Fire Ant Polymorphism (Hymenoptera: Formicidae): Factors Affecting Worker Size

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ABSTRACT Worker size distributions are apparently not homeostatically regulated in colonies of the fire ant *Solenopsis invicta* Buren. Pupae produced in artificially composed polymorphic, dimorphic, and small-worker colonies were not significantly different in either average size or frequency distributions. However, larger colonies produced significantly larger pupae. Average pupal size was tightly correlated with the logarithm of colony size all the way from single founding queens up to mature colonies with tens of thousands of workers. High larval density also resulted in significantly smaller pupae.

The apparent lack of homeostatic control combined with the influences of colony size and larval density, suggest that fire ant caste distributions do not track short-term environmental contingencies. Nevertheless, the general relationship between worker size and colony size is almost certainly adaptive.

WORKER SIZE VARIATION is an important aspect of fire ant population dynamics, energy metabolism (Porter and Tschinkel 1985), and social structure (Mirenda and Vinson 1981). Workers from the same colony may exhibit a 3-fold variation in length (Fig. 1) and more than a 15-fold variation in weight. Presumably, the frequency distribution of large and small workers in fire ant colonies represents some type of evolutionary optimum (Oster and Wilson 1978). However, the degree and nature of this optimization is not clear. Size–caste distributions might be fixed genetically and unresponsive to environmental changes, or they might be regulated to track broad changes in season (Markin and Dillier 1971), habitat (Davidson 1978, Bernstein 1980), or colony size (Oster and Wilson 1978). Conceivably, caste frequency distributions could even be adjusted to meet more ephemeral contingencies such as foraging, predation (Herbers 1980), or colony defense (Johnston and Wilson 1985).

Several factors affect fire ant caste distributions: First, the percentage of large workers in fire ant colonies increases markedly with colony size and age (Markin et al. 1973, Wood and Tschinkel 1981). Second, large workers are more common in the winter months than in summer months (Markin and Dillier 1971). Also, polygynous or multiple-queen colonies produce much smaller workers than monogynous colonies (Greenberg et al. 1985). Other potential extrinsic factors affecting caste distributions include temperature (Brian 1963), food (Brian 1975), the nature of brood care (Brian 1974), brood production rates (Brian 1953), and the presence or absence of major workers (Gregg 1942, Wheeler and Nijhout 1984).

The size distributions of workers in field *Solenopsis invicta* Buren colonies are extremely variable (Greenberg et al. 1985, Porter and Tschinkel 1985). The question is, does this variability reflect primarily genetic variation, developmental history of the colony, or facultative adaptation to the environment? While a definitive answer to this question is not the intention of this paper, we have nevertheless addressed several important aspects of the problem. Our primary objective was to investigate potential homeostatic control of worker size castes in small fire ant colonies. In conjunction, we also investigated the effects of colony size and brood production rate on the size of pupae produced.

Materials and Methods

To determine if altered worker caste distributions influenced the size range of pupae produced, we manipulated the proportions of large and small workers in experimental colonies. Workers were separated from brood and sorted into six size classes using standard testing sieves (mesh sizes 16, 18, 20, 25, 30, and 35; Porter and Tschinkel 1985). Average head widths for workers collected on each of the six sieves were, respectively, 1.35, 1.19, 1.01, 0.86, 0.74, and 0.68 mm. Corresponding live weights were 4.5, 3.3, 2.1, 1.3, 0.8, and 0.6 mg. Polymorphic colonies contained a standard percentage (by live weight) of workers from each sieve (largest to smallest: 6, 13, 9, 15, 30, and 27%). This frequency distribution was chosen to approximate the average observed in mature fire ant colonies (Porter and Tschinkel 1985). Small-worker and medium-worker colonies contained ants collected on sieve nos. 35 and 25, respectively. Large-worker colonies were composed of workers from sieve nos. 18 and 16 (67 and 33% by weight). Dimorphic

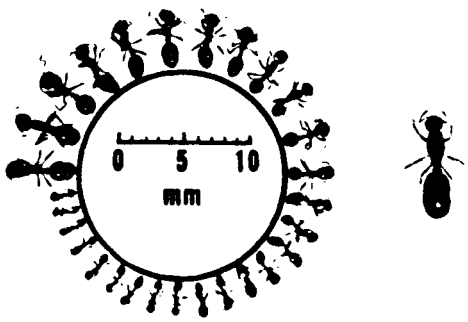

Fig. 1. Worker size variation in a mature colony of the fire ant, *Solenopsis invicta*. A colony queen is shown on right for comparison.

