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Fire ant thermal preferences: behavioral control of growth and metabolism

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Summary. Thermal preferences of well-fed and food-limited fire ant colonies (*Solenopsis invicta*) were studied in relation to colony growth and metabolic costs. The growth curve for well-fed colonies was strongly skewed toward warmer temperatures with maximal growth occurring near 32° C (Fig. 2A). The growth curve for food-limited colonies was skewed toward cooler temperatures with maximal colony size occurring around 25° C (Fig. 2B). Food-limited colonies apparently grew larger at cooler temperatures because metabolic costs of workers were reduced. A series of binary choice tests confirmed three predictions concerning fire ant thermal preferences (Figs. 3–4). First, well-fed colonies preferred brood temperatures very near the optimum for colony growth (31° C versus 32° C). Colonies were also able to select appropriate suboptimal growth temperatures when the optimal range was unavailable. Secondly, as predicted, a large percentage of colony workers (~30% in well-fed colonies) consistently chose cooler temperatures than those selected for the brood. This strategy probably increases longevity of workers not directly associated with brood care. Thirdly, food-limited colonies preferred cooler temperatures than well-fed colonies. Metabolic costs of food-limited colonies were reduced by approximately 7% because of (1) slightly cooler brood temperatures (30° C versus 31° C) and because (2) an additional 20–30% of the workers selected cooler temperatures. The addition of excess food reversed food-limited thermal preferences within 12 h for the brood (Fig. 5) and several days for the workers. Contrary to expectations, thermal preferences for brood in food-limited colonies did not match the food-limited growth curve, perhaps because fire ant colonies can choose to rear brood at warm temperatures while maintaining accumulated colony biomass at cooler temperatures.

Introduction

Temperature is a central factor in the life of ant colonies. As with most poikilotherms, the metabolic rates of ants are highly temperature dependent. Respiration rates approximately double with every 10-degree increase in temperature (Peakin and Josens 1978; Calabi and Porter 1989). Increased respiratory rates are, in turn, closely associated with increased rates of brood development (Porter 1988; Schmidt 1968) and reduced worker longevity (Calabi and Porter 1989). Temperature also has important effects on colony activity. For example, foraging is often inhibited or preduced at temperatures above or below certain ranges (Curtis 1985; Porter and Tschinkel 1987; Rogers 1974). Even within preferred ranges, rates of forager transit are proportional to temperature (O'Neill and Kemp 1990; Rissing 1982).

While temperature is the primary factor controlling colony activity and metabolism, ants not are completely subject to its vicissitudes. In fact, many species are very effective thermoregulators. A few ants are endothermic like honeybees; that is, they regulate colony temperatures with internally produced metabolic heat (Franks 1989; Horstmann 1990; Rosengren et al. 1987). Most ants, however, are strictly exothermic. These species thermoregulate by behaviorally tracking fluctuating temperatures in and around their nests. Some species augment their behavioral capabilities by constructing mounds which function as solar collecting devices (Seeley and Heinrich 1981). A few ants may also use the respiratory heat of decaying nest material (Coenen-Staß et al. 1980; Coenen-Staß 1988) or symbiotic fungus (*Atta*, unpub. data).

The fire ant, *Solenopsis invicta* Buren, thermoregulates by moving up and down in a labyrinth of earthen chambers as the mound warms or cools. On a spring morning when surface temperatures are cold, most of the colony is 40–50 cm under the mound. By midday, most of the colony moves up into the mound where temperatures on sunny days are often 10–20° C warmer than the surrounding soil. High mound temperatures

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in the afternoon or cool temperatures in the evening eventually drive the colony back down into the soil column. Each morning, the thermoregulatory cycle begins anew as mound temperatures rise above those in the surrounding soil.

Thermal preferences are a key element in the thermoregulatory behavior of ants. Colonies of several species appear to select temperatures affording maximal brood production (Brian 1973; Roces and Núñez 1989). Colony members may also have differing thermal preferences. Larvae are sometimes kept at cooler temperatures than pupae (Coenen-Staß 1985; Kipyatkov and Shenderova 1986; Roces and Núñez 1989). Also, inactive workers (Ceusters 1977) or queens (Kipyatkov and Shenderova 1986) may prefer cooler temperatures than their active counterparts. Season and prior acclimation temperature appear to have little effect on the thermal preferences of ants (Coenen-Staß 1987; Cokendolpher and Francke 1985), but low humidity can reduce thermal preferences substantially (Cokendolpher and Francke 1985; Kneitz 1966). Roces and Núñez (1989) reported that feeding levels affected thermal preferences for *Camponotus* brood with preferences varying according to a circadian rhythm.

This study investigated thermal preferences of the fire ant, *S. invicta*, as they relate to colony growth and metabolic costs. Three hypotheses were tested. The first was that fire ant colonies actively select temperatures which maximize colony growth. The second hypothesis was that, on average, workers select cooler temperatures than those they select for the brood. This disparity should occur because warmer temperatures are a net benefit for brood production (Porter 1988), but a net cost for workers since increased temperatures increase worker respiration and substantially reduce longevity (Calabi and Porter 1989). The third hypothesis was that food availability affects thermal preferences. When food is abundant, colonies should choose warm temperatures that maximize production. However, when food is limited, colonies should choose cooler temperatures which reduce worker respiration and replacement costs allowing the resulting energetic savings to be invested in maintaining larger colonies.

