Research article

Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius:* worker characteristics in relation to colony size and season

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Summary

As colonies of all monogyne ants grow from a single, colony-founding queen to a mature colony with many workers, they develop the species-typical characteristics of the mature colony. This ontogeny, and these species-typical characteristics and their seasonal changes were studied in the Florida harvester ant by excavating 31 colonies of the full range of sizes, on 4 dates representing major phases of the annual cycle. Worker characteristics varied strongly with colony size, location in the nest, and season. All but incipient colonies contained both major and minor workers. The proportion of the colony which was major workers was unaffected by colony size, averaging about 7%, but showed a small increase in mid-summer. Minor workers increased in size as colonies grew larger, but major workers did not. Most of the changes in minor worker weight were caused by changes in fat stores, which varied by 85% or more. The patterns of weight variation supported the following life and seasonal history of minor workers. The young, lighter-colored workers (callows), occurred near the bottom of the nest between June and October, confirming a strong age-stratification in the nest. For a given headwidth, callow minors were fatter than their older, darker sisters. In the course of the season, young workers gained lean weight, but lost fat as they moved to nest chambers ever closer to the surface. Finally, when their fat content was less than 10%, they became foragers on the surface. Along with these age-related changes, minor workers were lightest and least fat in July after the colony had produced its annual crop of sexual alates, and gained an average of 24% by winter. Workers were heavier and fatter if they came from a larger colony, and heavier and younger deeper in the nest. Seasonal variation in fat weight and dry weight was greater in smaller colonies than large. Although less variable, lean weight was lower in July and in the bottom of the nest, and higher in a larger colony. These patterns were similar, though less precise, for major workers.

Altogether, in the life history of harvester ant colonies, the large pulse of early-spring sexuals probably cannot be produced solely from current foraging intake. The metabolic and labor resources needed for sexual production are stored in the bodies of the young workers, whose fat content reaches the annual minimum after producing sexuals. After these sexuals have flown, the colony once again switches to producing workers and storing excess foraging intake as worker fat for over-wintering, and for producing the next year's sexuals. As colonies get larger, this proportional excess increases, giving rise to fatter and larger workers.

Introduction

Many myrmecologists have been struck by the apparent parallels between social insect colonies and individual organisms, giving rise to the superorganism concept (Hölldobler and Wilson, 1990). Whatever its shortcomings, this concept draws attention to the fact that (1) mature social insect colonies are the products of development, just as organisms are, and that (2) evolution shapes the life history of colonies just as it shapes that of individuals, because (3) the colony is the evolutionary, and to some extent, the functional counterpart of the individual in non-social animals. This suggests that application of life history theory to social insect colonies would lead to a better understanding of their evolution. Life history theory explores the association of life cycle characteristics with the ecological milieu in which these evolve. A life history tactic consists of a particular combination of the mean and variance of age at first reproduction, number of offspring, size of offspring, number of reproductive episodes per lifetime and time between them (Stearns, 1976).

Progress in this field therefore requires detailed information on colony composition (sociometry, Tschinkel, 1991) and function from all phases of the life cycle, from founding to senescence and death. In the majority of ant species, colony founding is non-social: without the aid of workers, queens found new colonies from metabolic reserves. All attributes of colonies are therefore the product of colony ontogeny (sociogenesis, Wilson, 1985). Furthermore, interspecific differences between mature colonies are the result of differences in their rules of sociogenesis (Tschinkel, 1991; 1993). The challenge of a life-history approach to social insect evolution is to identify which features are epiphenomena of no evolutionary importance, which are life history tactics and how these tactics affect colony reproductive success. Compiling age- and size-specific descriptions of colony features is obviously the first step toward meeting this challenge.

In social insects, the age-size-frequency distribution of workers is an important subject of study because it represents a central feature of the colony's adaptive suite of traits. The demography of non-social animals is the incidental outcome of the life history schedules of its component animals, and is an epiphenomenon without adaptive significance. By contrast, the demography of the workers in a social insect colony is shaped by natural selection to produce a schedule of births, deaths and worker sizes which is adaptive to the colony, a process called adaptive demography (Wilson, 1968; Oster and Wilson, 1978; Schmid-Hempel, 1992). In species within 40 of the 260 genera of ants this process has resulted in a large range of worker sizes and shapes (worker polymorphism: Oster and Wilson, 1978). Worker polymorphism is tied to life history tactics through division of labor, because: (1) it adds another dimension to the division of labor, and increases ergonomic efficiency (Wilson, 1983; Hölldobler and Wilson, 1990); (2) it may modify the course of age polyethism (Mirenda and Vinson, 1981); (3) it changes the demography of colonies, because larger workers live longer (Calabi and Porter, 1989; Beshers and Traniello, 1994, 1996). These changes are presumed to have fitness implications.

Where worker polymorphism is present in mature colonies, it is almost always absent from the newly-founded colony, appearing during colony growth and development. This sociogenesis of worker polymorphism has been described in detail for *Atta cephalotes* (Wilson, 1983a) and *Solenopsis invicta* (Wood and Tschinkel, 1981;

Tschinkel, 1988). In both species, the right-skewing of the worker size-distribution increased with colony size. In *S. invicta,* this skewing resulted from an increase in the proportion of major workers (Tschinkel, 1988).

As in any life history strategy, colonies make "choices" concerning investment of resources in growth (new workers) vs. reproduction (sexual alates). The particular choices depend on the age or size of the colony, and divide the life cycle into ergonomic and reproductive phases. Choices may also be seasonal. Resources may not be immediately invested, but stored for future use as worker body reserves (Kondoh, 1968; Tschinkel, 1987; Wheeler and Martinez, 1996) or liquid food (e.g. *Myrmecocystus*, Hölldobler and Wilson, 1990). Such investment/storage patterns have obvious fitness implications. For polymorphic species, colonies also make choices regarding the timing and amounts of investment in workers of specific sizes. Tschinkel (1993) provided an accounting of such investment patterns during the life cycle and seasonal cycle of the fire ant, *S. invicta*. He found that investment rates in minor and major workers, fat storage, reproductive alates and colony maintenance all showed strong relationships to colony size (sociogenesis) and season. Altogether, these patterns defined a large part of the life history tactic of this species, and were associated with variation in fitness.

The harvester ants of the genus *Pogonomyrmex* are found in the arid zones of North and South America where the diet of many species includes large proportions of seeds. The genus includes many large, conspicuous species which have been popular subjects of diverse studies, resulting in substantial knowledge of their behavior, natural history and ecology. For example, Golley and Gentry (1964) and MacKay (1985) reported on the production ecology and energetics, Gordon (1996) and Crist and Wiens (1996) focused on the population dynamics, spatial distribution and behavior, and numerous authors have investigated aspects of foraging (Traniello and Beshers, 1991; for review, see Traniello, 1989). The species of *Pogonomyrmex* are typically ground nesting, long-lived colonies (Porter and Jorgensen, 1988; Gordon, 1996b), with small to moderate numbers of workers (100 to 15,000; Hölldobler and Wilson, 1990). Foragers often proceed on trunk trails to their foraging grounds, where they collect seeds, which they store as food reserves in underground chambers (Hölldobler, 1976). Colonies are typically founded by haplometrotic queens, and grow to maturity in 4–5 years (Gordon, 1996b).

There are only two *Pogonomyrmex* species with polymorphic workers, *P. badius* and the Argentine species, *P. coarctatus*. *P. badius* is the only member of its genus found east of the Mississippi River, and is a characteristic component of the open pine forests of the southeastern coastal plain. In this first paper of a series on the sociogenesis and sociometry of *Pogonomyrmex badius*, I will describe patterns of allocation and changes of worker size and demography during colony ontogeny and across seasons. These patterns define part of the adaptive demography and life history tactics of *P. badius*.

Materials and methods

The 25 hectare study site was located in the Apalachicola National Forest about 16 km southwest of Tallahassee, Florida. Soils were very well drained, almost pure,

deep sands. Vegetation consisted of mostly sparse, young longleaf pines with an herbaceous groundcover containing abundant cactus (*Opuntia* sp.). The site supported a large population of *Pogonomyrmex badius* along with *Solenopsis geminata, Forelius pruinosus, Trachymyrmex septentrionalis, Prenolepis imparis,* and *Conomyrma pyramica.*

Colonies were sampled and excavated 4 times during 1989-90 to cover a one-year cycle: (1) April 25–May 23; (2) July 10–Aug. 10; (3) Oct. 16–Nov. 7; (4) Jan. 16–Mar. 5. These dates were chosen to coincide roughly with major phases of the seasonal cycle. Sexual production was captured in the April–May sample, worker production in the July–November samples, and winter inactivity in the January–March samples. These samples will be subsequently referred to as the May, July, October and January samples, respectively. At each of these times, surface features were used to choose 2 small, 2 medium and 2 large colonies for excavation. Choices were haphazard and were scattered widely throughout the area. In the following years, several incipient colonies were excavated, bringing the total number of colonies to 31.

