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## SOCIOMETRY AND SOCIOGENESIS OF COLONIES OF THE FIRE ANT *SOLENOPSIS INVICTA* DURING ONE ANNUAL CYCLE<sup>1</sup>

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**Abstract.** In social insects, colonies as well as individuals have evolving life histories. Identification of the life history tactics of a social insect requires data on colony attributes and their development. To this end a full range of fire ant (*Solenopsis invicta*) colony sizes was sampled and censused on seven dates throughout 1 yr. Data included: mound volume; the number, dry masses, and fat contents of sexual and worker adults and immatures; stratified nest temperatures; worker distribution within the nest throughout the year; duration of the pupal stages; and respiration rates. Analysis showed:

1. Colonies reached their annual maximum population size in midwinter and their maximum biomass in spring. During the spring sexual production period they declined to a midsummer minimum. Calculations showed that the magnitude of this decline increased with colony size. During January to July, worker mortality exceeded natality, causing colony decline, while from July to December, natality predominated, causing growth.

2. Mound volume was closely related to the total mass of ants in the colony, and varied with season paralleling the mass of ants.

3. The mean size and variability of workers, and the percent major workers, increased with colony size and changed over the year.

4. The fat content (percent fat) of workers increased with worker size and colony size. Worker percent fat was lowest in summer after sexual production, climbed immediately to the annual maximum and then declined gradually through winter and spring.

5. Although sexual male and female pupae were close in mean dry mass (2.55 mg and 3.10 mg, respectively), males gained only 6% during adult maturation while females gained 290%. Females gained fat more rapidly than lean tissue causing their percent fat to increase from 31% to 49%. Mean mass of male and female sexual adults did not change with colony size.

6. The cost of worker maintenance declined from nearly 100% of total colony cost in winter to 46% in late spring when brood production peaked.

7. Production rates peaked in spring, with colonies investing 50% of their daily production in sexuals. This peak production was not sustained through the summer, and was probably fueled by stored worker fat. Worker production dominated in the latter part of the summer. All measures of production rate as well as total annual production increased with colony size, but most did so less rapidly than colony size, resulting in a declining efficiency of production and a declining natality rate.

8. The percent of annual production invested in sexuals increased sharply in colonies of between 20 000 and 50 000 workers, then remained at  $\approx 33\%$  for the remainder of colony growth, showing that the transition from the ergonomic to the reproductive stages is sharp, and that colonies must grow in order to produce more sexuals.

9. Many quantitative colony attributes were related to one another by differential growth, and can thus be seen as isometric or allometric measures. Rules of relative growth may thus constrain the possible combinations of attributes and their evolution. The methods of morphometric size and shape analysis are discussed as tools for understanding suites of colony attributes, and comparing them among species.

10. The sociometric/sociogenic method is discussed as a way to compile, analyze and compare data on social insect colony attributes and their growth and development.

*Key words:* colony growth; colony size; efficiency; energy investment; life history; production rate; relative growth; seasonality; *Solenopsis invicta*; worker size.

### INTRODUCTION

The idea that the individual organism is much more than its adult form, that it is its life cycle as well, is generally accepted and has placed the study of devel-

opment and life history at the center of evolutionary biology. The application of such ideas to social insects, in which the colony is the counterpart of the individual, has not been as common or explicit. Yet it is no less

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true that the evolution, function, and species differences of social insect colonies must also be understood in terms of colony ontogeny and life history. Oster and Wilson (1978) provided a general framework for evolutionary studies of social insects, but progress has been slowed by a scarcity of data on colony-level attributes and their development. I have argued (Tschinkel 1991) that the collection and analysis of such social insect attributes, termed "sociometry," would benefit the study of social insect biology and evolution.

Life history theory has contributed important insights and testable hypotheses, and has suggested that the patterns of age-specific mortality and environmental variability shape life histories (Stearns 1976, Smith 1981). Application of such theory to social insect colonies would require schedules of colony mortality, reliable estimates of colony size, colony-level data on age at first reproduction, investment in sexuals, size and number of sexuals and workers, colony growth and longevity, seasonal patterns, and many other attributes (Oster and Wilson 1978). Unfortunately, the collection of such sociometric data has not often been a regular practice of social insect biologists. The available sociometric data are summarized in Hölldobler and Wilson (1990).

For social insects, a focus on life history tactics moves directly to the process of colony ontogeny, a process termed "sociogenesis" by Wilson (1985). Sociogenesis not only identifies the process by which the mature colony attains its form, but also illuminates phylogenetic constraints on the possible outcomes of natural selection through the existence of developmentally linked traits and trade-offs (Tschinkel 1991).

Wilson (1985) and Tschinkel (1988a) described some of the profound changes which occur during sociogenesis. Most apparent among these changes is that of worker size and variability, described in detail by Wilson (1983) and Tschinkel (1988a), but also noted by several other authors for a variety of species (see review in Tschinkel 1988a). Other such sociogenic changes include efficiency of reproduction (Michener 1964, Porter and Tschinkel 1985), investment in sexuals (Brian and Elmes 1974, Vargo 1988) and longevity of workers (Calabi and Porter 1989).

There are probably many other sociometric changes associated with colony growth. The timing and amount of allocation to workers (growth) vs. alates (reproduction) are important components of the life history tactics. Little information on these is available. In social insects, worker demography is not merely an epiphenomenon, it is adaptive (Oster and Wilson 1978). The relationship of worker size to longevity indicates that worker size is another important component of life history tactics. A description of sociogenesis ought to relate a large number of colony and individual attributes to colony size (and/or age) over the full colony growth range (Tschinkel 1991). Collection of such data would also allow assessment of correlations and func-

tional relationships among the attributes (Tschinkel 1991). Application to a number of species might allow detection of linked (pleotopic) traits and "rules of sociogenesis."

In this paper I apply a simple sociometric method to the sociogenesis of the fire ant, *Solenopsis invicta*. The method produced a cohesive description of an annual cycle as well as the relationships among diverse, simultaneously measured attributes and their ontogeny. The core of the sociometric/sociogenic method is the careful selection of colonies representing the full range of sizes on several well-chosen dates throughout the year. Colonies are subjected to a census, along with the determination of individual masses and fat content. Addition of development times, nest temperatures, individual longevities, and metabolic rates allow determination of most of the basic growth and production relationships throughout colony growth and the annual cycle. Such knowledge can provide a partial foundation on which a theory of colony-level life history tactics of social insects can be built.

#### MATERIALS AND METHODS

##### *Selection of colonies, sampling, and mound volume*

Colonies were sampled without replacement (Table 1) six times during 1 yr from two young monogyne populations separated by  $\approx 1$  km. Both were on recently (4–6 yr) disturbed, weedy sites. A seventh sample was taken 1–16 October 1988 from a more distant, more wooded site. On each sample date 25–30 colonies representing the full range of mound volumes were provisionally tagged. Ten to 16 of these colonies were then selected for sampling, with special care to include colonies of both size extremes. These samples were not random and were not intended to be normal. Nevertheless, the Shapiro–Wilk test (1965) for normality showed that only in the March sample and all samples combined was colony size significantly non-normal ( $P < .01$ ). A total of 89 colonies was sampled.

Justification of this sampling method is as follows: Most of the data were subjected to regression analysis in which the relationship of some predictor variable,  $x$  (most often colony size), to some dependent colony variable,  $y$ , was determined. The reliability of the estimation of a regression slope and intercept is increased by increasing the range of  $x$ , as was done above by choosing more very large and very small colonies than might have appeared in a random sample. Differences in the relationship between  $x$  and  $y$  among sample dates can then be determined by applying  $t$  tests to the regression parameters. In some cases, means of variables were calculated for the samples, often after stratifying by size class. Because only one of the seven samples was significantly non-normal, statistical tests on these means are not likely to be very biased.

Mound volume was estimated in litres from mound

TABLE 1. Sample dates and characteristics.

| Sample no. | Date                | Day of year | No. colonies | No. workers (thousands) |      |
|------------|---------------------|-------------|--------------|-------------------------|------|
|            |                     |             |              | Min.                    | Max. |
| 2 MAR      | 22 March 1988       | 82          | 12           | 0.99                    | 268  |
| 3 APR      | 30 April–7 May 1988 | 121         | 16           | 0.33                    | 206  |
| 4 JUN      | 31 May–1 June 1988  | 152         | 16           | 0.25                    | 127  |
| 5 JUL      | 13–15 July 1988     | 186         | 10           | 6.4                     | 116  |
| 6 SEP      | 25 September 1988   | 268         | 9            | 6.3                     | 184  |
| 7 OCT      | 1–16 October 1988   | 282         | 14           | 7.8                     | 213  |
| 1 JAN      | 9–10 January 1989   | 10          | 12           | 0.75                    | 334  |
| Total      |                     |             | 89           |                         |      |

dimensions as a prolate hemi-spheroid (Table 2, measure 1).

Colonies were censused as in Tschinkel (1988a) with some modifications. Each colony was excavated into a large bin(s) 45 kg at a time. Soil and ants were well mixed and, if more than one bin was required, a 1-kg sample was reserved from each bin. When the colony had been completely excavated, all 1-kg samples were mixed well together and three 200-g or 150-g samples were taken to the laboratory for census. All individuals of all stages were counted. For each of the eight types of individuals (pupae and adult workers, males, females; sexual and worker larvae), three estimates of colony population were calculated from the counts, subsample mass, and total mass of excavated soil (Table 2, measure 2). The means of these three estimates were the basic data of this paper (Table 2, measure 3). Standard errors were mostly <10–15% of the mean, but because of the sampling method, these were probably an underestimate and were not used. Because most regressions included colonies varying over four orders of size magnitude, such precision is acceptable and adequate.

#### *Dry mass and fat contents*

All individuals that were not damaged were killed and oven-dried for 24 h at 60°C to determine mean dry mass<sup>2</sup> of each of the eight types of individuals (workers, adult males, worker pupae, etc.). Sexu- als were weighed individually and averaged, but workers, worker brood, male pupae, female pupae, and sexual larvae were grouped by colony to yield a mean but no variance (Table 2, measure 4).

The combined workers from each colony were visually separated into five size classes based on equal increments of head width by comparison to a series of measured workers. The separated workers were placed into perforated gelatin capsules in a Soxhlet extractor, extracted with diethyl ether for 24 h, dried, and reweighed. The difference between the mean pre- and postextracted dry masses allowed computation of the

mean lipid mass and percent lipid for each size class of each colony (Table 2, measures 5 through 8). This method does not distinguish body lipid from oil stored in the crop.

Alate females were divided into three size classes (<4.0 mg; 4.0–6.99 mg; ≥7.0 mg) and those from each colony extracted as a group, as for workers above. Lipid mass and percentage were similarly calculated for each mass group by colony (Table 2, measures 5 through 8).

Energy content was calculated from the lipid and lean content using the values in Peakin (1972) (lipid: 39.33 J/mg; protein and carbohydrate [lean matter]: 18.87 J/mg) (Table 2, measure 21).

From these dry masses, lean masses, and energy contents, the colony totals were calculated by use of the population estimates (Table 2, measures 19 and 22). The sum of these for all types of individuals resulted in the total colony biomass and energy content (Table 2, measures 20 and 23).

#### *Respiration rate*

Respiratory rates of workers of three sizes at two temperatures were taken from Porter (1988). Elzen (1986) gives rates for major workers and alates only. The more general relationship of temperature and worker size to respiration rate was computed with an equation fitted to Porter's data (Table 2, measure 15).

The respiration rate of female alates ( $n = 11$ ) was determined in a constant-volume respirometer at 30°C in the presence of KOH. The O<sub>2</sub> consumption rate per unit dry mass at other temperatures was estimated using the equation  $\log(\mu\text{L}\cdot\text{mg}^{-1}\cdot\text{h}^{-1}) = -3.14(1000/\text{K}) + 10.65$ . Respiration of male alates could not be determined because they did not stop moving. Their rate was estimated from their dry mass by assuming the same relationship to temperature and dry mass as female alates.

Oxygen consumption rates were converted to energy-consumption rates by the factor 0.0201 J/μL O<sub>2</sub> (Table 2, measure 18) (originally published as 0.0048 cal/μL O<sub>2</sub> in Calabi and Porter 1989).

Worker pupal development rate in relation to temperature was taken from Porter (1988) (Table 2, measure 11).

#### *Basic computations*

1. *Respiration and maintenance energy.*—Because both respiration rate and development rate are temperature dependent (Jensen 1978a, b), the temperature and temperature variation experienced by colonies in each sample had to be estimated. Estimation was possible through the generosity of S. D. Porter who provided me with his data on the vertical distribution of fire ants in natural mounds in relation to temperature during one annual cycle in the vicinity of Tallahassee, Florida (S. D. Porter, unpublished data).

For 1 d during each month, these data consisted of the daily temperature cycle at four levels in the nest

<sup>2</sup> See Editor's note, page 456.

TABLE 2. Computations, estimates and variables used in this study. Abbreviations: ad = adult; pu = pupa; lv = larva; wkr = worker; m = male; f = female; sx = sex; wkr sz cl = worker size class; samp = sample; strat = stratum of nest; d = day;

| Measure  | Symbol          | Categories in subscript |               |               |
|--|-----------------|-------------------------|---------------|---------------|
|  |                 | <i>i</i>                | <i>j</i>      | <i>k</i>      |
| 1 Mound volume   | $V$             | ...                     | ...           | ...           |
| 2 Estimated population                                 | $N_{ijk}$       | Subsample               | ad, pu, lv    | wkr, m, f, sx |
| 3 Mean estimated population                            | $\bar{N}_{ij}$  | ad, pu, lv              | wkr, m, f, sx | ...           |
| 4 Mean mass, individual                                | $M_{ij}$        | ad, pu, lv              | wkr, m, f, sx | ...           |
| 5 Mean wkr mass  | $M_{ijk}$       | ad                      | wkr           | wkr sz class  |
| 6 Mean lean mass                                       | $L_{ijk}$       | ad                      | wkr, m, f     | wkr sz class  |
| 7 Mean fat mass  | $F_{ijk}$       | ad                      | wkr, m, f     | wkr sz class  |
| 8 Mean percent fat                                     | $\%F_{ad,jk}$   | ad                      | wkr, m, f     | wkr sz class  |
| 9 Temperature  | $T_{ijk}$       | strat                   | samp day      | samp time     |
| 10 Mean temperature, interval                          | $T_{ijk}$       | strat                   | samp day      | time int      |
| 11 Pupal period at constant temperature                | $P_{ijk}$       | pu                      | wkr, m, f     | °C            |
| 12 Pupal development rate                              | $1/P_{ijk}$     | pu                      | wkr, m, f     | °C            |
| 13 Estimated pupal period, field                       | $\hat{P}_{ij}$  | pu                      | wkr, m, f     | ...           |
| 14 Fraction of workers in stratum                      | $\%N_{ijk}$     | strat                   | ad            | wkr           |
| 15 Mean O <sub>2</sub> consumption rate                | $R_{ijk}$       | ad                      | wkr, m, f     | °C            |
| 16 Worker O <sub>2</sub> consumption daily, stratified | $R_i$           | strat                   | ...           | ...           |
| 17 Total worker O <sub>2</sub> consumption daily       | $R$             | ...                     | ...           | ...           |
| 18 Worker maintenance cost                             | Mn/d            | ...                     | ...           | ...           |
| 19 Biomass (dry)                                       | $B_{ij}$        | ad, pu, lv              | wkr, m, f     | ...           |
| 20 Biomass, total                                      | $B_{tot}$       | ...                     | ...           | ...           |
| 21 Mean energy content, per mg                         | $E_{ijk}$       | ad, pu                  | wkr, m, f, sx | wkr sz        |
| 22 Energy content                                      | $\hat{E}_{ijk}$ | ad, pu                  | wkr, m        | wkr sz        |
| 23 Total energy content                                | $E_{tot}$       | ...                     | ...           | ...           |
| 24 Natality, daily                                     | $n_i/d$         | wkr, m, f, sx           | ...           | ...           |
| 25 Natality rate                                       | $\%n_i/d$       | wkr                     | ...           | ...           |
| 26 Production rate, biomass                            | $b_i/d$         | wkr, m, f, sx           | ...           | ...           |
| 27 Total production rate                               | $b_{tot}/d$     | ...                     | ...           | ...           |
| 28 Production cost                                     | $e_i/d$         | wkr, m, f, sx           | ...           | ...           |
| 29 Total production cost                               | $e_{tot}/d$     | ...                     | ...           | ...           |
| 30 Total cost  | $C_{tot}$       | ...                     | ...           | ...           |

J (nonsubscript) = joule; tot = total; indiv = individual; int = interval; popul = population; temp = temperature; resp = respiration.