Materials and methods

Effects of temperature on colony growth and size. The effects of temperature on the growth of well-fed and food-limited colonies were studied so that thermal preferences could be interpreted in terms of the physiological consequences. Test colonies were reared in experimental chambers maintained at one of five temperatures (±0.5° C): 25, 28, 30, 32, 35° C; see Porter (1988) for details of handling and feeding procedures.

Twenty well-fed colonies with a mature monogyne queen, 1.0 g of workers, and 0.5 g of brood were divided equally among the five experimental temperatures. Excess quantities of crickets (*Acheta domestica*) and sugar water (1 M) were provided daily. Petri dish nests (15 cm) were added as needed so that excess nest space was always available. Worker production for these 20 colonies was reported by Porter (1988).

Thirty food-limited colonies were allocated equally among the five experimental temperatures. Each colony initially contained a mature monogyne queen, 1.5 g of workers and 0.5 g of brood. Each day, these colonies received 1/2 of a cricket and 0.2 ml of 1 M sugar water. Nest tubes (13 by 100 mm) were added as necessary to ensure excess nesting space. After 2 months, both well-fed and food-limited colonies were separated into workers and brood and then counted and weighed.

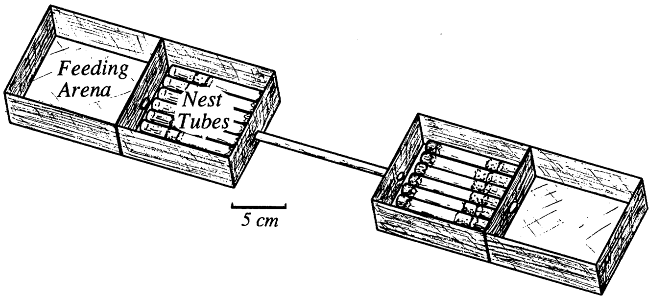


Fig. 1. Symmetrical design of nests used in binary temperature choice tests. Half of each nest was in one incubator and half was in the other. Colony members transferred back and forth between sides depending on incubator temperatures

Binary temperature choice tests. In order to determine fire ant thermal preferences, ten colonies were given a series of binary choices. This was accomplished by placing two incubators side by side. Temperatures in the incubators were changed every 12 h permitting colonies to make two choices each day. After each 12-h cycle, we estimated the percentage of colony workers and brood in each incubator. Fifteen different temperature combinations were compared in forty 12-h cycles over a 22-day period. Each temperature combination was repeated two or three times except 30 and 32° C, which was repeated nine times, and the combinations 30 and 36° C and 24 and 38° C, which were tried only once.

Experimental nests were constructed so that half of each nest was in one incubator and half was in the other (Fig. 1). Each half was connected to the other by a Tygon tube inserted through holes drilled in the walls of the incubators. The two central boxes each contained eight nest tubes (13 by 100 mm). Nest tubes were about one-third filled with water which was held in place by a cotton plug. Each tube had an aluminum foil cap with a ca. 3-mm puncture, allowing entrance to the area between the foil and the cotton. This arrangement kept nest humidity high and ensured constant availability of water. A small fan in each incubator circulated air and kept temperatures uniform.

Colonies were fed crickets and 1 M sugar water daily. Food was distributed equally between the two feeding boxes so that any feeding effects were symmetrical to the temperatures being tested. In order to test the effect of food availability on temperature preferences, five colonies received all the food they could eat, while the other five only received half a cricket and 0.2 ml of sugar water per day. Workers and brood were periodically removed from the well-fed colonies so that colonies in both feeding treatments contained 10000–15000 workers and brood.

Temperature preference data were analyzed with a four-way ANOVA. The four main factors were: "temperature" (15 paired combinations), "feeding" (well-fed or food-limited), "life-stage" (workers or brood), and "colony" (ten test colonies). The first three factors were fixed and fully crossed. The fourth factor was a randomized block with five test colonies nested in each level of "feeding"; this provided the necessary replication. Multiple runs of the same temperature combinations were averaged across test colonies. Percent preference data were arcsine-square root transformed to normalize their distribution, although this did not change which factors were significant. "Temperature" and "life-stage" were tested by their respective interactions with "colony". "Feeding" was tested directly by "colony". "Colony" and its interactions were not testable in this design.

In order to determine how rapidly colonies switched between well-fed and food-limited behavior, the incubators were alternated between 30° C and 32° C every 12 h. After 2 days, two food-limited colonies were switched to excess food and two excess food colonies were switched to limited food.

