

Research article

Thermoregulatory brood transport in the fire ant, *Solenopsis invicta*

C.A. Penick¹ and W.R. Tschinkel

Department of Biological Science, Florida State University, Tallahassee, FL 32306–4370, U.S.A., e-mail: Clint.Penick@asu.edu, tschinkel@bio.fsu.edu

¹ Current address: School of Life Sciences, Arizona State University, Tempe, AZ 85287–4601, U.S.A.

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Abstract. Nest structure in ants is often designed to optimize the colony's ability to thermoregulate, and this specialization is most highly developed in mound-building ant species. *Solenopsis invicta* invest a large amount of energy in building mounds and transporting their brood up and down in their nests as a means of thermoregulation. Because few ant species build true mounds, we wanted to determine the effectiveness of these mounds in harvesting solar heat as well as to distinguish what factors (temperature vs. circadian rhythm) govern where fire ants place their brood in the mound and when they place it. We measured temperature patterns in the mound over several days at different depths and under different conditions (under direct sunlight or shade), and then conducted a series of field experiments to manipulate the orientation and time of heating.

On cool mornings in spring or fall, surface temperatures of the mound rise at the fastest rate on the side receiving the most direct sunlight (usually the south side). This heating causes a temperature gradient through different depths in the mound, and shows little difference from outside ground temperature at a depth greater than ~40 cm inside the nest. In the morning, fire ants move their brood up into the mound on the side most directly heated, and when temperatures exceed optimal (~32°C) they move their brood down the temperature gradient to lower depths in the nest. In addition to this, mound temperature does not only increase due to direct sunlight, but temperature also increases higher than ground temperatures when the mound is in the shade due to its low specific heat.

Experiments in which sunlight was mirrored to the normally shaded side of the mound, or when mounds were heated at night, revealed that *S. invicta* primarily track temperature patterns and do not rely on behavioral habits or circadian rhythms for the thermoregulatory transport of their brood. When mounds were shaded, *S. invicta* brood was evenly distributed directly under the

surface of the mound rather than aggregating towards a specific side. The fire ant mound is important for thermoregulation because, compared to moundless subterranean nests, it absorbs heat more rapidly both in direct sunlight and shady conditions. Temperature tracking within the nest is key to understanding thermoregulatory placement of fire ant brood, as well as insight into the production of sexual brood and reproduction.

Keywords: Thermoregulation, brood rearing, mound construction, behavior, diurnal cycle.

Introduction

Fire ant mounds are conspicuous in disturbed habitats throughout the southern and eastern United States, however only a few ant species build true mounds (i.e., mounds of soil filled with a network of galleries and chambers that ants inhabit). The primary function of true mounds in all species is thought to be for microclimatic regulation, and this is especially important for brood rearing and production of sexual brood (Hölldobler and Wilson, 1990). Within a fire ant colony, thermoregulation and production of sexual brood are tied together and directly influence colony fitness.

Although some species of ants rely on metabolic heat production for thermoregulation, as for bivouacking army ants (Franks, 1989) or concentrations of reserve workers in *Formica rufa* mounds (Rosengren et al., 1987), most ant species are exothermic and track temperature in their environment. Although ground temperatures remain fairly constant throughout the day, they do change some, and ants that live in subterranean nests fine-tune nest temperatures by moving short distances within the nest (Seeley and Heinrich, 1981). Ground-nesting ants often build their nests beneath stones because the low

specific heat of dry rocks causes them to heat rapidly, and the ants migrate between warmer chambers under the stones during the day and lower regions in the nest during the night when surface temperatures (and stone temperatures) drop faster than temperatures deep underground. Mound-building ant species show an advanced condition of this temperature tracking behavior because they invest energy to build mounds that serve a similar purpose to the rocks used by ground-nesting species (Seeley and Heinrich, 1981).