| Units  | Applied to:       | Derivation, symbols, and notes  |
|--|-------------------|---|
| L  | colony mound      | $V = 4/3\pi \cdot a/2 \cdot b/2 \cdot ht$ ; where $a$ = length, $b$ = width, $ht$ = height.   |
| no.  | colony or stratum | $N_{ijk} = n_{ijk} \cdot (M_{tot}/M_{samp})$ ; where $n_{ijk}$ = count in subsamples; $M_{tot}$ = mass excavated soil; $M_{samp}$ = mass soil in sample.  |
| no.  | colony or stratum | $\bar{N}_{ij} = (N_{1jk} + N_{2jk} + N_{3jk})/3$ ; mean of 3 subsample estimates from measure 2.  |
| mg   | colony            | $M_{ij} = m_{ij}/n_{ij}$ ; where $m_{ij}$ = mass of $n_{ij}$ individuals from 3 subsamples combined. For sexuals, $M_{ij}$ = mean of $n$ indiv mass.  |
| mg   | colony            | $M_{ad,wkr,k} = m_k/n_k$ ; where $m_k$ = mass workers (from measure 4) in each of 5 head-width classes; $n_k$ = no. in each class.  |
| mg   | wkr sz cl, m, f   | $L_{ad,jk} = m_{ad,jk}/n_{ad,jk}$ ; where $m_{ad,jk}$ = mass after ether extraction; $n_{ad,jk}$ = no. in sample. For sexuals, $M_{ad,jk}$ = mean of $n$ indiv masses.                            |
| mg   | wkr sz cl, m, f   | $F_{ad,jk} = M_{ad,jk} - L_{ad,jk}$ ; measure 5 - measure 6; for sexuals, $F_{ijk}$ = mean of $n$ indiv differences.  |
| %  | wkr sz cl, m, f   | $\%F_{ad,jk} = F_{ad,jk}/M_{ad,jk}$ ; measure 7 ÷ measure 5; for sexuals, $\%F_{ijk}$ = mean of $n$ indiv.  |
| °C   | stratum           | $T_{ijk}$ measured at time of colony excavation.  |
| °C   | stratum           | $T_{ijk}$ averaged graphically from daily temp cycle for 4 strata.  |
| d  | pupae             | $P_{ijk}$ from literature or determined in laboratory at constant temp; for other temps, $\log P_{ijk} = -2.71 \log T + 4.985$ .  |
| h <sup>-1</sup>  | pupae             | $1/P_{ijk} = 1/(24 \cdot P_{ijk})$ ; fraction of pupal period passed/h.   |
| d  | pupae             | $\hat{P}_{ij} = 1/(\sum_{int} H_{int}/P_{ijk})$ ; where $H_{int} = h$ in the int; sum of all $H_{int} = 24$ h.  |
| %  | colony            | $\%N_{i,ad,wkr} = N_{i,ad,wkr} \div (\sum_i N_{i,ad,wkr})$ ; fraction of wkr popul in each stratum.   |
| $\mu\text{L} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ | adults            | $\log R_{ijk} = -0.27 \log M_{ijk} - 3.14 (1000/K) + 10.65$ ; $M_{ijk}$ from measure 4; temp in K.  |
| $\mu\text{L}/\text{d}$                                 | stratum           | $R_i = \sum_{int} R_{ad,wkr,k} \cdot H_k \cdot B_{ad,wkr} \cdot \%N_{i,ad,wkr}$ ; measure 15 · $H_k$ · measure 19 · measure 14, where $H_k = h$ at temp k. Sum wkr biomass × resp rate over 24 h. |
| $\mu\text{L}/\text{d}$                                 | colony            | $R = \sum_i R_i$ .  |
| J/d  | colony            | $\text{Mn}/\text{d} = R \cdot 0.0201 \text{ J}/\mu\text{LO}_2$ .  |
| mg   | colony            | $B_{ij} = N_{ij} \cdot M_{ij}$ ; measure 3 · measure 4.   |
| mg   | colony            | $B_{tot} = \sum_{ij} B_{ij}$ .  |
| J/mg   | wkr sz cl, m, f   | $E_{ijk} = (L_{ijk} \cdot 18.87 \text{ J/mg}) + (F_{ijk} \cdot 39.33 \text{ J/mg}) \div M_{ijk}$ ; (measure 6 · 18.87 + measure 7 · 39.33) ÷ measure 5).  |
| J  | colony            | $\hat{E}_{ijk} = E_{ijk} \cdot B_{ij}$ ; measure 21 · measure 19.   |
| J  | colony            | $E_{tot} = \sum_{ijk} \hat{E}_{ijk}$ .  |
| no./d  | colony            | $n_i/\text{d} = N_{pu,j} \div \hat{P}_{ij}$ ; measure 3 ( $i = \text{pu}$ ) ÷ measure 13; $sx = m + f$ .  |
| %/d  | colony            | $\%n_i/\text{d} = n_{wkr}/\text{d} \div N_{ad,wkr} \cdot 100$ .   |
| mg/d   | colony            | $b_i/\text{d} = (n_i/\text{d}) \cdot (M_{ij})$ ; measure 24 · measure 4.  |
| mg/d   | colony            | $b_{tot}/\text{d} = \sum_i b_i/\text{d}$ ; $\sum_i$ all measure 26.   |
| J/d  | colony            | $e_i/\text{d} = (b_i/\text{d}) \cdot (E_i)$ ; measure 26 · measure 21.  |
| J/d  | colony            | $e_{tot}/\text{d} = \sum_i e_i/\text{d}$ ; $\sum_i$ all measure 28.   |
| J/d  | colony            | $C_{tot} = (e_{tot}/\text{d}) + (\text{Mn}/\text{d})$ ; measure 29 + measure 18.  |



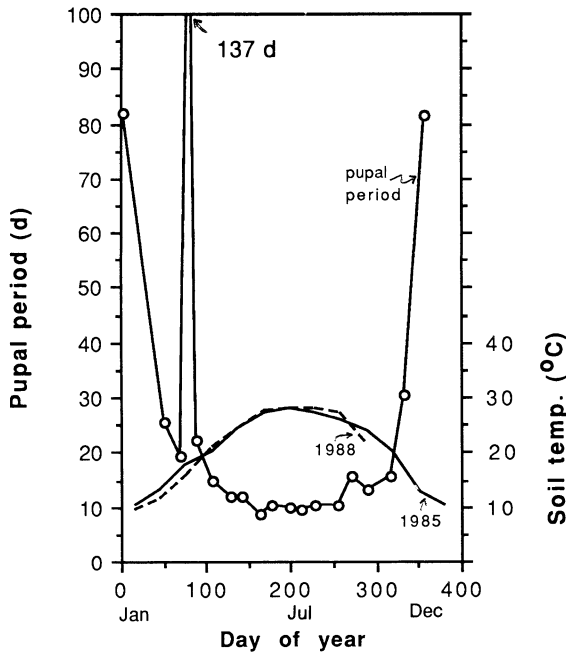


FIG. 1. Duration of the pupal period and soil temperature at 10 cm depth. Temperatures are given for 1985, the year of the temperature measurements, and 1988, the year of this study. The pupal durations used in this study were obtained from the smoothed curve of pupal duration. For relation between temperature and pupal period, see Table 2, measure 11. Soil temperatures are from Quincy, Florida,  $\approx 32$  km west of the study site. The single anomalously long pupal period in early spring was the result of an extreme cold spell which occurred on the sample day. Its effect was minimized during smoothing.

(Table 2, measure 10) and the percent of the colony's workers found at each level in the early morning and midday (Table 2, measure 14). Because Porter's sample dates did not coincide with mine, his data were all plotted against their dates, and the curves smoothed. From these smoothed curves, the temperature and percent of workers at each of the four levels, during morning and afternoon, was estimated for my sample dates. Because temperature cycled strongly in the mound sample (but not in deeper nest samples underneath the mound), the mean temperature (in the form  $1000/K$ ) for morning and midday was used (Table 2, measure 10). In this fashion, the approximate temperature exposure of the entire colony during a 24-h cycle was estimated.

Mass-specific oxygen consumption rate was computed for each level both morning and midday by using the estimated temperature and the mean worker dry mass found in the formula in Table 2, measure 15. This rate was converted to daily oxygen use (in microlitres) at each level (Table 2, measure 16). The sum of these stratified estimates gave the  $O_2$  use per day per colony (Table 2, measure 17). Multiplying this value by  $0.0201 \text{ J}/\mu\text{L } O_2$  gave the daily maintenance energy for each colony (Table 2, measure 18). These computations were similar to those of Jensen (1978a).

2. *Pupal development.*—To compute the worker pupal development rate, it was assumed that pupae were always found at the preferred temperature of  $31^\circ\text{C}$  if available, or the highest available temperature below  $31^\circ\text{C}$ , and that development did not proceed below  $24^\circ\text{C}$  (Porter 1988). This simplifying procedure probably underestimated realized pupal period somewhat. An equation was fitted to Porter's data to give the general relationship of pupal development in days ( $P$ ) to temperature (Table 2, measure 11).

When  $P$  was expressed in hours, its inverse gave the fraction of pupal period per hour (Table 2, measure 12). For each of Porter's monthly temperature cycles, the highest available temperature between  $24^\circ$  and  $31^\circ\text{C}$  available at any depth was plotted against time of day. The hours' exposure at constant temperatures was multiplied by the appropriate fraction per hour. For periods of changing temperature, the mean log temperature was used to estimate the fraction per hour and multiplied by the hours in their period. The inverse of the sum of these products for 1 d was an estimate of the pupal period for that date (Table 2, measure 13). These estimates for Porter's samples were plotted against date (Fig. 1). Pupal period for my sample dates were estimated from the smoothed curve. A small correction was made upon comparing the soil temperature at 10 cm for 1985 (Porter's sample year) with that of 1988 (my sample year).

To estimate sexual pupal development periods, the period at  $30^\circ\text{C}$  (males, 9.0 d; females, 11.3 d) was simply multiplied by the same proportion as workers using their rate at  $30^\circ$ .

3. *Natality and production rate.*—Dividing the estimated mean number of worker or sexual pupae from the census by the development period (in days) gave the number of new workers or sexuals eclosing per day (natality) (Table 2, measure 24) and dividing this by the number of workers in the colony gave the daily percent natality rate (Table 2, measure 25).

The product of natality and the mean adult masses resulted in the biomass of workers or sexuals produced per day (Table 2, measure 26), a value that could be converted to joules per day via the per-milligram energy content of adult workers and sexuals (Table 2, measure 28). Both computations included the energy and mass gain between the pupal period and mature adult mass. Pupae were consistently lighter than the mature adults in my samples, both for workers and sexuals.

The sum of daily production rate or production cost for workers and sexuals gave the total production rate and cost per day (Table 2, measures 27 and 29). Addition of worker maintenance cost gave total cost per day (Table 2, measure 30).

4. *Colony size classes through the annual cycle.*—In some calculations it was necessary to separate colonies into classes of size throughout the year, but this was complicated by the fact that colonies undergo a size-related decline from January to July during sexual pro-

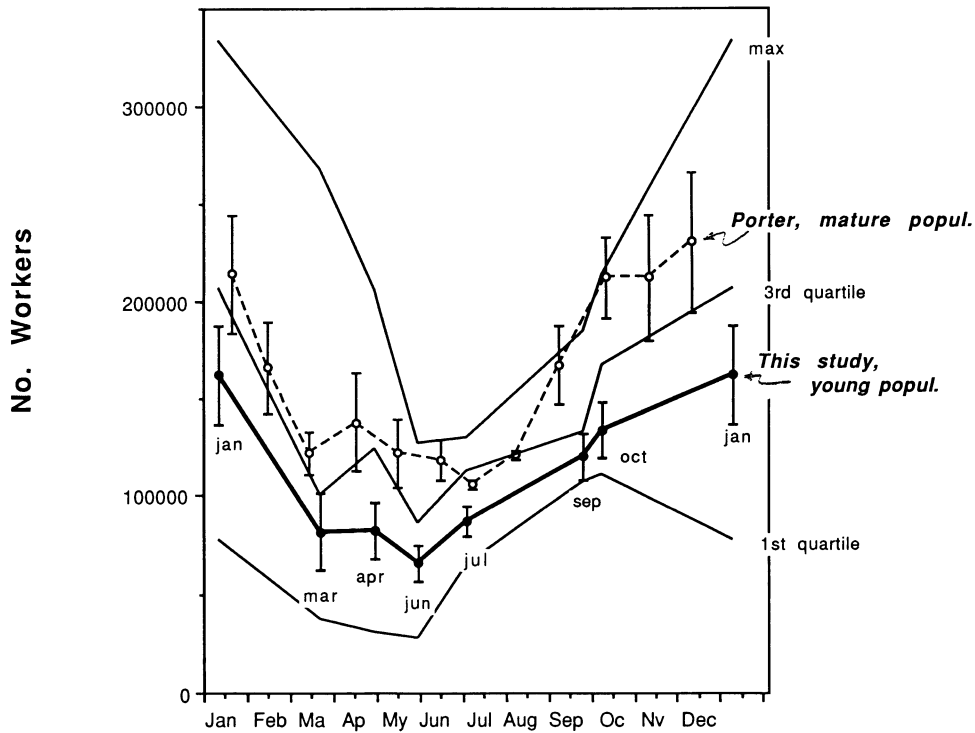


FIG 2. Mean worker population of colonies through the annual cycle for this study (lower curve) and that of S. D. Porter (*unpublished data*). Both studies are from the Tallahassee, Florida, area. For this study, first quartile, third quartile, and maximum colonies are also shown. The mean seasonal variation in colony size is similar in both studies, but the colonies in this study were smaller because they were drawn from a young population while those of Porter were drawn from a mature one. Larger colonies show more size fluctuation. Error bars =  $\pm 1$  SE.

duction and increase from July to December when worker production dominates (Fig. 2) (Tschinkel 1988a). In spite of choosing colonies to represent the full range of available sizes, mean colony size varied significantly over the year (ANOVA,  $F = 5.07$ ,  $df = 6, 82$ ,  $P < .001$ ) dropping from the January maximum of 162 000 workers to a June minimum of 66 000, then rising to 133 000 by October (Fig. 2). A similar but increasing pattern of annual fluctuation was also seen in proceeding sequentially from first quartile to third quartile and maximum size colonies (Fig. 2). Colonies too small to produce sexuals grow throughout the year, temperature allowing, and the size decline of sexual-producing colonies is probably proportional to the mass of alates produced. Thus to track a size-cohort of colonies through a year requires that the size-class brackets track these size changes appropriately.

Colony size-specific annual fluctuation was estimated from the mean logistic colony growth curve of Tschinkel (1988a) modified to reflect the annual fluctuation of growing colonies found in Tschinkel (1988a), Markin et al. (1973) and S. D. Porter (*unpublished data*). This consisted of adding a logistically increasing annual fluctuation to the mean logistic curve of Tschinkel (1988a) as follows.

$$N = \frac{165\,000}{1 + 83e^{-1.26t}} + \frac{\cos(6.28t) \cdot 55\,000}{1 + 150e^{-1.26t}}$$

where  $t$  = time in years. This equation fits the data reasonably well for colonies larger than 5000 workers (Fig. 3). The right-hand dividend was used to estimate the annual fluctuation as colony size and age increased.

January colony sizes were divided into six size classes in increments of 50 000 workers and the above equation used for graphical estimation of the size class brackets at all other sample dates (Fig. 4). Note that the size classes are composed of equal increments only in January, but that each size class includes corresponding colonies throughout the year. For example, colonies falling into the January class of 100 000–150 000 workers (class 3) would contain 77 200–94 000 in July. Size classes were designated 1–6 based on the January size. These size fluctuations are confirmed by parallel changes in mound volume in a population of repeatedly measured nests (E. S. Adams and W. R. Tschinkel, *unpublished data*).

Over the year, the ratio of actual mean colony size to the midpoint of its size class ranged from 0.7 to 1.1. Individual sample ratios were more variable because some colony sizes fell near the boundary values of their size classes (Fig. 4).

5. *Cumulative annual production.*— Mean daily production rates (number, mass, energy) were calculated for each size class on each sample date. Eight missing values were interpolated from the size class vs. production rate relationship for that date. The interval



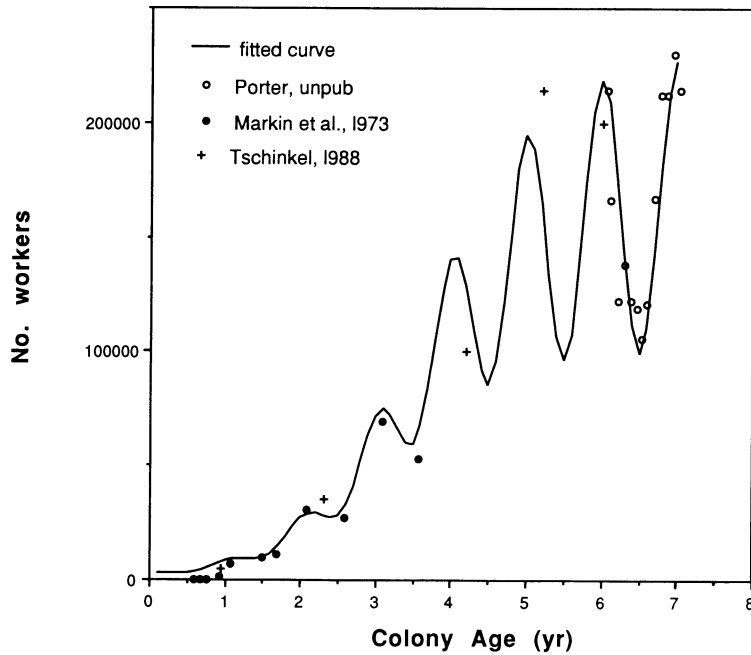


FIG. 3. Growth of the fire ant colonies. Curve fitted to the data of Porter (*unpublished data*), Markin et al. (1973), and Tschinkel (1988a) is a logistic function with a logistic increase of seasonal variation.

(days) between sample dates was multiplied by the mean of the rates for each pair of sequential dates to give the total production between pairs of sample dates. The sum of these products for 1 yr gave the total annual production in numbers, dry mass, energy content, maintenance energy, or total cost.

6. *Mortality*.—Mortality by colony size class and sample date was estimated indirectly. The change of mean colony size (number of workers) between sample

dates was calculated and divided by the number of days in that interval to give the change (+ or -) in number of workers per day. This value and all further calculations applied to the date midway between each pair of sample dates. Colony size for December was extrapolated and estimated mean size was substituted for any missing values. The mean daily worker natalities (from census) by size class were adjusted to the midpoint dates. Subtracting the daily change in work-

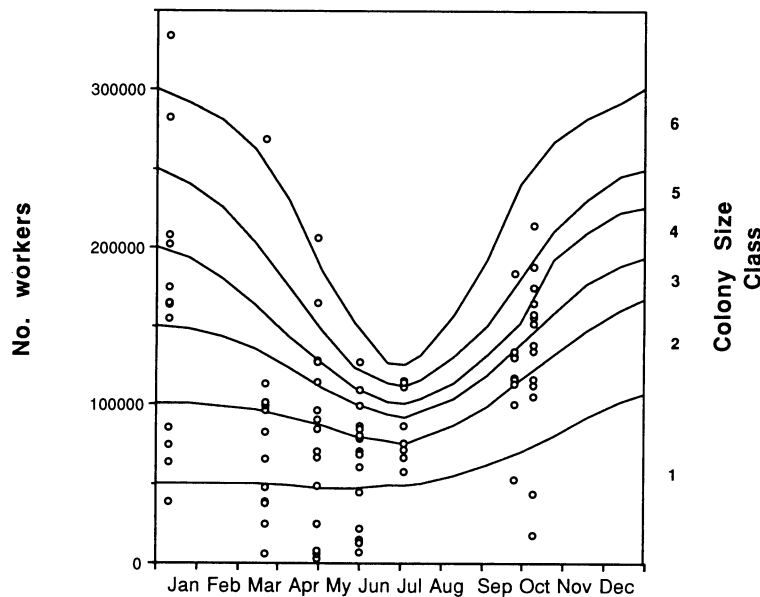


FIG. 4. Assignment of the sample colonies to size classes throughout the sample year. The curves show the size limits of classes set up in January in increments of 50 000 workers. All but the smallest colonies decline until midyear. The points show the censused size of all 89 sampled colonies. This graph was used to assign colonies to size classes throughout the sample year.

ers from the daily natality gave the daily worker mortality. (Note that worker mortality was forced by the change in colony size and natality.) Division of these numerical estimates by colony size (interpolated to midpoint dates) resulted in the percent change per day, percent natality per day, and percent mortality per day. All these estimates are approximate mean values for the intervals between samples. They apply to the mean colony in each size class.

7. *Data analysis.*—The data in their most basic form are available as a supplement.<sup>3</sup> Computations, regressions, and one-way analyses of variance were carried out on Minitab (Ryan et al. 1982). Data were transformed by taking logarithms (or arcsine transforms of proportions) as necessary to stabilize the variance. Linear regressions were carried out using dummy variables for the sample dates. Regressions were of Type I because the  $y$  variable was known to be causally linked to the  $x$  variable. Analysis of residuals allowed the choice of the best transformation and the elimination of any extreme outliers.

