations of the same species. All species, save for PCHO, grew as fast when small as when large. Significant components of regression printed with best estimated curve

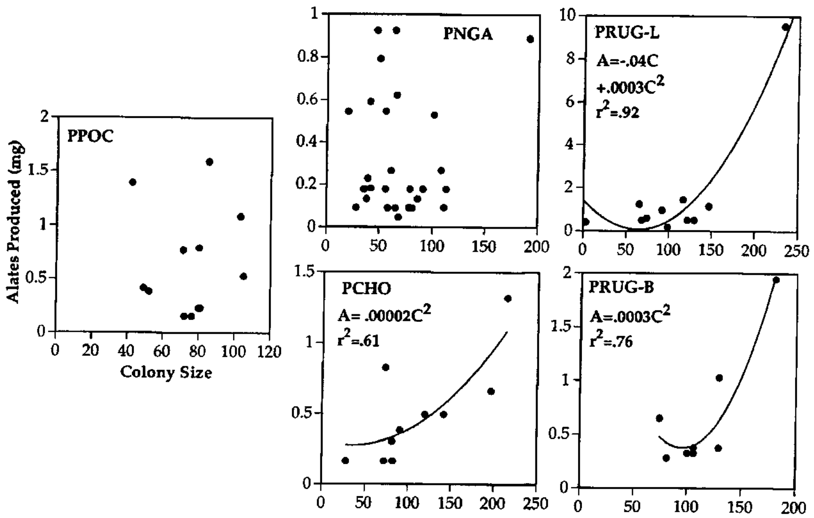

Fig. 2 Sexual biomass production failed to saturate, and often accelerated, with colony size in reproductive *Pheidole* colonies. Significant components of regression printed with best estimated curve

sexual biomass did not differ between queened and queenless colonies (Kruskal-Wallis test, $Ps > 0.5$) in any populations.

Colonies with alates had at least half-again more workers and soldiers as colonies without alates (PNGA: mean 69 vs. 43, $F = 19.0_{121,29}$; PRUG-L: 105 vs. 54, $F = 11.3_{38,11}$; PRUG-B: 113 vs. 42, $F = 19.3_{33,8}$; PCHO: 110 vs. 40, $F = 24.1_{31,10}$; PPOC: 75 vs. 46, $F = 24.1_{12,41}$, $Ps < 0.001$). However, none of these populations showed a saturating relationship assumed by the Oster and Wilson (Fig. 2). Instead, alate production accelerated with colony size in three populations (PCHO $F_{1,10} = 13$, PRUG-L $F_{2,11} = 145$, PRUG-B $F_{1,8} = 18.1$, $Ps < 0.05$) with regressions explaining 61–92% of the variance (Fig. 2). The other two species, PNGA and PPOC, although well sampled ($n = 29$ and 12), showed no clear relationship between colony size and alate biomass ($r^2 < 0.16$, $Ps > 0.1$, Fig. 2).

Prediction 1: soldiers defend sexual investment

Oster and Wilson (1978) predict an association between soldiers and sexuals. One of five monodomous populations (one of four species) had higher caste ratios in reproductive colonies (PNGA, Table 1). Nests with alates in the two populations of PRUG showed the same trend ($P < 0.1$). PPOC and PCHO failed to show any association ($P > 0.2$). In the polydomous species, PCCC, we tested the prediction of higher caste ratios in nest fragments with sexuals. This was not the case (Table 1, $P = 0.23$). If soldiers are allocated to defend sexual investment, it occurs at most in only two of five species tested.

