Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta**

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Summary. Colony size and worker polymorphism (headwidth) were determined for fire ant colonies ranging from incipient to 12 years of age. Colonies grew approximately logistically, reaching half size between $2^1/_2$ and $3^1/_2$ yr and reaching their maximum size of about 220000 workers after 4 to 6 yr. Colony size showed strong seasonal variation. There was some evidence that growth rate may vary with food density. Incipient colonies are monomorphic and consist of small workers only, but as colonies grow, production of larger workers causes the size-frequency distributions to become strongly skewed. These skewed distributions were shown to consist of two slightly overlapping normal distributions, a narrow one defined as the minor workers, and a much broader one defined as the major workers. Major workers differ from minor workers in having been subjected to a discrete, additional stimulation of body growth, resulting in a second normal subpopulation. The category of "media" is seen to be developmentally undefined. The mean headwidth of the workers in both of these subpopulations increased during the first 6 mo. of colony life, until colonies averaged about 4000 workers. Headwidth of minors declined somewhat in colonies older than about 5 yr, but that of majors remained stable. When the first majors appear, their weight averages about twice that of minors. This increases to about 4 times at 6 mo. and remains stable thereafter. The range of weights of majors is up to 20 times that of minors. Growth of the subpopulation of major workers is also logistic, but more rapid than the colony as a whole, causing the proportion of major workers to increase with colony size. In full sized colonies, about 35% of the workers are majors. Total biomass investment in majors increases as long as colonies grow, beginning at about 10% at 2 months and reaching about 70% in mature colonies. This suggests that major workers play an important role in colony success. The total dry biomass of workers peaked at about 106 g, that of majors at about 72 g. These values then fluctuate seasonally in parallel to number of workers. When colony growth ceases, the proportion of majors remains approximately stable. Colony size explained 98% of the variation in the number of major workers.

Introduction

The evolution and functional importance of worker polymorphism in ants have become central questions of the sociobiology of ants. Among the 260 genera of ants, 40 exhibit polymorphic workers, and of these 7 have dimorphic workers (Oster and Wilson 1978). Quantitative descriptions of some of these polymorphisms have been published (e.g., Gray 1971; Kondoh 1968; Topoff 1971; Wilson 1971). Other authors have addressed the relationship of worker size to polyethism (Busher et al. 1985; Corn 1980; Porter and Tschinkel 1985a; Wilson 1978, 1983, 1984), regulation of polymorphism in relation to season (Markin and Dillier 1971; Rissing 1987), habitat (Bernstein 1980; Davidson 1978) or colony defense (Johnston and Wilson 1985). The contribution of polymorphism to brood-rearing efficiency has been studied by Porter and Tschinkel (1985a). Brian (1957a), Porter and Tschinkel (1985b), Wood and Tschinkel (1981) and Markin et al. (1973) indicated colony size as a major factor affecting worker size. Oster and Wilson (1978) proposed a growth mechanism which might account for the ontogeny of polymorphisms.

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Ant queens which found entirely claustrally are an energetically closed system (Rissing and Pollock 1986) and sacrifice worker size for worker number. The first workers are therefore the smallest of their life cycle, the so-called minim or nanitic workers (Wilson 1971; Brian 1965; Wheeler 1910; Leutert 1962; Markin et al. 1972). The minims of most species in which workers in mature colonies are polymorphic, are monomorphic (Wilson 1971). The characteristic size variation or polymorphism develops as the colony grows, but the progress of this change has only twice been described in censused colonies (Wilson 1983, *Atta cephalotes;* Wood and Tschinkel 1981, *Solenopsis invicta*). Brian (1957a) reported that worker size gradually increased in the monomorphic *Myrmica rubra* until the colony reached about 300 workers, or 10% of its mature size. Rissing (1987) reported that mean worker size increased during the first year of colony life in the polymorphic *Veromessor pergandei*, but did not census the colony.

Queens of the fire ant, *Solenopsis invicta*, either singly or in groups, found colonies in the usual ant manner, producing a first brood of nanitic workers (Markin et al. 1972; Tschinkel and Howard 1983; Porter and Tschinkel 1986). Colony growth of *S. invicta* up to $3^{1}/_{2}$ yr was described by Markin et al. (1973), but their description of the increase of worker-size variation was mostly qualitative. Wood and Tschinkel (1981) described the appearance of worker size variation in colonies of up to about 6000 workers, showing that both the modal class and the skewness of worker head-width size-frequency distributions increase gradually as colonies grow.

While the increase of worker size variation in growing colonies is conspicuous (Bodenheimer 1937; Wilson 1971), there are no reports describing its full course quantitatively, nor is it clear whether size or variation continue to increase in mature colonies. In order to fill this gap, I present data relating the increase of worker polymorphism to both colony age and size. I also present the full colony growth curve of monogynous form *S. invicta*.

Methods

Fire ants are rare to absent in mature broadleaf forest, but are among the first to colonize newly cleared land, often doing so in high densities (Tschinkel 1987; Tschinkel and Howard 1983). At least for a few years after initial colonization, populations of fire ant colonies are essentially even-aged cohorts. By selecting sites cleared in the winter or early spring before mating flights occurred, I was able to sample populations aged 1.8, 3.7, 4.7 and 5.5 yr, with an uncertainty of about 3 mo. on the actual age. Colonies 1 week to 0.5 yr old were reared in the lab from newly-mated queens. Several field colonies aged 3

to 6 months were collected as a check on these lab-reared colonies. A 12–14 yr old population was also sampled. With increasing age, possible colony turnover makes the age of individual colonies increasingly uncertain.

Colonies were chosen haphazardly and collected during the winter or early spring. The 3.7 yr old population was near Gainesville, Florida. All the rest were in or near Tallahassee, Florida. Worker number was estimated as follows. The entire colony was excavated into a large bin(s). Each bin of soil and ants was mixed well and weighed. From each bin, five random samples of 100–200 g were returned to the lab for weighing and separation of workers from the soil. The total number of workers in a bin was estimated by dividing each sample count by the fraction of the total bin weight contained in the sample. Total colony estimates were made by averaging 5 sample estimates. Brood was not estimated. Large colonies were estimated in fractions and summed. All such estimates are probably 10–15% too low because they do not include foragers fielded at the time of excavation.

Worker size-variation for all but the smallest colonies was estimated on the basis of at least 200 headwidths measured by the method of Porter (1983). Minims were usually measured under a dissecting microscope with an ocular micrometer. Data were analyzed using several Minitab programs (Ryan et al. 1982). All colonies were of the monogynous form of *S. invicta*.