Results

Effects of temperature on colony growth and size

Well-fed colonies. Colonies with excess food grew very rapidly (Fig. 2A). The window or range of growth was between about 22° C and 36° C, with maximal growth near 32° C. Colonies at 32° C grew more than 40-fold in 2 months. Means for total colony weight and worker weight (Fig. 2A) were all significantly different from adjacent means except the 28° C and 30° C comparisons (1-way ANOVA; Scheffé's *S* test, $P < 0.05$). Between 28° C and 35° C, the ratio of workers to brood gradually increased (Fig. 2A). This pattern seems to indicate that relatively more workers are needed to rear brood at higher temperatures; however, this conclusion is confounded because larger colonies typically have lower brood production rates than smaller ones (Porter and Tschinkel 1985).

As expected, the growth curve was strongly skewed to the right. Growth at cooler temperatures was limited by slow developmental rates, while growth at higher temperatures was probably reduced by metabolic stress (Porter 1988). Fire ant colonies typically pile brood in clusters, but at 35° C colonies usually dispersed the brood around the nest chamber. This heat-stress behavior might help dissipate metabolic heat, although we were unable to detect heat accumulation in brood piles at cooler temperatures.

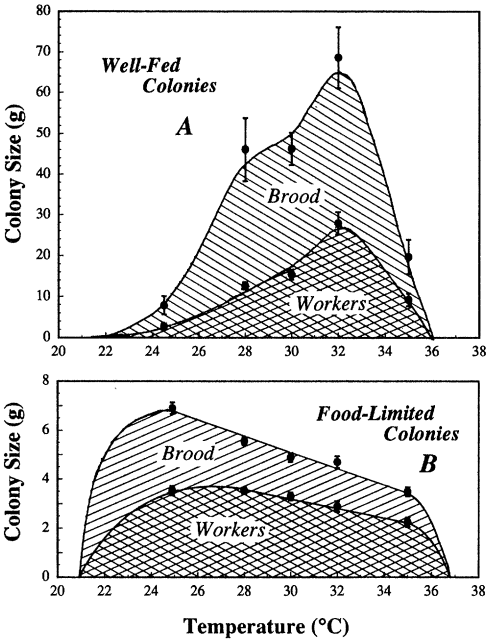


Fig. 2 A, B. Effects of temperature on the size of **A** well-fed colonies and **B** food-limited colonies after 2 months (note difference in *scales* for colony size). Each figure shows total colony weight separated into worker and brood portions. *Lines* were fitted by eye and *means* are shown ± 1 SE

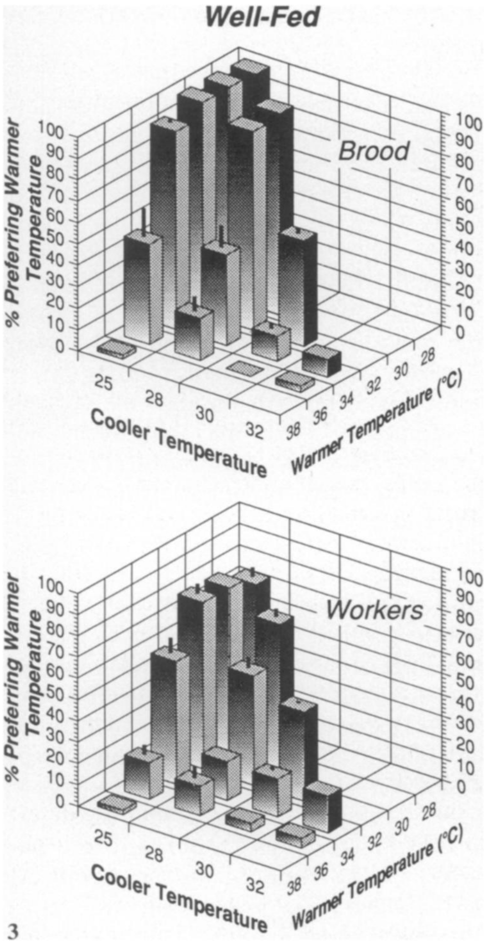
Food-limited colonies. The growth pattern of food-limited colonies differed considerably from that of well-fed colonies (Fig. 2). First, food-limited colonies apparently ceased growing after several weeks when they reached total weights of only 3–7 g. Secondly, as expected, food-limited colonies grew larger at cooler temperatures (linear regression; total weight, $r^2 = 0.84$, $P < 0.0001$; worker weight, $r^2 = 0.51$, $P < 0.0001$). Ratios of brood to workers were fairly constant between 28° C and 35° C, and consistently lower than corresponding ratios for well-fed colonies. The relative number of workers in food-limited colonies at 25° C may have been depressed slightly because this cool developmental temperature prevented colonies from attaining maximal worker populations by the end of the 2-month study period.

Binary temperature choice tests

Analyses of thermal preferences (Figs. 3 and 4) revealed significant differences in the following statistical factors: "feeding" ($P = 0.0015$), "temperature" ($P < 0.0001$) and "life-stage" ($P < 0.0001$). All interactions of these factors were significant ($P < 0.0001$) except "life-stage × feeding" ($P = 0.43$). "Temperature" was the most important factor in that the different temperature alternatives explained 75% of the variation in the ANOVA; this was because the general patterns of preferences in the four graphs in Figs. 3 and 4 were all quite similar. The "life-stage × temperature" interaction accounted for an additional 7.9% of the variation. The main factors "feeding" and "life-stage" accounted for 5.3% and 3.8%, respectively. The remaining 8.1% of the variation was distributed among "colony" and the remaining interaction terms.