Prediction 2: caste functions vary with reproductive state

Caste functions are curves relating soldier number to worker number. We analyzed the shape of caste functions using multiple regression with linear and squared worker terms. Three populations showed linear caste functions representing constant proportions of soldiers to workers (PRUG-L: $F_{1,149} = 68$; PRUG-B: $F_{1,39} = 91$; PPOC: $F_{1,52} = 90$; all $Ps < 0.001$, Fig. 3). Quadratic terms explained an additional 5% of the variance or less, none significantly. The remaining two species (PNGA: $F_{2,149} = 68$; PCHO: $F_{2,40} = 36$, $Ps < 0.001$) had concave caste functions and hence proportionately

Table 1 Comparing caste ratios (number of soldiers/number of workers) in colonies with and without sexuals. Caste ratios are higher in sexual colonies – as predicted by the life cycle model of Oster and Wilson (1978) – in one of five *Pheidole* species. Two populations of the same species, PRUG-L and PRUG-B weakly show the trend (see Fig. 3)

Species	Reproductive state	Caste ratio	No. nests	Kruskal--Wallis X^2	One-tailed P
PNGA	No sexuals	0.15	121	3.22	0.04
	Sexuals	0.20	29		
PRUG-L	No sexuals	0.05	15	2.41	0.08
	Sexuals	0.07	10		
PRUG-B	No sexuals	0.05	33	1.93	0.09
	Sexuals	0.06	8		
PCHO	No sexuals	0.11	31	0.13	0.35
	Sexuals	0.10	10		
PPOC	No sexuals	0.16	41	0.76	0.38
	Sexuals	0.17	12		
PCCC	No sexuals	0.10	170	0.54	0.23
	Sexuals	0.10	23		

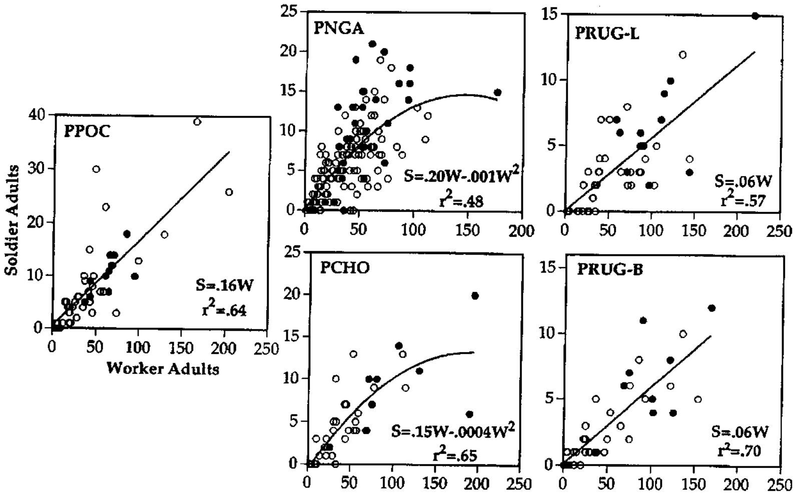

Fig. 3 The caste function was linear in three, and concave in two neotropical litter *Pheidole* populations. *Dark circles* are nests with alates: *open circles* lack reproductive adults or pupae

fewer soldiers in larger colonies. In none of the five populations was there a significant intercept, suggesting that soldiers in litter *Pheidole* are produced at or near the first brood.

Oster and Wilson (1978) predict a positive convex caste function in the reproductive season and a positive concave caste function in the growing season. At La Selva, Costa Rica we sampled in both the dry and wet season. For two common species, dry season nests (February and March) had a smaller proportion of sexuals than wet season nests (PNGA: 0 vs. 21%, Fishers exact test: $P = 0.008$; PRUG-L 8 vs. 35%, Fisher's $P = 0.032$). To test if PNGA or PRUG-L yielded caste functions matching the above prediction,we log-transformed soldier and worker number, linearizing their caste functions. In the resulting power function, $S = aW^x$, a positive convex caste function yields $x > 1$ and a concave, but still positive caste function yields $0 < x < 1$.