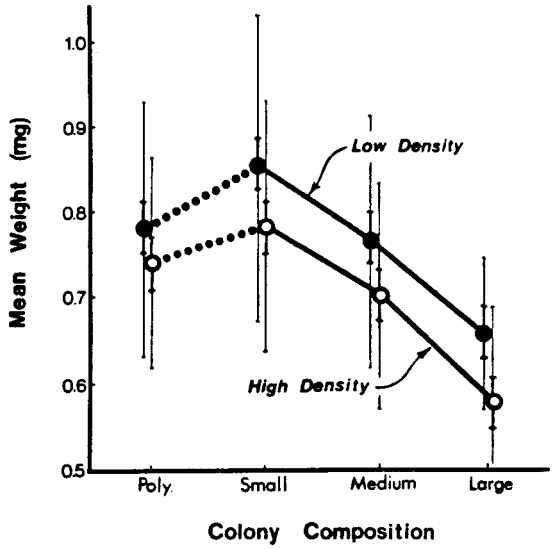

Fig. 2. Mean live weight of pupae produced in polymorphic fire ant colonies and monomorphic colonies composed of only small, medium, or large workers. Colonies were given either 1.0 g (high density) or 0.25 g (low density) of early fourth instars. Each point is the average of eight experimental colonies. Outer error bars are standard deviations; inner ones are standard errors of the mean after adjusting for larval batch and worker source.

colonies contained 50% small workers (sieve no. 35) and 50% large workers (sieve nos. 16 and 18).

The number of workers in each colony was adjusted so total worker weight remained constant across colony composition treatments. As a result, small-, medium-, and large-worker colonies contained ca. 1,640, 770, and 220 workers per gram, respectively. Similarly, polymorphic and dimorphic colonies contained about 1,020 and 960 workers per gram. We standardized worker weights rather than number so nest size and total colony biomass would be equal.

Workers from different colonies may differ widely in their brood-rearing capabilities. To account for this, we used worker source colony as a blocking or random effect factor (Porter and Tschinkel 1985) in each of the following experiments. This was accomplished by sieving a large colony (40–80 g of workers) and dividing it into fragment colonies of the appropriate size and worker composition. Each source colony was crossed with all experimental treatments and provided one replicate set of fragment colonies. This experimental design is the analysis of variance equivalent to a paired t test.

At the completion of each experiment, pupae were collected and sorted into six size classes by shaking them through a stack of six testing sieves (sizes 14, 16, 18, 20, 25, and 30). Average weights of pupae collected in each of the six sieves were, respectively, 3.2, 2.1, 1.2, 0.8, 0.5, and 0.4 mg. Corresponding mean pupal lengths were 3.4, 3.0, 2.4, 2.1, 1.8, and 1.6 mm. Pupal lengths (L) can be converted to worker head widths (W) using the formula $W = 0.35L - 0.07$.

Experimental colonies were maintained at 30.0 ± 0.7°C in constant darkness except during maintenance. They were fed ad lib. quantities of cockroaches (*Periplaneta* sp.) or tenebrionid larvae (*Zophobas* sp.) and 1 M sucrose soaked into small tissue wads. Colony collection, nest designs, and handling techniques have been described in more detail previously (Porter and Tschinkel 1985).