Results

Colony growth

Colony growth was approximately logistic but was complicated by strong seasonal fluctuation of colony size (Fig. 1A). Colonies reached $^{1}/_{2}$ maximum size in 2.5 to 3.5 yr and approached maximum size in 4 to 6 yrs. In order to determine the best fit to the data, the logistic equation was rearranged into the form

$$\ln\{(K/N_t)-1\} = -rt + \ln b$$

where K = maximum colony size, N_t = number of workers at time t (yr), r = initial growth rate, and b = a fitted constant. When $\ln\{(K/N_t)-1\}$ is plotted against t, a logistic function yields a straight line which can be subjected to linear regression. Colony growth data were plotted in this way, using K = 210 000 to 240 000 in increments of 10 000. Linear regression and analysis of residuals for all colony data showed that colonies younger than 5 mo. deviated from the logistic pattern. When these were excluded from the regression, colony age explained 84% of the variation in the complex function on the left side of the equation. Simply regressing colony size vs. age explained only 62% of the variance. The best logistic fit to the data was

$$N_t = 220\,000/(1 + 83e^{-1.26t})$$

Tschinkel and Howard (1983) indicated that up until 3 mo. of age, lab-reared colonies grew exponentially, a reasonable approximation to early logistic growth. However, as noted above, the fit
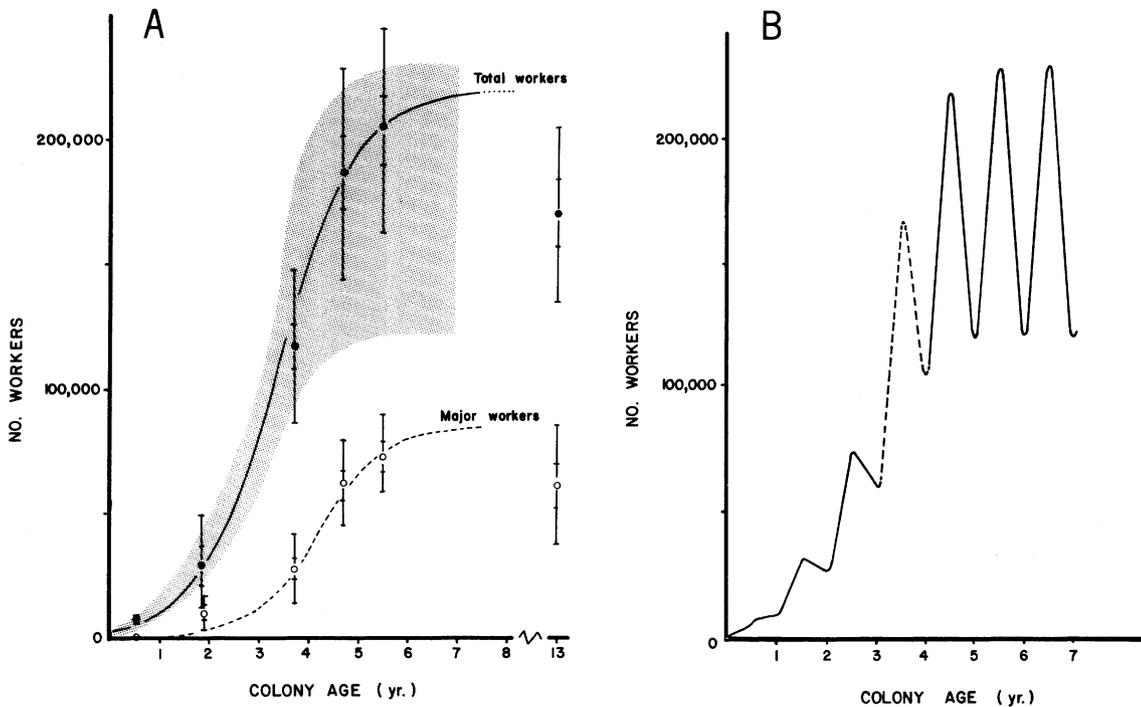
Fig. 1. A Growth of *Solenopsis invicta* colonies in total number of workers and major workers (see text for definition). All colonies except the 4.7 and 5.5 yr were sampled from different populations. *Curves* are the best-fit logistic function. The *shaded area* shows the limits of seasonal variation of mean colony size. Colonies less than $1/2$ yr old were too small to plot on this scale. Error bars show S.D. and S.E.M. **B** The probable real growth of monthly mean colony size, somewhat schematic. Data for colonies less than 3 yr from Markin et al. (1973) and this paper. Data for colonies older than 4 yr from Porter and Tschinkel (unpublished) and this paper. *Dashed portion* indicates interpolated portion

of the full logistic equation to early colony growth was not good. Solving the regression for $t=0$ indicated that colonies began life with about 2000 workers, a size they do not attain until 5 mo. of age. Is this lack of fit the result of using lab-reared colonies for early growth and field colonies for later growth, or it is some intrinsic deviation of early colony growth from logistic? A number of young field colonies were excavated to check early growth against that of lab colonies. Because their exact founding date was unknown, but must have coincided with one of the small number of early spring mating flights, they provide only crude verification. Eight such colonies with a most probable age between 3 and 6 mo. averaged 4710 workers (S.D. = 3950), comparing well with lab colonies of 5 mo. ($\bar{X}=1926$; S.D. = 560) and 6 mo. ($\bar{X}=8076$; S.D. = 2120). This suggests that the deviation of early growth from logistic is not an artifact of technique, but a colony characteristic.

Although Fig. 1A shows colony growth as a continuously increasing function, this is an artifact of sampling only during the winter and spring of each year. During the first 3 yr of colony growth, Markin et al. (1973) found that colony size (number of workers) actually *decreased* between

November and the following May. Porter and Tschinkel (unpublished, data to be published elsewhere) sampled a mature population of colonies whose annual means were stable from year to year. They found that the monthly mean size reached a maximum of about 230000 workers in December and declined to a minimum of about 120000 between March and August (annual mean = 161000 ± 46000 s.d.). Much of this annual fluctuation is probably the result of the spring switch to sexual production and emission, followed by a fall worker production. From these data, and those of Markin et al. (1973), the annual variation of mean colony size was estimated throughout growth and maturity (Fig. 1B) and is shown as the shaded area in Fig. 1A. Sampling growing colonies throughout the year would show that colony growth actually follows a sawtooth function which reaches a maximum in December and a minimum in midsummer of each year (Fig. 1B). The increase of the annual mean size was approximately described by $N_t=160000/(1+80e^{-1.5t})$. If colonies were sampled only during the winter maximum, their mean sizes would fall approximately on the upper bound of the shaded area (Fig. 1A), while sampling during the summer minimum would

cause mean sizes to fall approximately on the lower bound. The logistic curve drawn through the data in Fig. 1A must thus be seen as roughly the growth of colonies sampled during the winter and early spring (January to April). Sampling annually during the same month would have resulted in a curve roughly parallel to the upper and lower bounds of the shaded area of Fig. 1, and this curve would be moved upward as the sampling month changed from September to December and downward from December to August. The 1.8 and 3.7 yr samples were taken in April and March, respectively, while the 4.7 and 5.5 yr samples were made in February and January, respectively. Sampling all colonies during January would have pushed the 1 to 4 yr portion of the curve somewhat to the left, increasing r about 20%, but would not have resulted in a radical change of shape. Unfortunately, the magnitude of this seasonal variation was discovered after the samples in Fig. 1A had been completed.

