

WORKER LONGEVITY IN THE FIRE ANT *SOLENOPSIS INVICTA*: ERGONOMIC CONSIDERATIONS OF CORRELATIONS BETWEEN TEMPERATURE, SIZE AND METABOLIC RATES

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Abstract—We compared long-term economic costs of producing and maintaining different size fire ant workers (*Solenopsis invicta*) at two temperatures (24 and 30°C). Energetic costs for three sizes of workers were calculated from their biomass, longevity, respiration rates, and the energy content of worker tissue. Large workers lived considerably longer than small workers (50–140%, depending on temperature) and respired more slowly per mg of tissue (40%, independent of temperature). Overall, large workers cost about 30% less in cal/mo × mg than equal weights of small workers. However, on an individual basis, large workers were still four times more expensive than small workers because of a 6-fold weight difference. These data indicate that one large worker must provide services equivalent to at least four small workers, to justify the colony's energy investment.

Key Word Index: *Solenopsis invicta*, ergonomic, caste, longevity, metabolic potential, respiration, division of labour

INTRODUCTION

Many species of ants have a polymorphic worker caste (Wilson, 1971). This variation in worker size and shape is presumed to benefit colony fitness by allowing the colony to perform certain tasks more efficiently than it could if only one size of workers were present (Oster and Wilson, 1978; Calabi, 1988; Wilson, 1985; Porter and Tschinkel, 1985; Wilson, 1983a, b). However, the ergonomic value of producing different size workers must account not just for behavioural efficiency (frequency, rate and short-term metabolic cost of behaviour), but also for the long-term economic costs of maintenance (primarily respiration) and replacement (production of new workers). Ambient temperature and animal body size can markedly affect insect longevity (McArthur and Sohal, 1982; Sohal, 1981 and 1976; Sacher, 1977), respiration (Nielsen, 1986; MacKay, 1982; Sohal, 1982; Peakin and Josens, 1978) and activity rates (Ragland and Sohal, 1973; Sohal and Buchanan, 1981; Trout and Kaplan, 1970). Respiration and activity in turn affect longevity (Sohal, 1982; Sohal and Buchanan, 1981; Ragland and Sohal, 1975; Trout and Kaplan, 1970). Our primary objective was to compare the long-term economic costs of producing and maintaining different size ant workers at two temperatures: 24 and 30°C. Specifically, we wondered whether larger workers in some way offset or amortize their larger production costs, either by lower maintenance costs and/or increased longevity? Second, do such differences vary with temperature, thus potentially giving colonies some control over their economic and ergonomic costs? We were also interested in the association between worker

longevity and metabolic rates. Thus, we measured longevity and respiration of several worker size classes of the fire ant *Solenopsis invicta* Buren. Longevity of newly eclosed (callow) workers was measured in standard queenright colonies at three temperatures (17, 24 and 30°C). Worker longevity was also measured in queenless, broodless fragments at two of those temperatures (24, 30°C). Respiration was measured at the same two temperatures. Based on these data together with body weights and caloric values, we calculated lifetime costs for different size workers at two temperatures.

MATERIALS AND METHODS

Eleven large monogyne colonies of the fire ant, *Solenopsis invicta* Buren, were collected near Tallahassee, FL (30°39'N, 84°12'W) during the late summer or fall (1982–1983). During collection time, average daily maximal and minimal mound temperatures were 17 and 45°C at 2 cm depth and 25 and 28°C at 40 cm. Newly eclosed callow workers were collected from each colony and immobilized on crushed ice. Since head width and body mass/size are closely correlated, workers were measured under an ocular micrometer. The size classes with head widths of about 0.7 ± 0.03 , 0.9 ± 0.04 and 1.3 ± 0.04 mm were selected for marking, and called small, medium and large workers. (Several colonies at 30°C also contained two intermediate size classes.) Marking consisted of tying a loop of fine wire about the petiole of each ant (Mirenda and Vinson, 1979). Small workers were marked with 1 ml (0.025 mm) nichrome wire, while medium and large workers were marked

with slightly larger sizes (Horizon sales, Inc., P.O. Box 646, Framingham, MA 01701, U.S.A.). Ants were immobilized on crushed ice for a maximum of 45 min during sorting and marking procedures. About 20 ants were marked from each size class for each colony. Each experimental colony initially contained a queen, 1.5 g live weight of workers (about 2000) and 1.0 g of brood (about 1000). Colonies were maintained in constant darkness except during observation and care. They were fed *ad libitum* crickets (*Acheta*) or tenebrionid larvae (*Zophobas*) and 1 M sucrose solution soaked into small tissue wads (Porter and Tschinkel, 1985).