Experiments and Results

Larval Density Experiment. This experiment compared the size of pupae produced by polymorphic, small-, medium-, and large-worker colonies at two levels of brood production. Experimental colonies contained no queen, thus eliminating her effects on pupal size and allowing us to fix experimentally the brood:worker ratio (by weight). Eight experimental colonies were formed from each of eight worker source colonies (64 total). Experimental colonies were set up so that there were two from each source colony in each of the four treatments of colony composition (Fig. 2); 1 g of larvae (≈2,000) was then added to one of these experimental colonies (40% by weight) and 0.25 g (≈500) to the other (14%). These levels of brood density were chosen to approximate high and moderate rates of production found in field colonies (Markin et al. 1974). Each colony contained 1.5 g of workers (450–2,500, depending on worker size).

Medium-size larvae (mostly early fourth instars; Petralia and Vinson 1979) were collected and pooled from 15 to 20 laboratory and field colonies. Approximately 80 to 90% of larval growth (by weight) occurs during the fourth stadium. Four batches of larvae were used; two sets of source colonies were nested in each larval batch. Eleven days after setup, all pupae were collected, count-

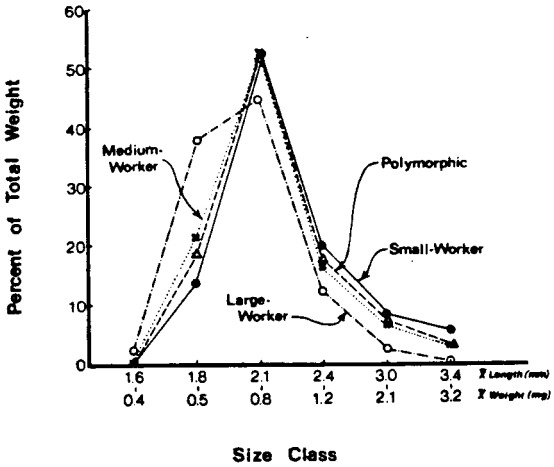

Fig. 3. Percentage of distribution of pupae (by weight) produced in polymorphic, small-, medium-, and large-worker fire ant colonies in the larval density experiment. Each curve is the averaged distribution of between 12,000 and 15,000 pupae collected from 16 experimental colonies.

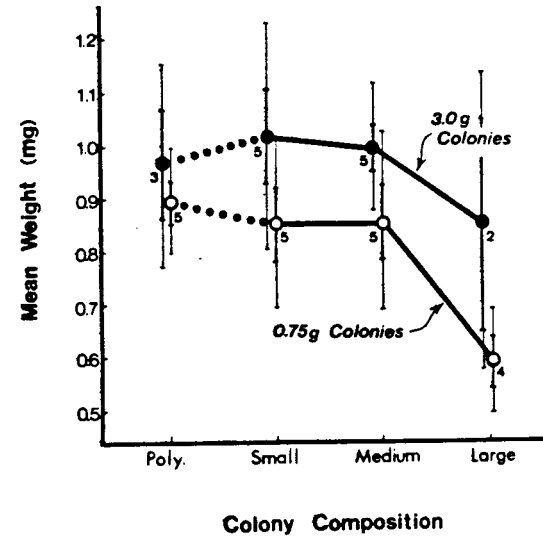

Fig. 4. Mean live weight of pupae produced in queen-right fire ant colonies containing either 3.0 or 0.75 g of workers. Colonies were composed of polymorphic, small, medium, or large workers. Number of observations is shown next to each point. Outer error bars are standard deviations; inner ones are standard errors of the mean.

ed, and sieved into size categories. Data were analyzed using a four-way analysis of variance. Worker source colony and larval batch were the blocking factors and colony composition and larval density were the experimental factors (Fig. 2). Worker source colony was nested in each larval batch; the other three factors were crossed with each other.

Pupae produced in colonies with high larval density weighed 9% less than pupae produced in colonies with low larval density ($P < 0.003$; Fig. 2). Similarly, mean pupal length declined 1.5% ($P < 0.03$) and the percentage of pupae in the three largest size classes declined 20% ($P < 0.01$). This effect was consistent across all treatments of colony composition (Fig. 2).