Twelve to 14 yr old colonies were significantly smaller than 5.5 yr colonies (Newman-Keuls test, $P < 0.05$). However, between January when the 5.5 yr colonies were sampled, and March when the 12–14 yr ones were sampled, mature colonies drop from 93 to 53% of their maximum (Dec.) size. The decline between the 5.5 and 12 yr points could thus be the result of seasonal variation, but site differences or a real decline in annual mean size may also contribute. The data do not allow a clear choice.

Food-limitation of colony growth rate

All of the field colonies in Fig. 1A were sampled from habitats of rather low standing biomass – sparse weedy land, lawns and grazed pastures. It seemed likely that growth rate would be dependent on the availability of the insect food upon which the fire ant depends. We have often noticed that lab colony growth is obviously dependent on feeding rate. Indeed, by feeding lab colonies an excess of food every day, it was possible to rear colonies in which individual founding queens produced 500 000 workers in 12 mo. For comparison, the field colonies in Fig. 1 produced an estimated 15 000 to 20 000 during their first year (3 × size at $^1/_2$ yr; 300% annual worker turnover; Tschinkel and Porter 1988).

In the course of a study on colony founding, I followed the progress of population establishment and early growth on a site that had been cleared of forest the previous winter. Such areas are rapidly colonized by founding queens during the early spring mating flights (late April–mid
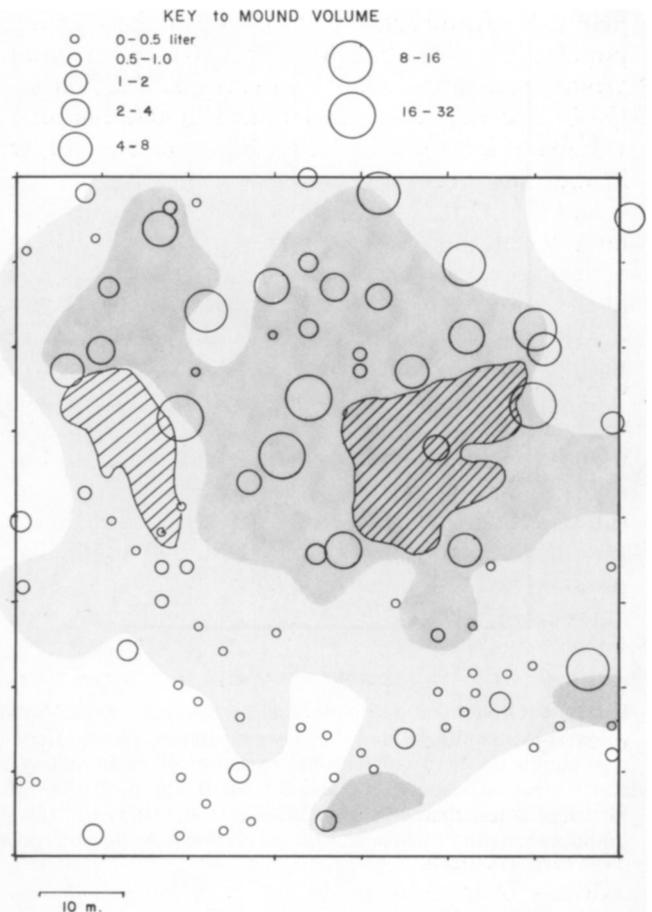
Fig. 2. Map showing the relationship between weed biomass and colony size 7 to 8 mo. after colony founding. Colony size was measured as the volume of the mound and is shown as *circles* of area proportional to the volume. The density of shading indicates the approximate weed biomass, ranging from areas with a high proportion of bare ground (*unshaded*) to dense weeds 1 to 2 m. tall (*dark shading*). All colonies were about the same age, but all large colonies were found in the area of densest vegetation and, therefore, highest food density. The *hatched areas* were flood prone depressions

May). At the same time, weedy plants become established and grow. Different parts of the site varied in quality depending on how much topsoil had been stripped in clearing, and therefore supported weed establishment and growth to different degrees (Fig. 2). In late December, after 5 to 7 mo. of colony growth, the fire ant colonies on this study plot were surveyed and their mound volumes measured. Weed biomass was estimated from the size and density of plants.

There was an obvious association between the standing biomass of weeds and the mound volume (colony size) of the fire ant colonies. I interpret this as resulting from the association of high insect biomass (fire ant food) with a high biomass of

plants. Foraging activity of fire ants in these young populations was heavily concentrated on and around plants, including on the roots. The majority of colonies in the barest areas still had a mound volume of less than 0.5 l after 5–7 mo., while those in the most vegetated areas were mostly between 4 and 32 l (Fig. 2). The area was resurveyed 1 yr later when the colonies were a little more than 1.5 yr old. Of those colonies that were still present at the same location, many of the smaller colonies in the sparser areas had increased a great deal in mound volume ($\bar{X}=40$ fold volume increase, S.D. $=33$; $n=10$), but those in the richer area that had already been large in the first survey showed modest to small increases ($\bar{X}=4.5$ fold; S.D. $=4.8$; $n=8$). This suggested that they were already near full size at the time of the first survey, a remarkable growth for less than one year! Though somewhat preliminary, these data suggest that the growth curve in Fig. 1 is valid for habitat of modest standing biomass, and may vary dramatically with the richness of the habitat. Confirmation would require comparison of colony growth across sites over several years.

Worker size variation in relation to colony age

The size-frequency distributions of headwidth for workers from colonies of increasing age (Fig. 3) suggest a number of age-related trends in worker polymorphism. 1) Incipient colonies consist of the smallest workers (the minim, or nanitic workers) whose mean headwidth is about 0.51 mm. 2) The modal head-width of workers increases rapidly for about 6 mo. and changes little after that. 3) Beginning as early as 1 mo. of age, the size-frequency distribution becomes positively skewed through addition of workers clearly larger (0.75 to 1.6 mm) than the modal class. 4) The proportion of these larger workers continues to increase up to about 5 years, but the majority of the workers is always found in the modal class between 0.55 and 0.75 mm headwidth.

