

Research article

Seasonality, division of labor, and dynamics of colony-level nutrient storage in the ant *Pheidole morrisi*

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Abstract. Nutritional provisioning is a critical component of life history strategies, and of particular interest in social insect colonies because of the role that division of labor plays in resource allocation. To explore the mechanisms that underlie colony nutritional strategies, I examined three populations of the ant *Pheidole morrisi* across a gradient of overwinter food scarcity over two seasons. *P. morrisi* colonies were found to employ a mixed strategy of fat storage with regard to a longer overwinter period: members of both worker castes increase their percent-fat in a graded manner, while the proportion of a specialized subcaste of majors known as “repletes”, also increased within the colony. Geographic variation in other colony traits such as mean colony size, mean worker size, and minor/major caste ratio were also found, although not always in a manner clearly relating to fat storage. These results indicate that colony demography responds to seasonal fluctuations in food availability through behavioral alterations (increased fat stores and recruitment of replete workers) rather than physical alterations (changes in lean body sizes or caste ratio). The findings illustrate the dynamic role division of labor plays in the success of insect colonies confronting environmental variability.

Keywords: Fat, seasonality, division of labor, caste, behavioral flexibility.

Introduction

The success of eusocial insects derives from the division of labor among individuals and/or castes that specialize in different tasks (Hölldobler and Wilson, 1990). Among the key life history traits of social insects, the nutritional storage of colonies in response to spatial and temporal

variation has been of considerable interest (Kondoh, 1968; Wilson, 1974; Rissing, 1984; Hasegawa, 1993).

Ant colonies exhibit dynamic patterns of nutrient storage in relation to latitude (Elmes et al., 1999), as well as season (Kondoh, 1968; Tschinkel, 1993; Blanchard et al., 2000). For example, studies on the fire ant *Solenopsis invicta* (Tschinkel, 1993) and the harvester ant *Pogonomyrmex badius* (Tschinkel, 1998, 1999) have demonstrated how colonies in the fall season store nutrients in the form of fats that can be used during overwinter periods of food scarcity, and during the spring to produce sexual brood (Tschinkel, 1987, 1998). However no studies have examined the dynamics of colony response to both spatial and temporal variation at the same time, leaving unaddressed the question of whether specific nutrient storage mechanisms in colonies differ with different kinds of environmental variation.

Among ants, a common mechanism of colony fat storage is for workers of both castes (minors and majors) to uniformly increase the amount of fat they hold in response to temporal changes in food availability (Hasegawa, 1993; Tschinkel, 1998), in what might be called “diffuse storage”. However it is also well documented that larger workers or members of the major worker caste will act as nutrient storage specialists, or “repletes”. These repletes carry and store a disproportionate amount of nutrients relative to other individuals in a colony and provide it to other colony members through trophallaxis in times of food scarcity (Kondoh, 1968; Wilson, 1974; Rissing, 1984; Tsuji 1990; Lachaud et al., 1992; Hasegawa, 1993; Borgesen, 2000). In the morphologically distinct worker castes of the genus *Pheidole* there is also a division of within the major caste itself, with a subpopulation of majors taking on the role of particularly fat-corpulent repletes (Tsuji, 1990; Lachaud et al., 1992). Furthermore, repletes in *Pheidole* have been found to

also be behaviorally distinct in their avoidance of defensive tasks compared to non-replete majors (Lachaud et al., 1992).

The goal of this study is to better understand the specific mechanisms by which ants use division of labor to store colony fat in response to both spatial and temporal environmental variation. I examined colonies of the worker-dimorphic ant, *Pheidole morrisoni*, over two seasons in three sites, whose separation of 10° latitude (~1500 km) make them ideal for investigating the response of ant colonies to varied seasonal regimes. We can then test a hypothesis of overwinter nutritional provisioning with three specific predictions: (1) that colonies should have higher levels of stored fat in the fall than the spring season; (2) that the amount of fat colonies store will increase with the length of overwinter period, and therefore with the latitude of the study site; and (3) that the geographical and temporal dynamics of fat provisioning will employ a division of labor that involves repletism.