True mound-building ant species usually occur in areas subject to temperature extremes, often in warmer temperate regions (Hölldobler and Wilson, 1990). Some ant mounds can reach impressive heights (over a meter) such as the mounds of *Formica polyctena* in northern Europe. These mounds (called thatch mounds) are usually made of decaying organic material, and are warmer deep within the mound rather than near the surface (Brandt, 1980). In this regard, these thatch mounds are fundamentally different from fire ant mounds and other mound building species, such as *Pogonomyrmex salinus* (Anderson and Munger, 2003) and *P. occidentalis* (Cole, 1994), which are constructed with excavated soil and are warmed mainly by the sun. The mounds of fire ants, resemble the heating properties of rocks in that they have a lower specific heat than the surrounding ground, and also have a higher surface area to volume ratio creating a greater area for heat transfer. Because of these physical properties, mound temperatures vary more than ground temperatures. While thatch mounds share these properties, they also combine the insulating properties of decaying organic matter with body heat production to maintain an inner core temperature within the mound (Rosengren et al., 1987), and these heat retaining/generating properties make thatch mounds different from the mounds of ants that do not build with mostly organic material.

The volume of a fire ant mound is positively correlated with the mass of ants in the colony and varies with seasonal trends in population (Tschinkel, 1993). At midmorning in spring, approximately 60–65% of the worker force and 90% of the brood is located in the mound (Hölldobler and Wilson, 1990), and the queen is usually in the mound as well. The mound itself is perforated with a network of narrow tunnels that extend 5 cm to 10 cm below the surface through the grass root system. Chambers appear 10–80 cm below ground level, and are connected by vertical shafts that radiate vertically from the subterranean portion of the nest to horizontal tunnels near the crust of the mound (Tschinkel, 2006). This orientation would facilitate movement of workers and brood from the mound to subterranean chambers in the nest. Nests can reach depths from 1–1.5 m below the surface (Cassill et al., 2002).

Fire ants characteristically move their brood up into the mound shortly after sunrise on the side most directly heated (this characteristic is so predictable that fire ant mounds could be used as a compass to determine the

direction of south by locating the side where brood is aggregated). As surface temperatures exceed optimal at the peak of the day or cool lower than the temperatures deeper in the mound at sunset, fire ants move their brood down a temperature gradient in the nest where temperatures remain almost constant between 16 ° and 24 °C year round (temperature data: Tschinkel, 1987). Brood-tending workers are the caste most likely to move the brood in response to temperature. The brood-tending caste is primarily determined by age polyethism, where younger workers attend to nest responsibilities and only the oldest workers leave the nest to forage (Hölldobler and Wilson, 1990).

This pattern of brood transport follows a daily cycle, and in some ant species it has been shown to exhibit a circadian rhythm. For example, Roces and Núñez (1989) discovered a photoperiodic circadian rhythm of temperature preferences for brood rearing in *Camponotus mus* in which nurse workers translocated the brood between two regions of different temperatures daily.

The rate at which brood develop is strongly correlated with temperature, a dependence which is the foundation of thermoregulatory brood transport (O'Neal and Markin, 1975). Increasing average nest temperature reduces development time in all castes of fire ant brood until temperatures exceed ~32 °C, which will negatively affect development and can cause brood mortality (Porter, 1988). Sexual brood is only produced when weekly mean soil temperatures (at 5 cm) rise above 20 °C (Markin et al., 1974). Thermoregulation of the brood has a large effect on reducing development time of sexual brood so that more brood can be produced in one season, and this will increase colony fitness.

The lower temperature limit for growth in *S. invicta* colonies is unusually high, where colonies cease growth when average nest temperatures fall below 24 °C (Porter, 1988). Low temperatures raise mortality rates of young larvae and eggs, but the queen may cease oviposition in response to these temperatures. Fire ants require unusually warm temperatures for colony growth.

There were two main parts to this study—first, a descriptive analysis of heating and cooling patterns within the mound, and second, a set of experiments to distinguish what factors influence brood placement. We hypothesized that temperature is the primary determinant of thermoregulatory brood placement in *S. invicta*, and that behavioral habits or circadian rhythms have little bearing on these behaviors.

Methods

Descriptive analysis of heating and cooling patterns within the nest

We recorded temperatures at different orientations and depths in fire ant nests in their natural setting by implanting iButton data loggers by Dallas Semiconductor in the mounds. The data loggers have a 16 mm diameter and are 5 mm thick. We attached strings to each iButton using

epoxy glue so we could easily locate and retrieve them from the nest for downloading the data through an interface onto a computer.

We examined two main aspects of nest heating and cooling: surface temperature differences between the north and south sides of the mound (the sun heats the south side most directly), and the temperatures at different depths in the mound. As points of reference, we also recorded ambient air temperature and outside ground temperature at 5 cm.

