Adaptive Value of Nanitic Workers in Newly Founded Red Imported Fire Ant Colonies (Hymenoptera: Formicidae)

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ABSTRACT Founding fire ant colonies, *Solenopsis invicta* Buren, with nanitic workers produced 17% more brood than experimentally modified colonies containing equal weights of normal-sized minor workers. As predicted, the number of workers in our founding colonies, not worker size, was the principal factor influencing brood production. These results provide the first empirical evidence substantiating the hypothesis that nanitic workers are indeed adaptive.

KEY WORDS *Solenopsis invicta*, nanitic, evolution, economics, ergonomics, colony founding

NANITIC WORKERS are miniature ants commonly reared in newly founded colonies (Brian 1965, Wilson 1971); they are frequently half the weight of the smallest workers in mature colonies. Nanitics, minims (Markin et al. 1973), or micrergates (Wheeler 1910), as these workers have been variously termed, are commonly associated with claustral colony foundation (Oster & Wilson 1978). Claustrally founding queens rear the first generation of workers entirely from material stored in their bodies before their mating flight (Toom et al. 1976).

According to sociobiological theory, the advantage of nanitics is that their small size allows founding queens to rear more workers from their fixed energy reserves (Oster & Wilson 1978). Incipient colonies have many pressing tasks, but relatively few workers to perform them. Production of additional small workers could benefit incipient colonies by allowing them to undertake competing tasks simultaneously rather than sequentially. Nanitic workers might also spread the risk of forager mortality over more individuals or allow colonies to perform certain tasks requiring a minimum number of workers to be successful (Oster & Wilson 1978).

Our objective was to investigate the adaptive value of nanitic workers in newly founded laboratory colonies of the red imported fire ant, *Solenopsis invicta* Buren. Specifically, we hoped to determine if the presence of nanitic workers in the first generation increased colony growth in the second generation. We also hoped to determine whether the value of nanitic workers was a consequence of their small size per se or their increased numbers.

We used colony growth as an approximate measure of colony fitness because rapid growth is essential for the survival of incipient fire ant colonies. Young colonies must produce hundreds or even thousands of workers before they can successfully defend a territory (Wilson et al. 1971), construct a mound, or survive the winter (Markin et al. 1973). Furthermore, young colonies are highly susceptible to subterranean predators (Buren 1983) and brood raiding from other founding colonies (Markin et al. 1973). In short, colony founding is a period of intense pressure selecting for rapid growth (Oster & Wilson 1978).

Materials and Methods

Colonies used in these experiments were reared from founding queens collected immediately after mating flights in May and June of 1984. Average queen weight was 15.5 ± 0.8 mg (standard deviations are shown unless otherwise indicated). Queens were placed individually in test tubes (13 by 100 mm) that had been partially filled with water, plugged halfway with a cotton ball, and then stoppered with a second one. Queens were maintained in darkness at 30°C and allowed to rear brood for 20 days. Experimental manipulations were performed 1 day before the first workers were to eclose; at that time, colonies contained an average of 31 ± 3 pupae (10.2 ± 1.0 mg), 4 ± 2 feeding larvae, ca. 35 eggs, and a queen weighing 8.0 ± 0.6 mg. Approximately one-fourth of founding colonies were eliminated before the experiment because the queen died or produced oversized male brood (Ross & Fletcher 1985). Founding colonies producing diploid males are almost never viable. During the actual experiment, all colonies produced worker brood and none were eliminated.

To investigate the adaptive value of nanitic workers, we experimentally modified the size and number of pupae (and prepupae) in newly founded colonies. All pupae were removed from 10 of 11 groups; larvae and eggs were not removed. Colonies in the 11th group served as undisturbed con-

Table 1. Number, weight, and size of pupae in study colonies

No. of pupae	Pupal weight (mg)		Head width (mm) after eclosure	Replicate colonies
	$\bar{x}$	Total		
Substitution groups				
5	1.92	9.6	0.95 ± 0.06	20
8	1.20	9.6	0.81 ± 0.04	20
16	0.64	10.2	0.67 ± 0.03	20
20	0.50	10.0	0.61 ± 0.03	20
Nanitic groups				
5	0.33	1.7	0.54 ± 0.01	10
8	0.33	2.6	0.54 ± 0.01	10
16	0.33	5.3	0.54 ± 0.01	10
20	0.33	6.6	0.54 ± 0.01	10
31[a]	0.33[a]	10.2[a]	0.54 ± 0.01[a]	20[a]
31 ± 3[b]	0.33[b]	10.2[b]	0.54 ± 0.01[b]	20[b]
50	0.33	16.5	0.54 ± 0.01	10

Colonies in the substitution groups contained varying sizes of pupae substituted from mature colonies, while colonies in the nanitic groups contained varying numbers of nanitic pupae.
[a] Experimental control colonies.
[b] Undisturbed control colonies.