Working from what is known about fat storage and division of labor in ants as discussed above, we can then also ask what specific mechanisms are employed when fat storage increases within a colony, whether colonies utilize diffuse storage or repletism, and by what means repletion accommodates increased storage needs. For example, one possibility is that the fatness of a given proportion of repletes will simply increase, another possibility is that more individuals will be recruited into the replete role, or some combination of these mechanisms.

Methods

Colony size and caste ratio estimation

The study populations of *Pheidole morrisoni* were located in Tallahassee, Florida (30°45' N, 84°30' W); Hoffman, North Carolina (35°03' N, 79°55' W); and Farmingville, New York (40°44' N, 73°04' W). Whole colonies were extracted from each site in June and July of 2000. In October of 2000, whole colony extractions were repeated for NC and FL, while mound samples were taken at the NY site, for a total of 15 NY, 29 NC and 29 FL colonies sampled. A random sample of both worker castes was collected from each colony and frozen at 0°C.

Colonies from all three populations were sampled, determining the percentage of majors in each colony, and the mean fat-free body masses of minor and major workers. The demographic sampling method was modeled after that of Tschinkel (1993). For each colony the soil (including all ants of the colony) was uniformly mixed, and four to six ~500g samples of this mix were sampled. With the total mass of the mix known, the number and proportions of the ants in a given soil sample (together with the absolute count of the frozen ants) provided an estimate of the total colony size and caste ratio of the colony. Estimates based on four to six samples were averaged and the resulting mean value for caste ratio and colony size was considered the measure for that colony. (Because only mound samples extending one to two feet into the soil were available in NY during fall of 2000, samples from this site and season were not included for estimates of colony caste proportions from the field). These values were then log-transformed for normality and compared by one-way ANOVA with *a posteriori* contrasts (Scheffé procedure) for 15 NY, 29 NC and 28 FL colonies pooled across both seasons. In the few instances where it was practicable to count the total number of workers this was done and considered as the measure for that colony. Inclusion of such colonies in the statistical analyses of the data

set did not significantly affect the results (one-way ANOVA), and so they were included in the final analysis.

Colony percent fat was calculated from the estimates of percent body fat for minors and majors (see below) multiplied by their proportions in that colony. These values and that of colony sizes were then analyzed by correlation. Spring colonies (n=10 FL, NC; n=9 NY), fall colonies (n=10 NC, FL; NY=not available). Fall-collected ants were also used for the analysis of colony size with percent-fat storage capacity; NY colonies were excluded from this analysis since colony size estimates were not available from fall mound samples at this site (see above).

Measures of worker body size and fat content

Body masses were obtained from frozen samples collected from colonies (n=10 colonies per site, per season; total n=60). The frozen sample sizes of ants averaged 461 ± 18 SE for minors and 117 ± 8 SE for majors per colony. Samples were sorted by caste and oven-dried at 65°C for 48 hours. Dried samples were then serially extracted in hexane to remove all fats, as follows: dried samples were put in a scintillation vial with ~5mL of hexane. These vials were rotated on an orbital shaker at 120 rotations/minute overnight at 27°C. The next day the hexane was decanted, samples air-dried for 2 hours and ants were massed again. Fresh hexane was added and the procedure repeated every day until the dry mass of the sample of ants no longer decreased between extractions (typically four rounds of extraction).

The dry, fat-free mass of all the ants in a sample was taken and divided by the total number to give a single mean value for the body mass of the caste in that colony. The mean absolute fat mass and fat percent-body mass of the minor and major castes in a given colony were then simply the numeric difference in mass before and after serial hexane extraction, and that difference in mass (multiplied by 100%) divided by the pre-extraction mass, respectively.

Estimates for a whole colony's percent fat were calculated by taking these mean values for minor and major workers and using the estimated colony size and caste proportions (see above) as multipliers to provide a value for whole colony percent-fat. This method does not distinguish lipids from other hydrophobic compounds such as cuticular hydrocarbons or phospholipids. However the findings of Blanchard et al. (2000) indicate that lipid/fat represents the large majority of such contents stored in the abdomen of worker ants.