Colonies with well-developed mounds were chosen in an open field in Tallahassee, Florida. The iButtons were set to record temperature every 10 minutes and were placed at 1 cm and 5 cm depths in a single fire ant mound on the north and south sides. Data were collected over five days starting February 13th 2005.

A mound in the same location was used to acquire temperature data at different depths in the mound starting at the surface (1 cm deep) and lower depths in 5 cm increments to 40 cm. The iButtons were again set to record temperature every 10 minutes, and the data were collected over four days starting March 14th 2005.

Tests for heat tracking versus behavioral habit and circadian rhythm

We conducted three field tests on fire ant mounds in Tallahassee, Florida, which included reversed heating patterns between north and south sides, general shading, and heating nests during the night (when mound temperatures are normally suboptimal). In the first test we wanted to see if reversing the heating pattern in the morning would cause the ants to bring their brood up into the mound on the side that was heated or if they would bring the brood up on the side normally exposed to the sun out of habit or other cues. We shaded the south side of the mound with cardboard and reflected sunlight to the north side with a large mirror to reverse the normal temperature pattern in which the south side receives the most direct sunlight.

Thermistor temperature probes were imbedded just under the surface on at least one test colony so we could monitor temperatures as they approached optimal (~32 °C), and iButtons set to record every minute were placed 1 cm under the surface on the north and south sides of the mound to record temperature data. Control mounds were left to natural heating conditions and their temperatures were also monitored. We used a standard sized spoon (15 mL) to take samples from the nest as the temperatures neared 32 °C (about two hours after sunrise) from the north and south sides of experimental and control groups. The brood in each sample was counted. These samples were not representative of the entire population of brood within a nest, but were used to detect the general presence or absence of brood in an all-or-none response. This test was done on fresh colonies on each of three separate days, (April 13th and 28th, and May 2nd, 2005) for a total of 8 colonies in each of the two groups: reversed heating and control.

In the general shading experiment we tested the response to non-directional heating. We used cardboard to shade all sides of the mound and left the top uncovered for ventilation. We again placed iButtons 1 cm under the surface on the north and south sides to monitor temperature. Control colonies were left open to natural heating and their temperatures were also monitored. Samples (15mL) were taken 2–3 hours after sunrise from the north and south sides of shaded and control colonies. The brood was counted in each sample. This test was done on two separate days, April 28th and May 8th, 2005; there were 8 colonies in each of the two groups, shaded and non-shaded (control).

In the heating experiment, colonies were heated at night between 12:00 midnight and 3:00 AM when brood is usually kept deep in the nest. Small grills were suspended ~10 cm above nests and five pieces of burning charcoal were put on each grill. Control colonies were left exposed to normal conditions. Thermistor temperature probes along with iButtons set to record every minute were used to monitor temperatures at the surface as well as 5 cm below the surface. A single sample (15mL) was taken from each nest approximately 2 hours after the nests were heated (when surface temperatures were ~32 °C), and brood was counted in each sample. This test was done on two separate nights, May 2nd and 8th, 2005; there were 6 colonies in each of the two groups, heated and non-heated (control).

Results

Descriptive analysis of heating and cooling patterns within the nest

Surface temperature on the south side of the mound was more variable and could reach temperatures 10–20 °C higher at midday in spring than the ambient air temperature or temperatures at any other location in the mound. Following sunrise, surface temperatures on the south side rose at a greater rate than air temperature and reached optimal (~32 °C) when the air temperature was ~5 °C below optimal.

There was an obvious difference in temperature between the north and south sides of the mound. Whereas the south side heated at a faster rate and to a greater degree, surface temperatures on the north side were almost exactly the same as air temperature (Fig. 1), and this was probably due to the increase in surface area of the mound that allows a greater exchange of heat with surrounding air temperatures. The outside ground temperature at 5 cm fluctuated little and was generally cooler than mound temperatures during the day and warmer during the night.

