

# Sociometry and Sociogenesis of Colony-Level Attributes of the Florida Harvester Ant (Hymenoptera: Formicidae)

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**ABSTRACT** This study addressed how collective, supra-organismal colony characteristics change during growth (sociogenesis) from the founding queen to maturity and through the seasons. A total of 31 harvester ant colonies representing a full range of sizes was excavated on 4 sample dates during the year. The data were analyzed for growth-related and seasonal patterns. The subterranean nests consisted of horizontal chambers connected by vertical tunnels. The total area of these nests increased more slowly than did the colony population, leading to an increase in mean worker density, which also varied seasonally. Nest area grew somewhat more rapidly through nest deepening and addition of new chambers than it did through the enlargement of chambers. The mean weight and headwidth of workers increased with colony size, but this size increase was limited to the minor workers. The major workers made up  $\approx 7\%$  of the worker population, a proportion that did not vary with colony size. The total weight and number of seeds stored by colonies increased isometrically with colony size, so that the milligram of seeds per milligram of ant biomass did not change. However, the weight of seeds increased more rapidly than did the population of dark (older) workers who collected them, so that the foragers of larger colonies each collected more seeds than their counterparts in smaller colonies. Large colonies contained up to 300,000 seeds. Colonies of fewer than 60 workers collected smaller seeds, but larger colonies showed no relationship between mean worker size and seed size. Brood production was limited to May-September. Sexu-als were produced only in the early spring, before any workers, by colonies with  $>2,500$  workers ( $\approx 1/3$  of maximal colony size). In the summer, colonies of all sizes produced only workers. The seasonal patterns of colony fat reserves suggest that colonies draw on these reserves to overwinter and produce sexuals, then they rebuild the reserves during the summer. The size of the fat reserves increased much more rapidly than did colony size, suggesting that changes in colony composition and function lead to better nutrition. All indicators of colony growth rate increased more slowly than did colony size. These included the ratio of brood to workers, callow workers to dark workers, and the number of developing follicles in the queen's ovaries. These decreases were also reflected in raw birth rates (individuals per day) that increased half as rapidly as did colony size, and colony growth rates (percent per day) that decreased by half with each 10-fold increase in colony size. These patterns are discussed in relation to colony function, ontogeny and life history.

**KEY WORDS** Florida harvester ant, colony size, colony growth, seed storage, development, seasonality

In SOCIAL INSECTS, individuals are organized into colonies, giving rise to 2 levels of biological organization—the organismal level and the colony level, or supra-organismal. Because colonies are, to a large extent, the primary units of natural selection in social insects, colony-level attributes and processes are the products of evolution. The existence of this additional level of organization has led to the formulation of the super-organism concept, drawing attention to social processes and structures that are analogous to those occurring in organisms (Wilson and Sober 1989, Hölldobler 1991, Ratnieks and Reeve 1992). By analogy with organisms, there is an expectation that social insect colonies also have a consistent size, arrangement of parts, and pattern of development. The characteristic mature colony size (worker number) of species of social insects ranges from a few dozen individuals to many millions (Hölldobler and Wilson

1990, table 3-2) and is always the product of growth and development. Tschinkel (1991) suggested that the inventory of colony attributes (sociometry) and development are important to understanding insect sociality. Wilson (1983) and Tschinkel (1993) described the ontogeny (called “sociogenesis” by Wilson) of 2 ant societies from the founding queen to the mature colony, and they showed that many attributes change in predictable ways, often with parallel changes in functions. In fire ants, colony size predicted many colony-level attributes, including mean worker size, proportion major workers, worker:brood ratio, mound volume, territory size, respiration rate, fat storage, sexual production, and production rates (Tschinkel 1993, Tschinkel et al. 1995). All these were related to each other through their relative rates of change with colony size, making analysis through the methods of morphometry particularly useful.

In social insects, knowledge of sociometry and sociogenesis are also important to any study of life history evolution at the colony level. Life history strategies are characterized by particular states of such attributes as colony size, colony age at 1st reproduction, investment in sexuals, colony growth, colony longevity, seasonal patterns, and many other attributes (Stearns 1992). Bourke and Franks (1995) reviewed theory and case studies of life history evolution in ants. Sociogenic data can be collected most conveniently from a series of colonies that span from newly founded to mature. By repeating such sampling on several well-chosen dates throughout the year, seasonal changes can also be determined (Tschinkel 1993). Systematic collection of sociometric and sociogenic data from many species will facilitate comparative study and contribute to an understanding of life history evolution in social insects. This article is 1 of a series on the sociometry and sociogenesis of the harvester ant, *Pogonomyrmex badius* (Latreille). Articles on worker characteristics and the spatial distribution of nest contents have been published (Tschinkel 1998, 1999). An article on nest architecture will follow.

### Materials and Methods

The 25-ha study site was located in the Apalachicola National Forest  $\approx$ 16 km southwest of Tallahassee, FL. Soils are excessively drained, almost pure, deep sands. Vegetation consists of mostly sparse, young longleaf pines with an herbaceous groundcover containing abundant cactus (*Opuntia* sp). The site supports a large population of *P. badius* along with *Solenopsis geminata* (F.), *Forelius pruinosus* (Roger), *Trachymyrmex septentrionalis* (McCook), *Prenolepis imparis* (Say), *Conomyrma pyramica* (Roger), and several other less common species.