Queenright colonies

Five colonies were maintained at $30 \pm 0.5^\circ\text{C}$ and six were kept at $24 \pm 0.5^\circ\text{C}$. These two temperatures were chosen because they were near the upper and lower limits of the temperature range suitable for brood production (Porter, 1988). Two additional colonies were included for comparison. They were collected in 1984 and set up at $17 \pm 2^\circ\text{C}$, however, since respiration rates were not measured at this temperature, they were not used in the analyses of energetic costs. Dead workers were collected from the refuse piles weekly and checked under a microscope for the wire marks. About 6% of marked workers died within 2 weeks of marking; these workers were assumed to have died because of handling and were therefore excluded from the analyses. Over 85% of the original 841 marked individuals were ultimately recovered from the refuse piles. Mortality rates for laboratory colonies were probably somewhat lower than those in the field because there was no predation, fewer environmental stresses, excess food, etc. However, since laboratory conditions were constant across treatments (except for temperature), the relative differences in mortality rates by treatment are both valid, and the point of interest.

By the end of the experiments, colonies at 30°C had grown to about 45 g live weight of workers and brood, while those at 24°C contained only 2–3 g. Colonies kept at 17°C gradually dwindled, since brood production completely ceased at that temperature (Porter, 1988).

Queenless colonies

Since marking ants with wire rings and recovering their remains from the refuse piles of growing colonies is very time-consuming, we also set up 10 small, queenless, broodless colony fragments, each composed wholly of 0.5 g live weight of callow workers. We wished to see how closely the mortality schedules of these workers matched those of callows living in normal, queenright colonies, and whether this experimental approach could be substituted for that of individual marking. Dead individuals in queenless colonies were also collected weekly. All were counted and their headwidths measured in a wedge micrometer (Porter, 1983); a random sample of 1470 workers were used for the final analyses. These fragment-colonies ultimately died out because no brood was present.

Respiration rates

Respiration rates were established using a modified

Scholander respirometer (see Porter and Tschinkel, 1985) on eight colonies collected in September and October. To avoid unduly stressing or disrupting the test colonies, respiration was measured on ants freshly removed from the field, rather than on laboratory colonies themselves. Workers were sieved into the three size classes on the day of collection, and held overnight in laboratory nests, with access to a 1 M sucrose solution soaked into tissue wads. On the second day, 0.1–0.2 g live weight samples of each worker size class were run at 30 and 24°C respectively ($N = 8$ for each size-temperature combination.) We used 0.1–0.2 g samples rather than individual ants, on the assumption that activity rates of ants in groups more nearly approximate those of ants in intact colonies. Also, since respiration rates may change with worker age, each sample included a full range of workers in approximately the natural age-distribution, based on careful sampling by worker colour and location from entire, intact colonies. Oxygen consumption of experimental samples was measured hourly for 3 h beginning 1 h after ants were placed into the respiration chamber. Following each run, the ants were killed, dried at 60°C and weighed. Workers averaged $53 \pm 6\%$ dry wt—percent water did not vary with size class, so all sizes are the same proportion wet to dry weight.

RESULTS

Longevity increased when either worker size increased or temperature decreased (Fig. 1). Overall, increased longevity was associated with decreased metabolic rates. These relationships substantially affected the production and maintenance costs of different size workers.

Longevity, worker size and temperature

Worker longevity increased significantly with worker size (ANOVA, $P < 0.01$; Fig. 1, Table 1). Large workers lived twice as long as small ones at 24°C , and nearly 50% longer at 30°C (Fig. 2). At 17°C the picture was not as clear, with medium workers outliving large workers, possibly because of the small number of colonies tested or confounding effect(s) due to the lack of brood production and consequent dwindling of colony size. There was also a 1 week period 49 weeks into the experiment when the temperature in this chamber rose to about 25°C .