The temperature patterns at different depths show that there was a significant decrease in temperature between 1 cm and 5 cm at midday. This explains why brood is generally spread maximally over the south side of the mound at a layer only a few centimeters deep. As temperatures at 1 cm exceed optimal, depths ranging to 5 cm stay close to optimal, so this is the region where most brood should be found after midmorning (Fig. 2). Temperatures near the surface of the mound also cool at a faster rate and to a greater degree than temperatures at lower depths in the nest, so after sunset warmer temperatures were found deeper in the mound (15–40 cm). Temperatures at depths between 1 cm and 15 cm heat and cool to a greater degree than the surrounding ground temperatures because of higher surface area to volume

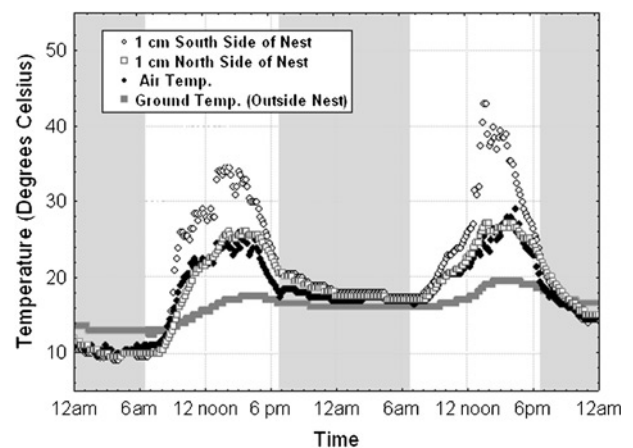


Figure 1. Temperature profile of *S. invicta* mound spanning 48 hours (gray areas indicate nighttime hours) in mid February.

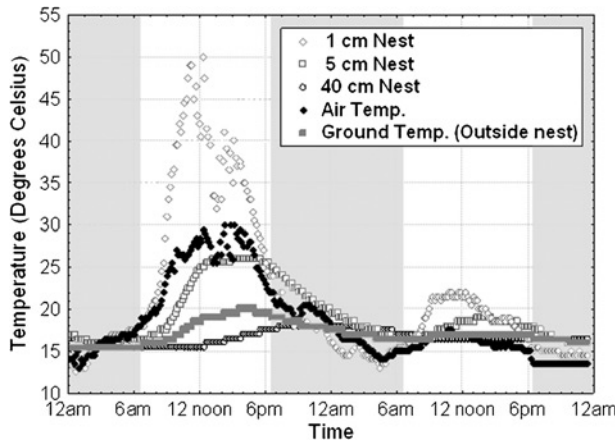


Figure 2. Temperature profile of *S. invicta* mound (south side) spanning 48 hours at four different depths (gray areas indicate nighttime hours) in mid March. The first day was sunny, while the second was cloudy.

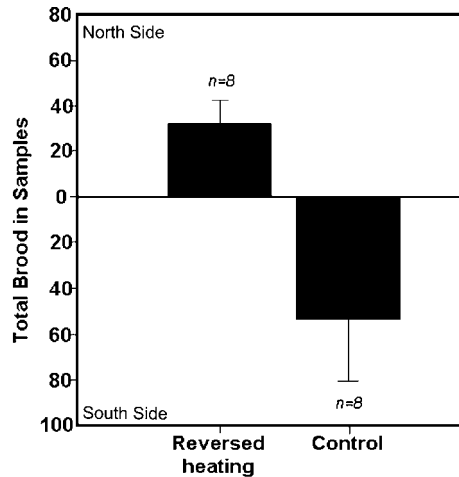


Figure 3. Average brood totals from north and south side samples from experimental (reversed heating pattern) and control colonies. Each group consists of 8 colonies. Bars indicate the mean brood in samples along with standard error bars.

ratio, which provides greater rates of heat transfer with the air surrounding the mound even on cloudy days.

Heating patterns in the mound were diminished under cloudy conditions, but surface temperatures still had a heating advantage over lower depths (Fig. 2). However, cloudy conditions reduce the difference in temperature between the north and south sides of the mound.

Tests for heat tracking versus behavioral habit and circadian rhythm

Reversed heating pattern. The response to reversed heating was all or none. By midmorning in control colonies, all of the brood was aggregated on the south side (most direct sunlight), and no brood was found on the north side. Reversing the heating pattern on the mound caused the exact opposite response with all brood being

located on the north side with no brood being found on the south (Fig. 3). When brood was present, the amount of brood in samples between the reversed heating and control groups was not significantly different—only their location was. Because no brood was found on the south side in reversed heating colonies, this suggests that *S. invicta* was tracking temperature primarily and that no habits or other cues were associated with this behavior.