“Replete” and “non-replete” majors, their body sizes, and proportion within colonies

Majors were considered repletes if they had visibly corpulent gasters meeting the criterion that two intersegmental sutures between tergites were visible by the naked eye due to abdominal distention. This criterion follows similarly to that of Tsuji (1990). Corpulence was assessed after oven-drying of the ants, helping assure that gaster distention was due to the presence of oil fats rather than aqueous nutriment that can also be stored in the gaster. This criterion follows similarly to that of Tsuji (1990). In this manner, repletes and non-repletes were sorted from the random sample of majors collected from field nests.

The proportions of repletes among majors were determined from the random field colony samples as described in *Colony size and caste ratio estimation*. For the comparison of replete and non-replete major body sizes, the mean of dry, fat-free body masses of majors from 16 NY, 15 NC and 14 FL colonies from both seasons were used, for a total of n=45 colonies. Body size and fat content were determined by the same methods as described above.

Defense behavior assays of majors

Three separate sets of 300 minor workers, 75 major workers, and one queen were placed in custom-made artificial nests of dental plaster (115×103×20 mm) and glass, covered with red cellophane, and kept in

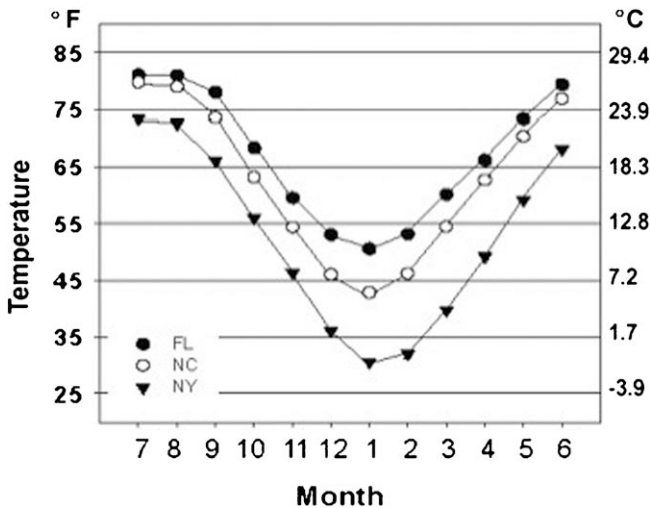


Figure 1. The 30-year mean monthly temperature for the three study sites in FL, NC and NY, respectively. Because *P. morrisi* workers typically do not forage when air temperature is below 55°F, the period of time when mean temperature is below this temperature was used as a proxy for the length of the food scarcity (overwinter) period for these three sites.

plastic bins of a standard size (38 cm×15 cm×6 cm) with walls coated in Fluon™ to keep the ants within the bins. All three trials used colonies sourced from the FL population.

The numbers of minors and majors patrolling outside of the nest in the arena were recorded; all majors patrolling outside at this time were observed to be non-repletes. 35 medium-size fire ants (*Solenopsis invicta*) were then added into the arena. After ten minutes, the numbers of replete and non-replete majors both outside the nest (confronting the fire ant aggressors) and remaining inside the nest were recorded. The numbers of minors were recorded similarly.

Statistical analyses

All statistical analyses and calculations were conducted in S-Plus 2000 Professional (Mathsoft, Inc., Cambridge, MA) and Microsoft Excel. The quantities, including percentages, were found to follow Normal distributions using quantile-quantile plots and were analyzed without transformation, unless otherwise noted. In Linear Mixed Effects (LME) ANOVA analyses (Pinheiro and Bates, 2000), individual colonies were considered random effects; all other effects such as caste, season and site were considered fixed.

Results

Worker fat storage in relation to site, season and caste

Both minor and major workers of all three populations exhibited a higher mean percent fat in the fall than the spring season, as well as an increasing percentage of body fat with increasing latitude (season effect: $t_{(56)}=22.56$, $P<0.0001$; latitude effect: $t_{(56)}=27.55$, $P<0.0001$, LME ANOVA), (Figs 2A, B). Colonies as a whole also followed the same trend (Fig. 2C).