What is the nature of these distributions? Preliminary analysis revealed no transformation which converted such a skewed distribution to a single normal one. However, for most colonies, plots of the normal scores of the headwidths (Ryan et al. 1982) vs. headwidth resulted in two straight line segments (samples in Fig. 4). Because linearity of this type of plot indicates that the data are distributed normally, Fig. 4 suggested that the skewed distributions of Figs. 3 and 4 were actually the sum of two different normally distributed subpopulations of workers. The workers in one of these sub-
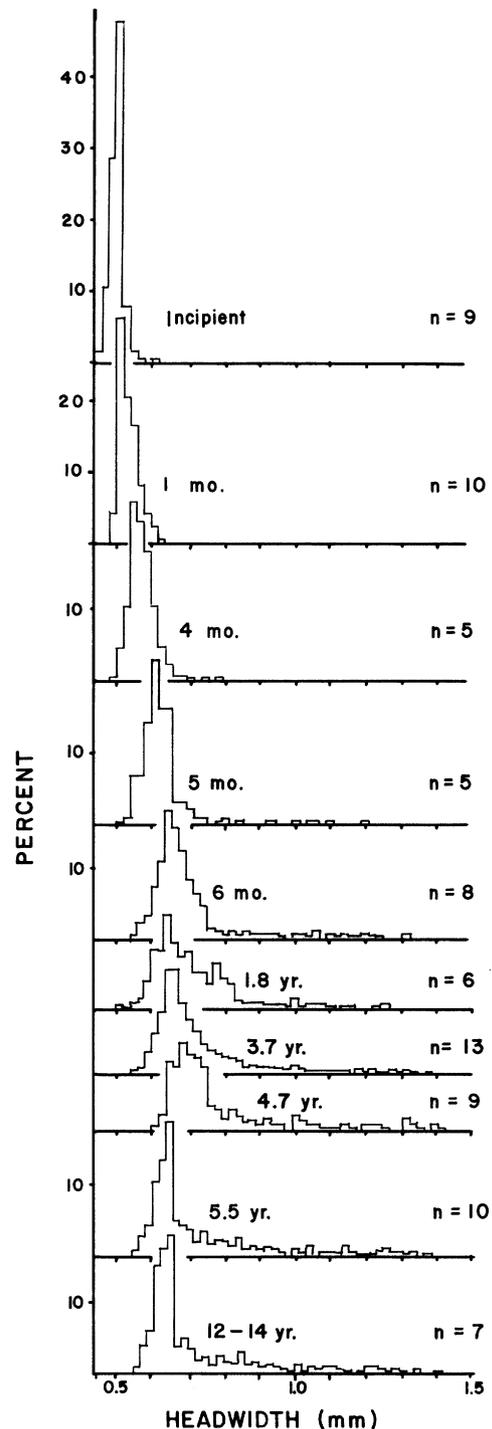
Fig. 3. Headwidth-frequency distribution of workers in colonies of increasing age. Each histogram is of the sum over all colonies (*n*) of that age and is shown as percent of total. Most of the change in these distributions took place during the first 6 mo. of colony life, and consisted of an increase in modal size and skewing. Mean colony size is given in Fig. 1

populations were much larger and more size-variable, and the two distributions overlapped slightly. The region of overlap could be recognized by a
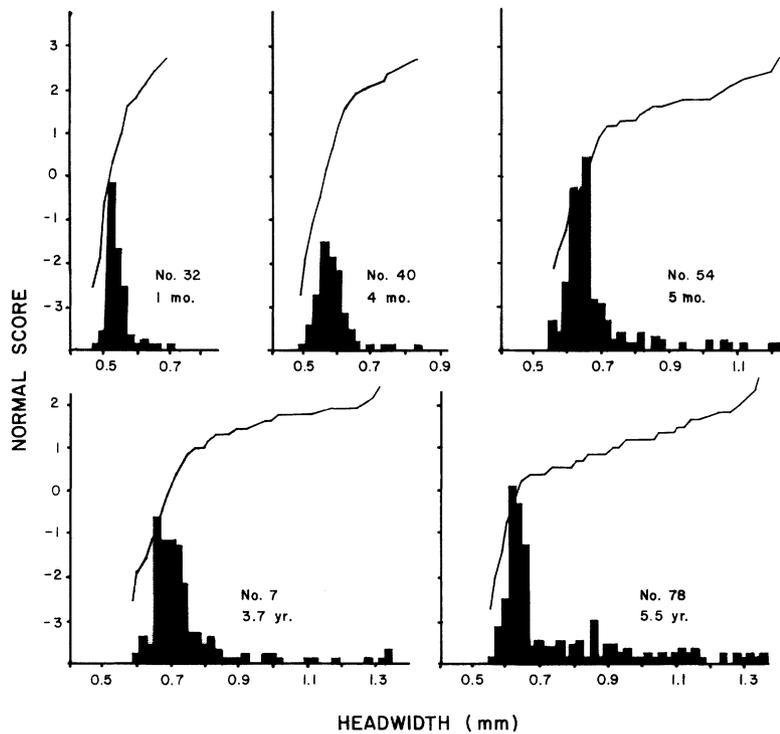
Fig. 4. Examples of headwidth-frequency distributions of individual colonies representing a range of ages. The smallest increment represents 1 worker, and each histogram is based on about 200 workers. The normal scores for each distribution are also plotted against the headwidth. All consist of two straight-line portions indicating that each distribution is the sum of two normal distributions of differing mean and variance. The smaller workers are minors and the larger are majors. The median has a normal score of zero
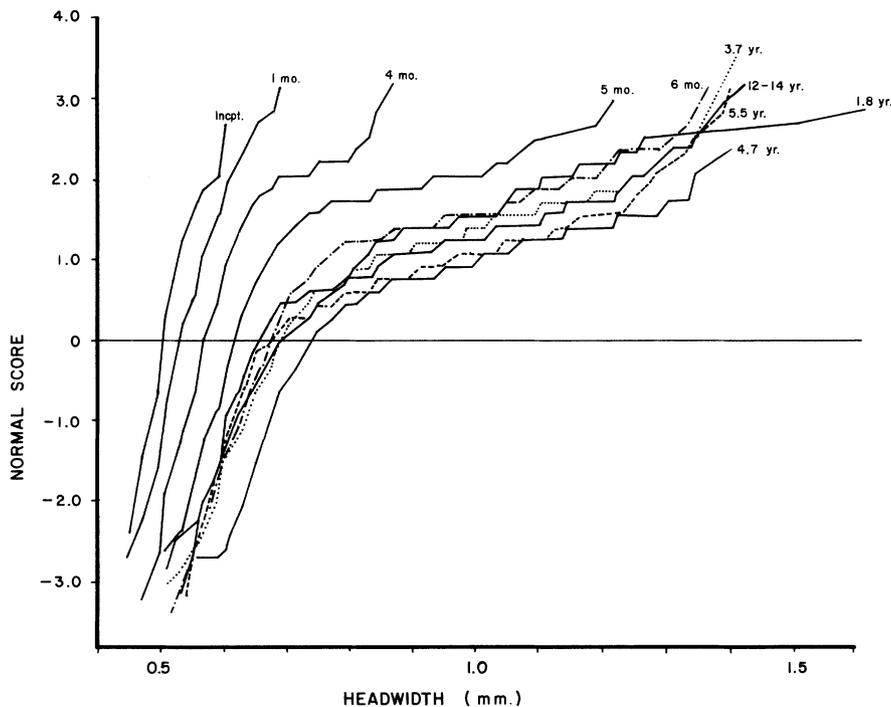
Fig. 5. Normal scores of the overall histograms for each age group (Fig. 2) as a function of headwidth, showing the nature of the early change in the distributions and the relative lack of change after about 6 mo. A normal score of zero identifies the median. The *kinked-straight line nature* of these functions indicates that the underlying distributions consist of the sum of two normal curves. Major and minor workers are defined by which of these two distributions a worker belongs to

