Research article

Food supplementation alters caste allocation in a natural population of *Pheidole flavens*, a dimorphic leaf-litter dwelling ant

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Summary. Caste ratio theory predicts that polymorphic ant colonies should be able to alter the ratio of worker sizes in response to changing environmental demands. We selected a common dimorphic species, *Pheidole flavens*, for a field manipulation to test whether caste allocation will change in response to food supplementation. We collected, without replacement, control and treatment colonies from 1 m² plots over a period of four months. Food was added to treatment plots every other day in either of two spatial presentations: clumped and split. Clumped food treatments received food in a single location in the center of the plot, while the split food treatments were spread throughout the plot area. To test how *P. flavens* responded to food supplementation, we compared the number of soldier pupae between control and treatment plots, as well as the ratio of adult soldiers to adult minor workers. We found a generalized increase in the number of soldier pupae produced within the treatment plots, which was not correlated with the duration of the treatment period. As the manipulation progressed, the ratio of soldiers to minor workers increased in the clumped food plots. The possible mechanisms for altered caste ratios include the absence of soldiers from their nests, increased frequency of interactions with competitors, and a change in the type of foods collected from the environment. The discovery that food resources can affect how ant colonies determine the ratio of sterile workers suggests that ants may change caste ratio in response to a number of environmental variables.

Key words: Caste ratio, polymorphism, food supplementation, nutrition.

Introduction

Organisms allocate resources to maintenance, growth, defense, and reproduction. In ants, polymorphic species have morphologically discrete worker castes, which often perform different colony functions (Wilson, 1980a; Porter and Tschinkel, 1985; reviewed by Hölldobler and Wilson, 1990). Caste ratio theory predicts that social insects should modify the ratios of worker castes within a colony in response to environmental conditions (Oster and Wilson, 1978). For the most part, experiments have not been able to find ecological variables that affect caste ratio (Gordon, 1996). Among geographically separated populations and among hetero-specifics, worker caste demography can vary with the environment (Davidson, 1978; Walker and Stamps, 1986; Calabi and Traniello, 1989; Gibson, 1989; Beshers and Traniello, 1994), but many reports show negative results (reviewed by Schmid-Hempel, 1992) and there is even less support for adaptive caste ratios within the lifetime of individual colonies.

Two experiments have reported adaptive colony level changes in caste ratios of ants. Gentry (1974) demonstrated that colonies of the Florida harvester ant, *Pogonomyrmex badius*, increased the size of newly produced ants in response to the systematic removal of workers, which he called "predation." In 1996, Passera et al. found that lab colonies of the dimorphic ant *Pheidole pallidula* continuously exposed to the odor of conspecific colonies produced more major workers, which we will refer to as soldiers for brevity. In both experiments caste ratio changes appeared to be responses to physical threats to the colony – actual removal of colony members, or the chemical communication of competitor presence. Messier (1996) also conclusively found the occurrence of ecologically adaptive caste ratios in colonies of a Neotropical carton-nesting termite. As demonstrated by experimental removal of soldiers from field colonies of *Colobopsis nipponicus*, which results in colony failure or reduced efficiency, defending soldiers increase colony success (Hasegawa, 1993a, 1997).

Can polymorphic ants alter their caste proportions in response to changes in their food resources? While soldiers in ant colonies defend nests, they also perform many food-

related tasks inside and outside the nest, including food storage (Lachaud et al., 1992; Hasegawa, 1993b), foraging (Wilson, 1980b), defending food resources (Detrain and Pasteels, 1991, 1992), and milling seeds (Creighton, 1966; Wilson, 1984). Manipulative studies upon caste ratio have been performed in the laboratory (for example, Passera 1974, 1985; Passera et al., 1996), but they have not been undertaken in natural conditions. Caste determination within natural communities can be studied by manipulating specific environmental factors, leaving the organisms intact within their habitat. By altering only the food resources and avoiding any other manipulation of the natural environment, we can learn if polymorphic ant behavioral and competitive responses to the food environment include changes of caste ratio.