There was a significant “caste effect” in the statistical analysis, indicating that on average members of the major worker caste store a greater percentage of fat than minors ($t_{(57)}=23.75$, $P<0.0001$). Absolute amounts of fat were

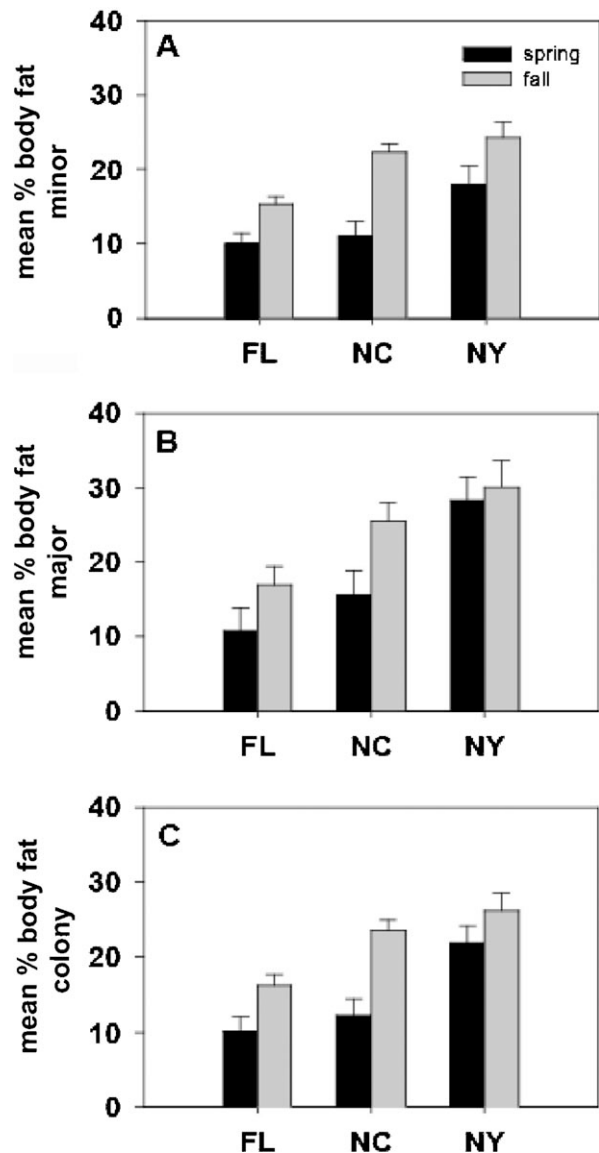


Figure 2. The relationship of fat storage to latitude and season in three *P. morrisi* populations (FL, NC, NY). (A) The mean percentage of body mass accounted for by fat in ants of (A) the minor caste, (B) the major caste, and (C) in the colony as a whole. As predicted by the overwinter food provisioning hypothesis, the amount of stored fat is greater in the fall than the spring season within sites, and greater at higher latitudes where the period of food scarcity is longer. Because caste proportions could not be measured in NY fall colonies, the colony percent fat for that site and season (right-most column) is an estimate assuming 10% majors, the average value for this population in the spring season.

higher in majors than minors, and fat also made up a greater proportion of major body mass. A significant caste-by-site interaction ($t_{(57)}=22.56$, $P<0.0047$) is consistent with the differential storage of fats within the major caste in the more northerly sites.

Table 1. Experimental trials of the behavioral response of replete and non-replete majors during an attack by *S. invicta* on their nests. Of the small number of majors found patrolling outside of the nest before the addition of *S. invicta*, all were all non-repletes. In all three trials, workers of all castes left the nest to confront *S. invicta*. Among majors, a disproportionate number of non-replete majors left the nest, while replete majors largely stayed inside, pressing themselves firmly into the sides of the nest walls. Significant behavioral associations with the major replete and non-replete subcastes were found in all three trials, Fisher's exact test, one-tailed. "–" designates unrecorded data.