Workers of all sizes lived substantially longer at lower temperatures (Fig. 2; ANOVA, $P < 0.01$; Table 1). An overall test of parallelism or colinearity of least squares regression lines for the three treatments showed that each differed significantly from the others ($P < 0.05$). Colonies at 30, 24 and 17°C were maintained for 23 ± 2 , 67 ± 2 and 97 weeks, respectively (5.8, 16.8 and 24.2 months): longevity declined about 80% with a temperature increase from 17 to 30°C . There was also a significant interaction between worker size and temperature, with large workers living longer than expected at 24°C compared to the other two temperatures (Fig. 2; ANOVA $P < 0.01$). [These data (Table 1, Fig. 1) are also the basis for monthly mortality calculations in Tschinkel and Porter, 1988.] For both analyses, individual variation in longevity within colonies was considerable, with

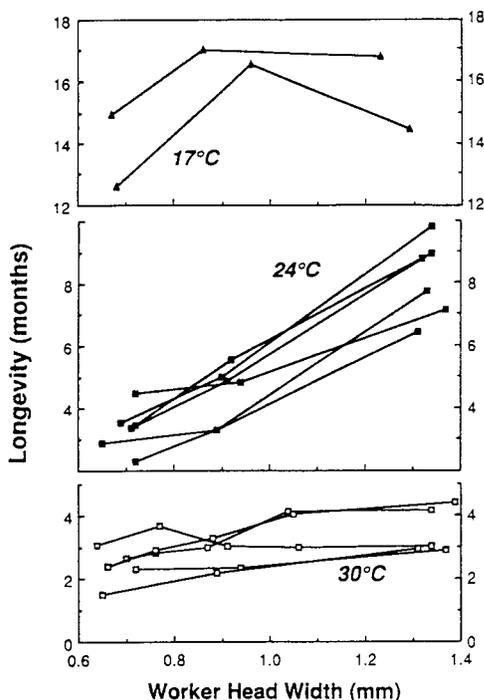


Fig. 1. Relationship between longevity (age) and worker size (head width) for the fire ant, *Solenopsis invicta*. Each line represents a different colony, and each point is the mean of 12–20 workers. Average longevity increased significantly (by ANOVA and regression, $P < 0.01$) with worker size for colonies at 24 and 30°C, but not at 17°C.

standard deviations averaging 40% of the mean (Table 1). Variation between colonies was also large, and required control during statistical analyses. Such variation gives the survivorship curves somewhat erratic shapes (Fig. 1), although the treatment averages were relatively smooth (Fig. 2). (They are probably best approximated by a Weibull distribution; Gladstein *et al.*, unpublished results.)

Worker longevity in the queenless, broodless fragments were extremely variable, suggesting a limited potential for using workers from queenless

Table 1. Mean longevity, months \pm one standard deviation, for each size class per colony, for queenright colonies only

Temperature (°C)	Colony no.	Worker size		
		Small	Medium	Large
17	12	14.9 \pm 4.7	17.0 \pm 5.4	16.8 \pm 7.5
	13	12.6 \pm 5.4	16.6 \pm 5.4	14.5 \pm 6.3
	mean	13.8 \pm 5.1	16.8 \pm 5.4	15.6 \pm 6.9
24	1	2.3 \pm 1.2	3.3 \pm 1.5	7.8 \pm 2.6
	2	3.4 \pm 1.0	4.8 \pm 1.4	8.8 \pm 1.5
	3	3.6 \pm 1.8	5.0 \pm 1.3	9.8 \pm 3.9
	4	3.5 \pm 1.6	5.6 \pm 2.0	8.8 \pm 4.0
	5	2.9 \pm 1.3	3.5 \pm 2.7	6.7 \pm 6.2
	6	4.5 \pm 1.7	4.8 \pm 2.7	7.2 \pm 5.1
mean	3.4 \pm 1.4	4.4 \pm 1.9	8.2 \pm 3.9	
30	7	2.6 \pm 0.3	3.0 \pm 1.2	4.1 \pm 1.7
	8	3.0 \pm 0.8	3.0 \pm 1.6	2.6 \pm 1.4
	9	2.4 \pm 0.6	3.3 \pm 0.8	4.4 \pm 1.5
	10	2.3 \pm 0.5	2.3 \pm 0.7	2.9 \pm 1.0
	11	1.5 \pm 0.5	2.9 \pm 0.3	3.0 \pm 1.0
	mean	2.4 \pm 0.5	2.8 \pm 0.9	3.7 \pm 1.3

Mean denotes mean per size class per temperature treatment. An overall ANOVA showed significant between-treatment differences ($P < 0.01$).