Surface features such as crater dimensions and charcoal deposits were noted, and all foragers in the vicinity of the nest were collected. Also included in this "surface worker" sample were any workers exiting the colony upon disturbance. A pit was dug next to the colony, and chambers were progressively exposed in their horizontal aspect, one at a time. Depth of the chamber floor from the surface was measured and the contents of each chamber were aspirated and stored in separate containers. The outline of each chamber was traced on a sheet of acetate laid over the exposed chamber floor, and the compass orientation of the chamber noted. From these tracings, chamber perimeter and area were determined. At intervals, soil temperature was measured as the dig proceeded. Depending upon size, 1 to 2 days were required to complete an excavation.

I needed assurance that the process of excavation did not affect the distribution of the colony within the nest. In one excavation, a 2 m pit was excavated next to the nest and covered with plywood. After 24 h, sheets of metal were driven horizontally into the wall of the pit in order to sever the vertical tunnels of the nest and prevent worker movement between chambers. The nest was then excavated as above, taking special note of any accumulation of workers or brood above or below the metal barriers. This excavation tested the assumption that excavation did not cause significant movement of ants within the nest, and that the distribution of ants among excavated chambers represented their real distribution in undisturbed colonies. This excavation method was repeated on a second nest, except that the barriers were driven in immediately and the nest was excavated without delay.

In neither case was there convincing evidence that the colony was redistributing itself in response to disturbance. In the first case, workers were more evenly distributed than non-barriers workers, but most of this was probably the result of the loss of much of the soil temperature gradient after the pit excavation and before nest excavation. In the second case, nest members did not differ substantially in their distribution from non-barriers nests. In neither case was there much accumulation of workers and brood either above or below the barriers, as would be expected if colony members were undergoing active net movement either upward or downward in response to disturbance.

In the laboratory, the workers and brood from each chamber were sorted, count- ed and oven-dried at 50 °C for several days. Light-colored workers were regarded as callows and were analysed separately from dark-colored workers. For analysis of worker size and weight, workers were combined according to which third of the nest (by measurement, not chamber count) they were found in. This yielded 8 combined samples for each colony: dark workers and callows for surface, upper third, middle third and bottom third. Twenty workers were randomly selected from these 4 sam- ples and individually weighed. After exhaustive extraction with ether in a Soxhlet extractor (Tschinkel, 1993), they were reweighed to determine the amount of fat through weight-loss. Finally, headwidth was individually measured using the wedge micrometer device of Porter (1983). The random measurement error (SD of repeat- ed measurements) of this device is 0.006 mm. Brood and sexuals were combined for the entire nest after counting, oven-dried and weighed.

For some analyses, colonies were grouped into 5 size classes based on the log of the number of workers (most effects of colony size are non-linear). The classes were: < 100, class 0; 100–750, class 1; 750–2000, class 2; 2000–4500, class 3; > 4500, class 4.

Seeds were oven-dried and, using standard testing sieves of decreasing mesh size, sifted into 10 size categories (sieve #s 8, 10, 12, 14, 16, 18, 20, 25, 30, 35). If there were fewer than 100 seeds in a chamber, the total sample was weighed and counted. For larger samples, the total weight of seeds was taken, and the number calculated from the weight of a subsample of 100 seeds.

Data and data analysis: The basic data are summarized in Table 1. Various totals and ratios were calculated from these. Data were analysed by regression and/or ana-

Table 1. The basic data reported in this paper are shown in italics. Colonies were sampled 4 times during a 1 yr cycle: (1) April 25–May 23; (2) July 10–Aug. 10; (3) Oct. 16–Nov. 7; (4) Jan. 16–Mar. 5. Reports on the remainder of these data will appear elsewhere

Basis	Items
chamber	depth (cm); area (cm^2); perimeter (cm)
chamber	count of dark workers and callow workers count of worker pupae, worker larvae count of male and female alates, male and female pupae, sexual larvae weight and count of seeds seed size distribution (weight or number by dimension)
nest thirds	total weight workers total weight of dark workers total weight of callow workers *worker weight and weight frequency distribution* *worker headwidth and headwidth frequency distribution* *worker fat content and fat-content frequency distribution* *callow worker weight and weight frequency distribution* *callow worker headwidth and headwidth frequency distribution* *callow worker fat content and its frequency distribution*
colony	total chamber area, perimeter, maximum depth total count workers, worker pupae, worker larvae total count sexual male and female adults, pupae, sex larvae total weight dark and callow workers; worker brood, sex brood total weight and count of seeds

lysis of variance (ANOVA). Transformations were applied as needed to stabilize the variance.

## Results

Separation of majors and minors

The headwidth-frequency distribution of workers is strongly skewed to the right as a result of the presence, except in incipient colonies, of small proportions of major workers among the predominant minor workers. A normal-score plot of such distributions results in a two-phase curve (Tschinkel, 1988), as in Figure 1. The left limb with the high slope and narrow range represents the minor workers, and the right limb with its lower slope, larger mean and wider range, the majors. The values of headwidth at which these two limbs intersect were used to separate minor from major workers on a repeatable basis. The headwidths of minors and majors were analyzed separately. Headwidths of minors were always normally distributed, but those of majors were occasionally leptokurtic, especially in large colonies where there was an excess of small and large majors over what would be expected from a normal distribution.
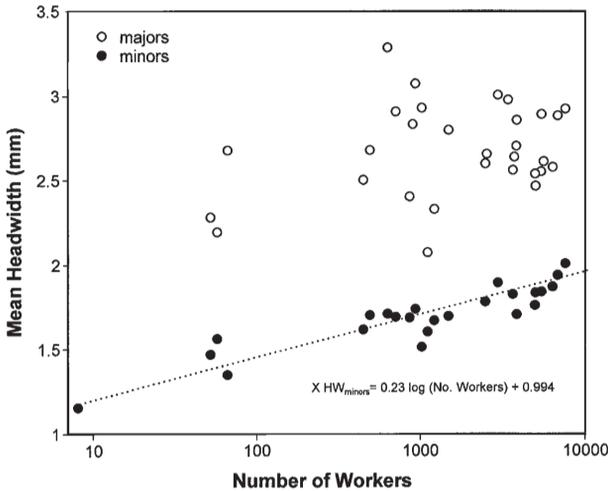

Minor worker headwidths

The colony mean for headwidth of minor workers increased as colony size increased (Fig. 2) (Regression: $HW_{minor} = 0.23$ (log no. workers) $+ 0.994$; $R^2 = 0.64$, $p < 0.00001$). The mean headwidth of minor workers in incipient colonies was 1.15 mm, whereas in colonies of 7 to 8 thousand workers, it was 1.90 mm. The mean headwidth of major workers was much more variable, and unlike that of minors, showed no significant relationship to colony size in a simple regression (Fig. 2, regression: $R^2 = 0.0004$, $p < 0.92$, N.S.).

Headwidth was further analyzed by analysis of covariance. Depth in the nest (4 levels) and date (4 levels) were used as the factors, while colony size (number of workers) was the covariate. In order to stabilize the variance, the covariate was log-transformed for the analysis of major workers, and both the covariate and the dependent measure (individual headwidth) were log-transformed for minor workers. In order to balance the design, the analysis was repeated without the surface samples, which were often missing in the winter sample.

Minor headwidth was significantly related to both depth in the nest ($F_{3, 14602} = 8.08$; $p < 0.00001$) and date ($F_{3, 14602} = 87.11$; $p < 0.00001$), but the effect of date was different at different depths (significant date-depth interaction: $F_{9,14602} = 20.25$; $p < 0.00001$). Headwidth increased significantly (Duncan's multiple range test) from 1.76 mm in May to a maximum of 1.80 mm in October and then declined slightly to 1.78 in January. However, whereas headwidth declined only from 1.78 to 1.77 between the surface and bottom nest samples in January, it declined significantly (Duncan's Test) from 1.83 to 1.71 mm, surface to bottom, in the May sample. The July and October samples were similar to each other, fluctuating between 1.78 and 1.82.
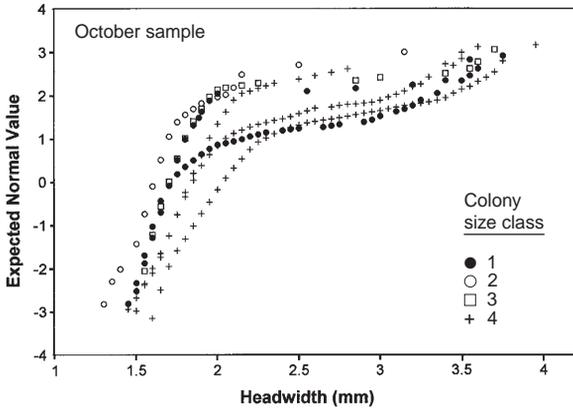
Figure 1. Probability plots of the headwidths of workers. The two-leg nature of these plots indicates that the underlying distribution consists of two contiguous normal distributions, the left one for minor workers and the right one for major workers. The transition to the lower slope marks the transition from minor to major workers, and was used to separate headwidths for further analysis
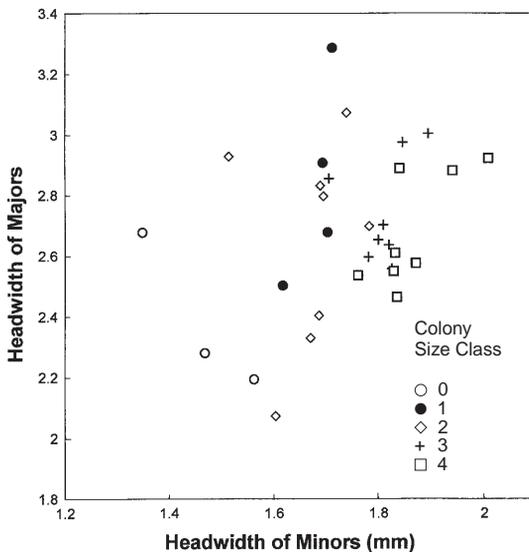