Colonies were sampled and excavated 4 times during 1989–1990 to cover a 1-yr cycle: 25 April–23 May, 10 July–10 August, 16 October–7 November, 16 January–5 March. These 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.

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 leaving the colony upon disturbance. A pit was dug next to the colony, and chambers were progressively exposed in their horizontal aspect, 1 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. Chamber height was almost invariant. At intervals as the dig proceeded, soil

temperature was measured. Depending on colony size, 1–2 d were required to complete an excavation.

In the laboratory, the workers and brood from each chamber were sorted, counted, and oven-dried at 50°C for several days. Light-colored workers were regarded as callows and were analyzed separately from dark-colored workers. The primary data for this study were counts of the different types of individuals in each chamber. Analysis of weights, 1999, fat content, and the vertical distribution of nest contents have been published (Tschinkel 1998). Data on nest architecture will appear elsewhere.

Seeds were oven dried and, using standard testing sieves of decreasing mesh size, sifted into 10 size categories (sieves number 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. For this study, the weight of seeds in all chambers was summed to give a colony total.

Queens were returned to the laboratory live, where they were weighed and dissected within hours of capture. Ovarian function was estimated as the number of vitellogenic (opaque) follicles. The contents of the spermatheca were dispersed in 1 ml 0.5 N NaCl, and the sperm were counted in a hemacytometer as in Tschinkel (1987).

**Data and Data Analysis.** The basic data consisted of the counts and weights of all types of colony members and seeds, as well as measurements of chamber area and nest depth. These were aggregated to the colony level, and were used to calculate various totals and ratios. Data were analyzed by regression or analysis of variance (ANOVA) using Statistica-W4.5 (Statsoft 1994). Log transformations were applied as needed to stabilize the variance. The effect of season was tested in regressions through the use of indicator variables. With a few exceptions, the best-fit regression model was one in which the intercepts were allowed to vary, but all groups shared a common slope.

### Results

**Nest Depth, Total Nest Area, and Chamber Number.** As colonies grow, they of course excavate larger nests. This increase could result from larger chambers, more chambers, deeper nests, or all of these. The majority of excavation is carried out by dark, older workers, but it is possible that callows help to deepen the nest. All measures of nest size increased more slowly than did measures of colony size. The maximal depth of the nest approximately doubled for every 10-fold increase in the worker population (Table 1, regression 1), and the total chamber area increased 7-fold (Fig. 1) (Table 1, regression 2). These relationships did not change with season (sample date), nor were there any interactions between date and worker number. The total area increased more slowly in relation to the total colony weight (sum of the weight of all colony members): a 10-fold increase in colony weight was associated with only a 5.6-fold increase in

Table 1. Summary of regressions of various dependent measures (y) against colony size (x), in the form  $\log y = b + a \log x$

Regression no.	Dependent variable (y)	Independent variable (x)	df	Mean slope	SE	t vs. 0	P	Sample date	y-Intercept	t of difference	P	Adj. R <sup>2</sup> , %
1	Max nest depth	No. workers	29	0.36	0.040	8.97	<0.00001	All	0.96	7.45	<0.00001	73
2	Total area	No. workers	29	0.87	0.044	19.6	<0.00001	All	0.55	3.98	<0.00004	93
3	Total area	Total colony weight	29	0.40	0.040	19.1	<0.00001	All	0.15	2.64	<0.02	92
4	No. chambers	No. workers	29	0.47	0.050	9.30	<0.00001	All	-0.31	-0.20	n.s.	74
5	Mean chamber area	Colony weight	29	0.34	0.035	9.83	<0.00001	Oct.	0.39	-2.36	<0.05	76
6	Workers/cm <sup>2</sup>	Colony weight	28	0.12	0.057	2.06	<0.05	Others	0.54	9.83	<0.00005	10
7	Workers/cm <sup>2</sup>	No. workers	28	0.14	0.12	1.21	n.s.	May, July	-0.52	-2.36	<0.05	27
8	Mean headwidth of minors	No. workers	29	0.22	0.018	12.3	<0.00001	Oct. Jan.	0.31	0.78	n.s.	84
9	Total weight seeds	Colony weight	28	1.10	0.067	16.5	<0.00001	All	0.71	2.41	<0.02	90
10	Total weight seeds	No. dark workers	28	1.29	0.075	17.1	<0.00001	All	1.03	18.0	<0.00001	91
11	Total weight seeds	No. brood	14	1.70	0.19	9.13	<0.00001	May, July	0.48	1.86	n.s.	85
12	No. of seeds	No. workers	27	1.17	0.094	12.4	<0.00001	May, July	0.10	0.2	n.s.	84
13	Mean seed weight	No. workers	29	0.16	0.055	2.96	<0.01	Oct. Jan.	0.86	3.01	<0.01	21
14	Mean seed weight	Mean minor headwidth	29	0.54	0.25	2.15	<0.05	All	0.50	2.20	n.s.	11
15	Total no. brood	No. workers	20	0.77	0.075	10.3	<0.00001	May, Oct.	-0.07	-0.51	n.s.	83
16	No. callow workers	No. dark workers	20	0.85	0.057	15.0	<0.00001	July	-0.28	-0.11	n.s.	91
17	Queen weight	No. vitello. follicles	18	0.10	0.035	2.98	<0.01	Excluding May	0.44	3.93	<0.001	25
18	No. vitellogenic follicles	Total worker weight	18	0.31	0.037	8.27	<0.00001	May, July	1.44	18.7	<0.00001	93
19	Worker birth rate (day <sup>-1</sup> )	No. workers	7	0.70	0.059	11.8	<0.00001	Oct.	1.56	2.69	<0.02	95
20	Worker/worker-day	No. workers	7	-0.30	0.059	-5.13	<0.005	Oct.	1.17	9.05	<0.00001	93
21	Sexuals/day	No. workers	2	0.30	1.01	0.30	n.s.	Oct.	-0.10	-15.5	<0.00001	95
22	Mg worker/mg worker-day	Total worker weight	7	-0.29	0.067	-4.40	<0.005	July only	-0.94	-5.48	<0.001	76
23	Total weight fat	Colony weight	27	1.24	0.040	30.7	<0.00001	May only	-0.15	-0.04	n.s.	70
24	Proportion worker fat	Colony weight	28	0.18	0.040	4.58	<0.00001	May, July	-1.74	-11.8	<0.00001	97
								Oct. Jan.	-1.50	3.11	<0.01	97
								Not Oct.	-1.37	-9.03	<0.00001	48
								Oct.	-1.21	-2.11	<0.05	