The size of workers in experimental monomorphic colonies strongly affected the size of pupae produced. Mean pupal weight decreased 25% as the size of workers in these experimental colonies increased ($P < 0.001$; Fig. 2). Similarly, mean pupal length decreased 7% and the percentage of pupae in the three largest size categories decreased ca. 50% (Fig. 3). Average weights of pupae declined significantly going from small- to medium- to large-worker colonies ($P < 0.05$, Duncan's multiple range test). Pupae produced in polymorphic colonies were intermediate between those produced in small- and medium-worker colonies. The frequency distribution of pupal biomass gradually shifted from small to large size classes as mean pupal size increased (Fig. 3). In other words, no unusual changes in frequency distributions were detected. Interestingly, larvae added to large-worker colonies pupated 1 to 2 days before larvae in the other three treatments.

Medium- and large-worker colonies might have produced smaller pupae because larger workers have low brood-rearing skills, the ratio of workers to larvae was smaller, or because of homeostatic regulation. The following two experiments, however, tend to discount the possibility that fire ant caste ratios are homeostatically regulated.

Queen-right Experiment. This experiment was designed to investigate the size of pupae produced from eggs laid naturally in queen-right colonies. We used a three-way factorial design. Colony composition and colony size were the two experimental factors and again source colony was a blocking factor. As before, colony composition consisted of four treatments: polymorphic, small-, medium-, and large-worker colonies. Colony size was chosen as a second experimental factor because it is correlated with the degree of polymorphism in field colonies. Our experiment contained two levels: small colonies with 0.75 g of workers and larger colonies with 3.0 g of workers.

We randomly adopted a mature queen from a laboratory stock colony into each experimental colony. Colonies were then allowed to rear brood at their own rate rather than an experimentally fixed rate as in the previous experiment. Pupae and larvae resulting from the adopted queen were removed after 4 and 7 weeks. These data were collected from pupae raised in the "main experiment" of our fire ant ergonomics and brood production study (Porter and Tschinkel 1985). Data for two polymorphic colonies and four large-worker colonies were missing either because the queen died or the colony failed to produce pupae (Fig. 4). Consequently, this experiment was analyzed

using BMDP's maximum likelihood analysis of variance (Jennrich and Sampson 1979).

Brood production during the first 4 weeks was generally low and irregular, probably because of the initial lack of brood in the experimental colonies (Porter and Tschinkel 1985) and stresses associated with setting up the experiment. Pupae collected during this period tended to be small and showed no significant size differences either across the treatments of colony composition or colony size. By week 7, brood production was twice as high as the first month and much more consistent. Overall, these pupae were 17% heavier than pupae produced in the previous larval density experiment. Less disturbance of the growing larvae or the presence of a queen may account for this difference.

The larger 3.0-g colonies produced significantly larger pupae (Fig. 4). Pupae in these colonies were 15% heavier ($P < 0.001$) and 4% longer than pupae produced in the smaller 0.75-g colonies. However, the rate of brood production per gram of workers was 50% higher in the smaller colonies (Porter and Tschinkel 1985). Consequently, larger colonies may have produced larger pupae because the ratio of workers to brood was higher. In fact, when the ratio of the number of workers to the number of pupae was used as a covariate (log transformed), the difference due to colony size was no longer significant ($P > 0.6$), but the covariate was very significant ($P < 0.007$).

Pupae produced in large-worker colonies were significantly smaller than the other treatments of worker composition ($P < 0.01$; Fig. 4). However, the sizes of pupae produced in polymorphic, small-, and medium-worker colonies were not significantly different. Unlike Johnston and Wilson (1985) with *Pheidole*, we found no correlation between the average weight of workers in the queens' original colonies and the average weight of pupae produced in their adopted experimental colonies ($n = 16$). Apparently, any size variation due to the queens' age or genetic makeup was swamped by other sources of variation. Fire ant queens removed from large field colonies and placed in small laboratory colonies invariably produced much smaller workers. Consequently, colony size appears to be much more important than the queen's age in determining worker caste distributions (Wilson 1983b).

Dimorphic Experiment. This experiment was undertaken to determine if the unusually high percentage of large workers in artificial dimorphic colonies would inhibit the production of large-worker pupae. Polymorphic and small-worker colonies from the same source colony were paired with each dimorphic colony (Table 1). Experimental colonies each contained an adopted queen and 3.0 g of workers. A sample of fourth instars was added to each colony. Two replicate sets (Table 1) were also allowed to rear brood from their adopted queen. Data were analyzed using BMDP's maximum likelihood analysis of variance (Jennrich and Sampson 1979).