For colony size class analyses, data were grouped by colony size classes based on January colony size and subjected to an analysis of covariance (SPSS-MAN-OVA program; Hull and Nie 1981). In this case colony size was a covariate and sample date the factor.

#### *Caveats*

Several caveats must be understood if a reasonable interpretation of data is to be made:

1. The *accuracy* of the colony population estimates was not verified, because no other methods for independent estimation were available. The reported populations are estimates of the excavated ants and are *precise* generally within 10–15% of the mean estimate. Only the mean estimates were used in this study.

Most colony census methods (including this one) do not include the foragers afield at the time of census (but see Nielsen et al. 1976 for an exception). If foragers compose a fixed percentage of the colony, this would lead to a fixed percent undercount of workers. However, if the percent foragers grows allometrically to colony size or changes with season, the undercount may skew the various parameters. Estimates of the proportion of a colony that forages range from 10 to 20% (MacKay 1981 and references therein, Porter and Jorgensen 1981) but its relation to colony size in the field or season is unknown. However, working in the laboratory, Miranda and Vinson (1981) found that the percent foragers fell greatly as colonies increased in size, suggesting cautious interpretation may be in order.

<sup>3</sup> See ESA Supplementary Publication Service Document No. 9303 for 6 pages of supplementary material. This document is available on 5¼" diskette or in printed form. For a copy of this document, contact the author or order from the Ecological Society of America, 328 East State Street, Ithaca, NY 14850-4318 USA. There is a small fee for this service.

2. While computation of investment on an annual basis is an improvement over single-sample methods, the units of that investment may well affect the outcome of the calculations. This is clear from a comparison of investment patterns based on energy embodied in biomass as opposed to total energy costs (biomass energy + maintenance energy). Even the last does not include the cost of doing work. Such changes in the basis will skew parameter estimates if the elements of the basis are differently related to colony size. For example, because the maintenance cost grows less rapidly than colony size, patterns of investment based on total cost are different from those based on biomass only. If the cost of work grows allometrically to colony size, addition of this measure will alter the patterns of investment based on biomass + maintenance.

3. The conversion of the pupal census to birth rate was made with the following simplifying assumptions: (a) All pupae were exposed to the optimal temperature (31°C), or if 31°C was not available, the highest nest temperature available. This somewhat overestimates the rate of development (and therefore birth rate) because in reality, pupae are exposed to a range of temperatures. S. D. Porter (*unpublished data*) found that workers placed pupae over a range of temperatures in field colonies and in a laboratory temperature gradient, and that the preferred temperature varied with the nutritional condition of the colony (S. D. Porter and W. R. Tschinkel, *in press*). (b) A single value was used for the worker pupal development time. Porter (1988) and D. Wheeler (*unpublished data*) indicated that large workers took several days longer to pass the pupal period. Because the relationship between pupal development and size was not known, I used a single value characteristic of minor workers. Inclusion of this factor would cause the birth rate estimates to be decremented progressively more as colony size (and therefore pupal size) increased. (c) Mortality during the pupal period is negligible. Significant pupal mortality would result in real natality that was lower than estimated. Together (a) and (b) suggest that I have probably overestimated birth rates and variables derived from them.

4. Estimation of basal maintenance cost was made only for workers because data were not available for larvae and pupae. This means that maintenance cost is underestimated more for small colonies than large because small colonies have proportionally more, smaller, and therefore more oxygen-consuming brood. However, considering the crudeness of respiration estimates and the fact that brood make up only 25–50% of most colonies, these factors are not likely to make a meaningful difference. Jensen (1978a) estimated brood respiration to be  $\approx 13\%$  of the total respiration in *Formica pratensis*.

5. The determination of worker fat content does not distinguish between body fat and oil contained in the crop. While workers' crops often contain droplets of oil, the amount of this oil is not known.

6. Many calculations inherently involved one or

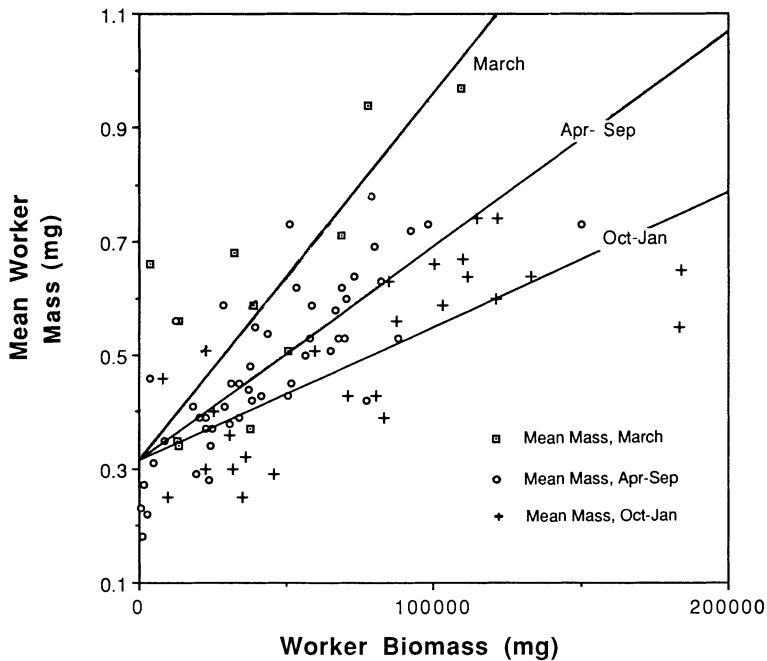


FIG. 5. Change in body mass of individual workers with changes in total worker biomass. The increase of mean body mass of individual workers with total worker biomass is most rapid in March, intermediate in summer, and least in winter. Colonies of a given biomass consisted of heavier workers in March than in summer or in winter.

more levels of smoothing, averaging, or interpolation. Examples include the estimation of development periods, temperature, natality, mortality, and all calculations based on colony size classes. This smoothing levels variation and gives the impression that variability is lower than it really is.

7. As a description of growth-related changes, it must be remembered that the patterns described in this paper result from an instantaneous "snapshot" of a population of small to large colonies, not from the tracking of a cohort of colonies during their growth.

## RESULTS

### *Colony population and structure*

Rationale: Body size and its social analog, colony size, are attributes with deep biological importance. Most colony descriptions begin with the number of workers, but a comprehensive description requires much more. An ecological, behavioral, or natural history slant demands knowledge of mean worker size, and if the worker population is polymorphic, the size-frequency distribution as well. The total worker biomass relates to the ecological impact of the colony, and the relationship among worker biomass, number, size, and energy cost bears on how a colony makes the trade-off between the size of workers and their number. The number, sex, size, and energy content of the alate reproductives are important fitness components. Finally, to the extent that these measures change with colony size and season, these changes are themselves important colony attributes. For this reason, all measures must be re-

lated to the size of their source colony and the time of the year.

### *Worker number.*—

Fig. 4 shows the variation of the number of workers in the six colony size classes through the year. For all but the smallest colonies, worker number declined during sexual production from January to midyear, then increased until the end of the year. The magnitude of this decline was greater the larger the initial colony size. The smaller the initial colony size, the greater the net increase in size by year end. Colonies in the largest size class, 6, merely returned to their initial size. Colonies in the smallest class, 1, showed almost no mid-year decline because they produced few sexuals. By the end of the year, if one were to reclassify the resulting colonies, the first three size classes would be in the next larger class, class 4 would be almost in class 5 and classes 5 and 6 would remain such.

### *Worker mean size.*—

Mean worker dry mass was regressed against the colony size (worker biomass) over all samples, using dummy variables for the sample dates (Fig. 5). Because the log-transformed data fit slightly less well, the regression of untransformed data is presented here. A common  $y$  intercept ( $0.32 \pm 0.02$  mg [ $\bar{X} \pm \text{SD}$ ],  $t$  ratio [= slope/ $\text{SE}_{\text{slope}}$ ] = 16.0) was assumed, reasoning that at very small colony size all workers have similar masses (0.13 mg for minim workers). The discrepancy between the extrapolated (0.32 mg) and observed (0.13 mg) initial worker masses was probably the result of strongly nonlinear increase of mean worker mass dur-

ing the first 6 mo (or 5%) of colony growth (Tschinkel 1988a). During this period, both major and minor workers actually increased in mean mass. Thereafter, the increase in mean worker mass was mostly the result of an increasing proportion of major workers (Tschinkel 1988a).

For any given colony size, worker size also varied throughout the sample year (Fig. 5). The regression slopes of the sample dates clustered into three significantly different groups: October to January ( $2.34 \times 10^{-6}$  mg/mg to  $2.27 \times 10^{-6}$  mg/mg), March ( $6.23 \times 10^{-6}$  mg/mg) and April to September ( $3.23 \times 10^{-6}$  mg/mg to  $4.76 \times 10^{-6}$  mg/mg). The larger workers in March colonies may be the result of the differential die-off of smaller workers during the winter when production of new workers is low.

Together, colony size (worker biomass) and sample date accounted for 61% of the variation in mean worker mass. The two variables in the previous regression are not entirely independent because worker biomass is the product of the number of workers and their mean mass. A log-log regression of worker biomass against the number of workers showed that this biomass increased more rapidly than did worker number (log biomass of workers =  $1.32 + 1.20 \log$  number of workers;  $R^2 = 94\%$ ). Only in March was this relationship significantly different, with worker biomass increasing more rapidly (slope = 1.23). The mean worker mass thus accounts for almost all the difference between the number of workers and their biomass.

When mean worker dry mass was regressed against number of workers, the proportion of explained variation ( $R^2$ ) dropped to 26%, and the significant difference between the October–January and summer slopes disappeared (slope =  $2.50 \times 10^{-7}$  mg/worker). Workers in March, however, were still clearly heavier for a given colony size (slope =  $6.13 \times 10^{-7}$  mg/worker), as in the previous regression. The common  $y$  intercept was once again larger than the mass of minim workers (0.37 vs. 0.13 mg).

#### Worker biomass. —

When the mean mass of workers was multiplied by the number of workers, the biomass was estimated. For the colony size classes, the mean of this variable peaked in March when the worker number was still fairly high and mean worker mass was high.

#### Analysis by worker size class. —

1. *Worker mass.* — The analysis above showed that, on average, workers became larger as colonies grew, and that mean worker size varied with season. Most of the increase in mean worker mass resulted from the increased proportion of major workers (Tschinkel 1988a). These patterns were further clarified by separating workers into five size classes in 0.2 mm head-width increments beginning at 0.5 mm, and analyzing worker mass (cube-root transformed) and lipid content (percent lipid, dry) in relation to sample date, worker

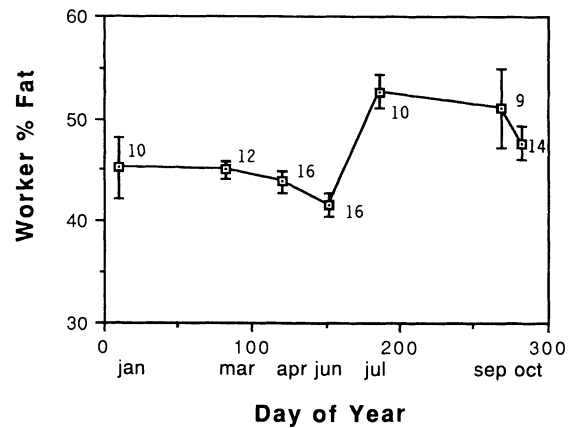


FIG. 6. Seasonal variation in the worker percent fat. Worker fat is greatest in midsummer to fall, then declines gradually through winter, reaching a minimum after the spring sexual production period. Values are the means over all worker and colony size classes, neither of which interact with season. Error bars =  $\pm 1$  SE. Number next to each point is sample size.

size, and colony size. All data were analyzed by ANOVA using sample date as the independent factor and colony size class and worker size class as covariates. Because the ANOVA was not balanced, factors and interactions were entered in several orders, and the extremes of the  $F$  ratios and  $P$  values are reported. In no case was there an interaction between worker size class and colony size class: the mass and lipid content of workers was related to worker size class in the same manner for all colony size classes.

Because worker mass is practically isometric to head width (Porter and Tschinkel 1985), worker size class should (and does) predict worker mass almost exactly. In the ANOVA, worker size class accounted for 97.6–98.5% of the explained variation in mean worker mass, depending on the model. This is a relatively uninteresting fact. The variation of worker mass with sample date and colony size class was much smaller and, while accounting for only 1.5–2.5% of the total variance, was highly significant ( $P < .001$ ), no matter what the order of entry of these factors into the ANOVA. For a given worker size class, worker mass increased significantly ( $F = 113$ ,  $df = 1$ , 396,  $P < .0001$ ) with colony size class, accounting for 0.5–1.6% of the explained variation. Sample date accounted for 0.4–0.5% of the variation in worker mass ( $F = 4.77$ – $6.19$ ,  $df = 6$ , 396,  $P < .001$ ). Worker size class also interacted with sample date ( $F = 3.07$ ,  $df = 6$ , 396,  $P < .006$ ), showing that the effect of worker size class on worker mass varied with season. This variation cannot be explained by the head-width class but is probably the result of the changing fat content.

2. *Worker fat content.* — The dry-mass fat content of workers (percent fat) changed significantly with season ( $F = 13.3$ – $16.8$ ,  $df = 6$ , 396,  $P < .001$ ). Worker fat content declined steadily (slope =  $-0.013$ ,  $t = 2.61$ ,  $P < .05$ ) from its high in July through the winter to



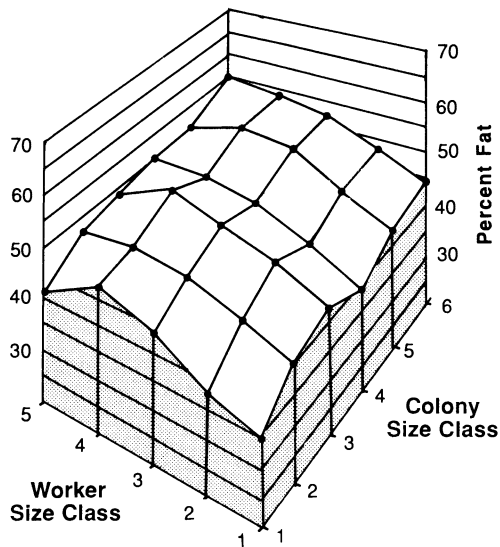


FIG. 7. The relationship of worker size and colony size to the worker percent fat (dry matter). The values are the annual means. The leanest workers are the smallest ones in the smallest colonies, while the fattest ones are the largest in the largest colonies. The pattern of seasonal variation in percent fat is similar for all worker and colony sizes (see Fig. 6).

its low in June (Fig. 6). This pattern was unaffected by colony size (colony size class  $\times$  sample date interaction,  $F = 1.37$ ,  $df = 6, 396$ , NS), i.e., colonies of all sizes showed similar seasonal changes in fat content.

In addition to the seasonal changes, worker fat content increased significantly with both worker size ( $F = 79.5-98.0$ ,  $df = 1, 396$ ,  $P < .0001$ ) and colony size, so that the highest content was found in the largest workers of the largest colonies and the lowest in the smallest workers of the smallest colonies (Fig. 7). This suggests that colony nutrition improved with colony size and that larger workers may function in part as energy depots (Porter and Tschinkel 1985); i.e., that energy storage is allometric to both colony and worker size. Indeed, a log-log regression of worker biomass (in milligrams) against total colony fat (in milligrams) showed a slope of 1.10, significantly  $> 1.0$  ( $t = 2.71$ ,  $P < .02$ ). In other words, for every 10-fold increase in worker biomass, the colony's total fat mass increased  $\approx 12.5$ -fold.

When percent fat was analyzed by colony size class within a sample date, it was clear that while percent fat generally increased with colony size, this increase was significant only between July and January (slopes = 0.014–0.027,  $P < .05$ –.0001). The March to June samples showed no significant slope, although workers in the smallest colonies were always the least fatty. Within colony size class, percent fat increased 2–4% for each worker size class ( $P < .0001$ –.02). However, the next-to-largest rather than the largest workers were the fattiest in 62% of the cases (Fig. 7), resulting in a significant interaction between worker size and sample date ( $F = 2.08$ ,  $df = 1, 6$ ,  $P = .05$ ).

3. *Other measures.*—A number of other measures correlate so highly with either mean worker mass or percent fat that their patterns of variation are essentially the same. Thus mean energy per worker, mean lean mass, and mean fat mass are, respectively, 99.5, 94.5, and 96.7% correlated with mean worker mass. Similarly, energy per unit mass is almost perfectly correlated with percent fat because the former was computed from the latter via constants. The preceding analyses of mean worker mass and percent fat are therefore almost identical with these other analyses.

4. *Proportion of major workers.*—Worker larvae that attain a certain size threshold early in development are reprogrammed to pupate at a larger size (Wheeler 1990). The resulting larger workers form a distinct subpopulation called major workers, while the remaining, un-reprogrammed workers are called the minor workers (Tschinkel 1988a). Size class 1 contained all the minor workers (head width 0.5–0.7 mm). All others were composed of majors (0.71–1.5 mm). As colony size class increased, the proportion of workers in all size classes of majors increased (i.e., right skew increased), while that of the minor class decreased. This relationship gave rise to the increase in mean worker mass noted in *Worker mean size*. These analyses confirm the findings of Tschinkel (1988a). Seasonal patterns in percent majors were less distinct: colony size class 1 (the smallest) showed the greatest annual increase in percent majors. Most colonies had a higher proportion of majors in the spring, peaking in April, perhaps as a result of differential mortality or differential production. The combination of the high proportion of majors with the still relatively high colony size resulted in a peak of worker biomass in March.

5. *Overview of worker analysis.*—The mean masses of workers increased several-fold with colony size, so that worker biomass grew more rapidly than did worker numbers. Most of the increase in mean mass was caused by an increased proportion of major workers. Majors composed up to 70% of worker biomass in large colonies (Tschinkel 1988a). Mean worker size fluctuated seasonally as well. For a given size of colony, workers were larger in spring and smaller in fall.