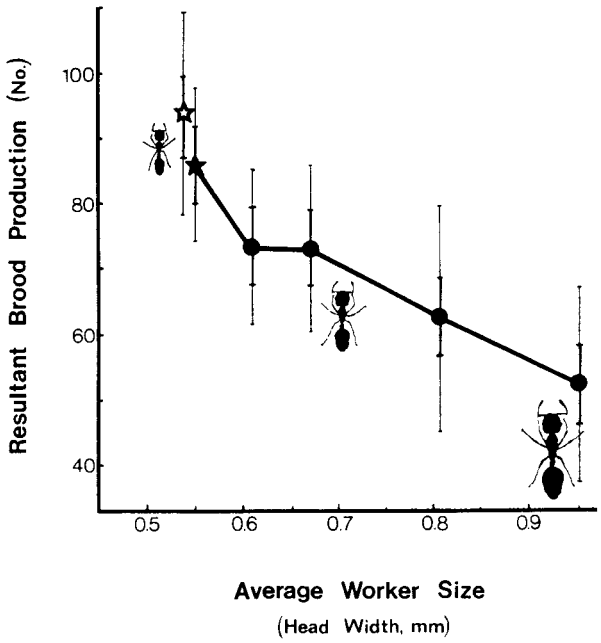

Fig. 1. Resultant brood production (larvae and pupae) plotted against the average size of first-generation workers in the artificially constituted incipient colonies. Each colony contained ca. 10.2 mg of workers, but the number of workers in a colony varied inversely with worker size (Table 1). ★, brood production by nanitic workers in manipulated control colonies; ☆, production in undisturbed control colonies. Each point is the mean of 20 colonies. Outer error bars are standard deviations; inner ones are pooled 95% CL for the means.

trols. Of the 10 treated groups, 4 received substitution pupae and 6 received nanitic pupae (Table 1).

The four substitution groups (Table 1) received pupae collected and pooled from 10 mature colonies. The number of pupae substituted into these groups was adjusted so that total pupal weight approximated that in undisturbed control colonies (10.2 mg). Consequently, the number of pupae introduced increased from 5 to 20 as pupal size decreased (Table 1). Pupae were sorted into size categories (see head widths, Table 1) by gently shaking them through a stack of geological sieves (Porter & Tschinkel 1985b). Only small through medium pupae were utilized because large workers (head widths >1.2 mm) are known to be poor brood tenders (Porter & Tschinkel 1985a).

The nanitic pupae removed from the 10 treated groups were pooled and sieved as above and then used to set up 6 groups of nanitic colonies (Table 1). These colonies received either 5, 8, 16, 20, 31, or 50 nanitic pupae. This series allowed us 1) to compare nanitic and substitution colonies having equal numbers of workers and 2) to assess the impact of colony size on subsequent brood production. Colonies receiving 31 pooled nanitic pupae (≈10.2 mg) served as manipulated controls for the experimental procedures.

This experiment was repeated twice. Our initial run contained six groups: the four substitution groups and the two nanitic control groups (Table 1). Each group contained 10 randomly selected colonies. Two weeks after the first run we set up a second run identical to the first, but it also included the five additional nanitic groups.

A day after the first workers eclosed, experimental colonies were unstoppered and fed daily, ad lib. (Porter & Tschinkel 1985a). Sixteen days after the experimental manipulations, all resultant second-generation pupae and larvae were counted and weighed.

Results were analyzed with analyses of variance and covariance. Duncan's multiple range test was used to determine significant differences between treatment means (Ott 1977).