We designed a manipulative field experiment to change the food available to *Pheidole flavens* – a common leaf-litter nesting dimorphic ant species in the lowland wet tropical forests of Costa Rica. *P. flavens* soldiers have been observed at food items placed on the forest floor, thus demonstrating a role in foraging or food defense outside the nest. To elaborate the role of food in caste ratio determination of *P. flavens*, we provided supplemental food in two presentations, "clumped" and "split," which were equal except for the spatial distribution of provided foods. The response to different food presentations may also determine whether the spatial scale of the foraging environment is a factor in determining caste ratio.

Methods

This study was located in an old-growth forest at La Selva Biological Station, Sarapiquì Canton, Heredia Province, Costa Rica. La Selva is a lowland wet tropical forest in the Carribean Lowlands of Costa Rica, and recieves ca. 4 m of rain annually, mostly falling in the wet season from June – December (McDade and Hartshorn, 1994). The exact location of the ca. 4 hectare site in the forest is described elsewhere (McGlynn and Kelley, 1999). We demarcated 290 plots of 1 m² size using wire flags and plastic flagging. These plot locations were at least 5 m apart and at least 20 m away from trails. In similar habitat at the same field station, Kaspari (1996a, 1996b) revealed that 1 m² plots placed 5 m apart from one another are far enough to ensure independent sampling of leaf litter nesting ant species. Microenvironmental variables of the control and treatment sites were not significantly different and not associated with leaf litter ant demography (McGlynn, 1999).

The plots were randomly assigned to three treatments: control, clumped food, and split food. Both food treatments received approximately 5 g (about 20 individuals) of *Nasutitermes corniger* termites, applied every 2 days. Termites were collected directly from arboreal carton nests at La Selva, and then frozen in a – 20 °C freezer. Termites were lightly coated with vegetable oil to attract a wide variety of foraging ants in the leaf litter community. In the clumped food plots, termites were placed in a single pile in an arbitrarily selected location inside a 20 cm circle located at the center of the plot. In the split food treatments, the same quantity of food was distributed equally among four quarters of the plot.

Treatments commenced in mid-January 1997, and continued through the dry season for a total of four months. During the month of February, the forest received uncharacteristically heavy rainfall, totaling over 500 cm. Flooding associated with the intense rainfall is likely to have affected the leaf litter ant community more than the experimental treatments, because the ants had very little opportunity to forage. However, the continuation of the experiment through March, April, and May enabled us to observe the effects of the food treatments in the third and

fourth months following the start of the treatments. At the end of the experiment, we had sampled 58 plots of each treatment and the control. Food addition was the only experimental manipulation of the plots. Researchers did not step in the plots, and visitors were excluded from the research area.

The schedule of treatments and nest collections were designed to prevent any disturbance or stress upon the field colonies. Consequently, plots were sampled destructively only once, with collections spread over the course of four months after the start of treatments. Approximately every 2 days, one plot per treatment was sampled. We collected leaf litter ant nests from the plots using the "intensive sampling" protocol described by Bestelmeyer et al. (2000).

P. flavens was by far the most common species, occurring in 55 of the 174 experimental plots. Inside each colony we counted the number of minor workers, minor worker pupae, soldier, soldier pupae, dealate queens, winged queens, pupal queens, males, pupal males, and larvae. Sexual individuals were relatively rare and are not included in the analyses. We identified species using Bolton (1994), and Longino and Cover (http://www.evergreen.edu/ants).

We used plots as replicates, rather than individual nests or colonies, to avoid pseudoreplication of any unknown plot effects. Using the plot as a sampling unit, rather than colonies, eliminates the errors caused by incorrectly designating colonies. The process of identifying colony units prior to the start of treatments would likely have resulted in a change in soldier production in response to the physical disturbance. While the identification of colonies would be useful to understand colony level processes, the identity of colony units could not be known; as a result, our interpretations are restricted to how the treatments affected all of the ants in the plot, rather than individual colonies. In many cases, single plots contained more than one *P. flavens* nest. While the majority of nests were collected with a single queen, many nests had no queen within them; one nest in a control plot had two dealate queens. However, Kaspari and Byrne (1995) found that queens are often the first to escape, and conclude that most *Pheidole* nests collected without queens at this location were queenright nests from which the queens escaped during collection.