Trial	Worker type	pre- <i>S. invicta</i>		post- <i>S. invicta</i>		Total #
		# in nest	# out	# in nest	# out	
1	Repletes	48	0	33	15	48
	Non-repletes	18	4	3	19	22
	minors	–	12	–	69	–
2	Repletes	43	0	38	5	43
	Non-repletes	30	2	18	14	32
	minors	–	35	–	73	–
3	Repletes	36	0	33	3	36
	Non-repletes	36	0	26	10	36
	minors	–	7	–	21	–

Major workers – repletism and defensive behavior

The degree of fat corpulence was not uniform among individuals, and this heterogeneity was most pronounced among members of the major caste. Although there was a continuum of degrees of corpulence, a qualitative distinction could be made among the majors on morphological criterion of abdomen distention (see Methods). Majors of the distended, provisional replete class were more than twice as fat as non-replete majors in terms of percentage of their total body mass that was comprised of fat (repletes: $32.1 \pm 1.7\%$, non-repletes: $15.7 \pm 0.9\%$; $P < 0.0001$, paired t-Test, one-tailed).

Repletes were also found to avoid confrontation with fire ants. In contrast to their non-replete counterparts, repletes disproportionately avoided confrontation, remaining inside the nest rather than exiting and engaging in "soldier-like" defensive behaviors against fire ants ($P < 0.05$ for all three trials, Fisher's Exact Test, one-tailed) (Table 1).

Replete majors were on average of greater body size, with heavier lean (fat-free) body masses than their non-replete counterparts (Repletes = 0.510 ± 0.011 mg, Non-repletes = 0.478 ± 0.007 mg) ($t_{(43)} = 3.75$, $P < 0.001$, paired t-Test, two-tailed).

The occurrence of repletes in relation to site, season, and colony size

There was a significantly higher percentage of repletes present in the major caste in fall colonies compared to spring colonies, and in northern colonies compared to southern colonies (season effect: $t_{(55)} = 3.20$, $P = 0.0023$, latitude effects: NY vs. NC: $F_{(1,55)} = -5.78$, $P = 0.0002$, NY/NC vs. FL: $t_{(55)} = 3.98$, $P < 0.0001$, LME ANOVA) (Fig. 3).

There was a positive relationship between the percentage of repletes within the major caste and the total colony percent fat ($r_{(47)} = 0.76$, $P < 0.001$, Pearson's cor-

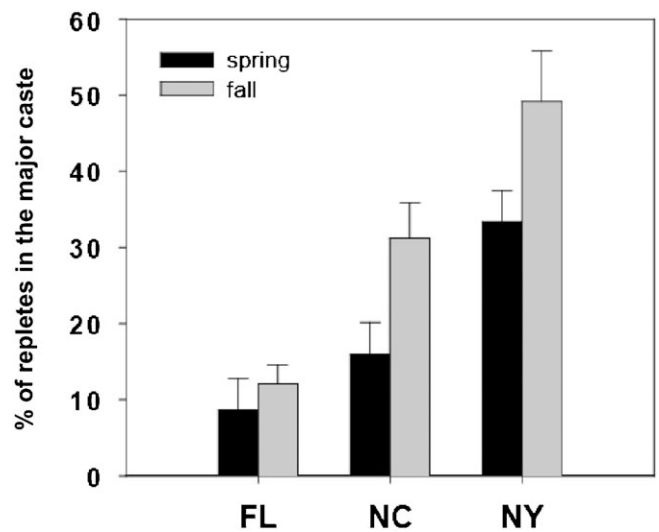


Figure 3. The percentage of the morphologically distinct replete individuals within the major caste by site and season. The percentage of majors that function as repletes varies in a pattern that mirrors fat storage in colonies as a whole (see Fig. 2C).

relation) (Fig. 3 vs. Fig. 2A), however no such relationship was apparent between the percentage of majors within a colony overall and the total colony percent fat ($r_{(47)} = -0.88$, $P > 0.05$) (Fig. 4).

Furthermore, no significant correlation was found between colony size (total number of workers) and the percentage of repletes in colonies when analyzed within a site, or when colonies across all sites were pooled ($r_{(47)} = 0.19$, $P > 0.05$).