Figure 2. The colony means for headwidths of minor and major workers in relation to colony size. Mean headwidth of minor workers increased significantly with colony size, but that of major workers did not. A regression line is fitted only to the minor worker data

The covariate, log colony size, accounted for 35% of the variation in headwidth: workers in larger colonies were larger. A significant interaction of colony size with date brought this up to 36%. The fixed factors and their interaction, on the other hand, although highly significant, accounted for only about 3% of the variance in headwidth, with date accounting for over 2% of this. In effect, sample date and depth shifted the mean minor headwidth 5 to 7%, whereas colony growth from incipient to maturity increased it about 40%.

Major worker headwidths

The headwidths of major workers were also significantly affected by sample date ($F_{3,1131}$ = 4.92; p < 0.002), depth ($F_{3,1131}$ = 4.16; p < 0.006). Inclusion of these factors exposed a significant increase of major headwidth with colony size (within-cells regression: $F_{3,1131}$ = 19.21; p < 0.00001). There was no significant date by depth interaction. Major headwidth reached a maximum of 2.75 in July and fell to a minimum of 2.50 in January. Major headwidth was highest in the upper third of the nest (2.75 mm) and declined to 2.63 mm at the bottom. Surface headwidths averaged 2.45 mm, but no surface workers were collected in the January samples.

Because major worker headwidths were more variable, the proportion of the total variance explained by the factors and covariate was small. Altogether, they accounted for 5.3% of the variance, with colony size explaining about 2%. Even small colonies produce major workers of almost "full" size, with relatively small increases as a result of subsequent colony growth. Nevertheless, the increase in mean major worker headwidth was linked to that in minor workers. Mean major worker headwidth regressed significantly on minor worker headwidth (Fig. 3) (HW_{major} = 0.63 HW_{minor} + 1.58; $F_{1,29}$ = 3.53; p < 0.07; R^2 = 8%). This suggested that major and minor headwidths converged as minors (and colonies) increased in size. However, when size class zero was removed from the regression, the relationship between major and minor headwidths became non-significant ($F_{1,25}$ = 1.11; N.S.), suggesting that most of the relative change in major and minor sizes occurred in very young colonies containing fewer than 100 or 200 workers. For larger colonies, the increase in mean headwidth of minors was not reflected in a signficant increase in major headwidths (Fig. 3).

Figure 3. The relationship between the colony means of minor headwidth and major headwidth. Colony size class is indicated by different symbols. Removal of the data for size class 0 resulted in a non-significant relationship
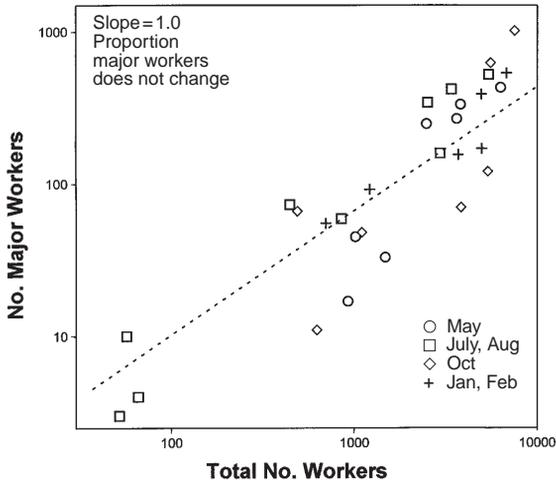
Figure 4. Number of major workers in relation to the total number of workers in colonies. Majors increase at the same rate as total number of workers, so that the proportion of majors does not change with colony size

Proportion major workers

As colonies grew, the number of major workers grew at the same rate as the number of workers (log no. majors = 1.06 log no. workers –1.48 (Oct-May); $F_{2,27} = 69.4$; $R^2 = 83\%$; $p < 0.00001$). The slope (1.06) was not significantly different from 1.0 (t-test, N.S.). As a result, the proportion of the colony which was majors did not change (Fig. 4), and averaged 7.4% (s.d. = 4.5%) over all colonies. The intercept for the July sample was significantly larger (–1.19) than the other three samples (–1.48), but still translated to the absence of majors in very small colonies. Solution of the regression indicated that the first major would be expected in colonies containing 14 and 25 workers, in July and other samples, respectively.

ANCOVA of the proportion majors (arcsine square-root transformed) by sample date and depth, with colony size as covariate, found a significant effect of sample date ($F_{3,80} = 3.40$; $p < 0.02$), but not of depth ($F_{3,80} = 1.53$; N.S.). Duncan's multiple range test confirmed that the proportion of majors in the July sample was significantly higher (10.6%) than in May (5.5%) but neither was significantly different from the October and January samples (7.2 and 5.7%, respectively).

Analysis of worker weights

Dry weights

For the analysis of dry weights, workers were again separated into minors and majors in order to overcome the strongly non-normal distribution of residuals resulting from analysis of the combined workers. Because sample size for weights was 20 or less for each group, and majors made up only 7 to 10% of the workers, results

for major workers were more variable and subject to sampling error. Dark and callow workers were also analyzed separately. Dependent variables were transformed as needed to stabilize the variance.

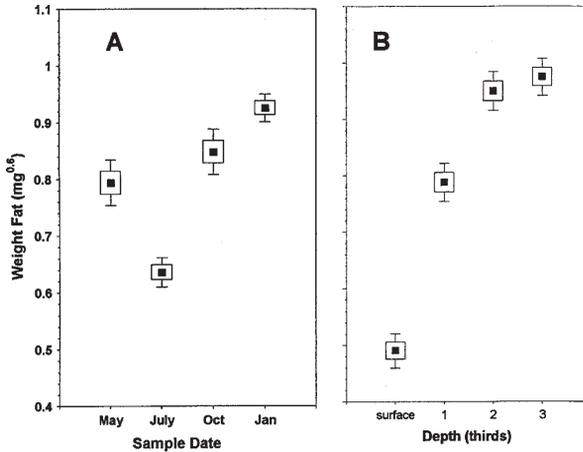### Dark minor worker dry weights

The mean dry weights of dark minor workers changed with season and depth in the nest (Fig. 5). ANCOVA of dry weight by sample date and depth, with colony size as a covariate showed significant main effects of both date ($F_{3,1837} = 68.3$; $p < 0.00001$) and depth ($F_{3,1837} = 52.6$; $p < 0.00001$). Workers were significantly different for all sequential pairs of months (Tukey's HSD test). They were lightest in July and 24% heavier in January. Workers in the middle third of the nest column were heaviest, and weight decreased significantly in going to the top third and the surface on the one hand, and the bottom on the other. However, relationship between depth and weight weakened in July, resulting in a significant date x depth interaction ($F_{9,1837} = 6.53$; $p < 0.00001$). A total of 48% of the variance in mean weight was explained, 6% by date, 5% by depth, $<2\%$ by a depth-by-date interaction, and 36% by the covariate, colony size.