In spite of the arcsine transformation, the variance of thermal preferences in some cells was probably not equal because certain temperature alternatives were avoided entirely by workers and/or brood (Figs. 3 and 4). In order to be sure that unequal variance did not confound the conclusions, the analysis was repeated after deleting temperature alternatives that resulted in a 0% preference for one alternative or the other (i.e. 24 and 30° C, 24 and 38° C, 30 and 36° C, 32 and 34° C, and 32 and 36° C). Cell variances in the resulting dataset were not significantly different (Hartley's test; F-max = 55.3; $df = 40{,}4$; $P > 0.05$). Most importantly, the ANOVA results were almost identical to those described in the preceding paragraph. Several additional ANOVAs were also conducted in which we deleted temperature alternatives that resulted in low or very low thermal preferences. Results of these analyses were very similar to those just described except that "feeding" was slightly more significant and "temperature" accounted for less of the total variance, as expected.

Well-fed colonies. The data for brood in well-fed colonies indicate either a preferred temperature of 31° C or a



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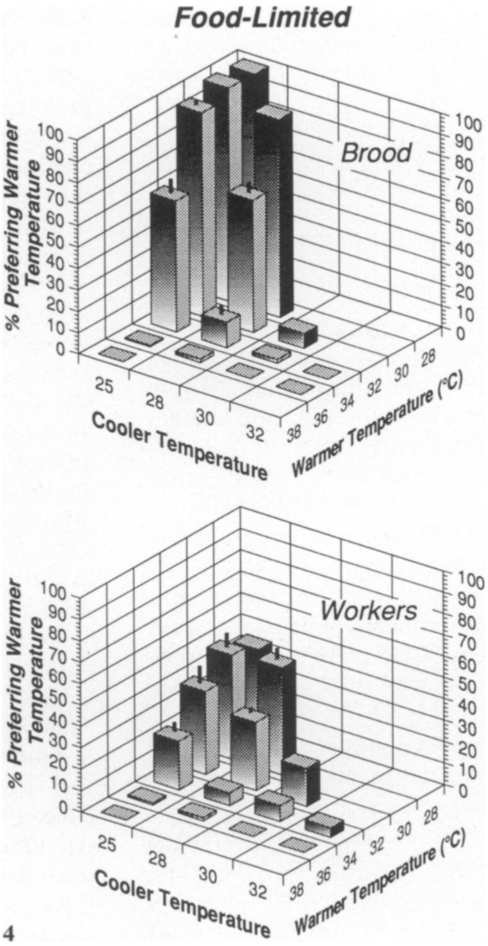

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Fig. 3. Thermal preferences of well-fed fire ant brood (*top left*) and workers (*bottom left*) in binary choice tests. Cells on the *horizontal plane* of each graph are formed by a matrix of warmer and cooler temperature alternatives. The height of the *bar* in each cell illustrates the percentage of individuals preferring the warmer of two alternatives. *Standard errors* are indicated for each bar when large enough to be seen ($n = 5$ colonies/bar)

Fig. 4. Thermal preferences of food-limited fire ant brood (*top right*) and workers (*bottom right*) in binary choice tests. See Fig. 3 for further explanation

preferred range of 30–32° C. This preference was determined by comparing sequentially higher pairs of temperature alternatives (Fig. 3 top; see diagonal row of bars with black side panels). At warmer alternatives of 30° C or less (i.e. 25 and 28° C, and 28 and 30° C) almost all brood were placed at the warmer temperature. At 30 and 32° C combination, the brood were nearly equally distributed between both temperatures, but at the 32 and 34° C combination almost all brood were placed at the cooler temperature. Larvae and pupae were not noticeably segregated between the different alternatives. Eggs and colony queens were not seen frequently enough to determine their thermal preferences. We have assumed, for the purpose of discussion, that workers select temperatures for the brood, but the brood may not be entirely passive; that is, they might communicate thermal preferences to the workers before or during transport.

The distribution of well-fed workers among the temperature alternatives (Fig. 3, bottom) was similar to the pattern observed for the brood (top). The major difference was that a substantial fraction of workers (20–45%) chose the cooler temperature, even when 90–100% of brood was at the higher temperature; this difference accounts for the significance of "life-stage" in the statistical analysis. The exception to this pattern was that slightly more workers (≤5% more) occasionally chose the higher temperature when the percentage of brood at that temperature was very low (i.e. ≤12%). This difference accounts for the significance of "life-stage × temperature" in the analysis. In other words, workers chose both warmer and cooler temperatures than those selected for the brood, depending on the particular alternatives; however, the general tendency was to choose cooler temperatures.

Careful inspection of Fig. 3 reveals that fire ants can adjust thermal preferences according to the options available. For example, 34° C was avoided by about 90% of the brood if the alternative was the preferred 30° C or 32° C. However, 40% or 90% of the brood was placed at 34° C when the alternative was 28° C or 25° C, respectively. Similarly, 36° C was avoided by 97–100% of the brood if 30° C or 32° C were the options, but 20% or 47% of brood was placed at 36° C if the cooler options were 28° C or 25° C, respectively. In short, workers would place brood at increasingly higher temperatures if forced to choose between increasingly cooler alternatives. Temperatures of 38° C were avoided by almost all colony members even when the alternative was 25° C.