We used two measures of soldier number to compare treatment plots and control plots. The first was the mean number of soldier pupae in each treatment. This comparison is valid because nests in control and treatment plots occurred at similar frequencies and were equivalent in the number of ants at the start of the experiment. Additionally, plots were collected in a similar time progression from the start of simultaneous treatments. This is an effective manner of comparing soldiers among the treatments because soldier pupae are temporary residents: once new soldiers are produced the age of adults is difficult to determine. The presence of soldier pupae in a nest is a relatively brief event, and is likely regulated by stochastic demographic and environmental variables. Therefore, soldier pupae production cannot be predicted as a function of time after the start of treatments. However, measurements of adult soldier numbers reflect earlier soldier pupae production. We predicted that a measurement of soldier ratio using adults would be tied to the duration of persistent food supplementation.
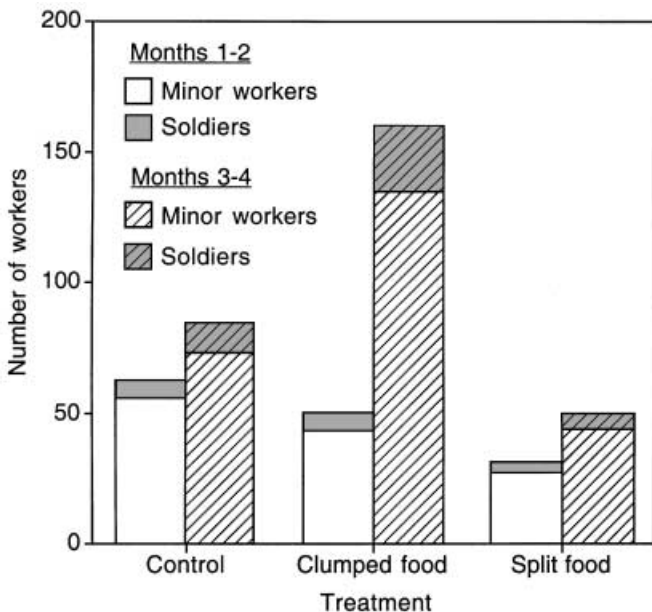
Results

The objective of these analyses is to determine if the production of soldiers varies among the control and treatment plots. Before discussing these comparisons, we present the general demographic response to the treatments. The supplemental food was consumed by nests of *P. flavens*: in addition to behavioral observations of *P. flavens* foraging at the supplemental food, several nests contained undigested chitin head capsules of *N. corniger* soldiers, suggesting that colonies of *P. flavens* carried termite soldiers back to their nests for consumption. No remains of *N. corniger* were found in ant nests

within control plots, though we did not quantify these differences because the discovery of head capsules was sporadic. The control and treatment plots contained similar frequencies of *P. flavens*: control, 24 of 58 plots; clumped food, 16 of 58; split food, 15 of 58 (χ^2 test, df = 2, χ^2 = 1.95, p = 0.38). Colonies were collected from plots at a steady pace throughout the experiment. While the ants were not collected on the same days in the four-month collecting period, the timing of collection, measured by days since the start of treatment, was not different among control and treatments (control mean = 50.0, SE = 5.8; clumped = 60.1, SE = 8.2; split = 59.0, SE = 6.7; Kruskal-Wallis test, df = 2, H = 1.21, p = 0.54). Because the development of workers occurs over a period of weeks, rather than days, the similar distribution of collection times among the plots permits comparison.
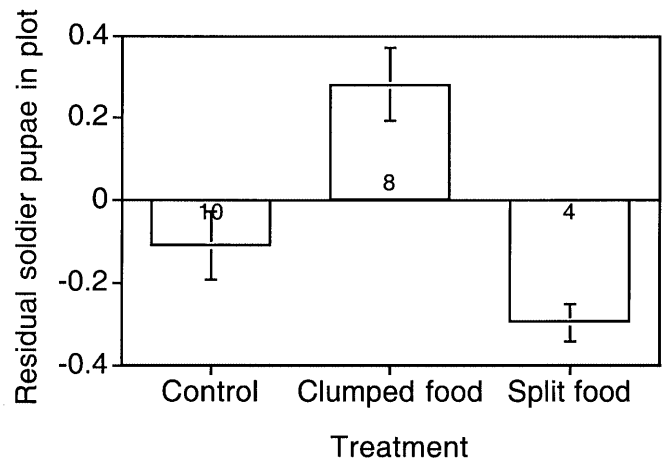
Worker number per plot, measured by the number of adults among all nests, was log transformed for normality in subsequent analyses. In the plots collected during the first three months after the start of treatments, there were no differences in worker number among the controls and treatments. In the first two months of experiments, plots contained similar numbers of workers (Fig. 1; ANOVA, df = 2.25, F = 0.923, p = 0.41), but in the second half of the experiment the clumped plots contained significantly more workers than the split plots (ANOVA, df = 2.24, F = 4.41, p = 0.031, Bonferroni-Dunn clumped vs. split p = 0.0099, control vs. split p = 0.22, control vs. clumped p = 0.085).