sharp kink in the normal score curves (Figs. 4 and 5). These figures allow the first non-arbitrary definition of minor workers to the left of the kink point, and major workers to the right. They also suggest that the concept of "media" has no developmental meaning.

When the normal scores of the combined headwidths for all colonies of each age group are similarly plotted against headwidth, the intersecting lines again indicate that we are dealing with 2 slightly overlapping normal distributions (Fig. 5), although the transition between them is less sharp

for these combined plots. These plots allowed easier quantification of the trends seen qualitatively in Fig. 3. As colonies grew and aged, the median headwidth (normal score = 0) increased up until colonies were about 6 mo. old, and then changed little. Similarly, the size ranges (spread of headwidths included in each straight segment) of the two subpopulations increased until 6 mo. but changed little after that. As colonies grew, the decreasing slope of both the upper and lower straight legs also indicated a broadening of the underlying normal distributions until 6 mo. of age. In all these characteristics, colonies aged 6 mo. to 12 yr appear fairly similar.

The kink point allowed the separation and separate analysis of the two subpopulations, the minor and major workers. Because the kink is not always sharp, the mean of two different methods was used for separation. The first used the graphically determined kink point, whereas in the second, any gradual transition between the two subpopulation curves was included with the minor worker subpopulation. With respect to the number of workers included in each subpopulation, the mean of these two estimates differed from the estimates by an average of 20%. About 80% of the estimates fell less than 35% from the mean. This mean value was used for all further analysis.

Separate analysis of the headwidth of the two subpopulations in relation to colony age (Fig. 6) showed that the mean headwidth of both minor and major workers increased until the colonies were about 6 mo. old, but remained about constant until 4.7 yr (minors ANOVA: $F_{1,60} = 36.6$; $P < 0.001$; majors ANOVA: $F_{1,60} = 33.8$; $P < 0.001$). This was followed by a significant decrease in the size of minors at 5.5 yrs and following (Newman-Keuls Test, $P < 0.05$), but majors showed no such decrease. Similarly, the parallel increase in the kink point indicated that both subpopulations shifted to larger sizes in parallel (ANOVA: $F_{1,63} = 15.2$; $P < 0.001$). The size of minor and major workers also became more variable as indicated by the mean within-colony standard deviations of headwidth (Fig. 6) (minor ANOVA: $F_{1,60} = 11.6$; $P < 0.005$; major ANOVA: $F_{1,59} = 23.0$; $P < 0.001$) until 6 mo. of age. The coefficient of variation (COV) of minors increased from about 2.5% to almost 9% at 6 mo., then fell gradually to 5%. The major workers showed a proportionally greater size increase. When they first appeared their mean headwidth was about 1.2 times that of minor workers. This increased to about 1.5 at 6 mo. and remained constant thereafter. The size variability of majors also showed a greater increase (Fig. 6) – the COV
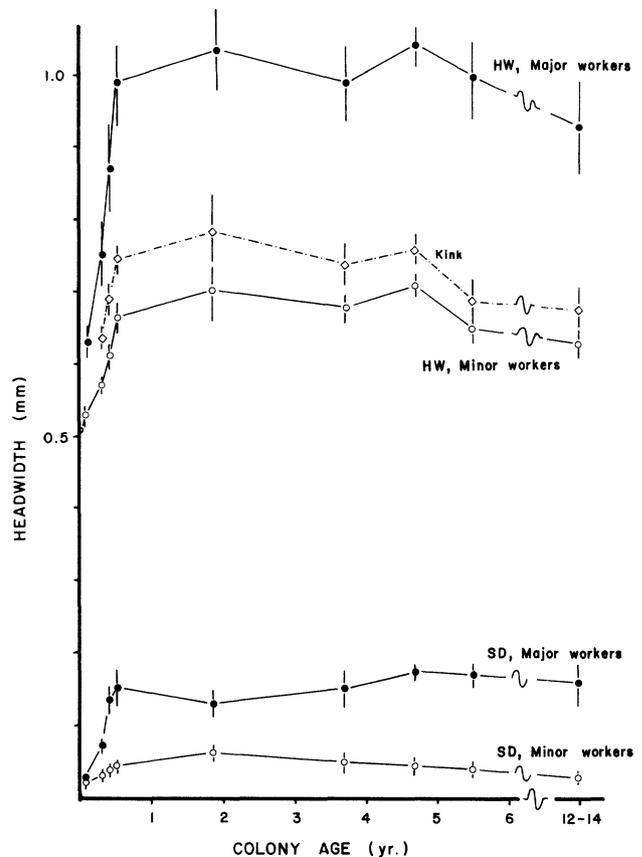
Fig. 6. The increase in the size and size-variability of major and minor workers in relation to colony age. HW-headwidth; SD = standard deviation of head-width. Also shown is the point of overlap (*kink*) between the 2 worker categories (see Figs. 4 and 5). All values increased until about 6 mo. of age, then remained more or less stable, with the exception of the mean HW of minor workers which declined significantly between 5.5 and 12 yr. Error bars = S.D. of the plotted means

for majors increased from 5% to about 15% at 6 mo. and remained stable thereafter.

The developmental origin of the major workers

Figures 4 and 5 indicate that minor and major workers belonged to two distinct normal distributions, implying that they differed discretely and discontinuously. A logical candidate for such a discrete difference might be that the majors resulted from larvae that had developed through a 5th instar, rather than the usual 4. To test this, worker larvae ranging in weight from about 0.3 mg to over 4 mg were sieved into 3 weight classes [mean weights = 0.54 mg (S.D. 0.13), 1.18 mg (S.D. 0.06) and 2.59 mg (S.D. 0.78)]. These larvae were cleared in 10% KOH, their mandibles were dissected, mounted on slides and measured under 400 × using an ocular micrometer. In spite of the almost

5 fold weight difference across the 3 weight classes, the dimensions of all mandibles fell into a single, unimodal distribution with a mean of about 0.1 mm (0.11, 0.099 and 0.10 mm, in order of increasing mean weight). Even sexual larvae, with a mean weight of 15 mg had a mean mandible length of 0.11 mm. There is thus no support for the origin of majors from a hypothesized 5th instar. It is more likely that a discrete event early in larval development reprograms majors to metamorphose at a higher weight. Wheeler (1986) suggested that this is the origin of the major workers in the dimorphic *Pheidole*.