The caste functions of PRUG-L did not differ with season ($F_{18,18} = 0$, $P > 0.5$). The *Pheidole* PNGA had a marginally steeper caste function in the wet (reproductive) season, as predicted ($S = -1.37W^{0.72}$ vs. $S = -0.41W^{0.60}$, ANCOVA $F_{18,120} = 2.7$, 1-tailed $P = 0.052$, Fig. 3). However, while the slope of the dry season caste function was concave the slope of the wet season caste function (0.72) was not convex (> 1) as predicted.

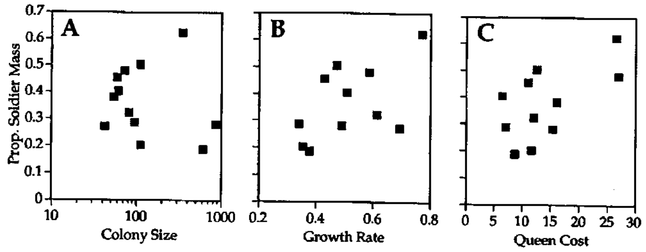

Fig. 4 Life history correlations among 12 Neotropical litter *Pheidole* species. The proportion of sterile caste biomass invested in soldiers **A** did not vary with colony size, **B** increased with growth rate (measured as the ratio of worker pupae to worker adults), and **C** increased with the relative cost (in multiples of worker biomass) of female alates. Species (see Methods) from top to bottom on the *Y* axisare: PNIT, PINT, PBIC, PPOC, PNGA, PNEB, PMIC, PCHO, PCCC, PEYE, PNIG, PHFB

In sum, the life histories of litter *Pheidole* did not closely match the life cycle model of Oster and Wilson. Most species did not appear to be food-limited, growing as efficiently when small as when large. Further, while larger nests produced more sexuals in all populations, the relationship between colony size and sexual production did not saturate. Only one in five populations, PNGA, had significantly more soldiers with sexuals and that species did not significantly change caste functions with reproductive season.

Evaluating between-species differences with plant defense theory

Six *Pheidole* species from Costa Rica and six from Panama yielded the minimum three nests for analysis. The 12 species of *Pheidole* differed in the relative cost of soldiers and alates. Soldiers were typically 4.5 times heavier than workers. Female alates (recovered from 11 of 12 species) were 14 times heavier, on average. Males (recovered from 10 of 12 species) were 4.2 times heavier. Moreover, while soldier cost varied only 1.6-fold between species, alates costs were more variable (males 3.4-fold, females 4.1-fold).

Of these 12 *Pheidole*, mean caste ratios (number of soldiers/number of workers) ranged from 0.047 to 0.43: a range of 25 to 2 workers for every soldier. The proportion of sterile caste biomass devoted to soldiers varied from 18 to 62% among the 12 species (soldier cost was unrelated to caste ratio $r_p = -0.03$, $P = 0.92$). The three plant defense models predict how this allocation should vary with growth rate, queen cost, and colony size.

The apparency hypothesis predicts that larger colonies should invest more in defense. Colony size investments. but as constitutive defenses, not as inducible defenses.

Two other models, the apparency hypothesis (Feeny 1976) and the growth rate hypothesis (Coley et al. 1985) seem to do less well. Both posit that defense investment increases with factors prolonging exposure to predators (size and slow growth rates). However, colonies of 850 workers do not appear to invest more in defense than colonies of 40 workers. Colonies that produce many pupae per worker – and hence are likely to grow more quickly – invest more, not less, in defense.

There are two reasons not to dismiss apparency as a useful concept to social insect ecologists. First, the *Pheidole* in this study represent only 1 order-of-magnitude difference in colony size. The ants, in contrast, represent an 8 order-of-magnitude span in colony size (Kaspari and Vargo 1995). A mature *Solenopsis invicta* colony (with over 200,000 workers) may invest 70% of its biomass in majors (Tschinkel 1988) more than any species studied here.