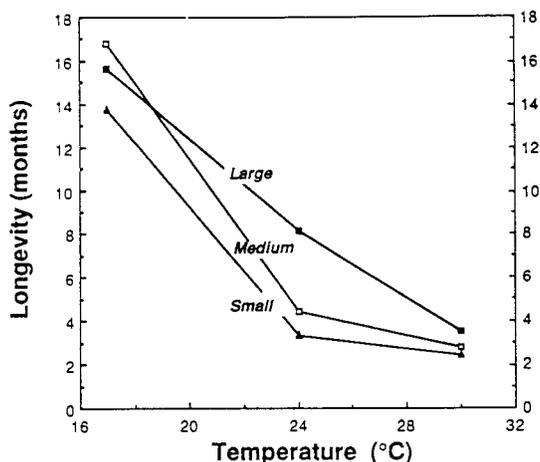


Fig. 2. Relationship between longevity of three sizes of fire ant workers (*Solenopsis invicta*) and temperature. Average longevity decreased significantly with increased temperature via ANOVA controlling for colony and worker size.

colonies to determine “normal” worker longevity. As in queenright colonies, larger workers lived significantly longer than small workers (both temperatures), and workers of a given size lived longer at lower temperatures. But the scatter was tremendous; R^2 values for regressions of longevity on worker size were about 0.02 for both temperatures. It was not clear whether the scatter was due to the absence of the queen and/or her brood. Queenless workers did live slightly longer than their queenright counterparts, although the queenless and queenright regression lines differed significantly only at 24°C.

Respiration and temperature

Respiration rates ($\mu\text{l O}_2/\text{h} \times \text{mg}$) increased with temperature, about 60% from 24 to 30°C (Fig. 3; $P < 0.01$, ANOVA with source colonies used as a randomized blocking factor). Rates at 30°C were about 25% higher than those reported by Porter and Tschinkel (1985). Variability associated with colony nutrition, season, and physiological adaptation to laboratory conditions may have contributed to this

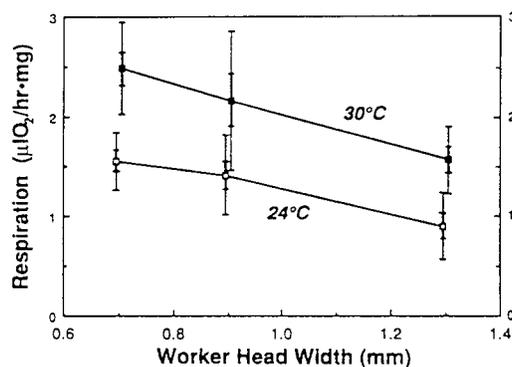


Fig. 3. Respiration rates ($\mu\text{l O}_2/\text{h} \times \text{mg dry wt}$) of different size workers at 24 and 30°C. Outer error bars are standard deviations; inner bars are standard errors of the means. Each point is the mean of several hundred workers (1–2 g) from each of 8 colonies. Respiration rate decreased significantly with both worker size and temperature ($P < 0.01$).

Table 2. Energetics of producing and maintaining different size fire ant (*Solenopsis invicta*) workers at 24 and 30°C