As colonies grew, they underwent seasonal size fluctuations of increasing magnitude, with a maximum colony size in midwinter and a minimum in midsummer. This is because worker production fell below replacement rate in the spring when production was shifted to sexuals (see *Costs and production rates: Production rates over the annual cycle and Production rates of colony-size cohorts.* . .). The worker fat content, and therefore the energy content, varied with colony size, worker size, and season. Fat content was lowest in the smallest workers of the smallest colonies and increased with both worker and colony size. The seasonal cycle of worker fat content was colony-size independent with a peak in July. Presumably, colonies drew upon worker fat during overwintering and during sexual production in the spring (see *Costs and production rates: Produc-*



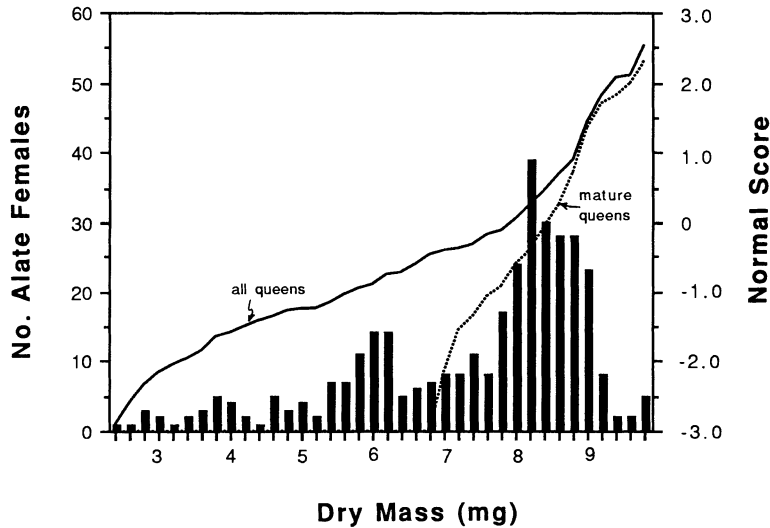


FIG. 8. Mass-frequency distribution of individual alate females over all samples. Females of  $<7.0$  mg are not yet mature, but are in the process of gaining mass. The normal score plots show the non-normality of the total population and the near-normality of the mature subpopulation ( $>7.0$  mg).

tion rates over the annual cycle and Production rates of colony-size cohorts. . .), so that fat content was lowest in June. Small colonies, because they experienced net growth, finished the year with more, larger, and fatter workers but few sexuals, while large colonies appeared to finish by simply having replaced dead workers and fat, but having produced large numbers of sexuals.

#### Mass and energy content of sexuals.—

1. *During maturation.*—Grand mean dry masses were  $2.66 \pm 0.30$  mg ( $\bar{X} \pm 1$  SD) ( $n = 285$ ) for male adults,  $2.51 \pm 0.38$  mg ( $n = 187$ ) for male pupae,  $7.48 \pm 1.16$  mg ( $n = 350$ ) for female adults, and  $3.06 \pm 0.41$  mg ( $n = 92$ ) for female pupae. Male mass increased 6% between the pupal and mature adult stage, while female mass increased by 275%.

Female mass gain during maturation resulted in a strongly non-normal distribution of masses (Fig. 8) with a mode at  $\approx 8.5$  mg and a strong left skew. The mean mass of female adults thus may include females that are not yet at flight mass, and thus underestimate the final investment of the colony in female alates. The mean mass of mature females caught in flight traps during one summer's mating flights was 8.07 mg with individual alate females ranging from 7.3 to 8.5 mg (D. McInnes, unpublished data). For the purpose of this paper, the modal class weighing  $>7.0$  mg was considered mature and flight-ready during the peak flight season. The mean mass of these females was  $8.42 \pm 0.60$  mg ( $\bar{X} \pm 1$  SD) and their mass-frequency distribution was not significantly different from normal (Shapiro-Wilk Test,  $n = 105$ , Corr. = 0.990; NS) (Fig. 8).

Fat extraction of female alates by mass class gave further insight into the process of maturation. Female alates from nine colonies were weighed and assigned to one of three mass classes:  $<4.0$  mg, 4.01–6.99 mg,

and  $\geq 7.0$  mg. Mean mass of individuals in each class was determined for each colony, the fat extracted, and the groups reweighed for determination of the fat and lean masses.

Maturation involved more than simply the addition of fat stores (Fig. 9). Both the mass of fat and the lean mass increased during maturation, but the rate of increase in fat exceeded the rate of lean mass gain (Fat mass =  $-1.87 + 1.35$  lean mass;  $R^2 = 76\%$ ) so that the percent fat in females increased according to: proportion fat =  $0.207 + 0.035$  fat mass;  $R^2 = 75\%$ ). The percent fat increased from  $31 \pm 2.7\%$  ( $\bar{X} \pm 1$  SD) in the lightest class to  $49 \pm 2.7\%$  in the heaviest, mature class.

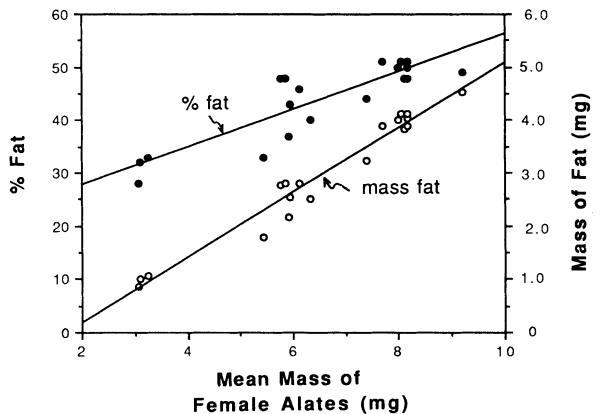


FIG. 9. The percent fat and mass of fat vs. female alate mass. As females gain mass during maturation, both lean and fat masses increase, but fat mass increases more rapidly, causing an increase in the percent fat. Females were assigned to one of three mass classes before extraction and each datum represents the mean value of a mass class for one colony. At maturity, females are  $\approx 50\%$  fat.

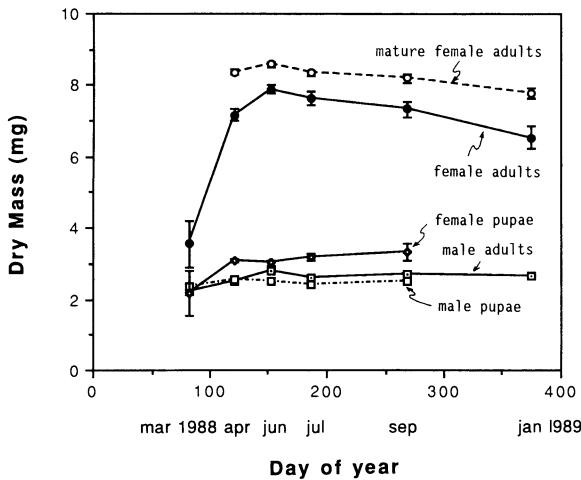


FIG. 10. Seasonal variation of the mean dry mass of sexual pupae and adults. Note the data begin with the March sample and end with the January sample. All except male pupae show significant seasonal variation. Error bars =  $\pm 1$  SE.

The increased mass and proportion of fat were reflected in an increased energy content, both per milligram and per female. The energy per unit body mass increased from  $\approx 25.2 \pm 5.6$  J/mg ( $\bar{X} \pm 1$  SD) at the start of maturation to  $\approx 28.9 \pm 0.47$  J/mg at maturity. This and the mass gain resulted in a per female energy content that rose from  $78.8 \pm 3.53$  J to  $234 \pm 15.7$  J at maturity, an increase of almost 290%. Energy per unit mass increased in relation to the mean mass ( $M$ , in milligrams) of the grouped females as follows:  $J/\text{mg} = 23.1 + 0.72 M$  ( $R^2 = 75\%$ ). Energy per female adult increased as follows:  $J = -21.7 + 31.4 M$  ( $R^2 = 99.3\%$ ). If this relationship is computed on the basis of overall mean female mass for the whole colony rather than by mass classes, it becomes  $J = -18.5 + 31.0 M$  ( $R^2 = 99.4\%$ ). This is the equation used in *Costs and production rates: Production rates over the annual cycle: 1. Regression of production rates to estimate energy content of female alates.*

While male mass increased significantly ( $t$  test  $P < .05$ ,  $df = 1, 472$ ) from the pupa to the mature adult ( $2.51 \pm 0.38$  to  $2.66 \pm 0.30$  mg,  $\bar{X} \pm 1$  SD), this represents only a 6% mass gain, much smaller than the nearly threefold increase in females. Moreover, male adults had an approximately normal mass-frequency distribution and did not show the skewing suggestive of a gradual maturation of overlapping cohorts. Mass gain is not a major part of male alate maturation.

2. *Seasonal variation.*—In addition to, or perhaps as a result of the maturational mass gain, there was a seasonally significant difference in mean mass (Fig. 10). Female pupae in March were lighter (2.16 mg) than they were in all other months (3.02–3.31 mg) (ANOVA:  $F = 3.71$ ,  $df = 4, 92$ ,  $P < .02$ ). A similar pattern but larger difference was found for female adults. These were lightest in March (3.57 mg), increased to 7.16 mg

in April, peaked at 7.89 in early June, and declined to 7.33 mg by mid-September (ANOVA:  $F = 7.85$ ,  $df = 5, 345$ ,  $P < .001$ ). These trends can probably be partly explained by the larger proportion of immature females during the early phases of sexual production, but the lower pupal mass suggests other effects as well, such as reduced nutrition during the early spring. When the analysis was repeated for mature female adults only (mass  $> 7.0$  mg), mass gain declined later in the summer, suggesting that the proportion of mature females is not sufficient explanation. This is further supported by similar trends in the mean masses of females captured in flight traps during mating flights (D. McInnes, unpublished data).

Male adults also show similar patterns in mass: they are lightest in March (2.24 mg) and peak in June (2.78 mg) (ANOVA:  $F = 11.08$ ,  $df = 5, 280$ ;  $P < .001$ ). Male pupae show no significant changes of mass with season.

3. *Sexual analysis overview.*—Most of the investment in female alates took place after adult eclosion and consisted of an almost threefold increase in mass and a rise in fat from  $\approx 30$  to 50%. This large energy investment represents stores upon which the alates draw during colony founding. Male maturation was accompanied by only a 6% increase in mass. Both sexes of alates peaked in mass during mating flight season, but neither changed mass or energy content in relation to colony size.

#### *Mound volume.*—

As a colony increases in size, it builds a larger mound. Because the mound is galleried, it represents living space, but it also represents soil excavated during the enlargement of the underground chambers below (Markin et al. 1973). Although the relationship of these two volumes is not known, an increment of mound volume represents a larger increment in total living space. Living space is an obvious element in a socio-metric study. That it may affect colony functions in important ways is a possibility that is largely unexplored. Feedbacks from living space could be important to sociogenesis, especially if the space did not increase at the same rate as colony size.

By measuring mound volumes and determining a packed volume of the mound soil, it was possible to show that the galleries compose  $\approx 66 \pm 6.9\%$  ( $\bar{X} \pm 1$  SD) of the total mound volume.

Because all excavation and building is carried out by workers only, the mound volume was first regressed against the worker biomass (log-log transformed data) by sample date. While this regression accounted for 78% of the variation, a better fit was obtained by regressing the mound volume against the total dry colony biomass (workers + brood + sexuals; log-log transformed) by sample date. This regression accounted for 89% of the variation, with a common slope for all values giving a somewhat better fit to the data (in Fig. 11, sample date, which accounted for 4% of the vari-

ation, is not included). A 10-fold increase in colony mass resulted in a 13-fold increase in mound size. A regression of mound volume per unit ant biomass confirmed this (multiple regression,  $F = 3.51$ ,  $df = 6, 68$ ,  $P < .01$ ).

The effects of sample date on mound volume were significant but rather small: for a given colony mass, mounds were  $\approx 1.6$  times larger in spring and summer than in fall and winter ( $t$  test of intercepts,  $t = 3.2$ ,  $P < .01$ ). Most of the variation in mound size resulted from variation in colony mass. The impression that mounds are larger and more conspicuous during the cool months must therefore be mostly the result of larger colony size during this season. In addition, worker biomass declined during the spring and summer and the decline was greater for larger colonies, possibly accounting for the larger volume factor during these seasons. A one-way ANOVA of the volume of mound per unit of colony biomass (log-transformed) by sample date confirmed these trends ( $F = 3.02$ ,  $df = 5, 69$ ,  $P < .05$ ). There was a mean of 2.12 mL/mg in January, rising through 2.9 mL/mg in March to  $\approx 3.5$  mL/mg during the summer and declining to 2.1 mL/mg in September. *Lasius flavus* builds mounds of similar size with  $\approx 1.6$  mL/individual (Nielsen et al. 1976).

The  $y$  intercept suggested that colonies should begin building mounds when their total dry mass was between 4 and 6 g, or 9000 and 14000 workers. The smallest sampled mounds ranged from 0.25 to 0.5 L and contained 4500–9400 workers, somewhat less than predicted by the regression.

Because the effect of sample date was small, a simple regression of the two log-transformed variables still accounted for 85% of the variation:  $\log(\text{mound volume}) = -3.82 + 1.06 \log(\text{mass of all ants})$ .

#### Costs and production rates

**Rationale:** The seasonal and life-cycle patterns of how colonies allocate resources are best seen in the rates at which the various options of production (workers, sexuals) and maintenance proceed. These allocation patterns are important life history components of each species. When allocation is measured as rates, it is not complicated by turnover as is standing biomass and is thus a better basis for estimates of investment. Production rates, in units of numbers, mass, or energy, are therefore key to sketching seasonal and life cycle investment patterns. Integrated over the life of a colony, production rates can give lifetime allocation patterns (see *Total annual production: Rationale and Allocation patterns and efficiency*). Production rates also bear on population dynamics. As long as birth rate (worker production) exceeds mortality rate, colonies grow. When they are equal, colonies enter stasis, and when mortality is greater, they decline (see *Annual cycle of mortality and natality by size class: Rates of mortality and natality and Cumulative natality and mortality*).

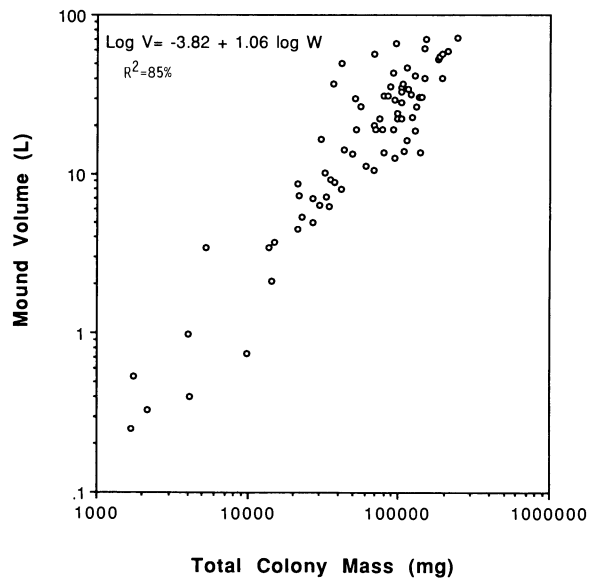


FIG. 11. Mound volume in relation to colony size. Total mass of ants in the colony explained 85% of the variation in mound volume. Seasonal effects were significant but relatively small.

#### Worker maintenance costs.—

Worker maintenance (respiratory metabolism) is a major cost for colonies of ants usually ranging from 65 to 75% of total costs (Jensen 1978b, Porter and Tschinkel 1985, Calabi and Porter 1989). In *Solenopsis invicta*, it ranged from 600 to 126 000 J/d, depending on colony size and season. A regression of maintenance cost against colony size (log–log transformed) showed that most of the variation in maintenance cost (in joules per day) was associated with colony size in milligrams ( $\log \text{maintenance cost} = 0.31 + 0.91 \log \text{colony size}$ ). Variation about the regression line was low because the maintenance cost was calculated mostly from means and constants, worker mass being the only source of sampling error in the calculation. The differences among the sample dates resulted from differences in the mean temperatures used in calculating respiration rates.

While several sample dates yielded significantly different  $y$  intercepts, the daily maintenance cost in July was only twice that in January (Table 3). Over the same period brood production increased 100- to 200-fold (Table 3, Fig. 13), depending on the particular measure. Thus, while brood production is practically zero in January, maintenance costs were still about half of July's value. This means that during winter, 99% of the operating cost of colonies is worker maintenance. This drops to  $\approx 45$ –50% during peak brood production (Fig. 12). A one-way ANOVA showed a highly significant effect of sample date upon the percent of total costs that was worker maintenance ( $F = 69.3$ ,  $df = 6, 82$ ,  $P < .001$ ). On the other hand, percent maintenance cost was not related to colony size (one-way ANOVA  $F = 1.62$ ,  $df = 5, 83$ , NS).

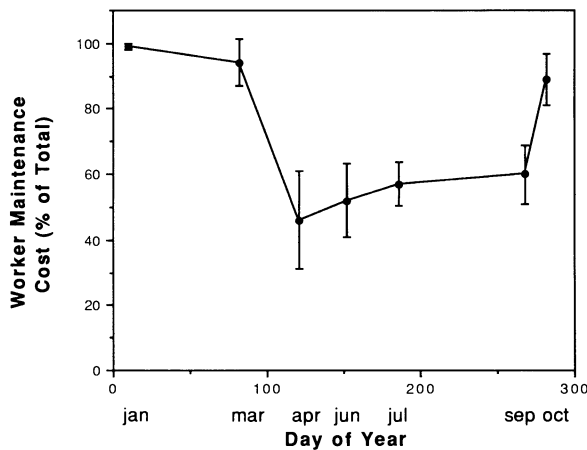


FIG. 12. The cost of worker maintenance as a percentage of the total daily colony cost. During winter, when brood production is near zero, almost all the cost is worker maintenance. In this figure, all nonmaintenance costs are brood production costs.

#### *Production rates over the annual cycle. —*

1. *Regression of production rates against colony size by sample date.*—The rates of production of workers, sexuals, and total ants were highly dependent on colony size and season. These rates were analyzed in stages: (1) The number of pupae of each type was estimated from the census; (2) The number of new individuals per day was computed by dividing the number of pupae by the pupal development period (*Materials and Methods: Basic computations: Pupal development*; Table 2, measure 24; Fig. 1); (3) This was converted to daily biomass production (in milligrams per day) by multiplying by the mean mass (Table 2, measure 26); (4) This in turn was converted to production cost per day (in joules per day) by multiplying by the joules per milligram determined from the fat extractions (Table 2, measure 28); (5) The daily maintenance costs of workers in joules was derived from colony temperature, respiration rate, and worker distribution in the nest (Table 2, measure 18); (6) The total daily cost of production in joules (= maintenance + production costs) resulted from the sum of (4) and (5) (Table 2, measure 30). Larval and pupal maintenance costs were not included but are probably a small proportion of total maintenance respiration (Jensen 1978b, Porter and Tschinkel 1985). Total cost does not include the cost of doing physical work such as moving brood, nest excavation, foraging, and so on (see Nielsen and Baroni-Urbani 1990 for an example of estimation of such costs).

Each of these daily production rates was then regressed against the total mass of workers (log-log transformed), using dummy variables for the sample dates (Table 3). In such regressions colonies were compared on the basis of their size at time of census, but because size changes throughout the year (Fig. 4), comparison

of colonies of a given size across months does not track the annual production history of a size-cohort of colonies. Rather, it is simply a comparison among colonies of the same instantaneous size across seasons (Table 3). Interpretation of the regressions is simplified if the effect of colony size on rates is the same throughout the year and each sample date simply multiplies the production rate by a characteristic factor. After log-log transformation, this meant that the sample months shared a common slope, but each would have a different  $y$  intercept. The data suggested that this was a somewhat better interpretation: a comparison of the correlation coefficients ( $R^2$ ), residual plots, normal score plots, and coefficient  $t$  values (not shown) favored the common-slope, variable-intercept interpretation over the variable-slope, common-intercept one, though not decisively. A mixed interpretation seemed unjustified and difficult.