Many plots did not contain soldier pupae; in some of these cases callow soldiers were present. The number of soldier pupae was correlated with worker number (Spearman rank correlation; Z = 3.908, p < 0.0001; r^2 = 0.187). We log transformed the number of soldier pupae to normalize the distribution. We then adjusted for the effect of colony size upon number of soldier pupae by using the residuals of log soldier pupae regression with log worker number (r^2 = 0.19, ANOVA F = 4.58, p = 0.045). The residual numbers of soldier pupae in clumped and split plots were significantly greater than in control plots (Fig. 2; ANOVA F = 9.78; Bonferroni Dunn clumped vs split p = 0.0008, control vs split p = 0.20; control vs clumped p = 0.0026). After detecting the increase in soldier pupae production in the clumped food plots, we tested whether this increase was a steady growth as the treatments progressed. The number of soldier pupae was not associated with the duration of the treatment (Fig. 3; r^2 = 0.021, ANOVA F = 0.419, p = 0.52). The difference in soldier pupae number in the treatments indicates a generalized and rapid increase in soldier pupae number in response to treatments, but no association with treatment duration.

Figure 2. Soldier pupae production among control and food supplementation treatments. Clumped food plots have significantly more soldier pupae than control and split food plots; analyses are in the text. Error bars represent standard errors


Figure 1. Worker number changes from the first two months after treatment, compared to the third and fourth months after treatment. In the third and fourth months, the clumped food plots have significantly more *P. flavens* workers; analyses are in the text
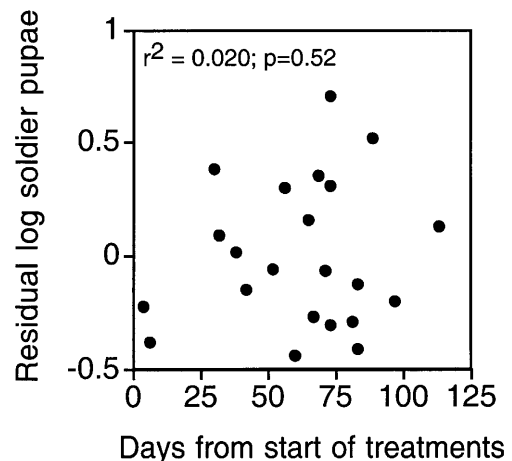
Figure 3. Soldier pupae production over time among all plots. There was no relationship between the number of soldier pupae and the time since the start of treatments in all plot types
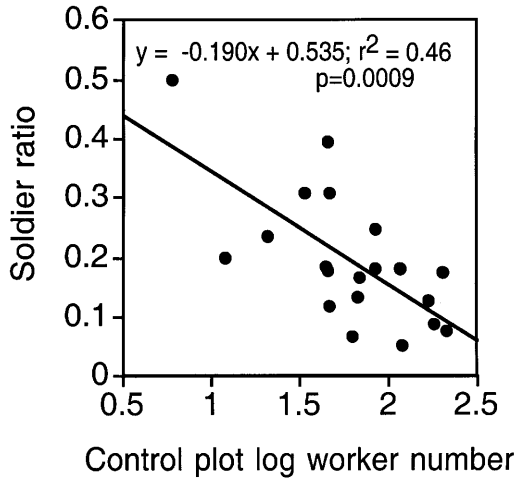
Figure 4. Worker number and soldier ratio in control plots. Soldier ratio is the number of soldiers/number of minor workers. In the absence of food treatment, soldier ratio shows a strong negative correlation with the number of workers. These data are used to correct for the effect of worker number on soldier ratio presented in Figure 5