Dark minor worker fat

Dry weight is composed of fat weight and lean weight, each of which can vary independently. Separate analysis can help identify sources of dry weight variation. Mean fat weight (0.6 power-transformed to stabilize variance) was analyzed by ANCOVA by sample date and depth, with colony size as covariate. Both sample date and depth had significant effects (date– $F_{3,1825} = 73.9$; $p < 0.0000$; depth– $F_{3,1825} = 203$;
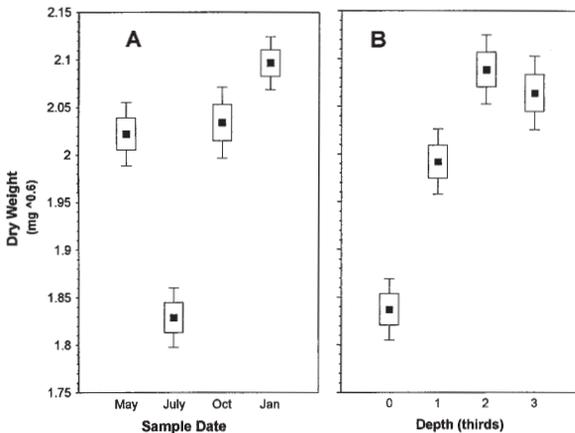
Figure 5. Mean dry weight (data 0.6 power transformed) of dark minor workers in relation to sample date and depth, from analysis of covariance. All means were adjusted for colony size. Error bars show 1.0 and 1.96 standard errors around the adjusted mean
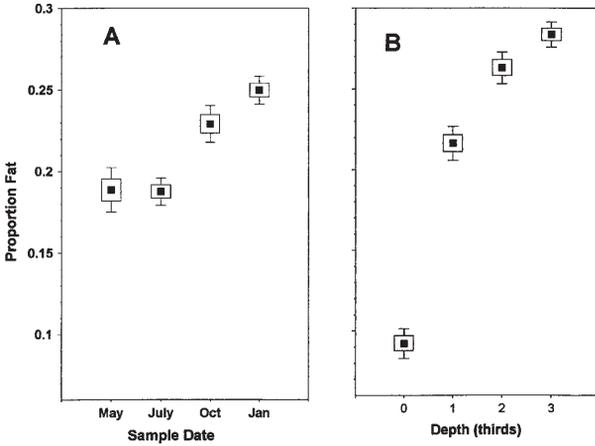
Figure 6. Mean weight fat (0.6 power transformed) of dark minor workers in relation to sample date and depth. All means were adjusted for colony size. Error bars show 1.0 and 1.96 standard errors around the adjusted mean

p < 0.0000) (Fig. 6). Again, mean fat content cycled between a July minimum and a January maximum. All except the October and May means were significantly different (Tukey's HSD test), suggesting a seasonal cycle of fatness with a minimum in July after sexual production, and a maximum in midwinter. Because the effect of depth on fat weight increased from May to January, there was a small but significant depth x date interaction ($F_{3,1825} = 5.58$; $p < 0.0000$). A total of 53 % of the variance in fat weight was explained, 16 % by depth in the nest, 3 % by date and 21 % by the covariate, colony size.

Total variance of fat weight was greater than that of dry weight. Throughout the year, mean dry weight varied 24 % (back-transformed adjusted means), while mean fat weight varied over 85 %. Together, this suggested that varying percent body fat was causing much of the variation in body weight. This was tested in an ANCOVA of % fat (based on dry weight) by sample date and depth, with colony size as a co-variate (Fig. 7). Both factors showed a main effect (date– $F_{3,1763} = 28.3$; $p < 0.0000$; depth– $F_{3,1763} = 117$; $p < 0.0000$). Fatness increased significantly from about 19 % at the May and July minimum to 25 % in January (Tukey's HSD test) (Fig. 7A). Fatness increased significantly from about 9 % in the surface workers to about 28 % in those in the bottom and middle thirds, which were not significantly different from one another (Tukey's HSD test). Fatness increased more strongly with depth in October and January, resulting in a small but significant depth x date interaction ($F_{9,1763} = 3.44$; $p < 0.0005$). A total of 36 % of the variance in % fat was explained, 3 % by date, 13 % by depth, 1 % by the date-depth interaction and 20 % by the covariate, colony size.

Dark minor worker lean weight

If dry weight varied largely because of variation in percent fat, then lean weight should be less related to the factors, and should be less variable than dry weight.
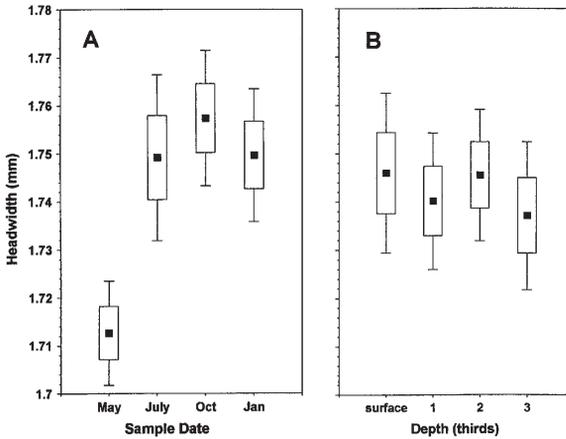
Figure 7. Mean percent fat of dark minor workers in relation to sample date, depth. Means were adjusted for the effects of colony size. Error bars show 1.0 and 1.96 standard errors around the adjusted mean
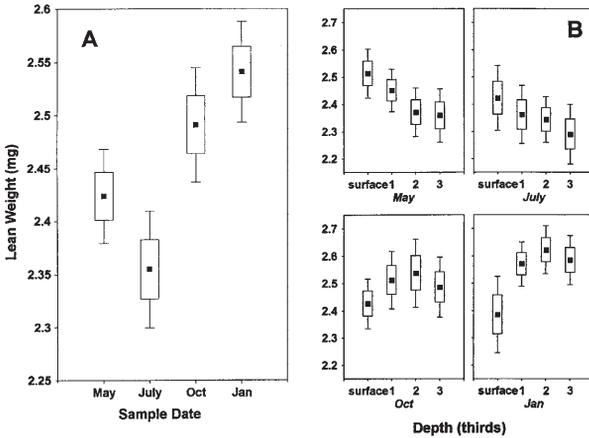
Figure 8. Lean weight of dark minor workers in relation to sample date and depth, from ANCOVA. All means were adjusted for colony size. Error bars show 1.0 and 1.96 standard errors around the adjusted mean

When the same analysis was run on lean weight of dark minor workers (0.6 power transformed), total variance dropped by almost 50%, and only sample date had a significant main effect ($F_{3,1816} = 11.2$; $p < 0.0000$) (Fig. 8A), with lean weights in July being significantly lower, and in January significantly higher than the other samples (Tukey's HSD test). Depth had no significant main effect. Lean weight declined with depth in May and July, but was not affected by depth in the other two samples, giving rise to a small but significant interaction between depth and date ($F_{9,1816} = 2.36$; $p < 0.02$) (Fig. 8B). A total of about 36% of the variance in lean weight was explained by the factors: Almost all of this was explained by the covariate, colony size, while only about 1% was explained by date and 1% by the interaction. Thus,
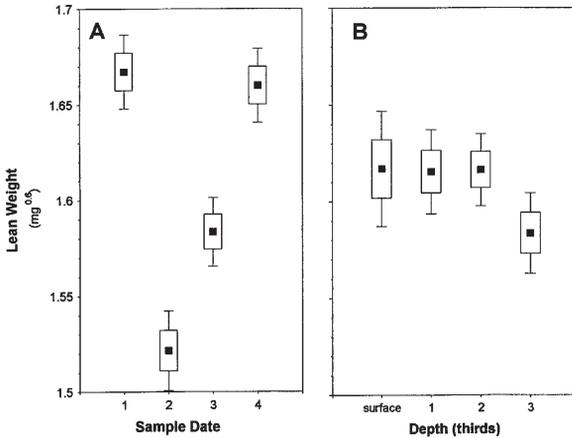
Figure 9. Headwidth of dark minor workers in relation to sample date and depth. The effect of colony size has been removed through its use as a covariate. Error bars show 1.0 and 1.96 standard errors around the adjusted mean

the removal of fat from the workers almost completely removed the effects of sample date and depth (their R^2 declined from 12% to 2%), while having no effect on the amount explained by the covariate. Removal of fat from the analysis also decreased the total variance by 50%. This suggested that the differences in dry weights caused by date, depth and colony size might result mostly from their effects on fat storage.

It seemed possible that the lean weight changes were the result of changing worker size, as measured by headwidth. Headwidth (dark minors only) was significantly related to date ($F_{3,1826} = 13.52$; $p < 0.0000$), but not to depth ($F_{3,1826} = 0.54$; N.S.) (Fig. 9). Headwidth of surface workers was significantly larger in May, showed no strong pattern in July and no significant differences in the other samples, giving rise to a small date-by-depth interaction ($F_{3,1826} = 2.78$; $p < 0.003$). The larger May surface workers may have resulted from differential survival of larger workers through the winter. Sample date explained only 1.2% of the total variance, while colony size explained 42%. Thus, almost all of the variation in mean worker headwidth was the result of differences in colony size.