Food-limited colonies. Food-limited colonies (Fig. 4) preferred slightly cooler temepratures than well-fed colonies (Fig. 3) making "feeding" a significant factor. The preferred temperature for food-limited brood was about 30° C compared to about 31° C for well-fed colonies.

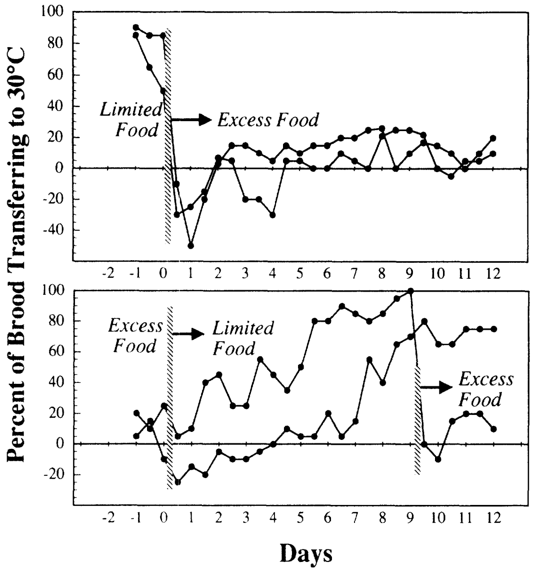

Fig. 5. Temporal change in thermal preferences of two fire ant colonies (*Solenopsis invicta*) switched from limited to excess food (*top*) and two colonies switched from excess to limited food (*bottom*). One colony in the bottom figure was switched back to excess food on day 9. Each *line* plots the percent of brood transferred from 32° C to 30° C with each 12-h switch in chamber temperature (a *negative value* indicates a net transfer to 32° C)

Food-limited colonies actively avoided placing brood at 32° C while well-fed colonies showed no clear preference for either 30° C or 32° C. Differences like this made the "feeding × temperature" interaction term significant. Food-limited colonies, like well-fed colonies, also adjusted thermal preferences according to the options available by placing brood at increasingly higher temperatures when faced with increasingly cooler options. Acceptable temperatures for food-limited colonies were about 2° C cooler than for well-fed colonies (compare well-fed brood percentages at the warmer temperatures of 36° C and 34° C with food-limited percentages at 34° C and 32° C, Figs. 3 and 4).

Workers in food-limited colonies also preferred cooler temperatures than their well-fed counterparts. In fact, the majority of food-limited workers were always found at the cooler temperature, even when a large majority of brood were found at the warmer temperature.

Switching between well-fed and food-limited behavior. In food-limited colonies, about 90% of the brood was routinely transferred from the warmer chamber (32°) to the cooler chamber (30° C) with each temperature alternation (Figs. 4 and 5). By contrast, brood in well-fed colonies were usually equally distributed between 30 and 32° C (Figs. 3 and 5). Similar differences can be found among other temperature combinations. Adding excess food to food-limited colonies caused a switch to well-fed brood preferences in less than 12 h (Fig. 5, top). By contrast, the switch from well-fed to food-limited brood preferences was much more gradual, generally requiring one or two weeks to reach maximal levels of brood transfer (Fig. 5, bottom). Percentages of workers transferring between temperatures were similar to that illustrated for the brood (Fig. 5) except workers never showed a negative transfer rate (net transfer to 32° C) and workers in food-limited colonies required 2–3 days rather than 12 h before they assumed the transfer pattern associated with well-fed colonies.

Discussion

Thermal preferences

The preferred temperature range for brood in *S. invicta* colonies was between 30° C and 32° C with a median of 31° C (Fig. 3). This median is 2.7° C warmer than that reported by Cokendolpher and Francke (1985), probably because we used intact colonies whereas Cokendolpher and Francke used isolated fragments consisting of 20–50 workers and some brood. Another important difference was that we monitored a colony's response to thermal change within their nest, whereas Cokendolpher and Francke monitored clustering behavior on a static and unfamiliar thermal gradient.

A preference of 31° C for brood is similar to, but slightly higher than, preferences reported for other ants: *Componotus mus*, 27.5–30.8° C (Roces and Núñez 1989); *Eciton burchelli*, 28.5° C (Franks 1989); *Myrmica rubra*, 21° C (Brian 1973); *Formica polyctena*, 23–29° C (Coenen-Staß 1987; Ceusters 1977; Kipyatkov and Shenderova 1986; Kneitz 1966). Other social insects also prefer brood temperatures of about 30° C including bumblebees (30–32° C, Heinrich 1973), vespid wasps (29–31° C, Gibo et al. 1974; Himmer 1931) and *Macrotermes* termites (30° C, Seeley and Heinrich 1981). Among social insects, honeybees appear to have the highest preferred temperature for brood rearing at 35° C (Fahrenholz et al. 1989).