Table 1. Mean wet weight (mg) of pupae produced in dimorphic, polymorphic, and small-worker experimental colonies

Worker source colony	Colony composition		
	Dimorphic	Polymorphic	Small-worker
1 A	0.80	0.74	0.67
B	0.84	0.77	0.83
2 A	0.93	0.92	1.05
B	0.79	0.70	—
3 A	0.81	0.82	0.90
4 A	0.82	0.76	0.76
Means ($P > 0.2$)	0.83	0.79	0.84

A, Pupae reared from pulse of fourth instars. B, Pupae reared from adopted colony queen.

The average weights of pupae produced in dimorphic, polymorphic, and small-worker colonies were not significantly different ($P > 0.2$; Table 1). Dimorphic colonies actually produced slightly more pupae in the two largest size classes than did polymorphic and small-worker colonies (5.4 versus 4.5 and 3.9%, respectively; $P > 0.07$). Furthermore, the shape of pupal frequency distributions were similar to those in Fig. 3 and essentially the same for all three treatments. The average weights of pupae reared from introduced larvae (A) and from eggs laid by the adopted queen (B) showed no consistent differences (Table 1).

Discussion

Unlike *Pheidole* (Gregg 1942, Wheeler and Nijhout 1984), large workers in *S. invicta* colonies probably do not inhibit the production of additional large workers. Pupae produced in polymorphic and small-worker colonies were not significantly different (Fig. 2 and 4). Similarly, pupae produced in dimorphic colonies (50% large workers) were no smaller than those produced in either polymorphic or small-worker colonies (Table 1). Colonies composed of only large workers (Fig. 2 and 4) did produce very small pupae, but this was probably because large workers are inept brood tenders (Mirenda and Vinson 1981). Eggs laid in large-worker colonies of the queen-right experiment seldom developed beyond the third stadium, and total pupae (g) produced by these colonies averaged only 3% of the totals produced by the other colonies (Porter and Tschinkel 1985). Large- and medium-worker colonies in the larval density experiment (Fig. 2) probably produced smaller workers because these colonies contained fewer workers per gram of larvae.

The presence of large workers apparently did not inhibit large worker production, nor did their absence stimulate production (Fig. 2 and 4; Wood and Tschinkel 1981). Small-worker colonies, for

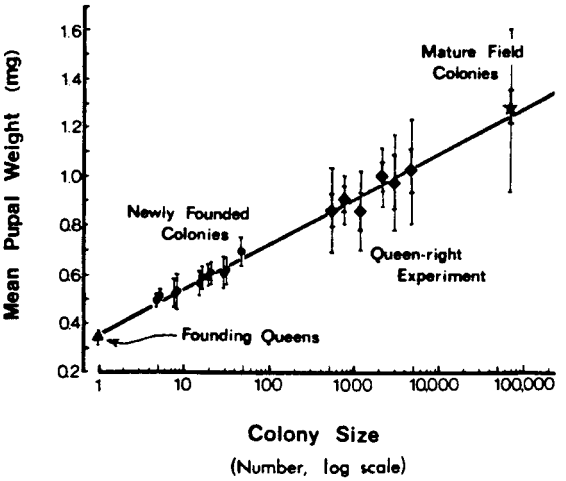

Fig. 5. Mean live weight of pupae produced in queen-right fire ant colonies plotted against colony size ($y = 0.35 + 0.19\log_2$, $R^2 = 98.8\%$). Data for "founding queens" and "newly founded colonies" are from Porter and Tschinkel (unpublished data). Each point is the mean of 10 to 20 colonies. "Queen-right experiment" colonies are from this paper (large-worker colonies were excluded). The pupae from 24 "mature field colonies" were collected in October 1984. We estimated the average size of mature colonies at 70,000 workers (Markin et al. 1973). Outer error bars are standard deviations; inner ones (where visible) are standard errors of the mean.

instance, might have produced medium and large workers preferentially, or medium-worker colonies might have produced extra small- and large-worker pupae. Careful inspection of size–frequency distributions in the larval rearing experiment (Fig. 3) and in the other two experiments as well revealed no effect of colony composition on the general shape of pupal frequency distributions (except for large-worker colonies). Similarly, when Wilson (1983a) excised the primary foraging class of leaf cutter ants (*Atta cephalotes*), experimental colonies did not respond by preferentially replacing that worker size group.