Population growth of the major workers and their numerical proportions

As colonies grew logistically, so did the *number* of majors ($N_m = 75000/(1 + 735e^{-1.6t})$; $R^2 = 84\%$; $n = 54$) (Fig. 1A, lower curve). Figures 7 and 8 show that the subpopulation of majors grew more rapidly than did the total population, so that the proportion of majors increased as long as colonies grew (5.5 yr) and then remained constant at about 35%, a minor/major ratio of about 2 to 1 (Fig. 7) (ANOVA: $F_{11,86} = 50.7$; $P < < 0.001$; The drop to 12–14 yr was not significant, Newman-Keuls test, $P > 0.05$). Almost all (98.5%) of the variation in the number of majors was explained by colony size (Log $N_m = 1.33$ Log $N_t - 2.22$; $R^2 = 98.5\%$; $n = 77$). For every 10 fold increase in colony size, the number of majors increased 21.4 fold (Fig. 8), leading to the increasing proportion of majors shown in Fig. 7. Colony size explained 80% of the variation in the proportion of majors (log prop. majors = 0.33 log no. workers $- 22.2$; $P > 0.001$; $n = 77$). Of course, age and size are confounded until colonies cease growing, but the stability of the proportion of majors once colonies reached their maximum size (Fig. 7) indicated that colony size rather than age, was the controlling factor.

Biomass and biomass proportions of major and minor workers

Obviously, the biomass of a colony increases as the colony population grows, but because worker size and the proportion of majors changes with colony size, the biomass increase is not related to the number of workers by a simple factor. Worker headwidths (HW, in mm) were converted to dry weight (W, in mg) using $W = 0.933$ HW$^{2.98}$ (Porter and Tschinkel 1985a). Dry weight averaged 47% $\pm 4\%$ (S.D.) of live weight, and this fraction was not significantly related to worker size. Each
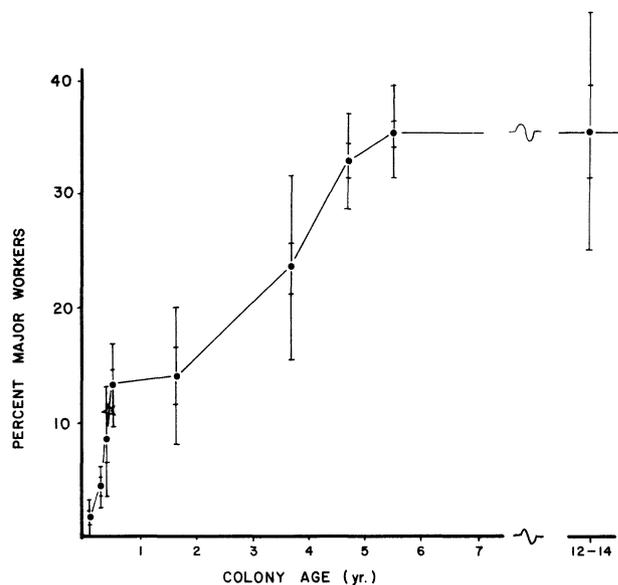
Fig. 7. The proportion of the total worker population which is major workers (see text for definition), as a function of colony age. The proportion increases as long as colonies are growing (up to 7 or 8 yr), but remains stable thereafter. The star indicates the mean value of 8 field colonies approximately 3–6 mo. old. Error bars show S.D. and S.E.M.

size-frequency distribution was converted to weight-frequency and its mean calculated. For each colony, the total dry weight of the worker population was calculated as the product of the mean worker dry weight and the number of workers. This computation was also carried out on the separate subpopulations of majors and minors, yielding mean, standard deviation and total dry weight for each subpopulation by colony.

As expected, the total worker dry *biomass* (g) of colonies paralleled the number of workers, increasing logistically with age (between 0.3 and 6 yr, $W_t = 110/(1 + 0.17e^{-1.33t})$; $R^2 = 89\%$; $n = 48$) to peak at 106 g (S.D. = 15.8 g) (225 g live weight) at 4.7 yr (Fig. 9). It then decreased significantly (Newman-Keuls test, $P < 0.05$) to 72.2 g (S.D. = 26.7 g) at 12 to 14 yr, paralleling the decline in number of workers (Fig. 1). This decline may be partly an effect of season, as noted above. Because the subpopulation of majors also grew logistically, its total biomass increased logistically, peaking at 72 g at 5.5 yr and then dropping significantly (Newman-Keuls test, $P < 0.05$) to 54 g at 12 to 14 yr (Fig. 9) [between 0.3 and 6 yr, $W_m = 83/(1 + 0.71e^{-1.61t})$ ($R^2 = 85\%$; $n = 51$)]. Because the average major weighed about 3 to 4 times as much as the average minor, the biomass growth of majors is much more rapid than growth of their numbers, peaking at over 70% of total worker dry