S. invicta colonies easily discriminated between temperature differences of 2° C; however, they are probably capable of much finer discrimination, perhaps as fine as the 0.25° C perception reported for honey bees (Winston 1987). Unlike many solitary insects, social insects generally have narrow thermal preferences for juvenile stages, possibly because feeding requirements do not interfere with thermal options. The preferred range for *S. invicta* brood was ≤2° C (i.e. 30–32° C); this compares to ranges of 6–12° C for solitary insects like house flies, roaches and grasshoppers (Fraenkel and Gunn 1961; Cornwell 1968; Uvarov 1977).

Thermal preferences and optimal growth

As hypothesized, fire ants do prefer temperatures that allow optimal or near optimal colony growth. The preferred temperature for brood in well-fed colonies (~ 31° C, Fig. 3) was about 1° C less than the temperature associated with maximal colony growth (~32° C, Fig. 2). Assuming thermal preferences for brood could be anywhere within the range of temperatures suitable for growth, 22–36° C (Fig. 2), these data indicate that evolutionary forces have optimized thermal preferences within about 7% of the maximum for colony growth. By way of comparison, Wilson (1980) reported that the size of *Atta* workers engaged in leaf-cutting was within about 8% of a theoretical maximum, a precision that he considered in accord with the concept of evolutionary optimization. The 7% difference in this study may reflect either natural imprecision or experimental imprecision; finer discrimination would require temperature increments of one degree or less for both growth and preference studies.

Thermal preferences of other poikilotherms are presumably closely associated with temperatures that permit optimal growth. Unfortunately, relatively few studies have adequately tested this hypothesis. In an especially thorough study, Brett (1971) showed that thermal preferences of sockeye salmon almost exactly matched the optimal growth temperature (15° C) for well-fed individuals. The ants *Campanotus mus* and *Myrmica rubra* apparently choose thermal optima in terms of pupal production and sexual differentiation, respectively (Brian 1973; Roces and Núñez 1989). The red wood ant, *Formica polyctena*, prefers 29° C for pupae (Coenen-Staß 1985) a temperature that is close to the developmental optimum of 30.5° C (Schmidt 1968). Garter snakes prefer temperatures (29–30° C) which maximize locomotion, tongue-flicking and digestion (Stevenson et al. 1985), but data on long-term effects of temperature on growth are unavailable. Honey bees maintain nest temperatures (35° C) which are close to the temperature at which brood develop best (Jay 1963) – brood reared much above 36° C generally have reduced survival while those reared at temperatures below 32° C have increased rates of wing deformity (Seeley and Heinrich 1981). These studies indicate that thermal preferences and optimal growth temperatures are correlated; however, the precision of this association has not been adequately determined in most cases. This is partly because thermal preferences in some species are so broad that comparisons would be meaningless (Fraenkel and Gunn 1961). In other cases, testing is complicated because thermal preferences vary according to the age (Uvarov 1977) or physiological state of an organism (Lazzari 1991). The major problem, however, is that most researchers simply have not evaluated thermal preferences in terms of their physiological effects on growth or reproduction.

Suboptimal temperature alternatives

Fire ant thermoregulation appears to be more sophisticated than a simple behavioral switch or thermostat where all warmer alternatives > 32° C are avoided. Binary choice tests showed that *S. invicta* colonies would choose increasingly higher temperatures if forced to choose between increasingly cooler alternatives. Furthermore, choices among suboptimal alternatives generally matched the growth curve for well-fed colonies (Fig. 2A). For example, growth at 34° C is much higher than it is at 25° C – as expected, 34° C was strongly preferred over 25° C (Fig. 3). Similarly, growth at 28° C was slightly greater than at 34° C; as might have been predicted, slightly more brood were placed at 28° C than at 34° C. Preferences for 36° C were higher than expected with the alternative of 25° C, but this could be because the growth curve actually tails off slightly above 36° C rather than ending abruptly as extrapolated (Fig. 2A). As expected, very few ants were found at 38° C when the alternative was 25° C. Temperatures above 36° C should be consistently avoided by colonies because such temperatures would necessitate very high metabolic costs while providing little or no benefit in terms of brood production (Porter 1988).

The ability to make appropriate choices among suboptimal temepratures may be an important component of fire ant thermoregulation because the preferred temperature zone of 30–32° C is often only a few millimeters thick in the mound, especially in the morning hours. This narrow band of preferred temperatures is probably quickly occupied by workers and brood, forcing the remaining individuals to choose between temperatures that are warmer or cooler than they would prefer. Very little information is available concerning this ability in other poikilotherms. The choice of appropriate suboptimal temperatures could be a general capability of many organisms, or it could be limited primarily to social organisms like ants which can effectively communicate thermal alternatives and compete for a limited zone of strongly preferred temperatures.

Thermal preferences of workers and brood

As predicted, a large prcentage of fire ant workers (~ 30%) consistently selected cooler temperatures than those selected for the brood (Fig. 3). The major metabolic benefit for workers is probably increased longevity. Each 2° C drop in temperature should increase the longevity of workers by about 14% (Calabi and Porter 1989). Food requirements would also be reduced because of lower respiratory rates, but this saving would normally not be important to colonies with access to excess food. Other social insects appear to employ similar strategies. Ceusters (1977) reported that a portion of workers in *Formica* colonies tended to cluster at cooler temperatures. Similarly, areas in honey bee hives with only workers tend to be cooler than those with brood (Winston 1987).