Colony size and fat storage

Colony size data was natural log (ln) transformed for statistical analysis. Mean ln(colony size) was different among the sites ($F_{(2,68)} = 4.68$, $P = 0.011$, one-way ANOVA) (Fig. 5). FL and NC mean ln(colony size)s

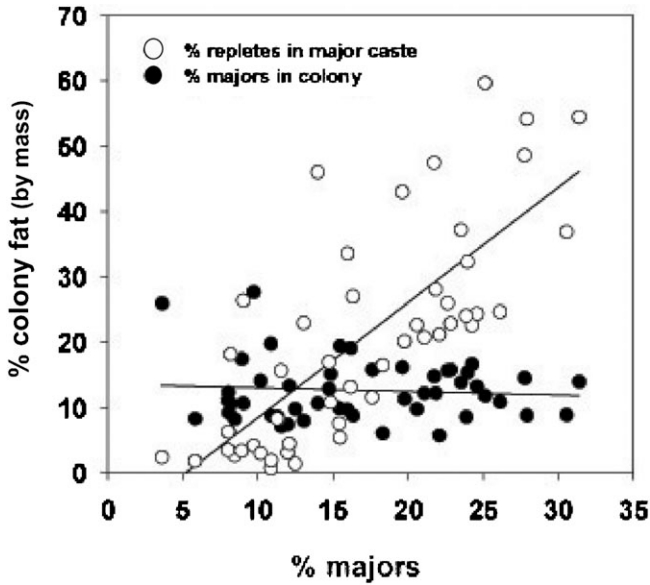


Figure 4. The percentage of repletes in the major caste increases with the percentage of fat colonies are storing (white dots) ($r_{(47)}=0.763$, $P<0.001$, Pearson's correlation), however the percentage of majors in the colony shows no particular pattern in regards to fat (black dots) ($r_{(47)}=-0.876$, $P>0.05$) (grouped data, all sites and all seasons). Although the major caste specializes in nutrient storage, for changes in fat storage the demographic shift of relevance is in terms of the behavioral castes within majors (repletes and non-repletes), rather than the proportion of physical castes (minor and major).

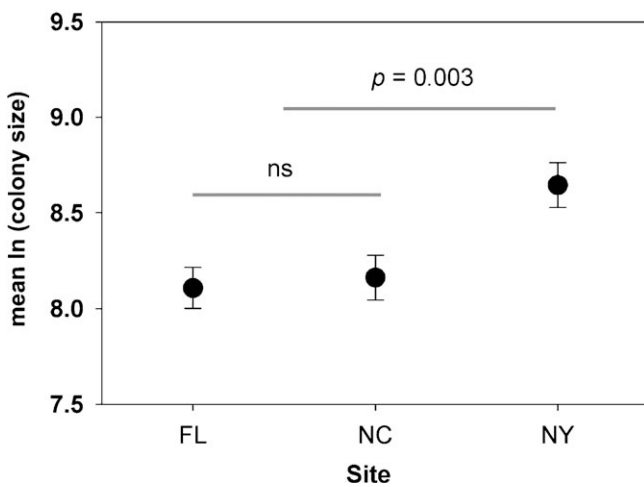


Figure 5. The relationship between colony size and geographic site. Black circles are mean of $\ln(\text{colony size}) \pm \text{SE}$. Mean $\ln(\text{colony size})$ was found to be significantly larger in NY compared to FL & NC ($F_{(1,69)}=9.72$, $P=0.003$, one-way ANOVA); FL & NC showed no statistical difference ($F_{(1,54)}=1.20$, $P=0.73$). NY, $n=15$; NC, $n=29$; FL, $n=29$.

were not statistically different from each other ($F_{(1,54)}=1.20$, $P=0.73$) and were grouped and compared to NY, which had a significantly larger mean $\ln(\text{colony size})$ than FL/NC ($F_{(1,69)}=9.72$, $P=0.003$, one-way ANOVA) (Fig. 6).

Within sites, no positive correlation between colony size and colony percent fat was observed in the spring or