Second, an ant colony, to grow quickly, must have its foragers out in the field. More foragers in the field may make a colony more apparent to predators. Behavioral studies suggest this is true: colonies sharply decrease foraging outside the nest in response to predators/competitors, which in turn may slow growth (Calabi and Nonacs 1994; Whitford and Bryant 1979). Thus a crucial distinction may exist between ants and plants: an actively growing colony (unlike an actively photosynthezing plant) is more likely to be noticed by predators and require more defense. This may help to explain the positive correlation between growth rate and soldier production in this study.

Costs and benefits of defense: two holes in our understanding of the soldier caste

A problem common to both plant and ant defense theory is precisely how to measure the cost and benefits of defense. For example, in this study we use mass to measure relative cost of different castes. However, cost may not be a simple function of body size when lifespan scales with body size (Tschinkel 1993). The relative cost of soldiers may be discounted by their tendency, in some species at least, to live longer (Porter and Tschinkel 1985).

A second puzzle involves the interacting roles played by different castes in the nest. Just as secondary compounds in plants may do more than defend against herbivores (McKey 1979), worker and soldier castes often show varied and flexible behavior. *Pheidole* soldiers may serve a number of functions in the nest, including milling and food storage (Wilson 1984). In the common litter *Pheidole* of La Selva and BCI, we have observed soldiers guarding both food and nest entrances (Wilson and Hölldobler 1985). These roles are also flexible: deprive a colony of soldiers, and workers defend the nest; remove the workers, and soldiers nurse brood (Johnston and Wilson 1985).

Note that behavioral flexibility within castes does not invalidate caste theory outright. The above models do not assume that soldiers *exclusively* defend, only that a gram of colony biomass invested in soldiers will result in better defense than a gram invested in workers. We are unaware of any experimental tests of this assumption. To this end, small twig-nesting species may allow us to manipulate, transplant, and monitor colonies in the field (Hasegawa 1993).

Caste and the ecology of large and small colonies

Studies of caste allocation have focused on large-colony species like the leaf-cutters (*Atta*, Wilson 1983), army ants (*Eciton* and *Neivamyrmex*, Schneirla 1957, 1961) and fire ants (Porter and Tschinkel 1985; Tschinkel 1993) although this emphasis is waning (Beshers and Traniello 1994; Hasegawa 1993). Most ant species have colonies numbering fewer than 1000 and the tropical *Pheidole* are an order of magnitude smaller than their temperate zone counterparts (Kaspari and Vargo 1995). Relatively little is known, however about the life histories of these small colony species (but see Byrne 1994; Herbers 1986, 1990; Ward 1983).

One difference between small and large-colony species may be the importance of resource depletion. Species like *Solenopsis invicta*, with colonies over 200,000 workers, may be immune to predation, buffered against catastrophe, and thus more prone to deplete food around the nest. *S. invicta* colonies show the decline in per-capita pupae production predicted for food-limited species (Brian 1956; Michener 1964; Porter and Tschinkel 1985). In contrast, pupae production decelerates with colony size in only one of five litter *Pheidole* populations tested here (Fig. 2). The litter *Pheidole* (and the stem-nesting *Leptothorax allardycei*, Cole 1984) are likely growing as efficiently at maximum observed size as they do when they are founded.

The accelerating alate production with colony size found here in three populations suggests that something is keeping colonies smaller than their reproductive optimum. If litter *Pheidole* occupy small, breakable nests, making colonies vulnerable to predators and random catastrophe (Byrne 1994; Herbers 1986; Yamaguchi 1992), then colonies may be perishing before reaching a size where resources limit colony growth.

Perhaps the litter *Pheidole* are at one end of a life-history continuum that ends with species like *Atta*, *Eciton*, and *Solenopsis* (subgenus *Solenopsis*). Studies of life history evolution in social insects are ripe for such theoretical and empirical exploration (Andersen 1992; Tschinkel 1993). Further contrasts of small-colony and large-colony species may begin to tell us why and how the Formicidae span colony sizes from 8 to 300 million individuals (Kaspari and Vargo 1995).

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