The relationship of thermal preferences to colony social structure is a subject that deserves further attention. Different castes and developmental stages may have different thermal preferences. For example, the large fraction of *S. invicta* workers at cooler temperatures (Figs. 3 and 4) may be reserve workers (Mirenda and Vinson 1981) trying to reduce metabolic rates. Workers selecting high temperatures could be foragers or scouts (Porter and Tschinkel 1987). Nurses, of course, should have preferences very similar to those chosen for the brood. Kneitz (1966) was unable to find differences in thermal preferences of *F. polyctena* workers; however, this possibility should be investigated with intact colonies. Newly eclosed alate queens might prefer warm temperatures while they are accumulating fat reserves, but mature ones might switch to cooler temperatures while they are awaiting a mating flight. The different brood stages may also have different thermal preferences. In *F. polyctena*, thermal preferences for brood gradually increased from eggs to pupae (Ceusters 1977; Coenen-Staß 1985; Kipyatkov and Shenderova 1986). We could not make this comparison in fire ants because eggs and young larvae were not normally visible in the experimental setup. Older larvae and pupae appeared to have similar preferences but subtle differences could have been missed. The thermal distribution of functional queens is another subject that deserves further attention especially in regard to their oviposition cycles. Kipyatkov and Shenderova (1986) reported that active *F. polyctena* queens selected higher temperatures than inactive ones. In short, differing thermal preferences may be an important aspect of colony social structure. If this is so, then ant colonies should grow best in thermal gradients where a range of temperatures is continuously available.

Thermal preferences of well-fed and food-limited colonies

As predicted, food-limited colonies did reduce metabolic costs by choosing cooler temperatures than well-fed colonies. This occurring in two ways. First, a higher percentage of workers in food-limited colonies consistently chose cooler alternatives when almost all of the brood was placed at the warmer alternatives (Figs. 3 and 4). Specifically, over 50% of food-limited workers chose cooler alternatives compared to about 30% for well-fed colonies. This was true even when the cooler alternative was 5° C less than the warmer one (i.e. the 25 and 30° C combination). The fact that workers switched from food-limited to well-fed behavior in 2–3 days suggests that direct changes in thermal preferences may be the primary reason for this switch, although the lower brood-to-worker ratios associated with food-limited colonies (Fig. 2) may also have been a factor. Energetic savings from worker preference shifts can only be roughly estimated because we did not measure percent distributions of workers across a thermal gradient. Nevertheless, a 2–4° C reduction in thermal preferences for an additional 25% of the workers should translate into a 3–6% reduction in total worker maintenance and replacement costs (Calabi and Porter 1989) during periods of food stress.

A 1–2° C reduction in thermal preferences for brood is the second way food-limited colonies reduced metabolic costs (Fig. 3–4). Test colonies required 1–2 weeks to fully develop food-limited preferences, but less than 12 h to switch back to well-fed preferences after receiving excess food (Fig. 5). The 1–2 week delay may be the period required for reserve workers (Glancey et al. 1973) to gradually exhaust food stored in their crops and body tissues. A 1–2° C reduction in thermal preferences for brood was much less than that predicted by the temperature growth curve for food-limited colonies (Fig. 2B). In fact, careful inspection of Fig. 4 indicates that the thermal preferences for brood in food-limited colonies more closely matches preferences that would be predicted if the growth curve of well-fed colonies (Fig. 2A) were shifted a degree or two to the left.

Why don't thermal preferences for brood in food-limited colonies match the growth curve of food-limited colonies? One possibility is that net brood production costs of fire ants are relatively insensitive to temperature, at least within the normal thermal range for brood production. In other words, the net cost of producing ten workers at 25° C is probably about the same as it is at 30° C (see "total costs", Calabi and porter 1989; also compare degree-days and pupal survival across temperature, Porter 1988). The reason food-limited colonies declined in size at warmer temperatures (Fig. 2B) is probably due to accumulating worker maintenance costs and not differential brood production costs. In fact, the 30% reduction in colony size between 25° C and 30° C (Fig. 2B) was nearly proportional to the 36% increase in metabolic costs over the same temperature range (Calabi and Porter 1989). The growth pattern in Fig. 2B is very similar to that observed for food-limited sockeye salmon (Brett 1971) and probably for the same reason; that is, increased respiratory costs at higher temperatures consume energy that would otherwise have been available for growth.

Under field conditions, entire colonies are never forced to occupy a single temperature. They almost always have a menu or more precisely a gradient of temperatures to choose from; this would generally allow reserve workers and other workers not directly engaged in brood care to select cooler temperatures. Given these conditions, it would seem best for food-limited colonies to rear limited numbers of replacement workers fairly quickly at warm temperatures while "storing" the bulk of the workers at cooler temperatures.