	Temperature (°C)	Worker size		
		Small	Medium	Large
Dry weight (mg)	—	0.36	0.68	2.46
Head width (mm)	—	0.7	0.9	1.3
Per cent* of colony by number†	—	41%	12%	2%
Per cent* by weight†	—	30%	15%	6%
Maintenance costs				
Respiration ($\mu\text{l O}_2/\text{hr} \times \text{mg}$)	24	1.55	1.41	0.90
	30	2.49	2.16	1.56
Energy units ($\text{cal}/\text{mo} \times \text{mg}$)	24	5.36	4.87	3.11
	30	8.60	7.47	5.39
Production costs				
Body tissue (cal/mg)†	—	6.66	6.90	7.09
Longevity (months)††	24	3.4	4.4	8.2
	30	2.4	2.8	3.5
Prorated costs ($\text{cal}/\text{mo} \times \text{mg}$)	24	1.96	1.56	0.86
	30	2.78	2.48	2.02
Total costs (Production + Maintenance)				
per unit weight ($\text{cal}/\text{mo} \times \text{mg}$)	24	7.32	6.43	3.97
	30	11.38	9.95	7.41
per individual ($\text{cal}/\text{mo} \times \text{ant}$)	24	2.64	4.24	9.79
	30	4.10	6.57	18.25
Lifetime costs (cal/mg)	24	24.9	28.3	32.6
	30	27.3	27.9	25.9
Metabolic potential ($\mu\text{l O}_2/\text{mg}$)	24	3.75	4.50	5.29
	30	4.27	4.32	3.93

*These values do not sum to 100% because of intermediate size classes not directly tested; †From Porter and Tschinkel (1985); ††Values for 30°C are the same as those reported by Porter and Tschinkel (1985). See results for explanations of calculations.

difference. Respiration per mg worker dry weight decreased as worker size increased, by about 40% at each temperature tested (Fig. 3, Table 2; ANOVA as above). This decrease was almost the same as found previously (Porter and Tschinkel, 1985). Respiration per individual, however, still increased significantly with worker size because large workers were six times heavier than small workers (Table 2).

Energy costs. The energetic costs of different size workers can be separated into costs associated with worker maintenance and production (see Table 2). Maintenance costs were estimated by converting worker respiration rates into units of energy at the rate of 4.8 cal/ml O_2 consumed assuming a mixed diet (Elliot and Davison, 1975). Thus, respiration in $\mu\text{l O}_2/\text{h} \times \text{mg}$ was multiplied by 0.0048 cal/ $\mu\text{l O}_2$ times 24 h/day times 30 days/mo, for energy units in $\text{cal}/\text{mo} \times \text{mg}$. Production costs (less larval respiration) were estimated by dividing the per mg energy content of the different size workers by their average longevity; this procedure prorated or distributed production costs over the entire life of the ant. Larval respiration was not determined for the different size workers, but since this cost accounts for only about 15% of total costs (Porter and Tschinkel, 1985), even fairly large differences in larval respiration would affect total costs of the different size workers by only a few per cent. Total estimated costs of the different size workers per month were obtained by summing production and maintenance costs. Note the difference between costs per "individual" and per "unit weight", and especially how per individual costs were calculated. Lifetime costs were calculated by multiplying total costs per month by longevity in months. Metabolic potentials per unit weight of workers were calculated by multiplying respiration rates by longevity.

At both temperatures tested, absolute maintenance costs of a given weight (not individuals) of large workers was about 40% less than that of an equal weight of small workers (Table 2), because large workers have lower metabolic and thus lower energy costs (Table 2).

Production costs include the energy incorporated into worker tissue and to a lesser degree larval respiration. Large worker bodies have a slightly higher caloric content (9%) than those of small workers (Porter and Tschinkel, 1985). Therefore, the absolute production cost of a given weight of large workers was more than that of an equal weight of small workers (Table 2). But because longevity of large workers was so much greater, their prorated production costs were 25% less at 30°C and 55% less at 24°C (Fig. 4).

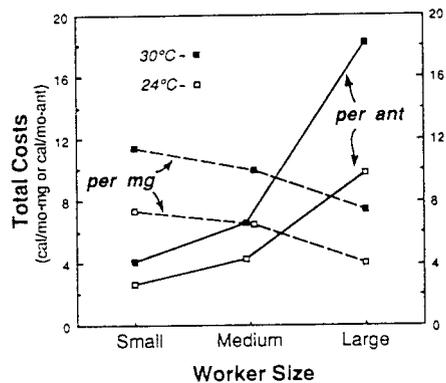


Fig. 4. Total costs per individual worker (—) and per mg of worker tissue (---), for three sizes of workers at two temperatures (24 and 30°C).

Since maintenance and relative production costs both decrease as worker size increases, their sum, or total costs, also decreases with size per unit weight, at both temperatures. However, because weight increases with worker size faster than costs decrease, total cost per individual increases as worker size increases, at both temperatures (Table 2, Fig. 4).