Log L.W. = 1.33 Log T.W. − 2.22
R^2 = 98.5 %   n = 77
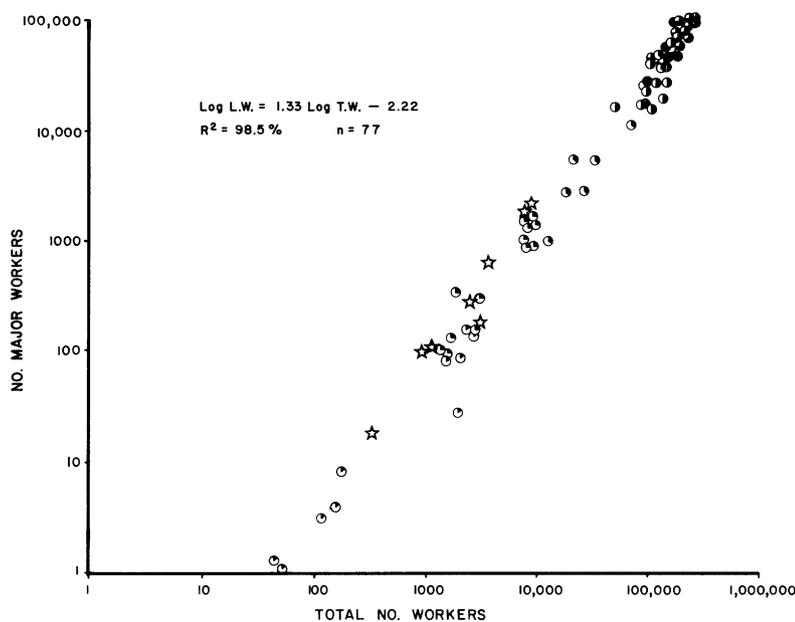
Fig. 8. The population of major workers as a function of colony size (total no. workers) for all colonies. Age is coded by the amount of each point blacked in and ranged from 1 mo. (*1/8th black*) to 12–14 yr (*all black*). Colony size explains more than 98% of the variation in number of large workers, irrespective of colony age. The *stars* indicate field colonies of inexactly known age (3 to 6 mo.) collected as a check on lab-reared colonies. Because the slope of the regression is greater than 1.0, the number of majors increased more rapidly than the total population, causing an increase in the proportion of majors
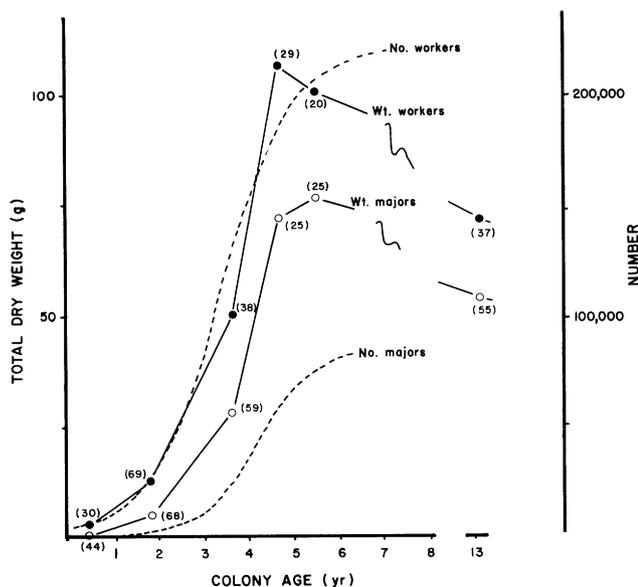
Fig. 9. Growth of total weight in workers and major workers as a function of colony age. For comparison, growth in numbers (*dotted lines*) is repeated from Fig. 1. *Numbers in parentheses* are COV's. Total weight in majors grows much faster than their number because they make up an increasing proportion of the population

weight. When the first discernable majors appear during colony growth, the ratio of dry weight invested in majors and minors is about 1 to 10, respectively. About midway through growth (3 yr), this ratio climbs through about 1 to 1 and levels off at about 2 to 1 in mature colonies. Thus, while minors outnumber majors about 2 to 1 in the average mature colony, the amount of material invested in majors is 2 to 3 times as much as in minors.

Increase of worker weight

In parallel to the increasing headwidths of minors during the first half year (Fig. 6), the mean dry weights of minors increased from about 0.13 mg in incipient colonies and leveled off at about 0.32 mg between 1.8 and 4.7 yr (ANOVA: $F_{1,63} = 33.7$; $P < 0.001$). It then dropped significantly ($P < 0.005$, Newman-Keuls test) to 0.25 mg at 5.5 yr and remained there at least until 12 to 14 yr.

The mean dry weight of majors followed a similar pattern. The earliest discernible majors weighed an average of about 0.22 mg (S.D. = 0.025). Minors in these colonies averaged 0.14 mg (S.D. = 0.016 mg). The mean weight of the majors increased until about 0.5 yr when it reached a mean of 1.0 mg (S.D. = 0.18) (ANOVA: $F_{1,16} = 26.6$; $P < 0.001$). It varied between 0.82 and 1.17 mg thereafter, but none of these values differed significantly from 1.0 mg. Unlike that of minors, the mean weight of majors did not decline after 4.7 yr.

The variability of the worker dry weights also increased in a similar fashion. The coefficient of variation (COV) of the dry weights of the separated major and minor subpopulations was used to estimate weight variability. For the minors, the COV's increased from about 8% in incipient colonies to about 26% at 1.8 yr, and then dropped gradually to about 14% in 12 to 14 yr colonies.

Major workers show much greater weight variability. The COV of the first discernible majors was about 9%. By 4 mo., it had increased to about 50% where it remained until 12–14 yr. As a result, the *range* of weights represented in major workers is up to 20 times as great as in minor workers, a fact of possible importance to division of labor.

Discussion

Although ant colonies may consist of several million workers, the average across species is probably in the hundreds (Brian 1965; Wilson 1971). In comparison, colonies of the fire ant, *S. invicta* are very large. They reach their maximum size after 4 to 6 yr of logistic growth. At its peak, such a colony contains over 200 g (live weight) of worker ants. During the height of brood production in the spring and summer, it also contains 40 to 60 g of brood in various stages (Tschinkel and Porter 1988), and every year it releases an average of 4400 sexuals (Morrill 1974) weighing a total of about 45 g. With an approximate worker turnover of 350% per year (Tschinkel and Porter 1988), this means that a mature colony produces about 700 to 800 g of ants per year.

My data agree generally with those of Markin et al. (1973), although these authors followed growth for only 3 yr. At that age, mean colony size was either 53000 or 110000 (their Table 1 and the text do not agree). They noted that "old" colonies contained about 120000 workers, and suggested that their 3 yr colonies were not yet fully grown. In my study, "old" colonies were somewhat larger, but variation from site to site is to be expected and the sampling month may have been different. Markin et al. (1973) also found substantial seasonal fluctuation in colony size, early summer colonies being smaller than fall ones. A larger size fluctuation was detected by Porter and Tschinkel (unpublished) in mature colonies. Colony growth models incorporating such seasonal effects were reviewed by Brian (1965). It seems likely that in the spring, colony growth potential is switched to sexual production, causing a worker deficit which is made up only after the sexual production ceases late in summer. Colony size therefore reaches an annual maximum during the late fall and winter. The annual fluctuation of colony weight is 50 to 60 g, and this is roughly in the range of the weight of sexuals produced annually by mature colonies (45 g, Morrill 1974; 60–70 g, Porter and Tschinkel unpublished).

Separate analysis of the minor and major worker populations showed that each grows logistically, both in number of workers and total weight, and that the proportion of majors increases until colony growth levels off. In mature colonies, minors outnumber majors about 2 to 1, but the total weight of majors is about twice that of minors, dramatically underlining the relative investment of production. Total energy investment favors majors somewhat less because, as a result of their lower metabolic rate and greater longevity, they are cheaper to maintain (Porter and Tschinkel 1985a). The ultimately high investment in majors suggests that these are very important to colony success, possibly through an increased role in production of sexuals. However, the ergonomic meaning of such gradual size shifts of workers size is presently unknown. For example, Rissing (1987) detected no ergonomic effects of the seasonal shift of worker size in *Veromessor pergandei*.