However, the patterns of headwidth changes did not parallel lean weight changes, especially in July. An ANCOVA of lean weight (0.6 power transformed) by sample date and depth in which the dependent variable was adjusted not only for colony size, but also for headwidth, showed that lean weight not only varied independently of headwidth (Fig. 10), but that the seasonal change of headwidth obscured part of the change in lean weight because they were opposite (compare Figs. 9 and 10). Adjusting for headwidth in addition to colony size therefore removed the obscuring effect of headwidth changes and doubled the amount of variance explained by date (from 1.2% to 4.6%) ($F_{3,1753} = 105$; $p < 0.00000$), and resulted in a significant effect of depth ($F_{3,1753} = 6.74$; $p < 0.0005$) and depth x date interaction ($F_{9,1753} = 9.72$; $p < 0.0000$). Between May and July, dark minor lean weight dropped from

Figure 10. The lean weight of dark minor workers adjusted for colony size and headwidth. Error bars show 1.0 and 1.96 standard errors around the adjusted mean

2.35 mg to 2.01, and then returned to 2.30 mg by the following January. Lean weight averaged 2.16 in the bottom third, but about 2.23 in the other levels. Lean weight did not change with depth in May, but declined strongly with depth in July. By October, this decline is slight and by January it has disappeared. It seems possible that these effects are the result of the large nutritional taxation caused by rearing sexual and worker brood, and the recovery from that taxation in the post-brood period.

Overview, dark minor workers

Summarizing the weight trends among dark minor workers, the largest fraction of the variation in all cases was explained by colony size. Colony size explained 36% of the variance in dry weight, 34% of lean weight, 53% of fat weight, 20% of percent fat and 42% of headwidth. The slope of this relationship changed little throughout the year for dry weight, lean weight and headwidth, with the exception that all increased more slowly with colony size in January than in other months. More specifically, workers in smaller colonies were relatively heavier (or larger) in January than in other months, reducing the slope of the weight (or headwidth)/colony size relationship (Fig. 11 A). For fat weight and percent fat, the slopes of the relationship to colony size were greatest in May and decline throughout the year until January (Fig. 11 B). Percent fat was unrelated to colony size in January. All colonies showed a strong annual cycle of fat storage, but the amplitude of this cycle is greater, the smaller the colony.

Much less of the variation in weight and size was related to sample date and depth: this was highest for fat weight and percent fat (23% and 17%, respectively), was moderate for dry weight (12%) and low for lean weight and headwidth (both 2%). Both dry and lean weight cycle between a minimum in July and a maximum
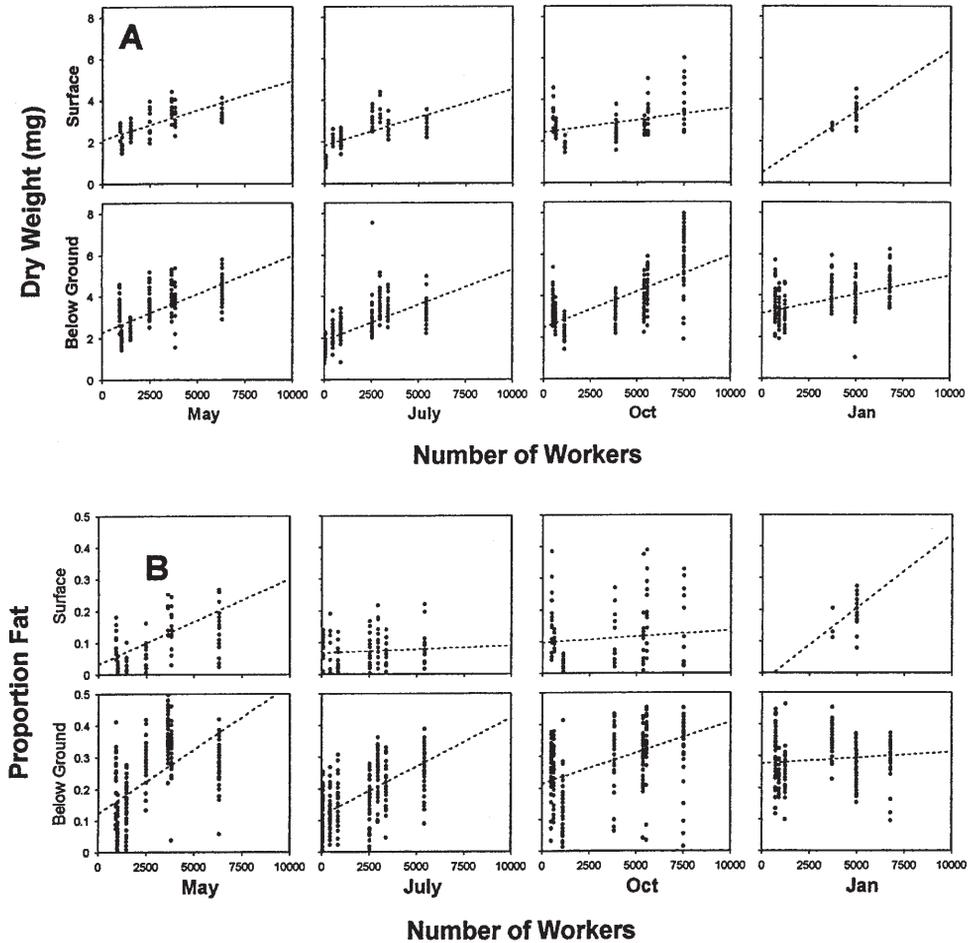
Figure 11. Dry weight and. percent fat in relation to colony size, categorized by date and depth. All below ground samples showed similar slopes were therefore grouped

in winter. Most of the weight variation is the result of changing fatiness with season, and these fatter workers are primarily located deeper in the nest, surface workers being quite lean at all seasons. Superimposed on these weight changes are smaller changes in mean headwidth whose direction was the opposite of weight changes for the first half of the year, reducing weight changes. Dark minor workers of a given headwidth and from a given colony size had the lowest dry and lean weights in July and the highest in January. Lean weight and headwidth decreased somewhat in the deepest stratum of the nest, but because the percent fat increased strongly with depth in all sample dates, dry weight was greatest in the bottom or middle thirds. Overall then, these patterns are consistent with an accumulation of fat in the second half of the year and the lower parts of the nest, probably as a result of the combined effects of the nutritionally taxing production of brood and the varying availability
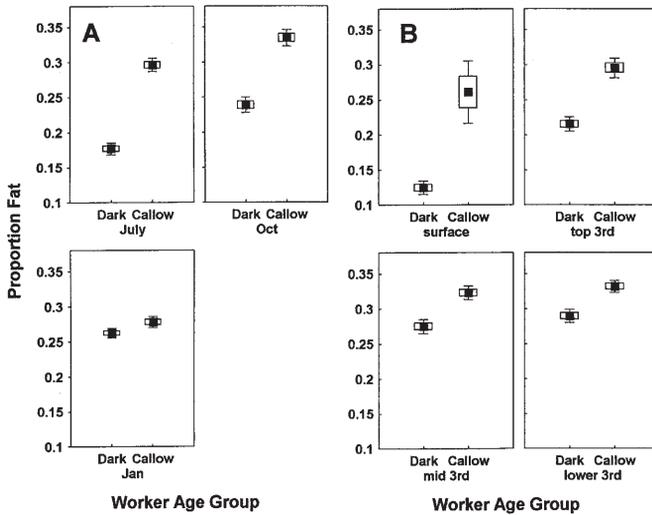
Figure 12. Comparison of % fat in dark and callow workers in relation to sample date and depth. Error bars show 1.0 and 1.96 standard errors around the adjusted mean

of food. The nutritional status of colonies improves with colony size, causing them to produce heavier, fatter and larger workers at any given time of the year.

Major worker headwidth and weights

As a result of greater variation, most effects were weaker for major workers than minors. Analyses omitted the surface workers because these were often small samples, and in order to balance the design. An ANCOVA of the headwidths of major workers by date, depth and worker age, with log number of workers as covariate showed no significant main effects of any of the factors. There was a significant interaction of headwidth with date, such that headwidth increased significantly with colony size in the July sample, but not in any others. Because this analysis accounted for the effects of date and depth, the within-cell regression of headwidth on log workers was significant ($F_{1,322} = 16.37$; $p < 0.0000$). This effect was not visible in a simple regression of major headwidth on log no. workers (see above).

As with minor workers, when it was adjusted for colony size, the dry weight of majors (0.6 power transformed) varied significantly with date (ANCOVA: Date main effect: $F_{3,187} = 3.35$; $p < 0.02$, $R^2 = 5\%$). Major workers were significantly lighter in July than in all other samples (Tukey's HSD test). Depth had no main effect on the dry weight of majors, nor was there a date-depth interaction. As expected, the within-cell regression of dry weight on colony size was significant ($F_{1,187} = 13.62$; $p < 0.0005$; $R^2 = 7\%$).

The pattern for proportion fat in major workers was almost identical to that in minors. After adjustment for colony size, date and depth both showed main effects as well as an interaction (ANCOVA: date – $F_{3,188} = 11.7$; $p < 0.0000$; depth – $F_{2,188} = 3.25$, $p < 0.05$; depth by date – $F_{6,188} = 2.49$, $p < 0.05$). Major workers

were significantly fatter in October and January than in May and July, and significantly fatter in the bottom third than at other levels. In the July sample, the effect of depth on fatness weakened, giving rise to the interaction.