Finally, effects of temperature and worker size on lifetime costs and on metabolic potential were mixed. On an individual basis, large workers were significantly more costly, although not as much so as expected based on their weight. But on a unit weight basis, at 30°C workers of all sizes had approximately equal overall lifetime costs per mg tissue, while at 24°C costs increased with size.

DISCUSSION

Longevity in fire ants was inversely associated with temperature and worker size; in short, as metabolic rates decreased longevity increased. However, the consequences of those associations differ markedly when considered per mg worker tissue or per individual worker, and thus have different economic and ergonomic implications. We consider each association in the context of related work, and suggest some general conclusions.

Longevity and metabolism

Fire ant longevity was closely associated with metabolic rates. This was reflected by the fact that large workers which have lower metabolic rates (Fig. 3) live longer than small workers (Fig. 2). Similarly, the cooler the temperature, the lower an ant's metabolic rate and the longer it lives.

Thermal effects. Temperature effects on longevity of other insects are largely, but not only, due to effects of activity. As temperature increases, longevity (both age-independent vulnerability to aging and aging rate) decreases (Sohal, 1975, 1985, 1986; Grigliati, 1985; McArthur and Sohal, 1982; Sacher, 1977; Lamb, 1968). Effects of temperature are less marked when activity is restricted (Ragland and Sohal, 1973, 1975). Activity also acts independently of temperature: generally, at fixed temperatures longevity decreases as activity increases (Sohal, 1982; Sohal and Buchanan, 1981; Ragland and Sohal, 1973, 1975; Trout and Kaplan, 1970). Presumably these effects of temperature, activity, and their interaction are consequences of the postmitotic nature of insects. Unlike in vertebrates, in which physical activity in the form of moderate stress can postpone senescence via morphological and physiological changes, in postmitotic cells such changes are limited or impossible, so physical activity acts as a stress factor and tends to shorten lifespan (Collatz, 1986; Sohal, 1976).

Although we did not distinguish effects of temperature from activity, our great increase in worker longevity at cooler temperatures, especially at 17°C, were presumably associated with lower activity rates as well as with lower basal metabolic rates. For colonies at 17°C an additional factor was lack of brood to tend, which decreased activity further. Enhancement of longevity due to relative inactivity is also suggested by the slightly greater average longevities of workers in queenless, broodless, fragments at

both temperatures. Certainly it seems that colonies could behaviourally regulate worker longevity. For example, workers could increase longevity by reducing activity and/or choosing cooler temperatures. They do enhance brood development by thermoregulatory movement within the mound. And colder seasonal temperatures must extend worker longevities through "winters".

Effects of worker size. Since metabolic rates (oxygen consumption) vary with temperature/activity (above), it is not surprising that longevity increases as temperature and metabolic rate decrease. Similarly, at a given temperature, the larger an ant, the lower its metabolic rate and the longer it lives. [Although metabolic rate does not correspond strictly to ambient temperature, since insects (Precht, 1958) and other poikilotherms (Newell, 1966) can show compensatory metabolic responses to temperature.] This relationship between worker body size and longevity seems to hold across ant species as well as within, with larger species generally outliving small ones (Haskins and Haskins, 1980; Nielsen, 1972; Brian, 1972; Peacock and Baxter, 1950). Studies not directly measuring longevity still show consistent increases in relative oxygen consumption per individual with increased size, both within species (Elzen, 1986; MacKay, 1982; Jensen, 1978; Jensen and Nielsen, 1975) and between species (Nielsen, 1986; MacKay, 1982). There may be variation by subfamilies as well: at a given weight, formicines consume proportionately more oxygen than do myrmicines (Nielsen, 1986; MacKay, 1982).

Metabolism and aging

The "rate of living" hypothesis implies that metabolic rate and aging are linked; specifically, that a given amount of energy will be expended per unit body weight during the lifetime of any particular genotypic group under specific environmental conditions (e.g. Sohal, 1986). In several insect species tested at different temperatures, their metabolic potentials were similar across temperatures, despite longevity differences due to temperature (McArthur and Sohal, 1982; Byzova, 1978; Miquel *et al.*, 1976; Trout and Kaplan, 1970). (An exception is *Musca domestica* in which metabolic potential at 18°C was 12% greater than at 25°C; Sohal, 1982.)