Figure 5. Soldier ratio changing over time in control and food supplementation plots. While soldier ratio increases significantly with supplementation of clumped food resources, there is no change in solider ratio within control or split food plots

To observe the cumulative effects of the rapid production of soldier pupae, we compared the adult soldier ratio in each plot with the time since the start of the treatments. If food supplementation disproportionately increases the number of soldiers compared to the number of minor workers, then the duration of the treatment should be correlated with the proportion of adult soldiers. In these analyses of caste ratio, we excluded the ten plots with few minor workers and no soldiers, because the absence of soldiers prevented calculation of a caste ratio. There was a strong association between soldier ratio and worker number (Fig. 4); we calculated the residuals of soldier ratio to subtract the effect of worker number. We tested whether adult soldier ratios varied with the duration of the treatment (Fig. 5). While there was a significant positive relationship in the clumped food plots, soldier ratio did not change over time in the control or split food plots.

The number of competing nests within the 55 plots containing *P. flavens* ranged from zero to 18, with a mean of 5.8 nests (SE = 0.524). Adult soldier ratios were independent of the number of competing nests in control ($r^2 = 0.019$), clumped food ($r^2 = 0.011$), and split food ($r^2 = 0.046$) plots. Only two 1 m² plots contained *P. flavens* and no competitors; because nearly all colonies faced high numbers of competitors nesting nearby, we could not compare soldier ratios between colonies with and without competition.

Discussion

Ants in plots subjected to clumped food treatments altered caste ratio to increase the number of soldiers. This effect was observed using soldier pupae – a momentary measure of soldier production – as well as the adult soldier ratio that reflects the cumulative effect of soldier production over time. By
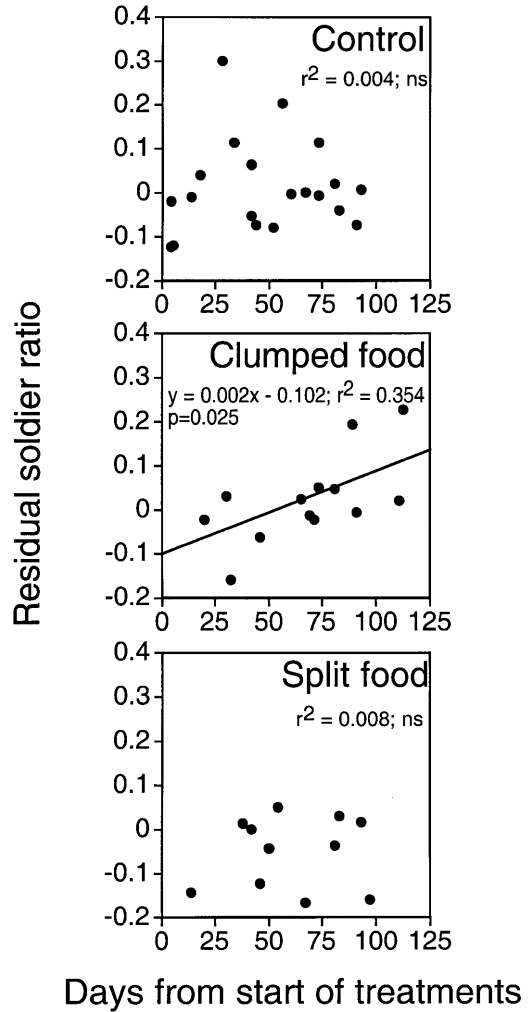
simply placing termites in a small clump on the forest floor, we found that the ants nesting near this supplemental food increased the production of soldiers, resulting in a net increase in the ratio of adult soldiers within the colonies. Therefore, we conclude that colonies in this Costa Rican population of *Pheidole flavens* altered their caste ratios in response to a specific change in its food resources. This interpretation agrees with predictions of caste theory that ants can adapt caste ratio in response to proximate ecological conditions.