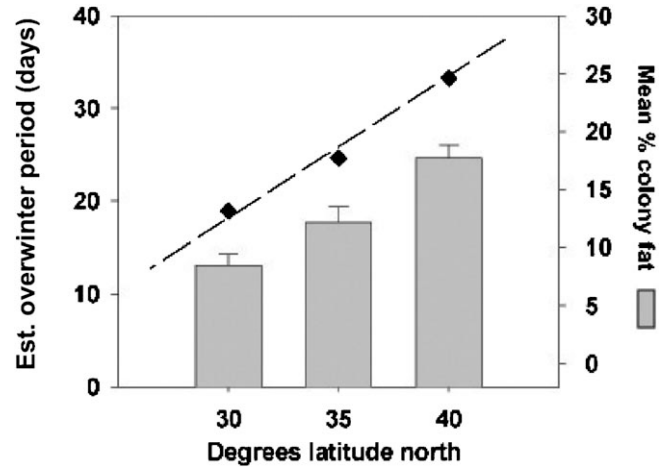


Figure 6. The number of months with a mean temperature below 55°F is a proxy for the length of the food scarcity (overwinter) period for these three sites (taken from Fig. 1). This time period plotted against the latitude of the three sites and exhibits a constant gradient (black diamonds). The latitudinal increase in the length of overwinter food scarcity is mirrored by an increase in the percentage of stored fat in colonies (bars are average \pm SE of spring and fall seasons combined, Fig. 2C).

in the fall. When spring colonies from all three sites were combined, a significant positive correlation between colony size and percent fat was found ($r_{(27)}=0.482$, $P<0.01$); however no such correlation was found when fall colonies across sites were pooled.

Discussion

The results presented support the three predictions of the overwinter provisioning hypothesis. Colonies of *P. morrisi* store more fat in the fall than spring season, and this seasonal pattern intensifies in northern populations that experience the longer winter periods (Fig. 6). Division of labor plays a significant role in this fat storage. In particular, increased recruitment of majors into the replete role appears to be the primary means by which colonies increased their seasonal nutrient stores (Fig. 3). The importance of repletes as colony fat storage specialists is illustrated by the fact that as only 7% of a colony's workforce is necessary to store over 35% of a colony's fat (Fig. 7).

Although repletes specialize in fat storage, we also see that all workers – minors and majors alike – contribute to the increase in overall colony fat levels through a graded increase in their percent body fat. Diffuse storage has been observed in other ants as a function of colony size (Hasegawa, 1993; Tschinkel, 1993, 1998), as well as a function of season (Tschinkel, 1993). Therefore, in response to seasonal differences colonies become fatter through two processes: (1) diffuse storage, a graded increase of the percent body fat of all worker castes, together with, (2) recruitment of more and more majors into the fat replete subcaste. This flexible combination of

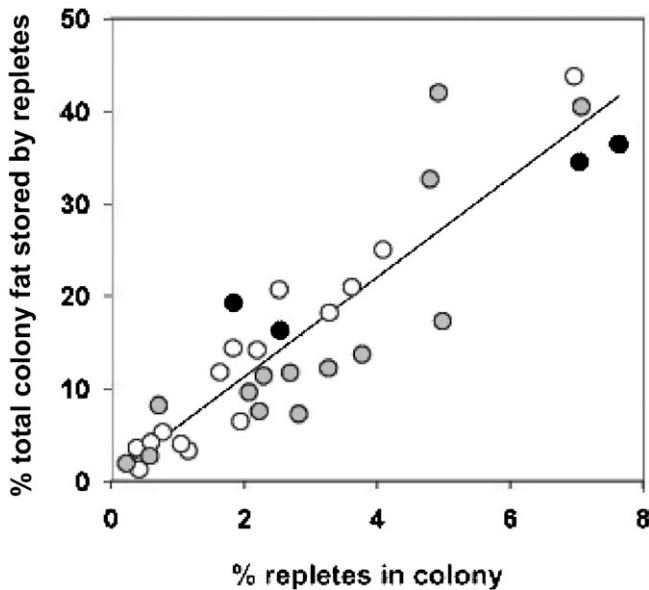


Figure 7. The percentage of total colony fat stored by the replete subcaste as a function of the percentage of the total worker force that repletes comprise, data grouped across all sites and seasons (black dots=NY colonies; gray=NC; white=FL). A small percentage of replete workers carry an inordinately large amount of colony fat, underscoring their role as nutrient storage specialists in *P. morrisi*.

caste specific responses (recruitment of replete majors), and caste non-specific responses (incremental increase of fat in all castes) appear to constitute a general mechanism of colony fat storage that is variably employed by *P. morrisi* across their geographic range (Fig. 2A,B; Fig. 7).