Results

Equal weights of larger workers were progressively less effective at raising the second generation (Fig. 1). Even though worker biomass remained constant, brood production declined up to 40% as the size of workers increased ($F_{5,114} = 22.9$; $P < 0.001$). Nanitic workers in manipulated control colonies produced 17% more brood than substitution colonies containing the smallest workers (head width = 0.61 mm; Fig. 1) normally found in monogynous colonies ($P < 0.01$; Duncan's multiple range test). Undisturbed control colonies produced more brood than manipulated controls (9%), but this was not quite significant ($P > 0.05$; Duncan's multiple range test). Experimental procedures might have reduced brood production because a few eggs were lost in the transfer process. Nanitic pupae eclosed at the same rates as the larger substitution pupae so differential eclosure rates were not a confounding factor.

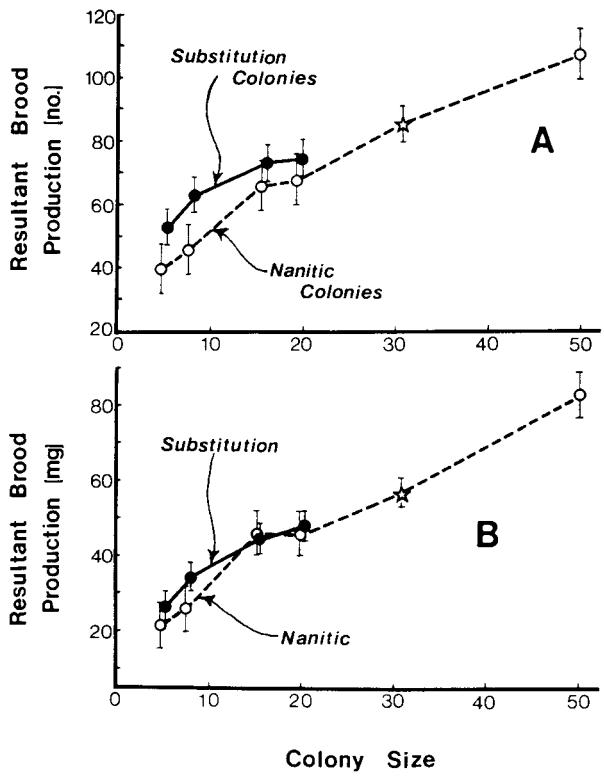

Fig. 2. (A) Resultant number of brood produced (larvae and pupae) as a function of first-generation colony size (number of pupae initially introduced). (B) Resultant weight of brood produced as a function of colony size. Nanitic colonies received nanitic pupae; substitution colonies contained 10.2 mg of progressively larger pupae transferred from mature colonies. Each point is the mean of 10 or 20 colonies (see Table 1). Error bars are pooled 95% CL for the means; ★, ☆, manipulated control colonies.

The number of workers in nanitic colonies distinctly affected the number of brood produced (Fig. 2A). Colonies that received 50 nanitic pupae produced almost three times as much brood as colonies receiving only 5. Colonies in the four substitution groups produced 10–40% more brood ($F_{1,117} = 19.0$; $P < 0.001$) than colonies containing equal numbers of nanitic workers (Fig. 2A); therefore, nanitics were actually less efficient on an individual basis. Nevertheless, the number of workers in nanitic and substitution colonies accounted for 31% of sample variation ($F_{1,117} = 62.2$; $P < 0.001$) while the difference between them accounted for only 10%. Curiously, first-generation brood production by the founding queen ($\bar{x} = 31$) was similar to that predicted for a second-generation colony containing no workers (30–40 brood; Fig. 2A).

When we analyzed the total weight of brood produced (Fig. 2B), results were similar to those just described for brood number (Fig. 2A), except that colony size accounted for 55% of sample variation ($F_{1,117} = 149.0$; $P < 0.001$), while the difference between nanitic and substitution colonies accounted for <2% ($F_{1,117} = 5.05$; $P < 0.03$ [Fig. 2B]). Larger colonies also produced larger pupae ($F_{1,117} = 98.4$; $P < 0.001$; Porter & Tschinkel 1985b). Pupae produced in substitutuion colonies were slightly larger than pupae from nanitic colonies ($F_{1,117} = 6.32$; $P < 0.02$), but this difference accounted for <2% of the explained variation. Whether brood size or number is the best predictor of colony success is somewhat problematic. Worker number was the primary factor affecting second-generation brood production (Fig. 2), but the rapid switch to near normal-sized brood in the second generation (Porter & Tschinkel 1985b) indicates that larger workers may be increasingly important in subsequent generations.