There are three plausible mechanisms *P. flavens* could have used to detect a change in resources and alter the production of soldiers in response. First, the absence of soldiers from the nest can result in increased soldier production (the soldier absence hypothesis). Ant soldiers are not genetically different from minor workers, but are produced by receiving greater amounts of food as larvae (Wheeler, 1986, 1991). Wheeler and Nijhout (1984) found that the presence of adult

soldiers in the nests of *P. bicarinata* inhibited the development of larvae into soldier pupae. Detrain and Pasteels (1991) found that larger quantities of food in the environment resulted in the increased recruitment of *P. pallidula* soldiers. Our study found an increase in soldier ratio in the clumped food treatment, but not in the split food treatment; other studies have shown that the spatial presentation of food impacts soldier absence from the nest. In *P. fallax*, clumped food items draw a greater number of soldiers from their nests than split food items (Itzkowitz and Haley, 1983). In *P. pallidula*, a single large food item draws more workers from their nests than an equivalent quantity of small food items (Detrain and Deneubourg, 1997). We observed that individual *P. flavens* soldiers will patrol large food items used as bait for over ten minutes at a time without bringing food back to the nest Therefore, the absence of soldiers collecting and defending the supplemental food could stimulate the production of new soldiers.

The second mechanism that could account for an increase in soldiers is a heightened frequency of interaction with neighboring competitors (the competition hypothesis). Large food items and foods of high quality can attract a greater number of workers from different colonies. As Passera et al. (1996) demonstrated with *P. pallidula*, the exposure of competing colonies to odors of one another, without direct physical contact, can result in increased soldier production. High quality food items, such as the supplemental food, can increase intraspecific and interspecific competition among colonies in proximity to one another (Torres, 1984; Tennant, 1994). These mechanisms can explain why the increase of soldiers in clumped food plots is more robust than the increase in split food plots. Elevated interspecific interactions, and enhanced soldier recruitment to the large clump of supplemental food could result in more soldiers being absent from the nest and increased competition among colonies in the litter. These are both known mechanisms for increasing soldier proportion.

Finally, the increase in soldier production may be the result of more food within the nest (the nutrition hypothesis). In laboratory experiments, Passera (1974) reported that *P. pallidula* increased the number of soldiers produced in reponse to supplementation of high-protein food. Our addition of food into the treatment plots probably increased the fraction of protein within the nests, which could have served as a trigger for soldier production.

We do not favor one hypothesis over another, and find evidence to support all three – soldier absence, competition, and nutrition hypotheses. These hypotheses are not mutually exclusive and might have operated simultaneously. However, behavioral responses to within-nest conditions are often different than responses to external environmental conditions (O'Donnell et al., 2000). The proximate within-nest stimuli from the "soldier absence" and "nutrition" hypotheses are not likely to evoke similar behavioral responses compared to external stimuli, such as interactions with competitors. If the competition hypothesis is true, then *P. flavens* must be able to produce a generalized response to many competing species. The increase in soldier ratio was not a response to one par-

ticular competitor (as in Carlin and Johnston, 1984), because there was no consistency in species composition of neighboring nests. *P. flavens* was the most common species in the experimental plots, and no other species was consistently found in a majority of plots containing *P. flavens*. Though the number of competing nests within the treatment plots was not associated with the change in soldier ratio, the competition hypothesis is not invalidated. The competition hypothesis proposes that an increased frequency of interaction with competitors would cause the colony to alter soldier ratio. While the number of competing nests was not associated with caste ratio, a previous study at the same site has shown that clumped food supplementation increases the frequency of encounters with competitors (McGlynn and Kirksey, 2000). Because the only previous studies that have shown an adaptive change in caste ratio have involved external threats to ant colonies, the competition hypothesis remains appealing.