Only significant effects were tabulated. n.s., not significant.



Fig. 1. Growth of the nest in relation to the number of workers, showing total chamber floor area, number of chambers, and mean chamber area. All measures increase more slowly than the colony population. See text for details.

total area (Table 1, regression 3). Again, there was no effect of sample date and no interaction.

Total chamber area increased both because the number and the size of chambers increased. Every 10-fold increase in worker number resulted in a 3-fold increase in the number of chambers (Table 1, regression 4) (Fig. 1) and a 2.1-fold increase in the mean chamber area (Table 1, regression 5) (Fig. 1). In October, colonies of a given size had smaller chambers, an effect of the higher worker density later in the year, not changes in mean chamber size. Chamber-size distribution of all but incipient colonies was highly skewed, with a few large chambers and many more small ones. When colonies were grouped into 4 size classes, the logarithms of their chamber areas were approximately normally distributed, except that the next to largest size class deviated somewhat from log-normal because of deficits in the abundance of middle-sized chambers and an excess in very large chambers. None of these differences, however, was very large. In all colonies, chamber size decreased with depth, a pattern described in Tschinkel (1999).

**Mean Worker Density.** Altogether, because nest area increased more slowly than any measure of colony size, crowding must increase with colony size. This was supported by regressing overall worker density (workers per square centimeter) against colony weight (Table 1, regression 6). Colony weight explained 10% of the variation in worker density, a 10-fold increase in colony weight resulting in an  $\approx 1.3$ -fold increase in worker density (Table 1, regression 6). Using the total number of workers as the colony size estimate explained 27% of the variation in worker density, but most of this was associated with the higher worker densities in October and January, rather than the effect of colony size, which was not significant (Table 1, regression 7). It is thus uncertain whether there is a true increase in worker density associated with colony size. It should be noted that density is highly unevenly distributed within the nest and differs for callow workers, older workers, and brood (Tschinkel 1998). These more geographically specific densities are probably more biologically meaningful than the overall density.

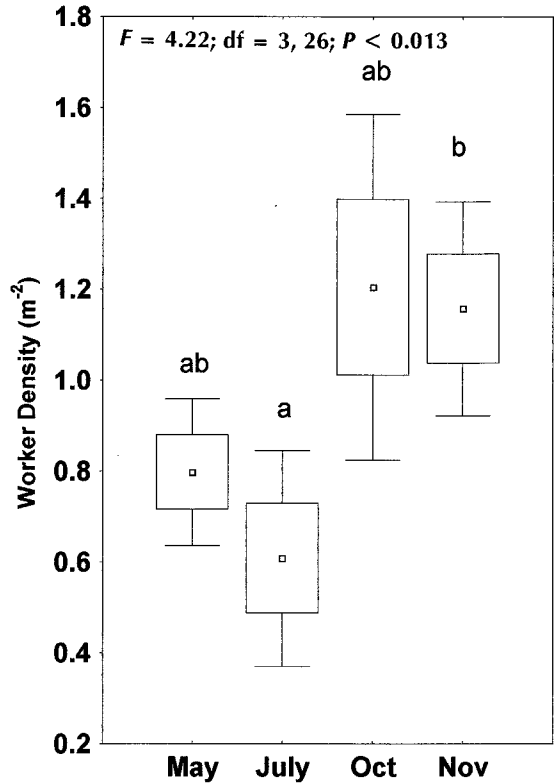


Fig. 2. Seasonal variation in mean worker density. Workers per square centimeter was significantly higher in the fall and winter than in spring and summer. This must have been at least partially the result of worker mortality without replacement during winter and spring. Means with the same letter are not significantly different (ANCOVA).