Overall, our results indicate that the size of workers in small fire ant colonies does not affect the size of workers which they produce. The potential of homeostatic control in mature colonies was not tested because of serious difficulties entailed in handling and manipulating these extremely large colonies. Nevertheless, we observed no hint of this possibility among colonies of different size in our queen-right experiment (Fig. 4). Furthermore, the presence of homeostatic control in large colonies seems unlikely because larger colonies produce progressively larger sized workers (Fig. 5).

In fact, the number of workers in a colony appears to be the principal predictor of pupal size. The average weight of pupae produced by queen-right colonies was very closely correlated to the logarithm of the number of workers in a colony (Fig. 5). Surprisingly, this relationship extended all the way from lone founding queens up to mature colonies with tens of thousands of workers. The general effect of this relationship is that the average weight of pupae produced increases very rapidly during the early stages of colony growth, but more slowly in the final stages. Variability in average pupal weights also increased with colony size; this in spite of the fact that queen-right and newly founded colonies were reared under controlled laboratory conditions. Apparently, the size range of pupae produced in larger colonies is inherently more variable than in smaller colonies.

What is the basis for the relationship between colony size and pupal weight? The rate of brood production per worker in *S. invicta* colonies decreases with increasing colony size (Porter and Tschinkel 1985). Possibly, lower rates of brood production per worker result in larger pupae because there are more workers per larva. Consequently, larvae might receive more food more often and grow larger (Brian 1953). This possibility is supported by the results of the larval density experiment (Fig. 2).

A positive correlation between colony size and worker size has been noted in other ant genera—*Myrmecia* (Gray 1971), *Atta* (Wilson 1983), *Myrmica* (Brian and Brian 1951), *Pogonomyrmex* (unpublished data). Since the rate of brood production commonly declines with colony size (Michener 1964), increasing worker to brood ratios would provide a simple explanation of why larger ant colonies generally have larger workers (Brian and Brian 1951). Similarly, high brood production rates in polygynous colonies (Greenberg et al. 1985) and small laboratory colonies may explain why workers in these colonies are distinctly smaller. Seasonally high brood production rates (Markin et al. 1974) may also help explain why fire ant colonies contain a greater proportion of small workers in the summer than in the winter (Markin and Dillier 1971).

Nevertheless, larval density may not be the only factor or even the major factor affecting pupal size; pheromones, various queen influences (Brian 1975), and food supplies may also be important mediating factors. Whatever the cause or causes, the effect of colony size on pupal size is remarkably consistent. The same process or processes which occur in incipient colonies also appear to occur in mature colonies with tens of thousands of workers.

The apparent lack of homeostatic control, combined with the effects of colony size, larval density, and developmental lag time of at least 3 to 4 weeks, argue against the possibility that fire ant colonies facultatively adjust caste distributions to track short-term changes in their environment. However, the gradual addition of large workers as colonies grow is almost certainly adaptive. Large workers in mature colonies appear to increase ergonomic efficiency primarily because they respire

at lower rates and live longer (Porter and Tschinkel 1985). Conversely, the absence of large workers in newly founded colonies is also adaptive because incipient colonies are more successful when they produce many nanitic (miniature) workers rather than fewer larger ones (Porter and Tschinkel, in preparation).

Nevertheless, much of the variation in worker caste distributions is probably not adaptive. If in fire ant colonies, worker size castes vary according to a single rule (Fig. 5), then caste ratios may not be optimized for all stages of colony growth. Likewise, seasonal changes in caste distributions may be more an outcome of low winter brood production or differential worker mortality than an adaptation to changing seasons.

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