The number of pupae of all types in colonies was greater during the warm months and in larger colonies (shown by intercepts for worker pupae, Table 3). Regression of the number of worker pupae vs. total mass of workers (log-log transformed) accounted for 73% of the variation. For a given size colony, the number of pupae increased  $\approx 4.5$ -fold from January to midsummer (Table 3) and fell during autumn. A 10-fold increase in colony size resulted in a 4.1-fold increase in the number of pupae, a large decrease in efficiency whose nature is explored in *Discussion: Efficiency and colony size*.

By dividing the censused number of pupae of each type by the development rate (days), the number of new individuals per day resulted. The lowest rates occurred in the winter and the highest in the summer.

2. *Relative production rates.*—In the regressions used here, the sample date, through changing temperature, acted as a multiplier of the rate/size curve. By taking the anti-log of the difference in  $y$  intercepts of two months, the factor by which the rates differ was derived. Because January production rates were consistently the lowest, they were used as the base sample against which others were compared.

The daily production rates for workers, sexuals, and total in terms of number, dry mass, production cost, and total cost were each regressed against colony size. All data were log-log transformed because this gave the best combination of stable variance, linearity, residual analysis, and high correlation coefficient for most analyses. Table 3 summarizes these regressions. The rates relative to the January rate show a number of clear patterns (Fig. 13). Most obvious of these is the strong effect of season. The total rate of production of number of individuals increased 115-fold between January and the early summer peak. In terms of total mass per day and production cost per day, the rate increase over this period was 200-fold (because mass per day and energy-production cost per day were so similar, only the latter will be discussed). The majority of total

TABLE 3. Regression of production rates (*y*) against colony size (*x*, as total worker biomass) in the form,  $\log y = b + a \log x$ . Values labeled with the same letter in a "group" row are not significantly different. SE = standard error.

| <i>y</i>                                 | Slope |        | Param-<br>eter | No. colonies |        |        |        |        |        |        | <i>R</i> <sup>2</sup><br>(%) |
|--|-------|--------|----------------|--------------|--------|--------|--------|--------|--------|--------|------------------------------|
|  | Mean  | SE     |                | JAN          | MAR    | APR    | JUN    | JUL    | SEP    | OCT    |                              |
|  |       |        |                | 12           | 12     | 16     | 16     | 10     | 9      | 14     |                              |
| <b>Individuals</b>                       |       |        |                |              |        |        |        |        |        |        |                              |
| No. worker pupae                         | 0.616 | 0.0093 | <i>b</i>       | 0.31         | 0.065  | 1.23   | 1.42   | 1.41   | 1.46   | 0.66   | 80                           |
|  |       |        | SE             | 0.10         | 0.10   | 0.088  | 0.088  | 0.11   | 0.12   | 0.094  |                              |
|  |       |        | group          | c            | d      | a      | a      | a      | a      | b      |                              |
| No. workers per day                      | 0.616 | 0.0092 | <i>b</i>       | -1.59        | -1.28  | 0.13   | 0.41   | 0.44   | 0.35   | -0.56  | 84                           |
|  |       |        | SE             | 0.010        | 0.010  | 0.88   | 0.088  | 0.011  | 0.012  | 0.094  |                              |
|  |       |        | group          | d            | d      | a      | b      | b      | a      | c      |                              |
| No. sexuals per day                      | 0.799 | 0.021  | <i>b</i>       | -3.75        | -2.56  | -1.37  | -1.56  | -2.00  | -1.87  | -2.11  | 59                           |
|  |       |        | SE             | 0.012        | 0.012  | 0.010  | 0.010  | 0.013  | 0.014  | 0.011  |                              |
|  |       |        | group          | c            | c      | a      | a      | b      | b      | b      |                              |
| Total no. per day                        | 0.673 | 0.0086 | <i>b</i>       | -1.87        | -1.44  | -0.027 | 0.20   | 0.20   | 0.80   | -0.80  | 85                           |
|  |       |        | SE             | 0.095        | 0.095  | 0.082  | 0.082  | 0.10   | 0.011  | 0.088  |                              |
|  |       |        | group          | c            | d      | a      | a      | a      | a      | b      |                              |
| <b>Biomass</b>                           |       |        |                |              |        |        |        |        |        |        |                              |
| Mass of workers per day (mg/d)           | 0.852 | 0.0079 | <i>b</i>       | -3.02        | -2.58  | -1.26  | -0.99  | -0.98  | -1.05  | -1.93  | 88                           |
|  |       |        | SE             | 0.20         | 0.20   | 0.18   | 0.18   | 0.022  | 0.24   | 0.19   |                              |
|  |       |        | group          | e            | d      | a      | b      | b      | a      | c      |                              |
| Mass of sexuals per day (mg/d)           | 0.738 | 0.018  | <i>b</i>       | -3.01        | -1.67  | -0.57  | 0.66   | -1.11  | -0.81  | -1.24  | 65                           |
|  |       |        | SE             | 0.10         | 0.10   | 0.089  | 0.089  | 0.11   | 0.12   | 0.095  |                              |
|  |       |        | group          | c            | c      | a      | a      | b      | a      | b      |                              |
| Total mass per day (mg/d)                | 1.02  | 0.0082 | <i>b</i>       | -3.82        | -3.12  | -1.62  | -1.51  | -1.64  | -1.76  | -2.62  | 89                           |
|  |       |        | SE             | 0.091        | 0.091  | 0.079  | 0.079  | 0.099  | 0.11   | 0.084  |                              |
|  |       |        | group          | d            | c      | a      | a      | a      | a      | b      |                              |
| <b>Energy content</b>                    |       |        |                |              |        |        |        |        |        |        |                              |
| Energy content of workers per day (J/d)  | 0.879 | 0.0078 | <i>b</i>       | -1.70        | -1.26  | 0.058  | 0.33   | 0.36   | 0.29   | -0.60  | 88                           |
|  |       |        | SE             | 0.087        | 0.087  | 0.075  | 0.075  | 0.095  | 0.10   | 0.080  |                              |
|  |       |        | group          | e            | d      | a      | b      | b      | a      | c      |                              |
| Energy content of sexuals per day (J/d)  | 0.723 | 0.018  | <i>b</i>       | ...          | -0.19  | 0.89   | 0.80   | 0.36   | 0.69   | 0.22   | 53                           |
|  |       |        | SE             | ...          | 0.10   | 0.088  | 0.088  | 0.11   | 0.12   | 0.094  |                              |
|  |       |        | group          | ...          | c      | a      | a      | b      | a      | b      |                              |
| Total energy content per day (J/d)       | 1.03  | 0.080  | <i>b</i>       | -2.44        | -1.76  | -0.26  | -0.15  | -0.24  | -0.36  | -1.23  | 89                           |
|  |       |        | SE             | 0.089        | 0.089  | 0.077  | 0.077  | 0.097  | 0.10   | 0.082  |                              |
|  |       |        | group          | d            | c      | a      | a      | a      | a      | b      |                              |
| <b>Maintenance cost</b>                  |       |        |                |              |        |        |        |        |        |        |                              |
| Daily maintenance cost of workers (J/d)  | 0.937 | 0.0066 | <i>b</i>       | 0.031        | 0.095  | 0.128  | 0.316  | 0.334  | 0.280  | 0.219  | 99                           |
|  |       |        | SE             | 0.0076       | 0.0076 | 0.0066 | 0.0066 | 0.0084 | 0.0088 | 0.0071 |                              |
|  |       |        | group          | c            | b      | a      | e      | e      | d      | c      |                              |
| <b>Total energy costs</b>                |       |        |                |              |        |        |        |        |        |        |                              |
| Total daily energy cost of workers (J/d) | 0.912 | 0.0014 | <i>b</i>       | 0.16         | 0.22   | 0.41   | 0.63   | 0.65   | 0.59   | 0.38   | 99                           |
|  |       |        | SE             | 0.014        | 0.014  | 0.012  | 0.012  | 0.015  | 0.016  | 0.013  |                              |
|  |       |        | group          | d            | b      | a      | c      | c      | b      | a      |                              |
| Total daily energy cost of sexuals (J/d) | 0.718 | 0.018  | <i>b</i>       | ...          | -0.019 | 1.03   | 0.90   | 0.48   | 0.81   | 0.34   | 54                           |
|  |       |        | SE             | ...          | 0.099  | 0.086  | 0.086  | 0.11   | 0.12   | 0.092  |                              |
|  |       |        | group          | ...          | c      | a      | a      | b      | a      | b      |                              |
| Total daily energy cost (J/d)            | 0.931 | 0.0022 | <i>b</i>       | 0.065        | 0.15   | 0.52   | 0.64   | 0.61   | 0.54   | 0.30   | 97                           |
|  |       |        | SE             | 0.025        | 0.025  | 0.022  | 0.022  | 0.027  | 0.029  | 0.023  |                              |
|  |       |        | group          | c            | b      | a      | e      | e      | d      | c      |                              |



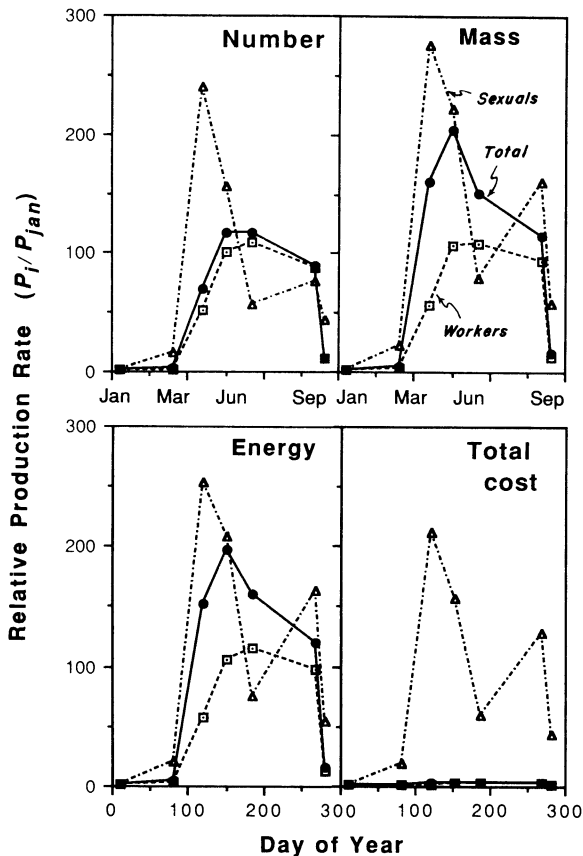


FIG. 13. The rates of daily production relative to the January rate, showing the effects of season and brood type. All colony sizes show similar increases of production with season, therefore the values are the means over all colonies. Note the sharp peak of sexual and total production in spring. When the cost of worker maintenance is included (total cost per day), the total and worker production rates only increase a fewfold over their January values. Symbols:  $\Delta$  = sexuals;  $\bullet$  = workers;  $\square$  = total.

cost per day (production + maintenance) was worker maintenance, a cost which varies only a fewfold through the year (Table 3). This led to relatively low seasonal variation of total cost of workers and the whole colony.

Worker production rates showed similar patterns except that they peaked in mid- rather than early summer. Worker production rate in numbers of individuals increased  $\approx 108$ -fold, that of energy produced 115-fold, and total cost  $\approx 3.1$ -fold.

Sexual production increased more sharply and peaked earlier than did worker production. The number of sexuals per day increased 240-fold between January and the April peak. By July this dropped significantly ( $t$  test,  $P < .05$ ) to 55-fold and then climbed slightly to 75-fold in September. When measured in energy produced per day, a 250-fold increase was seen by April, again with a significant ( $t$  test,  $P < .05$ ) dip in July. The origin of this dip may lie in the colony size minimum reached at this time. As colonies grew during

the remaining warm period, perhaps they achieved enough size to produce a second peak of sexuals in September. There was relatively little difference in production cost and total cost of sexuals (Fig. 13). Maintenance is a small proportion of the cost of sexuals because they remain in the colony only a few weeks.

With the onset of cool weather in October (day 282), all production rates dropped sharply. The effect of temperature on brood production is threshold-like: brood production essentially ceases below 24°C (Porter 1988).

3. *Relationship of production rates to colony size.*—Production rates were strongly related to colony size. A 10-fold increase in colony size increased the total number of ants per day 4.7-fold (anti-log of slope), of total production cost per day by 10.7-fold, and of total cost (production + maintenance) by 8.5-fold. Separating out worker production, these factors were 4.13 for numbers, 7.6 for production cost, and 8.2 for total cost. For sexual production, they were 6.3, 5.3, and 5.2, respectively. Viewed separately, both worker and sexual production increased more slowly than colony size, an apparent decrease in efficiency. However, taken together the total production rate of colonies kept pace with the increase in colony size: the slope of production cost per day was 1.03, not significantly  $> 1.0$  ( $t$  test of slope vs. 1.0, NS). From the point of view of instantaneous colony size, these data suggest that for one (production cost per day) of the three measures, there was no loss of efficiency with increasing colony size, while for the other two (total number per day, total cost per day), there was.

4. *Seasonality of investment in sexuals.*—Investment in sexuals was strongly seasonal (Fig. 14). The proportion of daily number and production cost which colonies invested in sexuals peaked in April at 19 and 47%, respectively. That is, almost half of the daily production cost was in sexuals at this time. This dropped to 12% in October. Interestingly, while the percent sex-

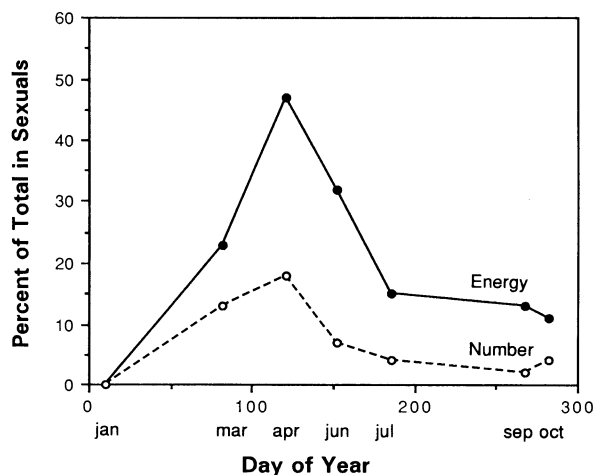


FIG. 14. The percentage of total daily energy production which is invested in sexuals in relation to season. About 50% of the energy of spring production is in the form of sexuals.

ual production remained at 13% in September, the production rate increased (Fig. 13), suggesting that this increase was the result of increased colony size.

*Production rates of colony-size cohorts through an annual cycle. —*

If we wish to follow what happens to production rates of a colony throughout the year, we must track such a colony through the spring decline and the fall increase of colony size. Choosing a colony size in January and simply solving the regressions in the previous section (Table 1) for this colony size does not result in the actual production rates over the year. By segregating the data from each sample date by size classes (see *Materials and Methods: Basic computations: 4. Colony size classes . . .*), the mean production rates of a representative class of colony can be tracked through the year in spite of the complex size changes (Fig. 4) it undergoes.

In Figs. 15 and 16, these annual cycles are shown for the means of the six size classes, using number per day and joules per day as the dependent variables. Missing values were interpolated from the regression within sample date. One outlier was substituted with an interpolated value. The figures share some obvious features: a sharp rise of production in the spring, a sharp drop in the fall, and a nonlinear increase in production rates as colony size increased.

During midsummer there was a distinct decline in both worker and sexual production rate. Colony size was at the annual minimum at this time, possibly accounting for the dip in production rates. By September, both colony size and production rates were higher, possibly giving rise to the minor rise in sexual production rate at this time. By October, temperatures had fallen enough to depress all production to very low levels.

The nonlinear increase in production rate with size class (Figs. 15 and 16) is of special interest. On the surface, the decreasing increments of production with increasing colony size class suggest that the efficiency of production declines with increasing colony size, an effect that is believed to be quite general in social insects (Michener 1964). However, it must be remembered that colonies decline in size until midsummer and increase thereafter, and that the magnitude of this decline is proportional to colony size (Fig. 4). Thus, a colony of 160 g (class 6) in January contains only  $\approx 90$  g in midsummer. Its production rate in midsummer is lower than expected on the basis of its January size in part simply because it is smaller.

Fig. 17 shows this effect for two colony sizes: the means of size classes 2 (35 g) and 6 (160 g). The vertical section of the regression surface across the year at 35 and 160 g shows the annual cycle of production rates that would be expected if colony size remained constant at its January value. The actual colony size is shown on the horizontal plane, with a large midyear dip for the large colony and a smaller one for the small

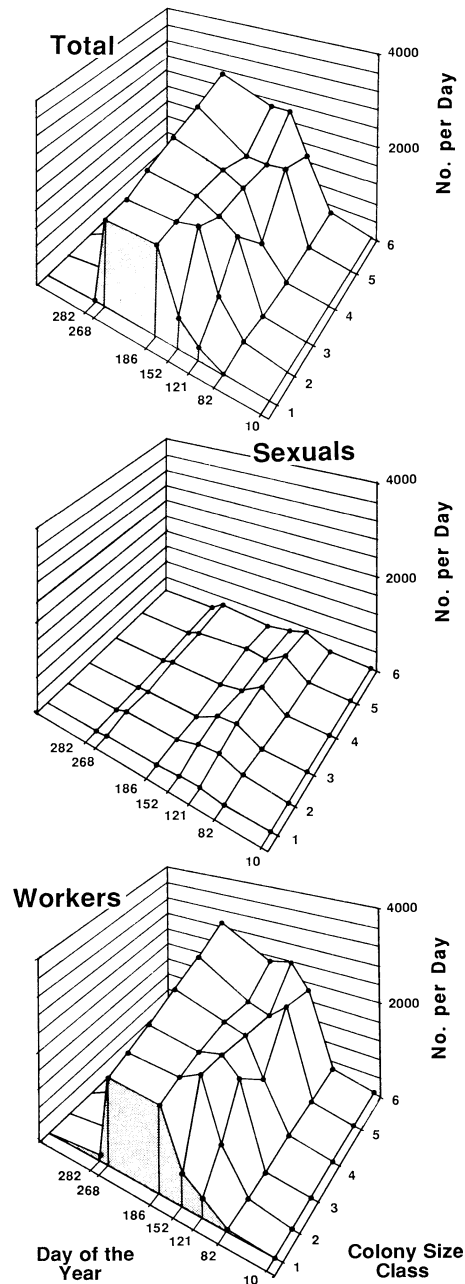


FIG. 15. Daily adult production rate in relation to colony size class and season.

colony. By September, the smaller colony exceeded its January size, indicating growth, while the large colony had not yet recovered its January size. When the actual colony size curves were projected vertically upward, their intersection with the regression surface defined the actual production rate during the year (i.e., these were the regression solutions using the actual colony sizes). Replotting these values against size class would result in an apparent decrease in production efficiency with colony size: production declines midyear because

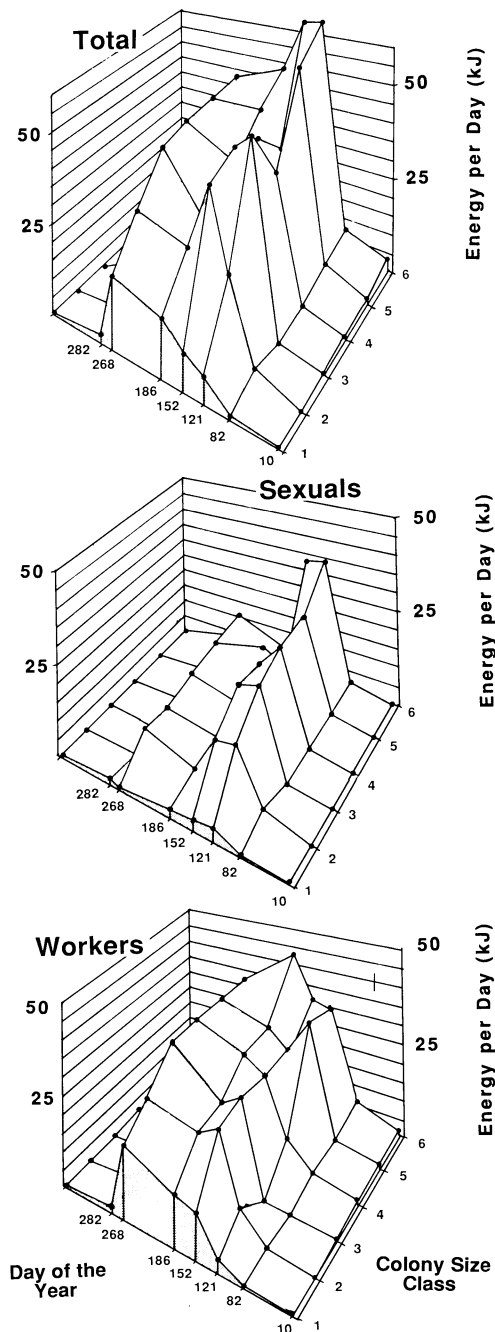


FIG. 16. Production rates (as daily energy cost) in relation to colony size and season. Sexual and total production peak in spring as colony size is falling. Production increases with colony size, but less than proportionally.

colony size declines, even though size *class* remains the same.