Logistic colony growth has been reported in several species of social insects (Bodenheimer 1937; Jonkman 1980; Weber 1982), and is the expected, though rarely demonstrated, mode of colony growth (Wilson 1971). Logistic growth results from negative feedback which slows the initially exponential growth (Brian 1965). Wilson (1971) suggested that the identification of such negative feedback should be made a central question in colony population dynamics. Several sources of such feedback can be suggested: (1) In all investigated social insects, the efficiency of brood rearing (larvae reared per adult worker) declines as colony size increases (Brian 1956; Michener 1964; Porter and Tschinkel 1985a). The ratio of workers per larva therefore increases with colony size. Brian (1956) suggested underdispersion of larvae and the "test-servicing" of larvae by workers as important causes of worker inefficiency. (2) Tschinkel (1988) found a similar decline of efficiency in the stimulation of queen fecundity by fire ant larvae. This leads to a regular decline in the per larva reproductive rate as colony size and larval population increase. Tschinkel also suggested that the queen's physical ability to lay eggs may set the upper fecundity, but was not able to make a clear choice between these alternatives. (3) The larger the worker, the less effective it is at brood rearing, at least in monomorphic colonies (Porter and Tschinkel 1985a). Perhaps as colony growth shifts worker size upward until 70% of colony weight is majors, this further depresses the worker brood-rearing efficiency. (4) The emission of sexuals diverts material from worker production, thereby slowing or

even reversing growth (Brian 1965), and giving rise to the seasonal variation of colony size in *S. invicta*. (5) Perhaps other functions, such as food gathering, nest construction, territorial defense, etc., also decline in efficiency as colonies grow. Undoubtedly, several factors act simultaneously to reduce overall colony growth rate gradually, until it ceases entirely.

Most claustrally-founding ants produce an initial brood of nanitic workers. With the exception of *Atta* (Wilson 1983), the initial worker broods of polymorphic ant species are monomorphic. Incipient *Atta* colonies contain a sufficient range of worker sizes to rear fungus, and as these colonies grow, they add both larger and smaller workers, gradually creating a strongly skewed size-frequency distribution. In *S. invicta*, all subsequent workers are larger than the initial brood, but skewing appears early, as in *Atta* (Wood and Tschinkel 1981).

In all three cases for which both census and size-frequency data are available, the full, mature size *range* and size *variability* of workers are achieved very early in colony life (10% of mature size in *Myrmica* (Brian 1957a); less than 5% in *S. invicta*; less than 1% in *Atta* (Wilson 1983)), suggesting this may be a general feature of colony development. On the other hand, at least in *S. invicta*, the proportion of large workers continues to increase as long as the colony grows. If this is so in *Atta*, it is to a lesser degree (Wilson 1983; and personal communication). Whether other polymorphic species continue to increase investment in majors remains to be seen.

A quantitative model of the ontogeny of polymorphism can be constructed from the following major elements. (1) As colonies grow, the brood-rearing efficiency of workers decreases, resulting in an increasing number of adult workers per larva (Brian 1956; Michener 1964; Porter and Tschinkel 1985a, b). (2) This in turn causes an increase in the amount of food per larva (Evesham 1985; Pisarski 1981), leading to an increase in worker size (probably up to a limit). A positive correlation between colony size and worker size has been reported in *Myrmecia* (Gray 1971), *Atta* (Wilson 1983), *Myrmica* (Brian 1957a), *Pogonomyrmex* (Porter and Tschinkel 1986), and *Solenopsis* (Markin et al. 1973; Wood and Tschinkel 1981; Porter and Tschinkel 1985b). In *Myrmica rubra* a higher proportion of larvae are fed at higher worker:larva ratios (Evesham 1985). Logically, an increase in mean weight requires increased food intake. This hypothesis is testable. (3) Larvae that attain

a certain threshold weight in one of the early instars (probably the third), are reprogrammed to enter metamorphosis at a higher weight (Wheeler 1986; Wheeler, personal communication). This reprogramming is a discrete event and results in the two normally distributed populations seen in Figs. 4 and 5. Such reprogramming has been reported in *Pheidole* (Wheeler and Nijhout 1981) where it results in complete dimorphism, with the size-variance of the majors only somewhat larger than that of the minors. In *S. invicta* on the other hand, the size variability of majors is much greater than that of the minors, suggesting that perhaps the larger larvae are fed preferentially and more variably by workers. Preferential treatment of different types of larvae by workers was reported in *Myrmica* (Brian 1957b). Alternately, Oster and Wilson (1978) theorized that continuous polymorphisms could arise if subsequent growth rate were an exponential function of the weight attained at an early stage. (4) As colony size increases, the improved feeding will cause an ever larger proportion of the larvae to exceed the weight threshold and to be reprogrammed to become majors. Those not reprogrammed become minors.

In this scheme, the proximate controlling factor is the ratio of workers to larvae. An increase in workers/larva increases the mean pupal size (Porter and Tschinkel 1985b). Thus, anything which alters the worker/larva ratio will also alter the polymorphism. For example, the proportion of minors rises during the summer and fall, seasons marked by low worker/larva ratios (Markin and Dillier 1971). The lower worker/larva ratio in polygynous colonies of *S. invicta* and *Formica exsecta* may provide a simple explanation of the lower proportion of majors and the lower mean worker size than in comparable monogynous colonies (Greenberg et al. 1985; Pisarski 1981). A non-ontogenetic factor affecting the size-frequency distribution is the greater longevity and stress-resistance of larger workers (Porter and Tschinkel 1985a). This causes an accumulation of larger workers in excess of their representation among the pupae.

The factor which drives the ontogeny of polymorphism must act at all colony sizes. Although I have tentatively suggested declining reproductivity (Michener 1964) and improving nutrition as the proximate driving force, the ultimate cause of the decline in reproductivity remains an open question. Brian (1956) suggested that the decline in brood rearing efficiency in growing colonies of *Myrmica* resulted from two sources: the tendency of the workers to limit access to larvae by piling

them up, and the "test-servicing" mode of larval care. Certainly, these are questions begging for investigation.

The use of normal score headwidth plots for discriminating minor from major workers offers a repeatable, biologically meaningful criterion for separating these subcastes. In continuously polymorphic ants such as *S. invicta* and *S. geminata*, most authors have arbitrarily set certain headwidths as separating "minors", "media" and "majors". This can be problematical if it captures different portions of the size distribution in small and large colonies. In addition, it is clear that the term "media" has no developmental meaning and should be dropped.

I have applied the normal score plot method to the size-frequency distributions of 13 species reported in the literature or from my own unpublished data. These included 3 monomorphic and 3 totally dimorphic species. The remainder showed some kind of bimodal or continuous polymorphism. Normal score plots of these species showed 9 reasonably linear or multi-linear plots (including *S. geminata*), 3 with some curvature and 1 with definite curvature. It seems likely that this method may prove generally useful for examining worker polymorphisms in ants.

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