After adjustment for colony size and headwidth, the lean weight of major workers (0.6 power) was significantly lower in July than in other samples, and decreased with depth (ANCOVA: date – $F_{3,187} = 18.44$, $p < 0.0000$; depth – $F_{2,187} = 3.08$, $p < 0.05$). Not surprisingly, the covariate headwidth explained 96 % of lean weight, whereas colony size added no further explained variance ($F_{2,187} = 2147$; $p < 0.00000$). Depth and date explained only about 1 % of the total variance, suggesting that their effects on the dry weight of majors ($R^2 = 5\%$) was almost all the result of their effects on fat content, as was the case for minor workers.

Callow workers

Callow workers were recognized by their lighter coloration, and occurred in all samples except May. In order to analyze callows, the May sample was deleted to yield a complete ANCOVA design. Callows were significantly different from dark workers in all measures. Overall, after adjustment for headwidth, the dry weight of callows was 4 % lower (Tukey's HSD test) than that of dark workers (main effect of worker age: $F_{1,2212} = 9.48$; $p < 0.005$). Including its interactions with depth and date, worker age explained about 1 % of the variation in dry weight. On the other hand, the relationship of worker age to lean weight was stronger (main effect, adjusted for headwidth, $F_{1,2194} = 125$; $p < 0.0000$; $R^2 = 2\%$) and callows averaged about 9 % lower in lean weight than did dark workers (Tukey's HSD test). This was the result of a significantly higher fat content in callows than dark workers (main effect of worker age, $F_{1,2204} = 85.3$, $p < 0.0000$). Callows averaged 30 % fat while dark workers averaged 23 % (significant, Tukey's HSD test), reducing the difference in dry weight compared to lean. Worker age and its interactions with date and depth explained 5 % of the variance in percent fat. The difference in percent fat between dark and callow workers decreased from May to January and with depth (Fig. 12), giving rise to significant age/date ($F_{2,2204} = 9.71$; $p < 0.0000$) and age/depth ($F_{3,2204} = 9.41$; $p < 0.00000$) interactions.

These patterns are consistent with the following worker life history. Callows eclose in the deeper portions of the nest, or segregate there early in their lives. Early in their lives, they have less lean matter but more fat than do dark workers. As they age, they gain lean matter, spend more time in the upper parts of the nest and lose fat. These opposed trends cause dry weight to peak when the workers are in the middle third of the nest. As callows age, they become indistinguishable from dark workers. Fat continues to decline until the workers become surface workers in the last days of their lives when their fat content is always lower than 10 %. Superimposed over these worker-age and depth trends are the annual cycles of fat content, lean weight and dry weight described above.

The samples did not contain enough callow major workers for a reliable analysis.
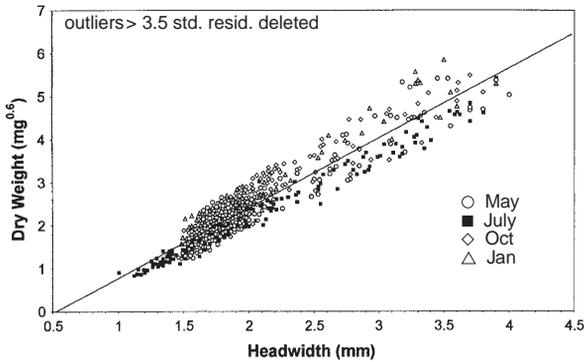
Figure 13. The relationship of dry weight and headwidth of dark workers, with the sample date indicated by symbols. A simple regression explained 83% of the variation whereas addition of sample date, depth and colony size class brought this up to 95%

The relationship between dimension and weights

The above analysis dealt with the variation of worker weight in relation to season, nest and colony size factors. However, the factor which causes most of the variation in worker weight is worker dimension (size). Worker weight increases as a power function of dimensions. If worker shape does not change with size (isometric growth), weight is proportional to the cube of the dimension, or dimension to the cube root of weight. When growth is allometric, as it decidedly is in *P. badius*, the exponent may be different from 3 (or 1/3).

Insect body weight can change within fixed dimensions by displacement of air sacs or other internal spaces, or by the expansion of telescoped parts. On the other hand, the dimensions of unjointed sclerotized structures, such as headwidth, are fixed at adult eclosion and are therefore an invariant estimate of body size. In this study, I used headwidth as an estimate of worker size and as the independent variable in a series of regressions.

Dry weight, lean weight and fat weight were transformed by raising each to the 0.6 power. This gave the best fit to linearity (as judged by analysis of residuals) in relation to headwidth in all subsequent regressions. A simple regression (Table 2) showed that lean weight was influenced by very little except headwidth ($R^2 = 95\%$), while fat weight (Fig. 14) was predominately under the influence of factors other than headwidth ($R^2 = 27\%$), these being sample date, depth and colony size. Dry weight was intermediate ($R^2 = 83\%$), as expected, because it is the sum of the lean and fat weights.

Indicator variables and interaction variables were then used in a multiple regression to test for effects of depth, sample date, colony size class and worker age on the intercepts and slopes of the headwidth-weight relationship. The best and most easily interpreted fit was obtained when each dependent variable was regressed such that slope was allowed to vary among the groups, but all were regressed to a common intercept (Fig. 13). When this model was applied to dark workers, the interactions of headwidth with sample date, depth and colony size class increased the explained variation over the simple regression by 12% for dry weight (Fig. 13), 52% for fat
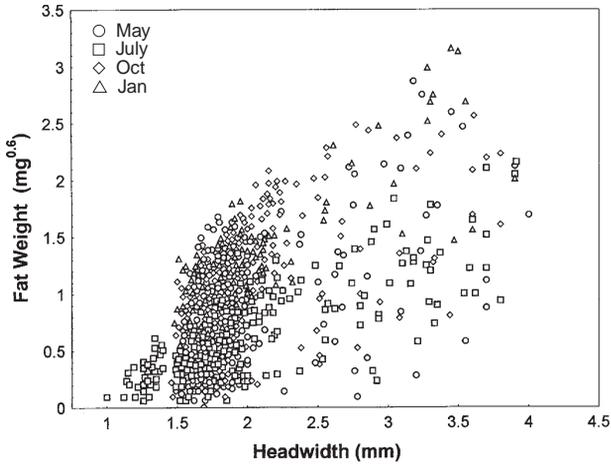
Figure 14. Fat weight of dark workers in relation to their headwidth. The sample month is indicated by symbols. Fat weight increased most slowly with headwidth in July and most rapidly in January. A simple regression explained only 27% of the variance, much of the remainder being related to sample date, depth and colony size

weight and 2% for lean weight (Table 2). In other words, the sample date, depth and colony size class determine most of the variation in fat weight, and very little in that of lean weight. Furthermore, this influence is mediated by the effect of the factors on the slope of the weight-headwidth regression. Thus, the largest slope of the lean weight regression was only 20% greater than the smallest. For dry weight, this was 33%, while for fat weight it was 600%.

The regression slopes describe the rate at which workers increase in weight with each increment in dimension. The variation of these slopes was the main cause of the differences in mean weights discussed above. This was clarified by regressing the cell means of dry, lean and fat weights from ANCOVA above against the slopes of each from the full models in Table 2 (Fig. 15). This showed that 95% of the variation in mean fat weight, 79% of the mean dry weight and 30% of the mean lean

Table 2. Results of regression of headwidth of dark workers against dry weight, lean weight and fat weight

Dependent variable	Independent variable(s)	Slope(s)	Intercept	R^2 (%)
Dry weight$^{0.6}$	Headwidth	1.63	−0.85	83
Dry weight$^{0.6}$	HW × Date, Depth, Size Class (61 combinations)	1.36 to 1.81	−0.70	95
Fat weight$^{0.6}$	Headwidth	0.64	−0.34	28
Fat weight$^{0.6}$	HW × Date, Depth, Size Class (61 combinations)	0.14 to 0.84	−0.056	80
Lean weight$^{0.6}$	Headwidth	1.41	−0.75	95
Lean weight$^{0.6}$	HW × Date, Depth, Size Class (61 combinations)	1.25 to 1.50	−0.74	97

weight was explained by slope. The fraction of the explained, full-model variation which was not explained by slope was probably partly the result of variation in mean headwidth among the samples (the cell means in Figure 15 were not adjusted for headwidth). Changes in the worker size distribution made relatively small contributions to these patterns.

In sum, mean worker dry weight varies in complex ways with colony size, sample date and depth in the nest. Most of this variation is the result of changes in the fatness of workers, but changes in mean headwidth also contribute. The magnitude of weight change increases with worker size, resulting in a positive slope in the weight-headwidth relationship. The effect of the factors on worker weight is mediated through their effect on the headwidth-weight relationship.

The weight of fat a worker contained increased with body weight, but did the proportion of fat differ with body size? When the proportion fat was plotted against dry weight (Fig. 16), it is apparent that majors and minors follow different rules of fat storage in relation to body weight. Whereas majors vary seasonally in proportion fat just as minors do, there is no relationship between their body weight and fattiness. Minors were therefore analyzed separately.