How well do the regression solutions (Table 3) using the size class midpoints agree with actual data? All colonies were assigned to size classes and the mean production rate for each size class and sample date was calculated. These "data" values were divided by the

regression solutions (Table 3). A ratio of 1.0 indicated perfect agreement. Sampling error can be expected to generate unpatterned scatter around the ratio of 1.0, but any regular deviation indicates that the regression solutions do not accurately reflect the measured values.

Overall, the pattern of deviation of the data from the regressions indicates that a different transformation might have fit the data better, one which gave higher production rates at small colony size and lower ones at greater size. Unfortunately, most such transformations lack the ease of interpretation found in log-log transformation. Some patterned deviation may have resulted from forcing a common slope on all samples in the multiple regression. It is also possible that the lack of agreement stems from errors in estimation of how colony size changes through the year (Figs. 3 and 4). If colony size were underestimated for small colonies and overestimated for large, the production rates from the regression equations would deviate from the data as observed. Colony-size related increases in mean pupal periods could also produce the observed deviations because these increases would reduce natality rate and production rate. Incorrect assignment of colonies to size classes could also achieve this result. The uncertainty cannot be resolved without repeated census of a cohort of colonies, a procedure for which methods are not available.

#### *Overview of production rates and costs.—*

All colonies showed a very high spring peak in total production (relative to their January rate) which occurred at the expense of worker fat and worker numbers. Almost half of April's production was devoted to sexuals causing colony size to decline as a result of the deficit in worker replacement rate. After midsummer, almost 90% of production consisted of workers, bringing about seasonal colony growth.

Total production rate increased at the same rate as did colony size. However, because only a portion of total production was invested in workers, the worker production rate failed to keep pace with colony size, slowing colony growth. However, this instantaneous picture does not take into account the variation of colony size during the year. When size cohorts of colonies were tracked through the year, production rates fell during the first half of the year because colony size fell, and rose during the second half of the year because colony size increased.

#### *Total annual production*

Rationale: Reproduction occurs on an annual cycle, making the year a meaningful unit over which to sum investment rates in order to determine investment patterns by, for example, colony size classes. For species in which queen and colony life spans are synonymous, summing the annual productions over the colony's lifetime gives lifetime investment patterns. The fraction of its lifetime resources which a

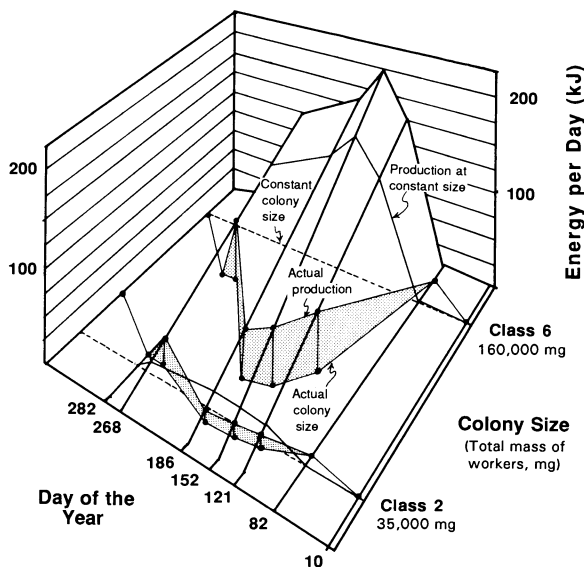


FIG. 17. The effect of seasonally changing colony size on production rate (as daily energy cost) for two representative colony sizes (classes 2 and 6). This figure also relates the regressions within sample date to the progress of the size class through the year. The vertical sections at 160 000 and 35 000 mg show production rates if colony size were constant at its January value. Actual colony sizes are shown on the horizontal plane for classes 2 and 6. Actual production rates are shown by the intersection of the vertical plane through the actual colony sizes and the regression surface (●).

colony devoted to “somatic” functions (workers, growth, maintenance) as opposed to reproduction (sexual alates) is an important component of its life history strategy.

Fire ant colonies can replace dead queens so that lifetime fitness and investment of colony and queen are not the same. In principle, queen lifetime production could be calculated, but could be different depending upon whether the queen founded her own colony or replaced a queen in a mature colony. Annual production by colony size class can be used to estimate lifetime production in either case.

*Allocation patterns and efficiency.*—Within each size class, the production rates in the foregoing section were converted to total production between sample dates by multiplying the number of days in the interval by the mean of the two production rates (i.e., rates were linearly interpolated). The first and last samples of the year were interpolated to the last and first samples, respectively, and the mean multiplied by the number of days to year-end or beginning, respectively. Summing these products over the year, this method thus cumulates the production by the *average colony* of each size class in spite of the annual cycle of changing size (Fig. 18). This cumulation was carried out for each dependent measure. From these annual totals, I calculated size-class specific proportion of investment in

sexuals and workers, ratio of cumulative production to initial colony size, and other measures of interest.

The total annual production curves all have a generally similar shape (Fig. 18). As expected, annual production rises with size class, but the patterns of this rise show some interesting features. In all cases, annual production increased more slowly than did colony size (Fig. 18), leading to declining efficiency of production by all measures (illustrated for total ants in Fig. 19). When the basis was number of individuals, a January colony of 25 000 workers (class 1) had produced 225 000 new workers by the end of December, or 9.0 workers for every original worker. Larger size classes produced more workers (Fig. 18) but the per-worker rate dropped from 9.0 in class 1 to  $\approx 1.5$ – $1.6$  in classes 5 and 6 (Fig. 19). In part, such declines are expected characteristics of logistic colony growth.

Because sexuals are much larger than workers, the cumulative number produced annually was much lower (Fig. 18). Nevertheless, production generally increased with colony size class, except again in class 6.

Because sexuals weigh more than workers, their share of the total dry mass was larger than their share of total numbers (Fig. 18). In addition, the curve showed a sharp break between classes 1 and 3, so that the annual mass production of classes 2 through 6 was a simple linear function of size, while that of class 1 was sharply lower. A class 1 colony starting out with 10.5 g of workers in January produced  $\approx 75$  g of workers and 13 g sexuals by the end of the year, a ratio of 7.1 g/g for workers, 1.2 g/g for sexuals, and 8.8 g/g for total. A colony in class 6 began with 161 g of workers and produced 362 g of workers and 121 g of sexuals by the end of the year, a ratio of 1.4 g/g for workers, 0.75 g/g for sexuals, and 2.2 g/g for total. The overall efficiency of production of class 6 colonies is thus only about one-quarter that of class 1 (Fig. 19).

The curves are fairly similar when the basis is production cost (Table 2, measures 28 and 29) (Fig. 18). While the energy-per-unit-mass values of workers and sexuals vary seasonally, they do so within rather narrow limits (Figs. 6 and 9), making the energy per year and mass per year curves rather similar.

Adding the daily worker maintenance cost to the production cost gave the total cost (Table 2, measure 30). Even during the season of highest brood production, worker maintenance costs exceeded the daily production costs of new ants by several fold. Because sexuals remained in the nest for only a few weeks (assumed 2 wk for calculation) and their maintenance rate per unit mass was low, their cost to the colony was mostly that of production. The relative cost of maintaining sexuals was less than that of workers. Larger colonies had proportionally higher worker maintenance costs (Table 1), decreasing the sharpness of the break at class 2.

*Relative investment in sexuals.*—Of special interest is the fraction of resources allocated to sexuals, an im-



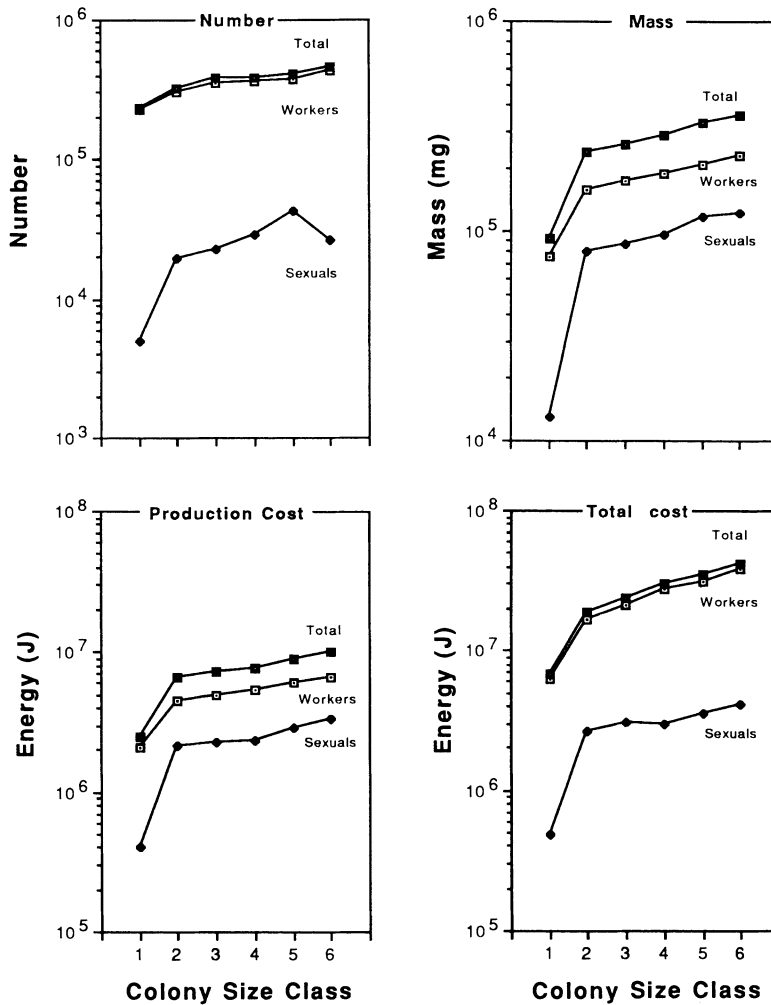


FIG. 18. Total annual production in number, mass, energy, and total cost in relation to initial colony size in January. The sharp break at size class 2 coincides with the transition from the ergonomic to the reproductive stage.

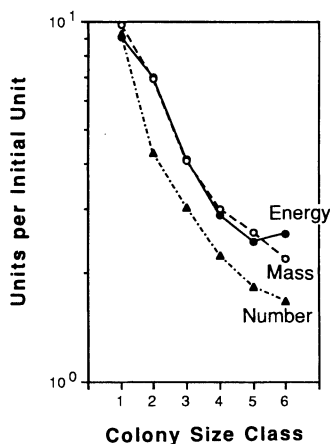


FIG. 19. Efficiency of production in relation to colony size. No matter what the basis (number, mass, energy), efficiency declines greatly as colony size increases.

portant element of the reproductive “strategy” of populations. *Solenopsis invicta* has been described as a “weedy” species (Tschinkel 1987a) and is thus expected to invest a large proportion of its production capacity in sexuals. There are very few data for comparison. The present data will form a basis for a future comparison with other species and populations. No matter what the basis, class 1 colonies invest a smaller portion of their annual production in sexuals, but all larger size classes invest a similar fraction (Fig. 20). On the basis of energy content, class 1 colonies allocate 16% while all larger classes allocate 30–34%, about twice as much (Fig. 20). The values are similar by mass (not shown): class 1 colonies allocate 16%, while all larger colonies invest 34–36%. It appears that once a colony leaves the ergonomic (worker producing) phase to enter the reproductive phase, the fraction it invests in sexuals remains constant. Class 1 spans from 0 to 50 000 workers in January and probably includes most of the ergonomic phase.



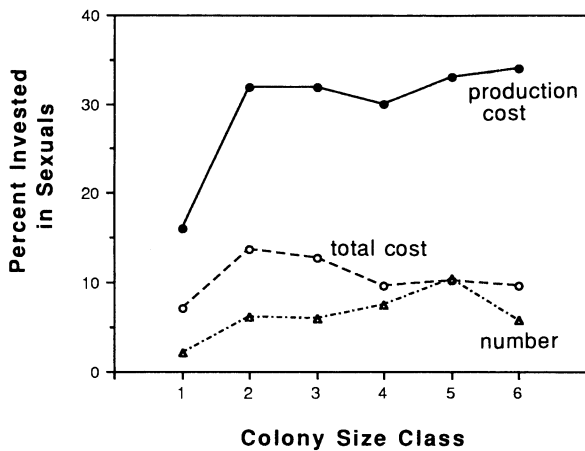


FIG. 20. The percent of the annual energy in biomass which is invested in sexuals. Colonies in size class 2 and larger invest about one-third of their annual production in sexuals. Values are lower when the basis is total cost or number. The transition from the ergonomic to the reproductive stage occurs in size class 1, resulting in lower investment for this class.

When the cost of worker maintenance was added to the production cost, the pattern changed somewhat. Because worker maintenance was relatively expensive, the fraction of total energy allocated to sexuals was lower for all size classes. In addition, the proportion allocated to sexuals peaked in class 2 and declined as size class increased (Fig. 20). This was the result of the relatively higher annual worker maintenance costs that larger colonies experience. As a fraction of total costs, classes 1 through 6 spend 62, 63, 67, 73, and 75% on worker maintenance. This was probably the result of the declining production efficiency as colonies got larger; i.e., it takes more workers to produce a given amount of new ants, with the consequence that worker maintenance was a larger fraction of the total cost.

When investment was estimated on the basis of numbers, the percent sexuals was lower still because sexuals were few in number, though large in mass and production cost. The pattern of investment remained similar, however.

*Overview of total annual production.*—All forms of annual production increased with colony size class, but none kept pace with colony size increase. Thus, the units of workers or sexuals produced during the year for each unit of worker present in January decreased by 75–80% in class 6 colonies when compared to class 1. Sexuals contributed to this decline because they do not contribute to future production.

Colonies of <50 000 workers (class 1) invested 16% of their production in sexuals, but all other classes invested  $\approx$ 33%. Larger colonies produced more sexuals simply because of their larger size, not because of greater proportional investment in sexuals. When the cost of worker maintenance was included, the percentage invested in sexuals declined between class 2

and class 6, probably because production efficiency declined and maintenance costs increased.

#### *Annual cycle of mortality and natality by size class*

**Rationale:** Worker natality and mortality and their relative rates are the direct causes of colony growth, stasis, and decline. Their values over the life cycle and the year are important ingredients of the socio-genesis and population dynamics of the colony, determining growth rates and colony size. Natality was directly determined in this study, but mortality was indirectly estimated.

*Rates of mortality and natality.*—Mortality and natality rates depended strongly on sample date and colony size (Fig. 21). As the soil warms in the spring, both mortality and natality rates rise (though not necessarily at the same rate), peaking sometime in midyear when soil temperatures peak. Worker mortality exceeded birth rate until midyear, causing the decline in colony size. The size of this deficit in worker production increased with colony size, reflecting the more extreme annual size fluctuation of larger colonies. In midsummer when sexual production slowed, worker natality began to exceed mortality, and colonies grew. This change from decline to growth occurred earlier (April) in the smallest size class because these invest little if any production in sexuals.

On all sample dates, both mortality and natality rate decreased with colony size. This decreasing birth rate is associated with logistic growth (*Costs and production rates: Production rates over the annual cycle: 3. Rela-*

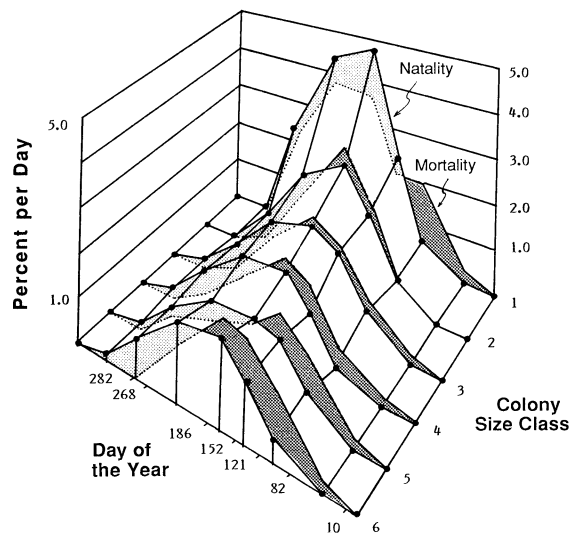


FIG. 21. Daily worker mortality and natality rates in relation to colony size class and season. Dark shading indicates the excess of mortality over natality during times when colony size is falling, while light shading indicates excess of natality over mortality when colony size is increasing. Mortality dominates during the first half of the year, while natality dominates during the second. Both mortality and natality decrease with colony size and peak midyear.