Rather than responding to variable fat storage needs through alteration of the physical caste proportions of minors and majors, colonies of *P. morrisi* flexibly change the allocation of workers to tasks within their behavioral repertoire. This kind of extensive behavioral plasticity in worker demography has been well-documented in other ants (Davidson, 1978; Herbers, 1980; Calabi, 1988; Calabi and Traniello, 1989; Gordon, 1989; Brown and Traniello, 1998; McGlynn and Owen, 2002). The results of this study are significant in demonstrating that a given mode of behavioral plasticity, in this case nutrient storage, may operate on large geographic scales according to local conditions. Further research on specific measures of foraging levels, food availability and competition at each of the three sites will be necessary to fully understand the behavioral dynamics outside of the nest and how increased levels of fat are in fact attained.

The results of this study confirm the documented role of the major caste as nutrient storage specialists in ant colonies (Kondoh, 1968; Wilson, 1974; Hasegawa, 1993). They also broaden our understanding of within-caste specialization in regards to defense behavior. Sorting majors as “replete” and “non-replete” on the basis of a morphological criterion reliably distinguished their propensities for participating in colony defense behavior (Table 1). Thus *P. morrisi* majors appear to contain true behavioral “subcastes” of non-replete individuals that

leave the nest and confront alien ants in a defensive role, and of repletes that specialize in the storing nutrients, but also tend to avoid defensive tasks. These findings are consistent with those of Lachaud et al. (1992) in *Pheidole pallidula*, in which the non-replete individuals were the members of the major caste most likely to leave the nest and confront aggressors. Indeed, this partitioning of tasks between repletes and non-repletes makes adaptive sense by minimizing the risk of loss of a precious colony resource: stored nutrition (Porter and Jorgenson, 1981; Blanchard et al., 2000).

The dynamic patterns of seasonal fat storage documented here inform the ongoing discussion over whether a Bergmann’s Rule-like trend of larger body sizes with increasing latitude (Bergmann, 1847) exists among eusocial insects and other ectotherms (Von Voorhies, 1996; Mousseau, 1997; Partridge and Coyne, 1997). Although such size trends have been found within ants (Cushman et al., 1993; Kaspari and Vargo, 1995), a number of studies have found the opposite trend in other social insects, such as bees and termites (Hawkins, 1995; Porter and Hawkins, 2001).

A number of hypotheses have been put forth relating increased size to increased overwinter survival. It is possible, for example, that larger colony size could in principle be an adaptation for overwinter survival if in fact colonies cannibalize their own brood and adults as a reserve source of nutriment (Kaspari and Vargo, 1995); likewise, larger individual worker size could be favored in higher latitudes if it increases metabolic efficiency (Cushman et al., 1993; Beshers and Traniello, 1994). However, the results of this study suggest that nutritional provisioning rather than simply size itself may be important in understanding social insect colonies’ response to seasonality in food availability. While the importance of size as a life history trait cannot be underestimated, other factors may need to be considered in examining apparent size trends. For example, the mean body sizes of both minor and major workers are larger in northern populations of *P. morrisi*, but this may be a consequence of selection on traits developmentally linked to body size rather than the result of selection on body size itself (Yang et al., 2004).

Finally, mean colony size was found to be larger the most northerly (NY) population in *P. morrisi* (Fig. 6). If there is a functional or adaptive significance to this, it may lie in the relationship between a colony’s workforce and the ability for it to acquire more resources during foraging (Oster and Wilson, 1978). By this hypothesis, larger colonies would garner more nutrients for storage and overwinter use. Studies in other species of ants have shown a clear relationship between increased colony size and increased fat stores (Hasegawa, 1993; Tschinkel, 1993, 1998); the relationship between colony size and percent fat were equivocal in this study (not found within sites, but detected across sites in the spring season). Although the functional significance of larger colony size with latitudinal site is in need of further examination, the developmental basis of larger northern colonies in *P.*

morrissi may be the consequence of variation in another life history trait: the monogynous versus polygynous colony modes of queens (Yang and Cover, in prep.). In the context of this and other fundamental life history differences between the three populations of *P. morrissi* (Yang et al., 2004), the flexible use of a common fat storage strategy by colonies across its large geographic range only highlights the important role behavioral plasticity plays in social insects adapting to their variable environments.

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