Our ability to assess the likelihood that soldier absence and nutrition effected a change in *P. flavens* is limited because of the challenges in performing related studies in the field. While studying the frequency of behavioral interactions at supplemental food presentations is possible, it is nearly impossible to disrupt colonies to track the food consumption and frequency of soldiers without destroying their fragile hollow twig nests. Previous studies on other *Pheidole* species validate the soldier absence and nutrition hypotheses. Both soldier absence (Wheeler and Nijhout, 1984) and supplemental nutrition (Passera, 1974) can trigger changes in soldier production, though there have been no reports of adaptive changes in colony-wide caste ratios. The occurrence of increased soldier ratio in the clumped food plots, and not the split food plots, could be caused by increased foraging efficiency and soldier recruitment to clumped foods (Itzkowitz and Haley, 1983). If the nutrition hypothesis is correct then the failure of the soldier ratio to increase in the split food plots could be caused by a smaller amount of food entering the nest, or by increased energy consumption during the process of retrieving the supplemental food. If the soldier absence hypothesis is correct, then the increased recruitment of soldiers to defend the clump of termites would trigger the increased production of new soldiers.

The discovery of ecologically adaptive caste ratios in *P. flavens* brings about an important question: why doesn't this occur more often with other polymorphic species in other systems? We offer some observations of our study system compared with studies that yielded negative results.

Colonies should not alter their caste ratios in response to the environment unless the developmental times of workers are faster than the transience of the environmental stimulus to which the colony responds (Oster and Wilson, 1978). While there is no existing sociometric study of *P. flavens* to inform us of developmental times (Tschinkel, 1991), studies of other ants (reviewed in Hölldobler and Wilson, 1990, p. 170) suggest that soldiers of this small sized tropical leaf litter dwelling species can be produced in less than two months. In our experiment, the food supplementation lasted for twice this period, with feedings every other day. The gen-

eral failure to find environmentally adaptive caste ratios in other species could result from manipulations with insufficient intensity or duration, or from measuring variables that sporadically affect colony fitness. In future seasons, it is possible that changes in the natural food availability would result in a different response to experimental food supplementation. While *P. flavens* does show the ability to alter caste proportion in the field, we do not yet know if colonies in the absence of experimental manipulations often change caste ratios because of natural changes in food availability.

Environment could play a significant role in regulating caste ratio in other polymorphic ant species, but this may have not been detected. Our experiment is fundamentally different from earlier studies. Most experiments on adaptive caste ratios have focused on species with larger colonies located in temperate climates, except for Wilson's work with Neotropical leaf-cutting ants (Wilson, 1980a, 1980b, 1983a, 1983b). While the demography of temperate ants is governed by the seasons (Brian, 1950; Herbers, 1985), leaf litter ants at La Selva grow and found colonies year round (Kaspari, 1996b). In this tropical climate, ants are not challenged by surviving winter, but are temporally restricted from foraging on a daily scale depending upon humidity (Levings, 1983; Kaspari, 1993). The lifespan of tropical leaf litter ant colonies are likely to be much shorter than temperate ants, as a result of frequent army ant predation, flooding, and patchy resources (Wilson, 1959; Kaspari, 1996b; Hirosawa et al., 2000) For these reasons, a four-month food supplementation can strongly impact the environment of these short-lived leaf litter ants competing with dozens of similar species in a patchy environment.

Gordon (1996) argued that the first experimental case of adaptive caste ratios in *P. pallidula* (Passera et al., 1996) was found in an unusual member of the cosmopolitan genus with a diverse variety of life histories. While colony defense was the key to unlocking the adaptive increase of soldiers in *P. pallidula*, presenting large amounts of food for sustained periods of time causes an increase of soldiers in *P. flavens*. The ability to respond to environmental changes may be more widespread than we have previously found. By performing basic sociometric studies to determine how environmental variables are associated with fitness and life histories, we might benefit by learning how adaptive caste ratios may have evolved in other species.

Acknowledgments

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