If net brood production costs in fire ants are relatively insensitive to temperature, why is there any decline in the preferred temperature for brood in food-limited colonies? The answer may be that rearing brood at cooler temperatures helps to buffer the negative effects of fluctuating food supplies. In particular, cooler preferences could reduce the chance of maintaining larvae at high temperatures without sufficient energy for growth. Cooler temperatures might also reduce the frequency of brood cannibalism (Sorensen et al. 1983).

A 1° C shift in brood temperature from 31° C to 30° C would decrease developmental rates by about 7% (Porter 1988). This decrease in developmental rates should result in a proportional 7% drop in metabolic costs and food requirements for the brood. A 1° C reduction in brood temperatures would also extend developmental time by 2.5 days and pupal development by about 1 day (Porter 1988). This delay could offer a slight benefit by deferring pupal eclosure until additional food was available to support the increased respiratory requirements of new workers (Roces and Protomastro 1988). A 1° C drop in thermal preference for brood would also reduce the production and maintenance costs of attending workers by about 6% (Calabi and Porter 1989). Assuming 50% of workers in food limited colones are involved in brood care, this would reduce total worker costs by about 3%. This percentage should be added to the 3–6% savings estimate calculated above for workers choosing cooler temperatures than the brood. Altogether, reductions in preferred temperatures in food-limited colonies would approximately reduce worker costs by 6–9% and brood costs by 7%.

It is unknown how frequently fire ant colonies are food-limited, but this is presumably fairly common in mature field populations. Another consideration is that the shift in thermal preferences will only be of benefit when mound temperatures reach about 28° C for workers and 31° C for brood. Mound temperatures of 28° C and 31° C are available about 60% and 30% of the time, from April to November respectively (unpublished data), the major period of brood production in north Florida (Tschinkel and Porter 1988). Food-limited colonies probably gain additional energy saving from reductions in brood production and worker activity rates.

More information is needed about the frequency, duration and types of food stresses found in field colonies. Studies of fire ant diet indicate that workers are fueled primarily by liquid carbohydrates while brood require proteins for growth (Tennant and Porter 1991; Porter 1989). Both carbohydrate and protein food sources were limited in this study. Future studies should determine if thermal preferences of workers and brood are affected differently by the type of food in short supply. Roces and Núñez (1989) reported that limiation of insect food delayed pupal eclosure in a *Camponotus* ant, but limitation of a sugar solution did not.

Food-limitation or starvation reduces thermal preferences in other poikilotherms. Stunz and Magnusson (1976) reported that bluegills with negative growth rates reduced thermal preferences by 1.4° C and metabolic rates by about 5%. Similarly, Javaid and Anderson (1967) found starvation reduced thermal preference by 2° C and 4° C for two of the three salmonid fish in their study. Berman and Quinn (1991) reported that prespawning salmon selected temperatures that were 2.5° C below ambient, a behavior that reduced metabolic costs by 12–20%. Regal (1966) reported that the thermal preferences of a constrictor snake were much lower when it was not digesting food. Two species of turtles had thermal preferences that were 1.5° C and 4.5° C lower before feeding (Gatten 1974). Deal (1941) reported mixed results concerning the thermal preferences of stored-product insects held in thermal gradients for 3 days with and without food. Thomson (1938) found that 80% of hungry mosquitoes avoided the warm side of his thermogradient, whereas recently fed ones showed no particular preference. Lazzari (1991) reported that unfed reduviid bugs (Triatoma infestans) gradually reduced their thermal preferences from 27–29° C to 25–26° C over a 12-day period, but this preference for cooler temperatures was reversed almost immediately after feeding.

Conclusions and suggestions for future research

This study has demonstrated that fire ants are capable of making fairly sophisticated thermoregulatory choices. Colonies not only selected an optimal or near optimal brood temperature, but they also selected the best suboptimal alternatives when the preferred temperature was not available. As predicted, a substantial fraction of colony workers consistently chose cooler temperatures than those selected for the brood. This strategy appears to reduce the production and maintenance costs for reserve workers and perhaps other workers not directly associated with brood care. The third major capability was that food-limited fire ant colonies chose cooler temperatures than those selected by well-fed colonies. Specifically, the preferred temperature for brood was reduced by 1–2° C and a larger fraction of workers in food-limited colonies consistently selected cooler alternatives.

These thermoregulatory capabilities are quite impressive from a behavioral standpoint, but additional work is needed to determine their ecological value under field conditions. In particular, it would be helpful to know how much temperature tracking behavior benefits field colonies in terms of increased growth potential. Another question is how frequently fire ant mounds become dry enough that humidity preferences (Potts et al. 1984) influence thermal preferences. Detailed behavioral observations are also needed of the thermoregulatory process itself. Specifically, how is it organized and which groups of workers are responsible for initiating it and carrying it out? Diseases might also affect thermal preferences of ants. A number of poikilotherms including crickets, lobsters, fish, frogs, and lizards are reported to create behavioral fevers by selecting temperatures that are 2–6° C above those normally preferred (Boorstein and Ewald 1987). The extensive thermoregulatory ability of ants and other social insects would seem to make them especially good candidates for behavioral fevers.

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