When we analyzed pupal production and larval production separately, the results were essentially the same as those described above. By the end of the experiment, queens had regained 4 mg of weight but this was not correlated with brood production or treatment. We also tried using the initial weight of the founding queen and the number of pupae produced in the first generation as covariates but neither was significant. The number of eggs in a colony at the beginning of the experiment was significantly correlated with brood production ($P < 0.01$), but this only explained an additional 3% of the variation. Finally, the differences between the first and second experimental runs were not significant ($F_{1,108} = 0.6$; not significant), so time was dropped as a blocking factor.

Colonies containing more workers produced more brood, but production per worker declined >60% as colony size increased ($F_{10,99} = 18.7$; $P < 0.001$). Furthermore, the per-worker brood production in much larger laboratory colonies containing several thousand workers (Porter & Tschinkel 1985a) was one-half to one-third the observed rate in our newly founded colonies. This negative correlation between individual output and colony size exists in many other social insect societies (Michener 1964, Brian 1965).

Discussion

Our results support the hypothesis that nanitic workers increase the fitness of incipient colonies. Manipulated control colonies with nanitic workers produced substantially more brood (17–63%) than colonies containing equal weights of progressively larger-sized workers (Fig. 1). The number of first-generation workers was the principal factor influencing second-generation brood production (Fig. 2). Nanitics are apparently beneficial because their small size allows founding queens to produce more workers, not because miniature workers are inherently more proficient at brood rearing. On the contrary, nanitics were actually somewhat less proficient at rearing brood than equal numbers of larger-sized substitution workers (Fig. 2A).

Natural selection has apparently operated at the group level to maximize the overall efficiency of founding colonies at the expense of individual

worker efficiency. Presumably, founding colonies do not produce subnanitic-sized workers because costs associated with smaller size would outweigh the benefits of further increased numbers. Unfortunately, the absence of subnanitic-sized workers precluded a test of this hypothesis. Perhaps this limitation could be overcome by using growth hormones or regulating feeding rates.

The advantage of nanitics apparently disappears rapidly as colonies grow and are able to forage during brood development. Workers in the second generation weighed almost as much as those in the first (0.60 versus 0.33 mg). This discontinuous size distribution raises the possibility that nanitic workers have been able to evolve traits somewhat independently of larger workers. Indeed, the evidence does suggest that nanitics are behaviorally and biochemically specialized (Vander Meer 1986) for colony founding.

Energetically, nanitics should be the most expensive worker size class to produce and maintain per unit weight. Extrapolating from data in our previous paper (Porter & Tschinkel 1985a), we estimated that nanitics would have 10% higher metabolic rates and 5% shorter life spans than our smallest size of substitution workers. Overall, then, nanitics would be ca. 8% more expensive to produce and maintain than an equal weight of minor workers.

After dividing brood production rates (Fig. 1) by estimated energy costs, nanitics were still ca. 9% more efficient than any other worker size class in terms of brood produced per unit of energy expended. Nevertheless, short-term growth potential is probably more important to incipient colonies than longer term energetic efficiency; this would be especially true when food resources were not limiting (Porter & Tschinkel 1985a) such as during a seasonal flush of food or the chance death of a large insect nearby.

The impact of nanitic workers on the success of their mother queen almost certainly occurs in the first few weeks of colony growth; high rates of nanitic mortality and rapidly growing colony size reduce nanitics to <10% of colony population after ca. 6 weeks. Nevertheless, their impact on colony fitness is probably not trivial. Colony founding is a period of intense selection; <5% of founding queens ever survive the early stages of colony growth (Markin et al. 1973, Morrill 1974). A trait that improves initial colony growth potential by almost 20% (Fig. 1) must be very important.

The fact that nanitic workers are so widespread, even among entirely monomorphic groups of ants, suggests that the production of miniature workers was an important stage in the evolution of claustral colony foundation (Haskins 1970). Indeed, some evidence indicates that primitive species whose queens still forage during colony foundation are less likely to produce nanitic workers (Haskins & Haskins 1955). It would be interesting to know how well the presence or absence of nanitic workers is associated with the different modes of colony foundation in ants generally.

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