When worker density was adjusted for any effect of colony size, it clearly varied with the seasons, reaching a high point in the autumn and winter and a low in July (analysis of covariance, ANCOVA: effect of sample date,  $F = 4.22$ ;  $df = 3, 26$ ;  $P < 0.02$ ; Fig. 2). The fact that the total nest area was not related to season (Fig. 1) suggests that the worker populations were fluctuating on an annual cycle within nests of fixed or irregularly increasing size or both. Most of the year's workers were produced between July and October, probably accounting for the increase in density over the summer. May colonies produce very few workers (they produce sexuals instead), which suggests that the density decline between January and July resulted from worker mortality without replacement. Of course, the spring density decrease could also have resulted from excavation of more space, or both processes could operate together. It will be necessary to track the populations of individual colonies throughout the year to separate these 2 sources of density-variation.

**Worker Size (Minor, Major).** Mean worker size increased as colonies grew, but this was almost entirely due to the increase in the size of minor workers, whose headwidth increased by 1.7-fold over the range of colonies in this study (Table 1, regression 8).

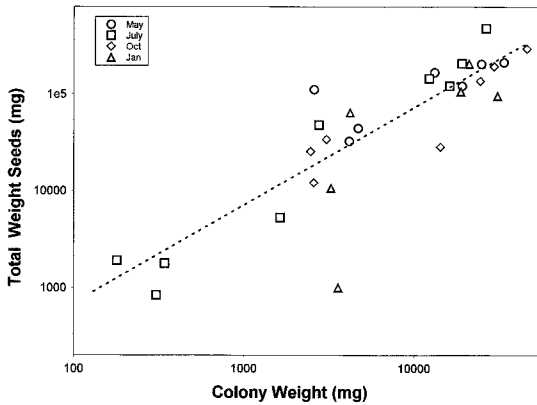


Fig. 3. Total weight of seeds stored in relation to colony size. The slope of the log-log regression was 1.07, not significantly different from 1.0. Colonies therefore store the same weight of seeds per milligram of ant, no matter what the colony size.

Worker size–colony size relationships are analyzed in more detail in Tschinkel (1998). The populations of major and minor workers increased isometrically with one another, so that their proportion did not change with colony size (Tschinkel 1998).

**Seed Stores.** The storage of seeds increased in direct proportion to colony needs (Table 1, regression 9; Fig. 3). The slope of this relationship was not significantly different than 1.0, suggesting that the seed stores grew isometrically with the colony biomass. However, the seed stores increased almost twice as fast as did the population of dark workers collecting them (Table 1, regression 10), suggesting that collection efficiency increased with colony size. When the total weight of seeds was adjusted for the number of workers in the colony (ANCOVA), no significant effect of season was found. If the worker population undergoes an annual

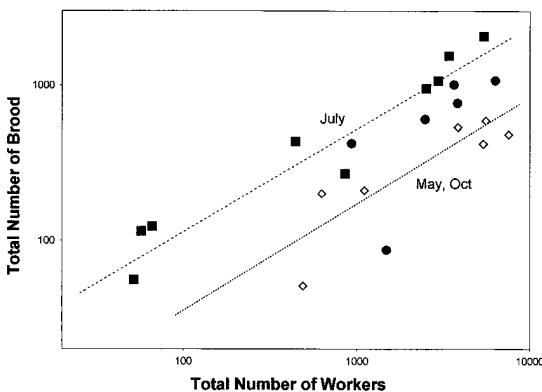


Fig. 4. Number of brood increases more slowly than does the number of workers. For every 10-fold increase in worker number, there is an  $\approx 6$ -fold increase in brood number. Whereas the number of brood is lower in May and October, the relationship of that number to colony size is the same (slopes not significantly different).

cycle of increase and decrease (as suggested by worker density), then seed stores must vary in parallel.

However, if it is primarily the larvae that are fed on seeds, the seed stores grow much more rapidly than the population of larvae (Table 1, regression 11). A 10-fold increase in the number of larvae is associated with a 50-fold increase of seed stores. Whether this leads to improved larval nutrition is an open question.

Large colonies stored up to 300,000 seeds, the result of a minimum of 300,000 forager trips. At the other extreme, the single incipient colony had only 20 seeds. The number of seeds increased somewhat more rapidly than did the number of workers (Table 1, regression 12) but was not significantly different from isometry (1.17 versus 1.0;  $t = 1.8$ ,  $df = 27$ ; not significant). For colonies of a given number of workers, colonies contained fewer seeds in October and January than in May and July, but these differences were not large. They probably resulted from increases in the worker population rather than decreases in seed stores.