The proportion fat (arcsine-square-root transformed) of dark minor workers was regressed against dry weight, using dummy variables for sample date. Variability of proportion fat was very high, even within sample dates. Dark minor workers ranged from 2 to 45 % fat in October and May, from 15 to 45 % in January and from 2 to 35 % in July. About 54 % of this variation was explained by dry weight, with the highest slope and lowest intercept in May and the lowest slope and highest intercept in July. These effects, however, were the result of dry weight being higher *because* of the higher fat content. When proportion fat (arcsine-square-root transformed) was regressed against headwidth instead of dry weight, there was little relationship of proportion fat to body size, although the expected relationships of season and colony size were apparent in the significant differences among the intercepts (Fig. 17). Several date-by-colony size groups showed significant slopes, but these were weak
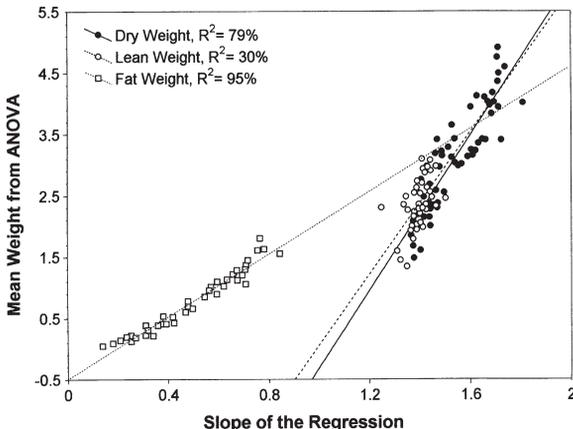
Figure 15. The mean dry weights of dark workers in relationship to the slope from the full model of the weight-headwidth regression. Slope explains 30 to 95 % of the variation in mean weight
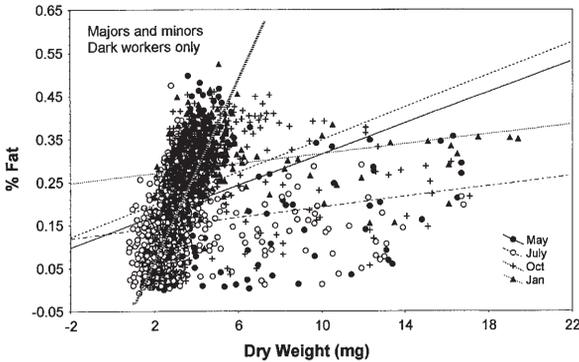
Figure 16. The proportion of fat in dark workers in relation to their body size (dry weight). Symbols and regression lines indicate the sample dates. The dense cluster of minors on the left shows a clear increase in proportion fat with body weight, whereas the scattered majors on the right do not
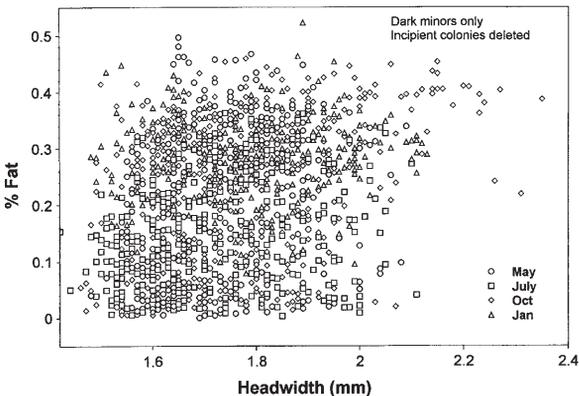
Figure 17. The proportion fat is unrelated (weakly in a few cases) to the size of dark minor workers, although fattiness varied with colony size, sample date and depth

relationships and as likely to be negative as positive. Thus, the proportion of body fat in dark minor workers depends upon factors other than its body size.

Discussion

The worker population of a colony of ants is the analog of the soma of an individual organism. Just as subdivisions of the soma carry out diverse functions in the individual, so do subdivisions of the worker population carry out the diverse functions of a colony. At least some of the seasonal and colony size-related variation among workers of *P. badius* must represent investment patterns that are part of the species' life history tactics. Variation of labor in relation to worker size and age has been

described for many ant species (Hölldobler and Wilson, 1990; Gordon, 1996a), but it has become increasingly clear that there are additional shifts of allocation and metabolism that parallel the changes of behavior. Superimposed on these behavioral changes are changes in metabolic rate (MacKay, 1983), dry weight, lean weight, fat storage, protein storage and location in the nest. Many of these change with season as well. Some of these shifts give rise to the patterns described in this paper.

Let us follow the life history changes of a typical *P. badius* worker. Our focal worker ecloses as either a minor worker, or more rarely, a much larger major. These are two subpopulations separated by a discrete developmental event (Wheeler, 1990). The linear size of our minor worker is likely to be as much as 40% or more larger if the worker eclosed in a large, rather than a small colony, and it increases by another 5% or so later in the season, but decreases somewhat if the worker was found deeper in the nest. A major worker is also likely to be smaller early in the season and deep in the nest, and larger in larger colonies, but high variability makes prediction of its size less precise. Most significantly, if our major worker was captured outside the nest, it is likely to be 12% or more smaller than one in the top third of the nest. Perhaps the largest majors are retained inside the nest as seed millers. In all but the smallest colonies, the size of majors and minors was not related, and the proportion of the population which was majors remained about 5–7% as colonies grew, but changed seasonally, rising to about 10% in July.

Our focal minor worker was most likely to have eclosed between June and October, and could be recognized by its lighter coloration. Shortly after eclosion, it was most likely to be found near the bottom of the nest. For a given linear size, it eclosed lighter and fatter than its older, darker sisters, and in the course of the season, it gained lean weight, but lost fat as it moved to reside in nest chambers ever closer to the surface. Finally, when it was of sufficient age, and its fat content was below 10%, it became a forager on the surface. At the same time that these age-related changes occurred, the worker was likely to be lightest in July after the colony had produced and flown their annual crop of sexual alates, and to gain an average of 24% by winter. It was also likely to be heavier if it came from a larger colony, and to be heavier and younger deeper in the nest.

Most, but not all, of these changes in weight were caused by changes in fat stores. Thus, our focal worker was likely to be less fat in July than at any other time, to be less fat the closer to the surface it was found, and to be more fat the larger its colony. Across all conditions, its fat content was likely to vary by 85% or more, and the variation, especially seasonal, was larger in smaller colonies. Because weight changes seem related mostly to fat storage, the lean weight of workers of a given linear size varies less than dry weight or fat weight. Nevertheless, for a given linear size, lean weight is likely to be lower in July and in the bottom of the nest, higher in a larger colony. Much of this change in lean weight may be storage protein, used for overwintering and rearing sexual brood in the early spring. These patterns were similar, though less precise, for major workers.

Altogether, these trends describe part of a colony life history in which the resources, both metabolic and labor, needed to produce sexuals early in the spring are stored in the bodies of the young workers, who also serve as the labor force to produce these sexuals. Workers reach the annual minimum fat content after producing sexuals, suggesting that the large pulse of sexuals is too expensive to be pro-

duced solely from current foraging intake. After these sexuals have flown, the colony once again switches to producing workers and storing the excess foraging intake as worker fat for overwintering and the next year's sexual-production. As colonies get larger, this proportional excess increases. It is presently unknown if these stored reserves are used *only* for sexual production, or whether colonies may "opt" to forego sexual production and invest the reserves in colony growth instead. It is possible that the improved nutritional condition of larger colonies is both the result and consequence of larger workers. An economy of scale may also contribute.

Throughout the year, the worker force is highly stratified by age within the nest. The upward movement within the nest first brings workers from the deep brood chambers into the seed chambers and finally to the surface. This migration is coordinated with changing worker behavior, resulting in division of labor. As in other species then, worker age polyethism occurs in parallel with the centripetal movement of workers away from the brood area of the nest (Hölldobler and Wilson, 1990).

My findings confirm the highly stratified organization of *Pogonomyrmex* nests. Porter and Jorgensen (1980, 1981) found that nest-defending workers of *P. owyheei* were stratified by order of emergence, and foragers were stratified among foraging trails, rarely mixing with the below-ground workers. MacKay (1983) found that workers of three species of *Pogonomyrmex* were vertically stratified in the nest, with the heavier, fatter, and metabolically slower ones near the bottom of the nest, and the older, leaner workers near the surface. However, he did not analyze fat content of callows and older workers separately, as I did, nor did he take colony size and season into account. Both MacKay (1983) and Porter and Jorgensen (1980, 1981) showed that fat content dropped sharply as workers became foragers, and that foragers suffered high rates of mortality. All these authors interpreted this as an energy-saving adaptation for the colony. Whereas I collected no behavioral data, my weight and fat trends are congruent with those reported by MacKay (1983) and Porter and Jorgensen (1981), suggesting that *P. badius* workers spin out their lives in much the same way.