Our data for fire ants suggest an approximate average per mg cost—a worker can consume only about 4.2 ml O₂/mg dry weight before the molecular machinery wears out and the ant dies (Table 2). However, while this may be true in a general sense, our estimates of metabolism and longevity were not sufficiently precise either to support the rate of living hypothesis or to exclude other possibilities. At 30°C, metabolic potential (average total lifetime oxygen consumed) appears to be independent of body size—large ants had about the same potential as small ants. At 24°C, cost increased with worker size, but the average was still about the same as at 30°C (4.2 mg ^{ml O₂/mg}). In other words, changing temperature apparently did not have much effect on metabolic potential. Larger workers at 24°C did have a higher lifetime cost than small workers, but the variability in estimates of respiration and longevity were such that this difference as well as the lack of difference at 30°C

may fall within the range of experimental error. It would be interesting to calculate the metabolic potential of fire ant queens, which are reported to live about 6 yr (Tschinkel, 1987).

Total lifetime costs showed the same pattern as metabolic potential, primarily because respiration accounts for about 70% of these costs.

Ergonomic and economic efficiencies

On a per individual basis, the economic (production plus maintenance) costs of *Solenopsis invicta* large workers were about four times those of small workers (Fig. 4, Table 2). While this was a considerable improvement in cost over the 6-fold difference expected on the basis of worker live weight alone (Table 2), large workers were still substantially more costly than small workers. It has been suggested that in some ant species, large workers and small workers have equal maintenance costs (Oster and Wilson, 1978); however, this was based on erroneous data (Golley and Gentry, 1964; see Porter, 1986). Economic data imply that one large worker must provide service to the colony equivalent to that of four small workers. However, with respect to amortizing costs of large workers, the per worker economic costs are only part of the picture. The largest *S. invicta* workers constitute on average only 2% by number of individuals and 6% by weight of a mature colony (or 6 and 18% respectively, if the next size class is also included; Table 2; Porter and Tschinkel, 1985; also see Tschinkel, 1988), so their absolute economic cost to the colony is much less than that invested in small and medium workers. More important is their "behavioural" value. Unfortunately, their role in the colony is unclear, making it difficult to measure their behavioural value and translate it into ergonomic units (Oster and Wilson, 1978). They preferentially carry larger particles of food and debris (Wilson, 1978); they can improve brood production if food is limited (Porter and Tschinkel, 1985); and they can perform other of the quotidian tasks of the colony (Mirenda and Vinson, 1981; Wilson, 1978), although they are disproportionately likely to be inactive "reserves" (Mirenda and Vinson, 1981; p. 418). Majors also forage only during the last 25% of their lives, vs the entire latter half of their lives as for the medium and small workers (Mirenda and Vinson, 1981). Since foragers suffer disproportionately high mortality (Schmid-Hempel and Schmid-Hempel, 1984; Porter and Jorgensen, 1981; Shaffer and Whitford, 1981), such delayed onset of foraging suggests some "protecting" of large workers; or at least that foraging is not their primary task. Indeed, this general pattern of *S. invicta* large worker behaviours—performing various behaviours but at lower frequencies than other size workers, and with no obvious caste-specific behaviour(s)—suggests that their primary behaviour has yet to be seen. The data argue for some ergonomic value not related to the daily round, at least not as seen in the laboratory conditions under which we know this species. It could be defense, as for large workers in many size-variable and dimorphic species (Calabi, 1988; Oster and Wilson, 1978). Perhaps *S. invicta* shows enemy specification (as e.g. *Pheidole dentata*; Carlin and Johnston, 1984), against some enemy restricted to the

Matto Grosso. Another possibility is that major workers are important in transporting the large sexual brood in and out of the mound during thermoregulation. Whatever the case, the primary task of large workers should be selectively important. Presumably the proportion of large workers in mature colonies of any polymorphic ant species represents an average selective trade-off between the proportionately greater expense of large workers, and their behavioural contributions to colony fitness. Our data quantify the greater expense of large workers, but only direct field observations will provide estimates of their behavioural value.

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