The size distributions of seeds in all nests overlapped broadly. Differences in the seed-diameter distributions were tested using the proportion of seeds in each seed-diameter class (sieve) for each colony. Colonies in the very smallest size class contained mostly very small seeds, whereas the distributions of all larger colonies were fairly similar, middle sized seeds being of greatest abundance. Thus, the smallest 3 seed classes made up 46% of the total number in colony size class 0, and 19% in size class 1, but only 8–11% in the largest 3 size classes. By contrast, the 3 middle classes of seeds made up only 30% of the total in size class 0, but nearly half in larger colonies. These shifts in relative abundance resulted in a significant colony size by seed-diameter interaction (ANOVA of proportion, seed size class by colony size class interaction:  $F = 1.96$ ;  $df = 32, 219$ ;  $P < 0.005$ ;  $R^2 = 16\%$ ).

**Sieving Separates Seeds by Diameter.** I used the mean weight of seeds in each diameter class to estimate mean seed weight by colony. For the ANOVA, mean seed weight of each seed-diameter class was weighted by the number of seeds in that class. I found that mean seed weight varied significantly with colony size (ANOVA of log seed weight by colony size class, sample date. Main effect of size class:  $F = 4,310$ ;  $df = 4, 1,865,939$ ;  $P < 0.000001$ ;  $R^2 = 0.9\%$ ). The mean weight of seeds increased significantly with each size class (Tukey honestly significant difference [HSD] test), from 0.72 mg in colony size class 0 to 2.00 in size class 4. This effect was also reflected in a significant relationship between the colony mean of seed weight and the number of workers (Table 1, regression 13). Seed weight also changed with sample date (main effect of date:  $F = 7928$ ;  $df = 3, 1,865,939$ ;  $P < 0.00001$ ;  $R^2 = 1.2\%$ ), being larger in July and October than in January and May (Tukey HSD test).

Because seed weight is approximately proportional to the cube of the diameter, the small differences in seed-diameter distribution detected by sieving, combined with very large sample sizes (>1.8 million seeds), resulted in significant differences in mean seed weight, but very little explained variance ( $\approx 2\%$ ).

These differences in mean seed size probably have little biological importance, except in the very smallest colonies whose tiny workers seem to collect mostly the smallest seeds. Regression of mean minor worker size against mean seed weight showed that colonies with smaller workers collected smaller seeds (Table 1, regression 14), but this effect was barely significant and was entirely due to the smaller seeds collected by the tiny workers of colonies with fewer than 60 workers. For all larger colonies, there was no relationship between mean worker size and mean seed size. If larger colonies collect larger seeds as a result of the increasing body size of their worker force (Table 1, regression 8), these effects are not detectable.

**Brood:Worker Ratio.** The decline of colony growth in larger colonies is reflected in a lower ratio of brood to workers. Every 10-fold increase in workers was associated with an  $\approx 6$ -fold increase in the number of brood (Fig. 4) (Table 1, regression 15). The brood number is lower in May and October, but the slope of the relationship with worker number was not significantly different from that in July. Considering only the July sample, this means that the colony-level brood:worker ratio declined from an average of 1.4 in incipient colonies of  $\approx 60$  workers to 0.33 in colonies of 6,000 workers. This is similar to the 4-fold change in birth rate noted below. However, minor workers get larger as colonies get larger, so that a simple count somewhat underestimates the total production of new biomass.

**Ratio of Callows to Dark Workers.** As with brood, the populations of callow workers increased less rapidly than did those of dark workers (Table 1, regression 16). A 10-fold increase in dark workers was associated with a 7-fold increase in callows. This is in line with the decline in all measures of colony growth with colony size. When the May sample, which lacked callows, was eliminated from the analysis, the number of callows did not vary seasonally (there were no significant differences in the intercepts for sample dates). This is somewhat surprising, but is probably the outcome of processes with opposite directions—the production of new callows by dark workers, the aging of callows into dark workers, and the death of dark workers through aging.

**Queen Reproductive Activity.** Queen body weight did not vary significantly in relation to either colony size or sample date. Apparently, the queen's reproductive output does not require enough ovarian hypertrophy to have much effect on her body weight. Using only the samples in which ovaries showed substantial activity (May and July), the queen's body weight was found to increase significantly with the number of vitellogenic follicles (Table 1, regression 17), but the rate of increase was small and explained  $< 20\%$  of the variation in queen weight. Other sources contribute much more to queen body weight variation than does ovarian development. Queens were significantly heavier in October than in other months.

However, the queen's ovarian function was strongly related to both colony size and sample date (Fig. 5, January excluded). Every 10-fold increase in colony

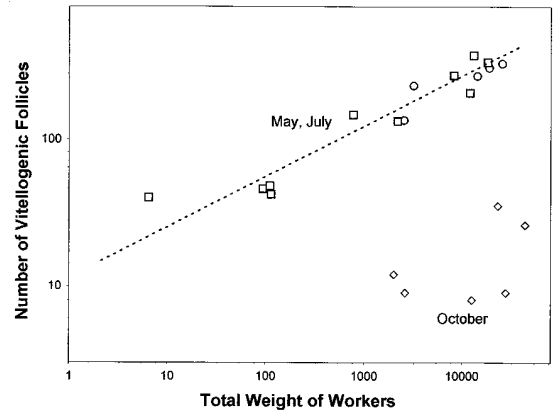


Fig. 5. Queen's reproductive activity, as estimated from the number of vitellogenic oocytes, increased more slowly than did the population of workers. By October, the queen's reproductive system was shutting down, and in January it was inactive.

size increased the number of vitellogenic follicles in the queen's ovaries by 2-fold (Fig. 5; Table 1, regression 18). The relationship in May was not significantly different from that in July, but in colonies of similar size in October, the number of follicles was only  $\approx 5\%$  of the value in the summer (Table 1, regression 18). As with other estimates of reproductive rate, this measure lagged colony size, probably contributing to the slowing of colony growth and the attainment of a maximal colony size.