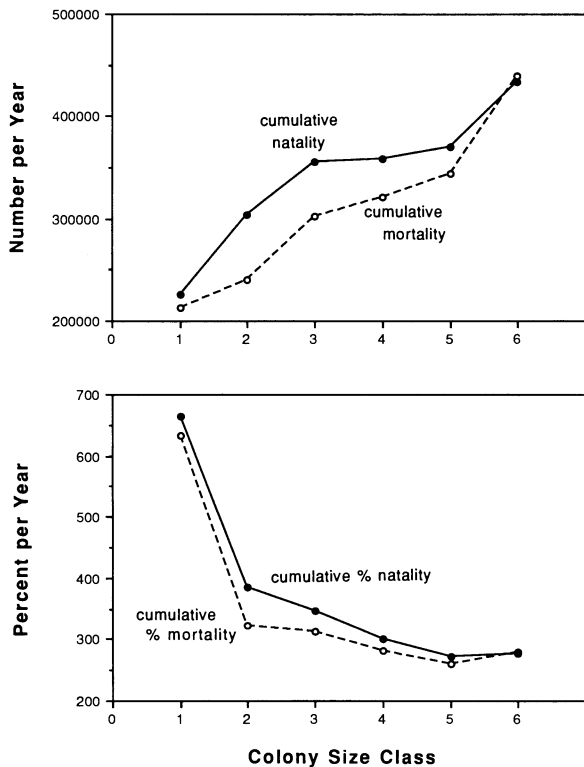


FIG. 22. Cumulative annual mortality and natality in number and percent in relation to colony size class. Total natality exceeds mortality in all but the largest size class, resulting in net colony growth at the end of each year.

relationship . . . and Production rates of colony-size cohorts . . .). The decrease of mortality rate with colony size is less expected, but may be the outcome of the greater longevity of the larger workers produced in larger colonies. Improved colony nutrition, as reflected in percent fat, may also increase longevity and decrease mortality rate. Whatever the cause, worker turnover (annual sum of daily percent natality) slows from  $>600\%$  per year in size class 1 to  $\approx 270\%$  in classes 5 and 6.

*Cumulative natality and mortality.*—Cumulation of natality and mortality over 1 yr (Fig. 22) showed that annual natality exceeded mortality for all size classes except the largest, leading to growth in the first 5 classes and a return to maximum size in class 6. These were average values of course. Individual colonies may suffer different fates. It should also be noted that these estimates were approximate; they were based on size classes whose annual size changes were estimated from the logistic growth curve and the size variation of a mature and a half-grown population of colonies (Tschinkel 1988a). In addition, of the 42 mean values (6 size classes  $\times$  7 sample dates), 8 were missing values and 2 were clear outliers. The mean values for the class were used in these cases. To an undetermined extent, the clarity of the patterns in Figs. 21 and 22 was the result of the inherent smoothing of these methods of estimation.

*Overview of mortality and natality.*—Worker mortality exceeded natality during the spring in colonies of all sizes, ever more so for ever larger colonies. This caused colony size to decline more for larger colonies than for small. After midyear, natality exceeded mortality resulting in colony growth. Summed over the year, the excess of births over deaths declined with colony size until in the largest size class, there was no net annual growth. Annual percent natality and mortality were both highest in the smallest colonies, resulting in a 600% worker turnover. These rates declined with colony size, resulting in a turnover of  $\approx 270\%$  in the largest colonies. These trends were probably caused by the greater longevity and lower productivity of the larger workers in larger colonies, further emphasizing the importance of worker size to sociogenesis.

## DISCUSSION

### Overview

Fire ant colonies undergo many changes during growth. Mound size and gallery volume increase. Workers become more numerous, but they also become larger and more of them are majors. The fat content and cost per milligram of workers and colonies increases, their mass-specific maintenance cost decreases, worker longevity doubles, and worker turnover decreases. Reproductive stage colonies invest a fixed fraction of their annual production in sexuals. Most of the total annual cost of colonies is worker maintenance, which increases from  $\approx 60\%$  of the total to 75% as colonies grow. The rate of production of new ants increases, but the increase does not keep pace with colony growth, causing a decline in the efficiency of production. This decline is associated with logistic growth and the attainment of a maximum colony size.

Superimposed upon these growth-related changes are many seasonal changes. Production of all brood is highly seasonal, but the production of sexuals is almost limited to the spring when about half of colony production is shunted into sexuals. This causes colony size to decline in proportion to its midwinter size and sexual production. Worker fat reaches a minimum at the end of sexual production. About 60% of workers are born in the second half of the year, causing colony size to rise again. Workers are larger in spring and smaller in fall. The cost of worker maintenance drops from almost 100% of total cost in winter to 45–50% in summer. Because the mound gives colonies the ability to maintain workers at higher than ambient temperatures, winter maintenance costs are still substantial (S. D. Porter, unpublished manuscript).

### Ergonomic and reproductive stages

While the existence of distinct ergonomic and reproductive stages in colony development is generally accepted (Hölldobler and Wilson 1990), my data (Fig. 20) offer some of the first and most convincing evidence that the percent invested in sexuals does not rise grad-

ually as colonies grow. Rather, it rises quickly to  $\approx 33\%$  by the time colonies contain  $\approx 50\,000$  workers, and remains at that value for the remaining 80% of colony growth. This transitional size agrees well with that found by Vargo (1988) in laboratory colonies (22 500–32 500 workers, only  $\approx 10\%$  of maximum colony size) and that of Markin et al. (1973) in field colonies ( $\approx 25\,000$ ). Vargo (1988) also showed that this transition was related to colony size, not age.

The constant fraction of production invested in sexuals means that, on average, greater sexual production is a simple and direct consequence of larger colony size. This sociogenic rule indicates that populations of *Solenopsis* colonies produce more sexuals by growing or evolving to larger size. We can expect the average fraction of production invested in sexuals to be a species character as it is in nonsocial individuals (Ito 1980). However, it should be noted that when worker maintenance cost is included, larger colonies invest a somewhat lower fraction because their relative maintenance costs are higher. This underlines the importance of the particular measure of investment used.

#### Seasonality

During the annual cycle, total production peaks in spring at rates that are apparently not sustainable, even though temperatures remain favorable. Production per milligram of worker peaked in April, even though soil temperature did not reach its maximum until July. Conversely, although the soil temperature in May and September were the same, production per milligram in September was only  $\approx 60\%$  that in May. These early unsustainable rates are probably fueled by energy stored in worker fat. During sexual production, worker birth rate falls below replacement levels, implying that colonies have no production reserve at any time. Energy invested in sexuals is drawn from worker production or fat storage. Viewed differently, colonies at maximum size cannot produce sexuals because they invest all production in workers (Hölldobler and Wilson 1990). In any case, colony size declines to a midyear low of half or less of the maximum size. The size of a single sampled colony of *Formica pratensis* varied by similar amounts through the year but peaked in June and was minimal through the winter (Jensen 1978a).

After sexual production slows in midyear, increased worker production brings colony size back to or above (depending on original size) the midwinter maximum. This seasonally asymmetric worker production not only causes strongly cyclical colony growth (Tschinkel 1988a), but also results in seasonal changes in worker size, as it does in *Veromessor pergandei* (Rissing 1987) suggesting that the age structure of workers is seasonally asymmetric as well, with young workers predominating in the fall and older workers in the spring. For larger colonies,  $\approx 60\%$  of workers are produced in the second half of the year. This asymmetry may contribute to the spring decline in colony size as the old workers live out their lives and may contribute to the cycle

of fat content because old workers contain less fat. Also implied is a seasonal shift in worker demography and possibly the type of labor available. The spring brood are reared, on average, by older (as measured by clock time) workers. Physiological age might differ less, at least in those species subjected to cool conditions in winter. Of course, such age asymmetry is probably true of most temperate zone ants to some degree, and probably varies from the discrete, single-cohort of workers in *Prenolepis imparis* (Tschinkel 1987b), through the overlapping summer and overwintering generations of *Myrmica* (Brian 1957) and other temperate ants, to the moderate asymmetry of *Solenopsis*, to perhaps constant production in some aseasonal environments.

The annual cycle of fat content was similar to that found by Ricks and Vinson (1972) in *Solenopsis richteri*, but the values in my study were higher, as were those of Passera and Keller (1987) on *Iridomyrmex humilis* workers. *S. invicta* workers appear to store energy during the latter half of the year, use this energy reserve to pass the winter, and then use the reserve for the otherwise unsustainable rate of spring brood production. Jensen (1978a) described a similar pattern in *Formica pratensis*, and it is probably quite widespread among ants. Workers of *S. richteri* also lose protein during peak brood production periods (Ricks and Vinson 1972). Also, workers of some ants lose fat as they age (Passera and Keller 1987). The annual change in fat content also parallels the changing proportions of young and old workers. Young workers predominate in the autumn, old in spring.

#### Investment in sexuals and workers

The seasonality of sexual and worker production makes it clear that total investment in sexuals (a component of fitness) cannot be realistically estimated from samples taken only during the sexual production season, as is normal practice. Fire ants, for example, invest 50% of production costs in sexuals during reproductive season, but total only 30% over the annual cycle. Colony growth and fat storage outside the reproductive season are probably an integral part of sexual production during season. Colonies with larger midwinter size probably produce more sexuals during the next spring. The best fitness estimate is one based on lifetime production of colonies or queens. For species such as *S. invicta* where queen replacement (Tschinkel and Howard 1978) makes colonies potentially immortal, it might be possible to apply genetic techniques to estimate lifetime fitness of queens. For this study, total annual production must suffice.

The proportion of production invested in sexuals is a life history tactic. A single colony of *Formica pratensis* invested 4.4% of annual production cost in sexuals (Jensen 1978a) while three species of *Pogonomyrmex* invested 8–50% (MacKay 1985). Information for other ants is typically based on single-sample determinations and is difficult to compare across species. From Brian and Elmes' (1974) data, I estimated annual

sexual investment to average  $\approx 33\%$  in *Tetramorium caespitum* by assuming a complete turnover of workers every year. Single-sample estimates for *Myrmica sulcinodis* were 11% of spring production (Elmes 1987a). For three species of termites, the proportion of standing biomass or "energy" invested in sexuals varied from 15 to 50%, depending on species (Nielsen and Josens 1978, Thorne 1983). *S. invicta*'s proportional reproductive investment is apparently similar to that of *Tetramorium caespitum* (Brian and Elmes 1974), but these studies are not strictly comparable because only in *S. invicta* was total annual worker production accounted for. Inclusion of the annual worker production in single-sample cases would lower the percent sexuals. Until percent sexual investment is reported in comparable form across species, comparison with confidence will remain difficult. Rates of investment in *S. invicta* might be relatively high as an adaptation for the effective colonization of disturbed habitats (Tschinkel 1987a).

Most worker production is replacement of those workers that have died and does not contribute to colony growth (Fig. 22). Furthermore, turnover rate of workers in small colonies is more than double that in large colonies (Fig. 21). Presumably, higher turnover is the outcome of the lower longevity of the smaller workers in smaller colonies. Thus, while a small colony may grow 100% in a year, it suffers a 600% worker turnover to do so. Large colonies suffer  $\approx 300\%$  turnover simply to maintain their size. Using both the birth rate and worker longevity, Tschinkel and Porter (1988) calculated annual worker turnover in a population of full sized colonies in which annual worker production just replaced mortality. Their estimates of 380% and 320%/yr are somewhat higher than my estimate of  $\approx 270\%$ , but are within the same range. Their daily estimates during the warm season agree reasonably with mine, ranging between 1 and 2%/d. In *Formica pratensis*, an ant of roughly similar worker size, Jensen (1978a) estimated turnover at 270%/yr. Jensen (1978b) reviewed turnover for nine ant species and reported values from 80 to 300%/yr. Most species' turnover exceeded 100%/yr.

#### *Efficiency and colony size*

The declining efficiency of production by workers as colony size increases (Michener 1964) is an expected attribute of logistic growth (Hölldobler and Wilson 1990) and is a major factor in limiting the size of colonies (Tschinkel 1988a,b). Porter and Tschinkel (1985) and Vargo (1988) showed that larger laboratory colonies produce less brood per gram of workers than do small colonies. This decline in efficiency was noted earlier by Brian (1956) and Michener (1964) and has been confirmed several times since. Tschinkel (1988a) discussed the possible role of declining efficiency in the development of worker polymorphism.

This declining efficiency is evident well before colonies are half grown and applies to all phases of brood

production. Tschinkel (1988b) showed that fourth instar larvae stimulate queen oviposition and that the efficiency of this stimulation (in eggs per hour per larva) declines continuously as larvae increase from 1 to 10 000. Porter and Tschinkel (1985) showed similar loss of efficiency when workers reared brood. These effects also apply to groups other than workers. For example, in groups of colony founding *S. invicta* queens, there is a 50% or greater decline in brood per queen as the number of queens increases from 1 to 10 (Tschinkel 1993). Similar declines were found in *Myrmecocystus mimicus* by Bartz and Hölldobler (1982). The causes of such declining efficiency are unknown. Brian (1956) suggested that it results from the tendency of workers to pile larvae up, leading to interference during servicing.

The units used to estimate production rate affect the conclusion as to whether efficiency changes with colony size. When production rate is measured in number of individuals per day (as is common practice), a 10-fold increase of colony size results in an  $\approx 50\%$  decline in new ants per milligram of colony (slope = 0.56; Table 3). When mass or energy per day are the estimators of production, there is no decline in efficiency. A field colony of 10-fold greater size produced 10 times as much mass or energy in new ants per day (slope = 1; Table 3). In large part, this is because larger colonies are producing larger, more energy-rich workers causing a decline in the *number* of workers contained in each gram or joule of production. When the cost of worker maintenance is included in the daily production rate, a 10-fold colony size increase results in a 15% decline in the per-milligram production rate, probably because the percent of total cost spent on worker maintenance rises from  $\approx 62\%$  to 75% as colonies grow from class 1 to class 6. The full meaning of these trends is uncertain, but it is clear that the measure of efficiency must be carefully specified.

The finding that, based on mass or energy per day, there is no decline in efficiency with colony size contradicts Brian (1956), Michener (1964), and Porter and Tschinkel (1985). In the laboratory experiments of Porter and Tschinkel (1985), a fourfold increase in colony size led to a 36% decline in production efficiency (in grams per gram per month). How can these findings be reconciled? Perhaps it is important that one is a field study on natural nests, the other a laboratory study using nests of unnatural structure. Brian (1956) provided evidence that the group form or geometry is important to efficiency. It is possible that the high degree of colony subdivision among the myriad chambers and tunnels of the natural nest have the effect of increasing colony efficiency and making it, at least by some measures, independent of colony size. If this were true, it would suggest an important function for nest geometry, inviting comparative and experimental study.

A second finding is in apparent conflict with the lack of efficiency loss. When efficiency is estimated from



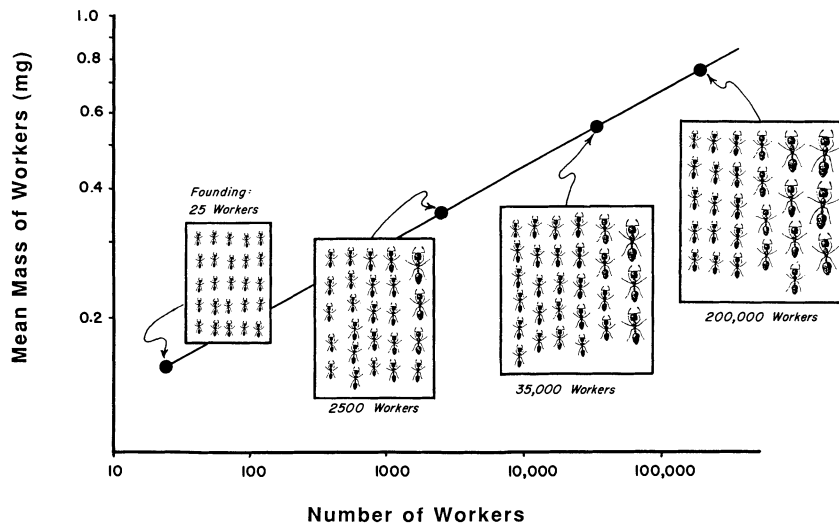


FIG. 23. As colonies grow, mean worker mass increases fourfold. Boxes show a typical selection of 25 workers from nests at four stages of growth and illustrate the changes in the sizes making up the worker populations.

total annual production (Fig. 19), larger colonies show lower efficiency no matter what the estimator. This can be reconciled as follows: annual efficiency is calculated on the basis of starting colony size (January). Whereas production of workers leads to higher production rates in the next generation, production of sexuals does not. The larger the starting colony size, the larger the sexual production during the year, the more colony size and therefore instantaneous production rate decline. Thus, even though the efficiency at any sample time does not decrease in relation to colony size, the falling size and its associated falling production rate causes the annual efficiency (in units per unit per year) to decrease with colony size. The switch from worker to sexual production and the accompanying colony size decline is felt, in part, as a decrease in the annual production efficiency.

#### *Changes within individuals*

The sociogenic increase in worker size may be ubiquitous in ants (Oster and Wilson 1978), not simply limited to polymorphic species such as *S. invicta* (Tschinkel 1988a) or *Atta* (Wilson 1983). Mean size of workers increases during colony growth in monomorphic species such as *Myrmica* (Brian 1957), *Tetramorium caespitum* (Brian and Elmes 1974), and others. In polymorphic species such as *S. invicta*, the nature of this changing worker population can be readily visualized from Fig. 23, which shows typical samples of workers drawn from colonies of the full range of sizes. Because worker size is linked to varying degrees to worker task (Wilson 1978, 1983, Mirenda and Vinson 1981, Porter and Tschinkel 1985, Calabi 1988), there may be profound, as yet undescribed, changes in the available labor pool during colony growth, both as a direct result of changing worker size and as an indirect

consequence of the increased longevity of larger workers (Porter and Tschinkel 1985, Calabi and Porter 1989) and its effect on worker demography. This changing demography is underlined by the decline of worker turnover from  $>600\%/yr$  in small colonies to  $\approx 270\%$  in large colonies, implying an increase in mean worker life span from  $\approx 2$  mo to  $4\frac{1}{2}$  mo. To some degree, worker size, through its effect on worker capacities, must define ecological role (Chew and DeVita 1980). To the degree that this is so, ecological role, at least in *S. invicta*, may shift substantially as colonies grow and mean worker size increases fourfold (Fig. 23).

The seasonal cycle of worker fat content may be very general among ants (see review in Tschinkel 1987b) and may represent a means by which production during a season unfavorable for colony reproduction may be stored for use during a favorable season. The increase of fat content with colony size may be driven by the improved nutrition per individual, which in turn may be driven by the changing producer-to-consumer ratio, the same factor which brings about the increase of worker size.

Female, but not male alates show a large (275%) mass increase between adult eclosion and maturity. This is typical of species in which queens found colonies claustrally (i.e., in isolation and without workers) (Keller and Passera 1989). In most such species, as in *S. invicta*, the post-eclosion mass of fat increases more rapidly than the body mass, so that the percent fat increases during maturation. In *S. invicta*, the lean mass also increases, indicating that maturation is more than simply fat deposition. Queens of independently founding species generally have fat contents exceeding 40% (Peakin 1972, Boomsma and Isaaks 1985, Nielsen et al. 1985, Keller and Passera 1989). The value of 50% fat for *S. invicta* is thus typical of claustral colony-



founders. It is interesting that fat content of gynes and mass of males are independent of colony size, perhaps because they are constrained by the needs for successful mating and colony founding. The meaning of the seasonal variation in alate masses is unknown.