In addition to fat, part of the metabolic stores of *P. badius* workers is almost certainly stored protein. Variation in such protein stores is probably the source of the 15–20% annual variation in worker lean weight (Fig. 10). Most insects sequester specialized storage-protein for situations in which demand for materials and energy exceeds income, e.g. metamorphosis. In ants, these same types of storage proteins are sequestered by virgin queens in preparation for colony founding (Wheeler and Martinez, 1995). They are also sequestered by workers during seasons in which food income exceeds demand, to be used when demand exceeds food income. Because nutrients move preferentially to brood, workers gain stores during seasons when brood are absent, resulting in a negative correlation between brood and worker metabolic stores (Wheeler and Martinez, 1995). In *P. badius*, both fat and lean weight are high in the early spring before brood production begins, drop to a minimum in July after the sexual brood have been reared, and climb back to a maximum at the end of the year. This pattern suggests that this species relies heavily on metabolic stores for rearing its first brood of the year. The use of such metabolic stores "may not be unusual" in the genus *Camponotus* (Wheeler and Martinez, 1995). In *Formica japonica* (Kondoh, 1968) such stores are reported to be used for brood rearing.

Tschinkel (1993) has argued that *Solenopsis invicta* rears its early spring sexual brood largely by drawing down the metabolic stores of its workers. An extreme example is *Prenolepis imparis*, in which all larvae are reared in a sealed nest on the metabolic stores of workers who last fed 5 to 7 months previously (Tschinkel, 1987).

As in many species of ants, workers increase in mean body size as colonies grow. The nature of this increase, however, is diverse among species, and may be related to maximum colony size. In monomorphic species such as *Myrmica rubra*, worker headwidth increased only during the first 10 % of colony growth (Brian, 1957). In *Solenopsis invicta*, both major and minor workers increased in mean size for about 5 % of colony growth, then remained constant. All further increases in mean worker size (minors and majors together) were achieved by increasing the proportion of majors in the worker population (Tschinkel, 1988). Majors and minors increased in size for only 1 % of colony growth in *Atta* (Wilson, 1983). In contrast, *P. badius* majors neither increased significantly in size as colonies grew, nor did their proportion of the total worker population change. However, minor workers continued to increase in size throughout colony growth. Thus, most of the increase in mean worker size in *P. badius* was caused by the increasing size of minors.

The worker headwidth-distribution of *P. badius* is similar to that in *S. invicta*, in that both consist of two more-or-less normally-distributed, slightly overlapping subpopulations (Tschinkel, 1988). Based on mechanisms proposed by Wheeler (1986), Tschinkel suggested that the major and minor subpopulations of *S. invicta* were separated by a single, discrete developmental event, such that majors were reprogrammed to pupate at larger and more variable sizes. This mechanism applies equally well to *P. badius* (Fig. 1). The larger than expected number of majors of extreme size may be the result of some upper size limit.

The relationship between weight and headwidth in *P. badius* is decidedly allometric, with an exponent of 0.6, compared to 0.33 for isometry. In this regard, *P. badius* is similar to *Atta* and other allometric, polymorphic species (Wilson, 1953; 1954), rather than to the isometric *S. invicta* (Porter and Tschinkel, 1985b; Wilson, 1978).

The life history strategy of *P. badius* thus includes worker size and fatness increases as the colony grows, predictable age-related patterns of distribution and upward movement within the nest, and complex fat and weight changes as workers age and the seasons wax and wane. Whereas many of the larger weight changes can be reasonably related to some aspect of fitness, some of the minor variation may be epiphenomena without adaptive significance. For example, the small seasonal changes in minor worker headwidth may be an incidental consequence of colony nutritional status or changes in worker-to-brood ratio (Porter and Tschinkel, 1985a). Ultimately, the importance of all such variation to the sexual output of the colony must be shown before a conclusion about adaptiveness can be drawn. Studies such as this one are the first step on this path.

Acknowledgements

References

Beshers, S.N. and J.F.A. Traniello, 1994. The adaptiveness of worker demography in the attine ant, *Trachymyrmex septentrionalis*. *Ecol. 75*:763–775.

Beshers, S.N. and J.F.A. Traniello, 1996. Polyethism and the adaptiveness of worker size variation in the attine ant, *Trachymyrmex septentrionalis*. *J. Ins. Behav. 9*:61–83.

Brian, M.V., 1957. The growth and development of colonies of the ant *Myrmica*. *Insectes soc. 4*:177–190.

Calabi, P. and S.D. Porter, 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. *J. Insect Physiol. 35*:643–649.

Gordon, D.M., 1996a. The organization of work in social insect colonies. *Nature 380*:121–124.

Gordon, D.M., 1996b. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecol. 77*:2393–2409.

Hölldobler, B., 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav. Ecol. Sociobiol. 1*:1–44.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Belknap/Harvard Press, Cambridge, pp. 732

Kondoh, M., 1968. Bioeconomic studies on the colony of an ant species, *Formica japonica*. I. Nest structure and seasonal changes of the colony members. *Japan J. Ecol. 18*:124–133.

MacKay, W.P., 1983. Stratification of workers in harvester ant nests (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc. 56*:538–542.

Mirenda, J.T. and S.B. Vinson, 1981. Division of labor and specification of castes in the red imported fire ant *Solenopsis invicta* Buren. *Anim. Behav. 29*:410–420.

Oster, G.F. and E.O. Wilson, 1978. *Caste and Ecology in the Social Insects*, Princeton Univ. Press, Princeton, NJ, pp. 352.

Porter, S.D., 1983. Fast, accurate method of measuring ant head widths. *Ann. Entomol. Soc. Amer. 76*:866–867.

Porter, S.D. and C.D. Jorgensen, 1980. Recapture studies of the harvester ant, *Pogonomyrmex owyheei* Cole, using a fluorescent marking technique. *Ecol. Entomol. 5*:263–269.

Porter, S.D. and C.D. Jorgensen, 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? *Behav. Ecol. Sociobiol. 9*:247–256.

Porter, S.D. and C.D. Jorgensen, 1988. Longevity of harvester ant colonies in southern Idaho. *J. Range Managem. 41*:104–107.

Porter, S.D. and W.R. Tschinkel, 1985a. Fire ant polymorphism (Hymenoptera: Formicidae): factors affecting worker size. *Ann. Entomol. Soc. Amer. 78*:381–386.

Porter, S.D. and W.R. Tschinkel, 1985b. Fire ant polymorphism: the ergonomics of brood production. *Behav. Ecol. Sociobiol. 16*:323–336.

Schmid-Hempel, P., 1992. Worker castes and adaptive demography. *J. Evol. Biol. 5*:1–12.

Traniello, J.F.A., 1989. Foraging strategies of ants. *Annu. Rev. Entomol. 34*:191–210.

Traniello, J.F.A. and S.N. Beshers, 1991. Polymorphism and size-pairing in the harvester ant *Pogonomyrmex badius*: a test of the ecological release hypothesis. *Insectes soc. 38*:121–127.

Tschinkel, W.R., 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol. 22*:103–115.

Tschinkel, W.R., 1987. Seasonal life history and nest architecture of the winter-active ant, *Prenolepis imparis*. *Inectes. soc. 34*:143–164.

Tschinkel, W.R., 1991. Sociometry: a field in search of data. *Insectes soc. 38*:77–82.

Tschinkel, W.R., 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecol. Monog. 64*:425–457.

Wheeler, D.E., 1986. Developmental and physiological determination of caste in social Hymenoptera: evolutionary implications. *Am. Nat. 128*:13–34.

Wheeler, D.E., 1990. The developmental basis of worker polymorphism in fire ants. *J. Insect Physiol. 36*:315–322.

Wheeler, D.E. and T. Martinez, 1995. Storage proteins in ants (Hymenoptera: Formicidae). *Comp. Biochem. Physiol. 112B*:15–19.

Wilson, E.O., 1953. The origin and evolution of polymorphism in ants. *Quart. Rev. Biol. 28*:136–156.

Wilson, E.O., 1954. A new interpretation of the frequency curves associated with ant poly-morphism. *Insectes soc. 1*:75–80.

Wilson, E.O., 1968. The ergonomics of caste in the social insects. *Am. Nat. 102*:41–66.

Wilson, E.O., 1978. Division of labor in fire ants based on physical castes (Hymenoptera: Formici-dae: *Solenopsis*). *J. Kansas Entomol. Soc. 51*:615–636.

Wilson, E.O., 1983a. Caste and division of labor in leaf-cutter ants: IV. Colony ontogeny of *Atta cephalotes*. *Behav. Ecol. Sociobiol. 14*:55–60.

Wilson, E.O., 1983b. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) III. Ergonomic resiliency in foraging by *A. cephalotes*. *Behav. Ecol. Sociobiol. 14*:47–54.

Wilson, E.O., 1985. The sociogenesis of insect colonies. *Science 228*:1489–1495.

Wood, L.A. and W.R. Tschinkel, 1981. Quantification and modification of worker size variation in the fire ant *Solenopsis invicta*. *Insectes soc. 28*:117–128.