Sperm counts ranged from 0.3 to 1.5 million, but were unrelated to colony size.

**Birth Rates and Colony Growth Rates.** Colony birth rates were estimated from the number of pupae present, the soil temperature of the chambers in which they were found, and the length of the pupal period (days) at that temperature, as determined in the laboratory. Both raw birth rates (workers per day, sexuals

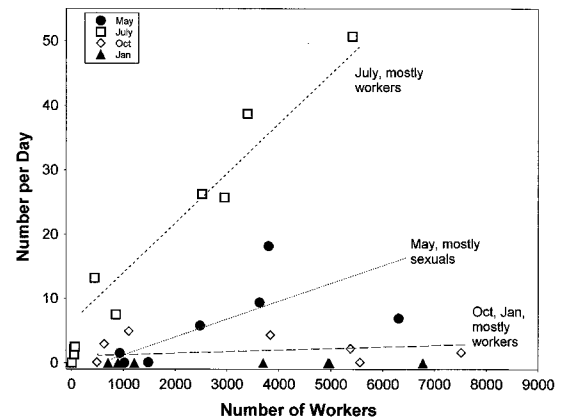


Fig. 6. Colony birth rate (workers per day) in relation to colony size and season. High rates of worker production were observed only in July. Colonies produced only sexuals in May, and ceased brood production in the fall.

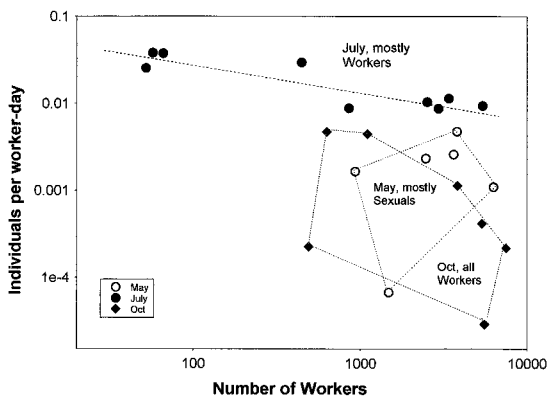


Fig. 7. Specific birth rate (workers per worker-day) declines as colonies increase in size. This relationship can be reliably estimated only in the July sample. In May, colonies produce almost only sexuals, and in October, brood production is shutting down. In July, each 10-fold increase in colony size is accompanied by a 50% decrease in the specific birth rate.

per day) (Fig. 6) and colony growth rates (workers per worker-day, sexuals per worker-day) (Fig. 7) were computed. High worker birth rates were observed only in July. May colonies produced almost only sexuals. Birth rates in October were much lower, averaging <5% of the July rates and showing no significant relationship to colony size (Fig. 7). In the winter, colonies shut down brood production entirely.

Birth rates were thus analyzed only for the May and July colonies. In July, larger colonies had higher raw birth rates (Table 1, regression 19), but these increased only  $\approx 5$ -fold for every 10-fold increase of colony size. As a result, the colony growth rate (workers per worker-day) declined by 50% for every 10-fold increase in the number of workers (Table 1, regression 20). The growth rates of colonies at the lower end of the sampled size range were thus  $\approx 3\%$  per day,

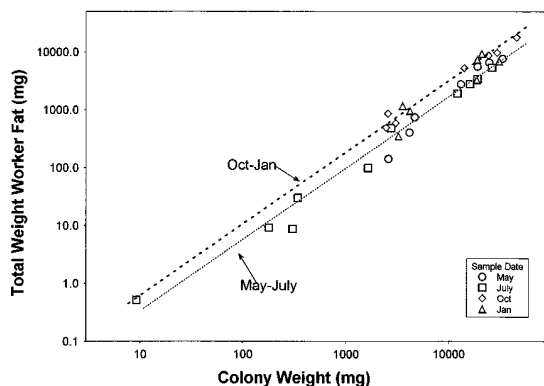


Fig. 8. Total weight of fat stores increases more rapidly than does colony weight, so that there is more energy reserve per individual in larger colonies than small. This fat reserve is drawn down during overwintering and early-spring sexual production, so that fat stores are smaller in the 1st half of the year than in the 2nd.

whereas those at the upper end were <1% per day. Such decreases are undoubtedly associated with logistic growth and the attainment of an upper, stable colony size limit.

The birth rates of sexuals followed a radically different pattern from that of workers. Only May colonies larger than 2,000 workers produced sexuals (Fig. 7). Considering only colonies that produced sexuals, there was no significant relationship between the sexual birth rate ( $\text{day}^{-1}$ ) and colony size (Table 1, regression 21), but this finding is based on only 4 colonies, and so must be considered tentative. Small May colonies produced neither sexuals nor substantial numbers of workers.