#### *Calculation of natality rate*

The calculation of worker birth rate by dividing the pupal census by pupal development time seems not to have been applied to ants before Tschinkel and Porter (1988). Yet this method is simple and requires only a census, the pupal development rate at several temperatures, and a record of the ambient temperatures in the area of the nest where the pupae are found and worker distribution in relation to temperature. In principle, this method can be used to calculate any stage's transition rate, if the development time and temperature exposure of the stage is known. If stage specific mortality can be determined, the method could give a complete life table and budget (Southwood 1978). The method can be refined by using a substage such as the pigmented pupal stage (Tschinkel and Porter 1988), but this must be weighed against the weakening of the statistical tests through the reduction of the sample size.

Even in species with only one or two generations of workers per year, it is desirable to estimate annual production from the production rate and time, rather than from a single census. Because workers eclose over a considerable interval, estimation of production from the standing biomass usually underestimates production. In some cases, the census and temperature data were collected, but the natality calculations were not made (MacKay 1981) because developmental rates were not known.

It should be possible to relate the daily natality of adults to the egg-laying rate of the queen some time previous. The adult eclosion rate should be the egg-laying rate decremented for pre-adult mortality and lagged for development time. Tschinkel (1988*b*) showed that fourth instar larvae stimulate queen fecundity in a log-log relationship. Does a similar relationship exist between daily natality and number of larvae in field colonies?

The natality (ants per hour) of the April and June samples was used because optimal temperatures were always available in the nest at these times. The natality was regressed against the total number of larvae (log-log transformed) and showed that natality increased 3.6-fold for every 10-fold increase in the larval population. For comparison, the egg-laying rate of queens in naturally growing laboratory nests increased 4.9-fold for every 10-fold increase in larval population. On the other hand, the intercepts of the regressions indicated that laboratory queens without larvae had egg-laying rates much lower than similar field queens, so that both converged on similar rates at high larval populations.

#### *Comparative sociometry/sociogenesis*

Most quantitative attributes of colonies are the products of growth. As colonies grow, their quantitative attributes often grow at different rates, so that the ratios among the attributes depend upon colony size. This is analogous to the changing relative dimensions of individual animals during growth, where the changing proportions are used as estimators of changing shapes. The same methods that have been used for the analysis of allometric growth, size, and shape of individuals (Mosiman and James 1979) can yield insights into the allometric growth and changes of colony "shape" (proportions). After stabilizing the variance with log transformation there are two basic types of plots: (1) a plot of the log ratio (or proportion, or percent) vs. log colony size which makes visible any change in proportion as a non-zero slope; (2) a log-log plot of the two variables of the ratio against one another which describes their relative growth and yields a slope significantly different from 1.0 if the ratio changes with size (allometric growth).

A number of analyses in this study are of this nature. For example, the population of majors grows more rapidly than the total worker population (slope of log-log plot  $> 1.0$ ), so that the proportion of majors has a positive slope with respect to colony size. This is also true for the percent worker fat, cost per worker, mound volume per ant, and others. On the other hand, neither the percent of production invested in sexuals (after an initial increase) nor the cost per sexual shows a relation to colony size. In a third type of relationship, the variable grows more slowly than colony size resulting in a negative slope. Examples are the worker oxygen consumption per milligram per hour, and production rate per milligram (or per joule or per individual).

The importance of these observations is twofold: (1) No colony description is fully useful without knowledge of colony size, and all quantitative descriptors of colonies must be accompanied by colony size data. (2) Because many colony attributes are colony size specific, it is not valid to make direct comparisons of attributes between species or populations. Unless a variable has been shown to be isometric, one must compare the *relationship* between variables and colony size, i.e., compare allometric or size/proportion relationships. Fig. 24 shows an example of such an interspecific size/proportion comparison based on data on percent majors. I have attempted to make the data as comparable as possible. Several attributes are easily seen: (1) the range of colony size; (2) the range of variation in percent major workers; (3) the rate at which the percent majors changes with colony size (note that percent majors can decline with colony size, as in *Camponotus impressus*); (4) the colony size range over which this change occurs; (5) the variability in percent majors for any given colony size (i.e., the degree to which other factors affect percent majors). Comparisons can be made

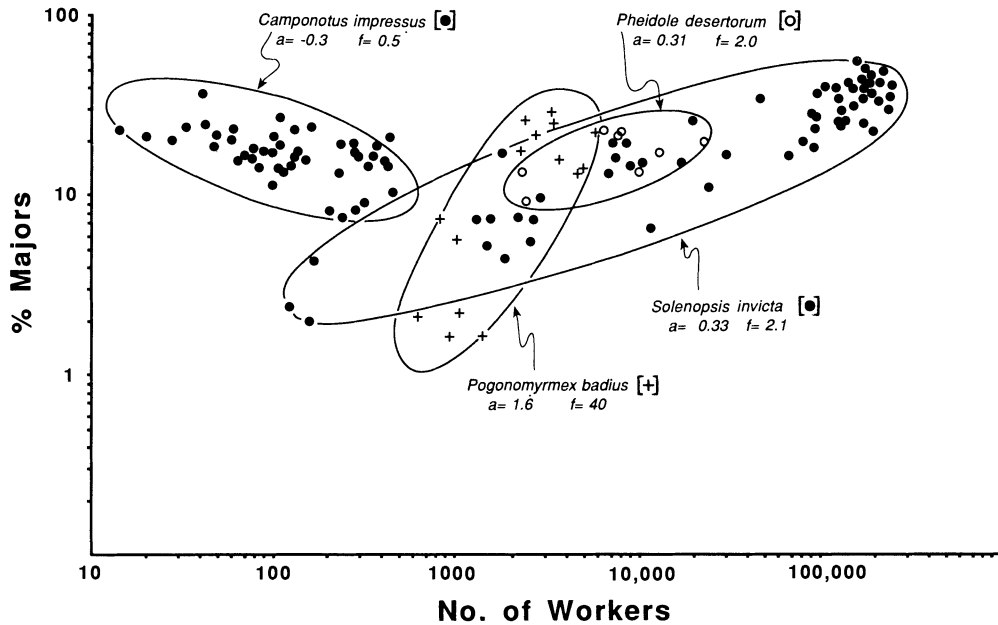


FIG. 24. Size/proportion analysis of the percent majors for four species of ants. Differences in the percent majors, the rate of increase (or decrease) in the percent majors, colony size, and size range are all readily visible. Data for *Camponotus impressus* from Walker and Stamps (1986); *Pheidole desertorum* from K. Helms (*unpublished data*); *Pogonomyrmex badius* from Tschinkel (*unpublished data*); *Solenopsis invicta*, this study.  $a$  = slope of log-log regression;  $f$  = factor of increase in percent majors for a 10-fold increase in colony size.

both visually and statistically using standard statistical methods such as regression and  $t$  tests. Fig. 24 also makes clear that single comparisons of percent majors among species may lead to erroneous conclusions if colony size is not taken into account. Results such as these were predicted by Oster and Wilson (1978: 159) when they wrote, "if the [caste distribution function] of a species is truly adaptive it will change as the colony ages, since the selective forces act differently on young as opposed to mature colonies."

The second example is an allometric plot (Fig. 25) showing the growth of the total mass of sexuals in relation to the total mass of workers. Again, much can be learned by visual inspection of Fig. 25: (1) the range of colony size (worker mass) of each species; (2) the range of the mass of sexuals for each species; (3) the rate of increase of sexual investment relative to worker investment; (4) the proportion of mass invested in sexuals (relative height of the data cloud on the  $y$  axis). Again, the figure makes it apparent that valid comparisons are not possible without specification of colony size. The critical fact may not be that species A produces more sexuals than species B, but that A does so at a particular colony size. It is also interesting whether species invest in sexuals by the same or different rules; similar slopes and intercepts suggest that similar rules operate and any difference in the amount of sexuals produced is simply the result of differences in colony size.

Fig. 25 is offered primarily for the purpose of illus-

trating the allometric method of comparing several species. The data are not all strictly comparable. In spite of these problems, Fig. 25 suggests several interesting relationships. (1) Most species overlap the isometric line, that is, most tend, at the upper limit, to contain about equal masses of workers and sexuals. (2) Most also contain small colonies probably just beginning to reproduce and therefore containing very low proportions of sexuals, giving the data clouds a parallelogram shape. (3) Two species (*Prenolepis imparis* and *Myrmica limanica*) contain much lower masses of sexuals than workers, possibly suggesting lower investment. However, none of the single samples comprising this figure is appropriate for estimating investment in sexuals. (4) Overall, all seven of these species seem to follow similar allometry relating worker mass to sexual mass. None are radically above or below the isometric line, and none seem to have radically different slopes, though sample sizes are small.

In general, allometries based on differential growth suggest sociogenic constraints on the possible colony proportions in a manner analogous to the constraints on possible worker shapes resulting from the rules of allometric body growth (Franks and Norris 1987). In other words, populations of colonies evolve changes in their attributes under constraint from the other attributes to which they are linked by the rules of allometric growth. The regulation of these various growth rates represent the sociogenic rules by which colonies develop. The changes in these rules represent the means

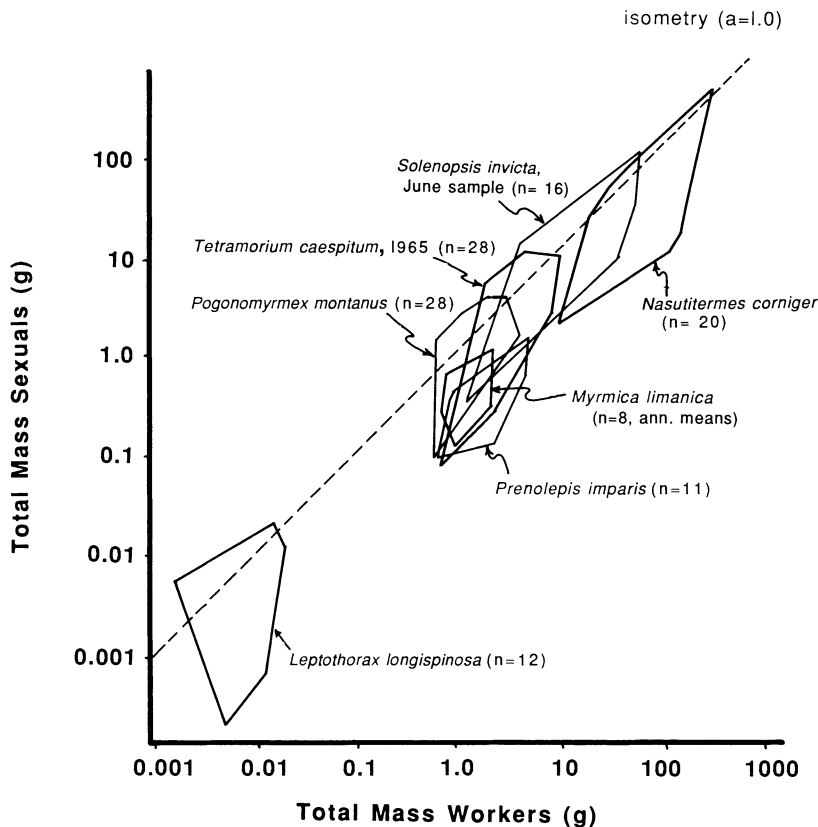


FIG. 25. An allometric plot showing the relationship between total mass of workers and sexuals for six species of ants and one termite. Polygons connect the outermost points. Most species straddle the line of isometry, indicating that they are able to contain as much or somewhat more mass in sexuals than in workers. Two species fall significantly below the isometric line. Most data points represent the mass of sexuals and workers contained in terminally sampled colonies, but those for *Myrmica limanica* are eight annual population means (Uchmanski and Petal 1982). *Solenopsis invicta* (this study, May sample), *Nasutitermes corniger* (Thorne 1983), and *Tetramorium caespitum* (Brian and Elmes 1974) are samples taken on a single date, but *Pogonomyrmex montanus* (MacKay 1981), *Prenolepis imparis* (Talbot 1943), and *Leptothorax longispinosa* (Headley 1943) represent several samples taken during 1 yr. In all cases, sexual immatures were treated as though mature. The masses of *Prenolepis imparis* sexuals were estimated from their size relative to workers. Data were analyzed using multiple regression.

by which populations of colonies evolve. Population attributes and their evolution can best be understood through sociogenic rules of colony growth and development. The differences among species can then be seen as differences in the sociogenesis of their traits, and the evolutionary changes as changes in the sociogenic rules.

#### *Life history tactics*

The reproductive unit in social insects is more or less the colony, and as a first approximation, the traits of colonies are the grist for the life history theory mill (this simple picture is complicated, however, by some species with colonies that contain multiple queens who may or may not be related to each other). The life history strategy of a social insect colony consists of the specific values of each of the components of fitness, among them the number and size of sexuals, the age (or colony size) distribution and magnitude of reproductive effort, the effect of reproductive effort on col-

ony mortality and future reproduction, and the variation of these traits among the colony's progeny (Stearns 1976, Oster and Wilson 1978, Smith 1981). The specific values of these components are thought to be shaped by the age-specific schedule of mortality imposed by the environment, and by the variability and predictability of that environment. Thus, it matters a great deal whether the environment is stable, predictably fluctuating, or unpredictable, whether juvenile mortality exceeds adult mortality, or whether populations are typically expanding or stable (Stearns 1976).

*Solenopsis invicta* appears to be an opportunistic species dependent upon ecological disturbance (Tschinkel 1987a). There is always a substantial fraction of fire ant populations which is expanding in areas of recent disturbance. In the absence of human disturbance, colonizable habitat is unpredictable in time and space, leading to high failure rates of dispersing sexuals. Of founding queens finding suitable sites, only  $\approx 20\%$  survive the claustral period. Even among incipient colo-

nies in vacant habitat, initial mortality rates are 5–6%/d and only  $\approx 0.1\%$  of queens survive after 3 yr (Tschinkel 1992). In areas already occupied by *S. invicta* colonies, mortality may be even higher because resident workers kill newly mated queens whenever they come upon them. Under natural circumstances, it seems likely that during some years, reproductive failure may be complete.

The early and high investment of *S. invicta* in large numbers of sexuals can be tentatively understood as a response to high juvenile colony mortality. Perhaps high likelihood of reproductive failure has led to the evolution of perennial colonies. An increase in the number of sexuals could evolve at least three different ways. Colonies might invest a larger proportion of their production in sexuals, they might increase colony size, or they might produce smaller sexuals. There is preliminary suggestion that the proportion invested in sexuals is under some genus-level constraint; the allometry between biomass sexuals and biomass workers is similar for *S. invicta* and *S. geminata* (D. McInnes and W. R. Tschinkel, *unpublished data*). It follows that *S. invicta* colonies, which are more “weedy” in their habits than *S. geminata* (Tschinkel 1988c), produce more sexuals than *S. geminata* mostly because their colonies are larger. It is also interesting that *S. geminata* alate females are  $\approx 20\%$  heavier and males  $\approx 25\%$  lighter than those of *S. invicta*. Whether these differences represent trade-offs between founding success of queens and their number is not known.

Seasonal variation in reproductive success is predictable and regular. Incipient colonies produced after midsummer lack time to grow to a size that can survive winter. This situation may have produced the tactic of restricting investment in sexuals to only the first half of the warm season and alternating this with storage of production as worker fat in the second half. In its native habitat, the salient seasonal feature may be rain-fall more than temperature.

While Oster and Wilson (1978) suggest that worker demography and size distributions are adaptive, the environmental characteristics selecting for particular demographics and size distributions are obscure. Major sources and schedules of worker mortality may play a role, but Oster and Wilson (1978) emphasized the probable role of efficiency. Some features of caste distribution functions are widespread among ants. Workers in incipient colonies of most independently founding species are unusually small (Hölldobler and Wilson 1990). Worker size increases gradually as colonies grow (Wilson 1985, Tschinkel 1988a). For founding queens, it is probably important to spread the risk of worker loss (Porter and Tschinkel 1986), and therefore improve juvenile colony survival. This could be of importance for a considerable period of early colony growth. In fire ants, major and minor workers increase in mean size until colonies contain  $\approx 10\,000$  workers (Tschinkel 1988a). Alternately, birth rate and colony

growth are more related to worker number than biomass. A colony of small workers would grow more rapidly than one consisting of the same biomass of larger workers (Porter and Tschinkel 1986), effectively reducing the period of high risk of colony mortality.

It is too early to make anything more than tentative hypotheses concerning the life history tactics of ants. There simply are not enough comparative data to identify syndromes of coadapted life history traits among social insects, and thus to tease out just what constitutes the tactics of the various social insect life cycles.

#### *Data gaps*

Ideally, a sociometric/sociogenic study would provide a full description of all major attributes during colony growth, the allometries among those attributes and the computation of all basic population dynamic and life table parameters over the span of colony growth and throughout the year. In reality, there are both practical and technical limits. The most serious was that in this study, mortality was estimated indirectly from birth rate and the changes of colony size within each size class. This links the estimate mathematically to birth rate and colony size. A direct determination of mortality would have been preferable, but convenient methods are not available. Their availability would allow computation of a complete schedule of birth, death, growth, and decline on a seasonal and colony size basis. I also made no attempt to determine territory size. Larger colonies have larger territory size (Wilson et al. 1971), and preliminary data showed that territory area is isometric to colony biomass (E. S. Adams and W. R. Tschinkel, *unpublished manuscript*). I also did not determine the percent of the worker force functioning as foragers, which when combined with colony and territory size would result in forager density in the field. Most other data gaps are of the nature of refinements rather than major gaps in the grand colony equation.

#### *Final remarks*

There exists a substantial literature of colony censuses of social insects, some based on large efforts and many colonies. Of the 25 or more studies on ants in which 10 or more colonies of a species were censused, only three gave data on the masses of individuals and thus allow an estimate of investment patterns in relation to colony size. While counts are certainly of interest, insight into numerous ecological aspects requires body mass (at least) as well. The ecological impact of animals is related to their biomass as well as their number. Future censuses should at least take the small additional effort to include the mean dry masses and, if possible, the percent fat of each of the types of nest inhabitants. Furthermore, data on development or growth should always be taken at specified temperatures. Together, such data would give a more realistic and complete picture of patterns of investment and



growth. Sociometric data should be reported on a colony basis, so that the data can be used for further analysis by others.

The methods described in this paper offer a simple, inexpensive way to collect and analyze sociometric data. Perhaps many researchers already collect some of these data in the course of other research, but without a coherent framework, these data languish unpublished. It is hoped that this study will help to provide such a framework as well as a stimulus for further sociometric/sociogenic studies.

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#### EDITOR'S NOTE

It is the policy of this journal to use the term "weight" when something is weighed with a spring scale, and the term "mass" when something is weighed with a mechanical or electronic balance. (Frequent calibration of the balance is assumed.) The author of this paper believes that this policy is based on incorrect science, but has changed "weight" to "mass" throughout the paper as required by the journal.

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