**Production Rate (mg/mg).** The birth rates for May and July (workers per day, sexuals per day) were converted to milligrams produced per day by multiplying them by the mean weight of workers and flight-ready sexuals, adding these. Dividing this sum by the total weight of workers in the colony resulted in the fractional daily increase of biomass (mg/mg-day). One July colony was eliminated from the regression because it contained very few pupae ( $n = 8$ ). In July, a 10-fold increase in the total weight of workers was associated with a 50% decrease in the production rate (Table 1, regression 22). The smallest colonies had daily growth rates in the range of 3% per day, whereas the largest grew  $\approx 0.6$ –0.8% per day. In May, there was no relationship of colony size to production rate, probably because small colonies were producing neither workers nor sexuals.

**Total Colony Fat.** In addition to storing seed reserves, colonies store metabolic fat reserves in the bodies of their workers. As a colony grows, its workers gain fat faster than the colony gains total weight. For every 10-fold increase in colony weight, worker fat weight increased 17-fold (Fig. 8) (Table 1, regression 23). This means that the total proportion of fat reserves stored by colonies increased as colonies grew, from a colony-wide mean of  $\approx 10\%$  in small colonies to  $\approx 25\%$  in large ones. The fat storage also varied seasonally—the intercepts for May and July were significantly lower than those for October and January (Fig. 8; Table 1, regression 23). May and July were not significantly different from one another, nor were October and January. During the summer and fall, colonies therefore store fat for overwintering and spring brood production. Large colonies have more excess energy to store than small ones. A log-log regression of the percent worker fat confirmed these trends, with colony weight explaining 46% of the variation in worker proportion fat, and May and July being less fat than October (Table 1, regression 24). Every 10-fold increase in total colony fat was associated with a 1.5-fold increase in worker percent fat.

It is important to note that fatness is distributed unevenly among workers of different ages, different positions in the nest, and in different seasons. These patterns are discussed in detail in Tschinkel (1998).

**Estimating Investment Over an Annual Cycle.** An estimate, however rough, of the proportion of production invested in sexuals is of interest because it

represents an important parameter of the life history strategy. To estimate total annual weight of sexuals produced, it was assumed that all sexual forms present in the May samples survived and attained flight-ready adult weights. To estimate total annual weight of workers produced, it was assumed that the July relationship between milligram of workers per day and worker number ( $W_{wk}/d = 0.026 N^{1.06}$ ) prevailed for a 120-d worker-brood season (approximately June–September). Colonies with fewer than  $\approx 2,000$  workers did not invest in sexuals ( $n = 3$ ), whereas larger colonies invested a fixed proportion ( $\approx 20\%$ ; SD 2.71;  $n = 4$ ) of annual production in them. These estimates are based on small samples, are not in energetic terms, and do not include the costs of maintenance or work. They must therefore be considered tentative.

### Discussion

One of the most important goals of social insect research is to understand the evolution of colony life histories (Franks et al. 1990, Bourke and Franks 1995), including the manner in which colonies grow from founding to maturity. The size-related trends described in this article constitute the developmental pathways, or sociogenesis, of harvester ant colonies. As colonies grow from incipient to mature, their minor workers get larger, they collect more seeds, build larger, more complex nests, store more fat in worker bodies, produce more new workers, and upon exceeding a threshold of colony size, invest in sexuals. Some of these increases occur at the same rate as colony size, some faster and some more slowly. These linked changes imply the existence of rules that guide the development of the super-organismal colony and suggest that the relationships among characteristics may have social functions. They also demonstrate that many colony characteristics depend on the size of the colony and suggest that colony size ought to be taken into account in all colony-level studies (Tschinkel 1991).

Among previous studies, the most comparable is that on *S. invicta* (Tschinkel 1993). Many relationships are generally similar in the 2 species, but the data sets differ in what they do well. The large sample size ( $n = 90$ ) for the *S. invicta* study assured high statistical power, but nest structure (other than mound volume) was not included, nor was the distribution of items within the nest. The current *P. badius* study yielded precise data on nest structure and distributions of items within it (Tschinkel 1998, 1999), but it sacrificed high statistical power because of modest sample sizes ( $n = 31$ ). The most similar other study is that of MacKay on *P. montanus*, *P. subnitidus*, and *P. rugosus* (MacKay 1981). Although several measures of colony growth rate in MacKay's samples declined with colony size, a reanalysis of his data revealed that quantitative comparisons could not be made because the range of colony sizes he sampled was generally 1 order of magnitude or less. Tests of size-effects increase in power with the range of sampled colony sizes. In contrast

with MacKay's, my samples of *P. badius* and *S. invicta* ranged over 4 and 5 orders of magnitude, respectively.

Nest characteristics were particularly tightly coupled to colony size. Total area grew by coupling chamber enlargement, addition of new chambers, and nest deepening. The distribution of old workers, young workers, brood, and seeds within the nest was highly predictable and made up the spatial and temporal structure of the colony (Tschinkel 1998). This highly structured nature of colonies is probably an important component of social organization and function (Franks et al. 1990; Sendova-Franks and Franks 1994, 1995).

An increase of worker size with colony size is a common feature of ant colony development (Tschinkel 1988a). In monomorphic species, mean worker size typically increases to a limit. In some polymorphic species, mean worker size changes because the proportion of major workers increases (e.g., fire ants [Tschinkel 1988a]), or decreases (Walker and Stamps 1986). In harvester ants, the mean size of minor workers increases, much as in monomorphic species, but the proportion of majors remains the same. The primary function of major workers in *P. badius* is probably seed milling. If so, the body size of the majors would have evolved in relation to the size distribution of seeds collected by the minors, and the unchanging proportion of majors would match the unchanging seed size distribution (incipient colonies excepted). The unchanging proportion of majors also suggests that their duties do not include larval care, because the larval population grows much more slowly than does colony size, but are associated with an isometric colony variable, the seed stores.

All measures of reproductive rate indicate that colony growth rates decline as colonies get larger. Such declines eventually result in the attainment of a maximal colony size and are typical of all hymenopterous social insects (Michener 1964, Tschinkel 1993), although the underlying mechanisms are not clear. However, to the extent that fat storage and worker body size are indications of colony nutrition, colonies become better nourished as they grow larger. This trend was also seen in *S. invicta* (Tschinkel 1993), and may be general among ants. Fat stores increased more rapidly with colony size in *P. badius* than in *S. invicta*. The decline of fat stores in association with sexual production in both species also suggests that the effect of colony size on sexual reproduction may act partly through nutrition. Tschinkel (1993) argued that fire ants cannot rear early spring sexuals from foraged food alone, but must draw on fat reserves placed in worker bodies the previous year to achieve the high production rates necessary for sexual production. This also appears to be true for harvester ants. Worker fatness declines to a minimum after sexual production, and it builds up in the 2nd half of the year in time for the winter shut-down.

As in many other temperate ants, the early spring sexual brood of harvester ants is accompanied by almost no worker production (Hölldobler and Wilson 1990). That is, sexual production is almost completely



separated from worker production. Because workers are relatively short-lived, colony size declines during periods of sexual production, and this decline is much greater for fire ants (50%) than it is for harvester ants ( $\approx 25\%$ ) because the workers of the former are much shorter-lived ( $\approx 4$  mo). The longevity of harvester ant workers is probably somewhat more than a year, reducing the seasonal colony size variation to the point of being detectable primarily as variations in worker density. The alternation of worker and sexual production can be seen as a strategy in which the capital and labor needed for sexual reproduction are alternately built up and spent.

Although the data are preliminary, it appears that once harvester ants exceed the size necessary for sexual reproduction, they invest a fixed proportion of their biomass in these sexual males and females, much as fire ants do (Tschinkel 1993). Larger colonies thus produce more sexuals by virtue of their larger size, not because they invest a larger proportion in sexuals. The preliminary calculations also suggest that harvester ants invest substantially less in sexuals ( $\approx 20\%$ ) than do fire ants ( $>30\%$ ). In addition, whereas fire ants begin producing sexuals when they attain  $\approx 10\%$  of their maximal colony size, harvester ants do not do so until they are  $\approx 30\%$  of this size. These traits would be expected from the habitats with which each is associated (stable versus weedy, early succession).

Like many temperate ants, harvester ants are strongly seasonal. Queens become reproductively functional in May, and they cease laying eggs before October. If egg-laying rate is proportional to the number of vitellogenic follicles, the queens' egg-laying rate only doubles for each 10-fold increase of colony size. This is similar to fire ants, in which egg laying is stimulated by the population of metamorphosing larvae (Tschinkel 1988b), and a 10-fold increase in these results in approximately double the egg-laying rate in the queen. Do larvae stimulate oviposition in harvester ants as well? The correlation between vitellogenic oocytes and number of larvae was not better than that with total worker weight. Tschinkel (1988b) suggested that the link between larvae and queen evolved to achieve high egg-production rates needed for large colonies and high worker turnover. Compared with fire ants, harvester ant queens have relatively low reproductive output, colony size is relatively small, and worker turnover relatively low. Perhaps no special mechanisms may be needed for queens to achieve the necessary egg-laying rates. Unlike fire ants (Tschinkel 1987), there was no relationship between colony size and the residual sperm supply in the queen's spermatheca. Perhaps sperm supply is not limiting to harvester ants, or perhaps the study population was not very old, so that even the largest colonies had only lived out a fraction of their lives.

The finding that the seed supply does not vary with season is surprising, considering that seed storage probably originated as a hedge against seasonal food scarcity. Perhaps seeds are always freely available so that constant stocks can be maintained. Seed usage would thus need to be determined by turnover rather

than standing stocks. As Rissing (1981) found in *P. rugosus*, there was little relationship between the mean seed size and mean worker size, except in the incipient colonies.

This study clearly has limitations. The number of sample dates and the number of sampled colonies represent a compromise between the desirable and the possible, and limit both the precision of the estimates and the fineness of pattern determination. This limitation is especially apparent for derivative calculations such as the annual totals. As in the fire ant study, no method for estimating worker mortality rate directly was available, so the estimation of population dynamics is incomplete. This will have to await future studies.

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