General shading. Without directionality of heat from the sun, brood was found in samples from both the north and south sides of the mound fairly evenly. Control colonies still showed the all or none response where brood was only located on the south side (Fig. 4). Surface temperatures on either side of the mound were close to the same, and were about the same as ambient air temperature. There was not a significant difference between totals in brood samples between the north and south sides of shaded colonies, so it can be assumed that brood was distributed evenly in the absence of directional heating. Without strong directional heating, fire ants were able to choose the largest area that was near optimal temperature to aggregate their brood.

Heating during the night. When fire ant mounds were heated during the night, they brought brood just under the surface of the mound in significant amounts. Because temperatures at lower depths in the nest are usually warmer than mound temperatures at night, control colonies did not bring their brood up into the mound (Fig. 5). Samples were taken about 2 hours after heating, which is about the amount of time it takes fire ants to bring their brood into the mound following sunrise. Since the time it took the ants to detect the change in temperature and transport their brood into the mound was not significantly different from the time it takes them to do this at sunrise, there was no time lag for brood

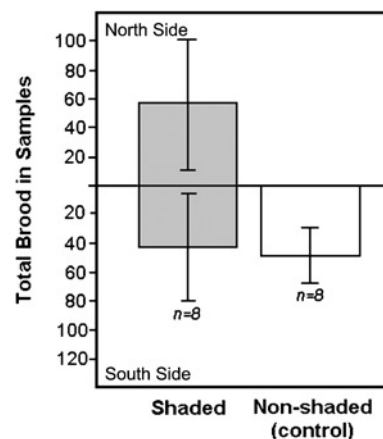


Figure 4. Average brood totals in samples from the north and south sides of experimental (generally shaded) and control (open to direct sunlight). Each group consists of 8 colonies. Bars indicate the mean brood in samples along with standard error bars.

placement. A time lag would be more noticeable if the ants were following a circadian rhythm.

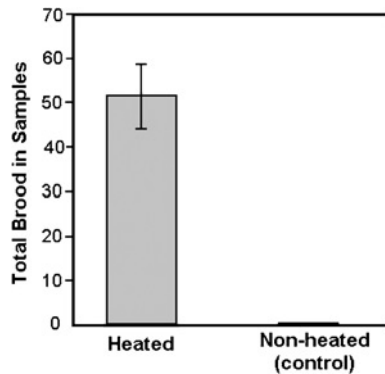


Figure 5. Average brood totals from samples taken during the night from heated and control colonies. Each group consisted of 6 colonies. Bars indicate the mean brood in samples along with standard error bars.

Discussion

Surface temperatures on the south side of the fire ant mound rise faster and higher than subterranean nest temperatures or ambient air temperature (Fig. 1). Because of the low specific heat of the mound and its increased surface area, rising air temperatures cause it to heat at a faster rate and to a greater degree than surrounding soil, even under shaded conditions (Fig. 2). Under shady conditions the heating is non-directional and surface temperatures of both the north and south sides are equivalent. This daily cycle of heating correlates strongly with fire ant brood placement in the mound, suggesting that fire ant thermoregulatory behavior is adaptive.

Because brood is moved into the south side of the mound most often, nest architecture could influence this daily migration or be influenced by it; however, there was no clear difference observed in the time it took to move brood into the mound between the reverse-heated colonies and control colonies. On a finer scale, slight differences in transport time could possibly be observed because of differences in nest architecture. The south sides of mounds were often sloped more than the north and free of grass that would shade the mound (presumably the ants are weeding), which is common in other mound-building species (Seeley and Heinrich, 1981; Vogt et al., 2004) excepting mounds of *Lasius flavus*, which are located in grasslands and usually covered with various grasses (Waloff and Blackith, 1962). During the winter, mounds are extended on the south side and cause nests open to direct sunlight to have a north-south axis of elongation, which contributes to the nest shape and may be linked to temperature tracking (Hubbard and Cunningham, 1977). In *Solenopsis richteri*, Vogt et al. (2004) showed that mound size was smallest just before winter and reached a maximum in May, which means that energy

involved in mound construction peaks at the same time temperature tracking is most important (during Spring sexual production). A similar pattern has been shown in *Pogonomyrmex occidentalis*, with the southeast-facing slope having a larger surface area, and the nest entrance usually located on this side as well to allow the ants to forage earlier (Romey, 2002). Within regions of the fire ant range that do not go through large temperature fluctuations there is a reduction in mound height, and mounds are usually shorter and have a decreased volume when temperatures are increased (Vogt and Smith, 2007). Fire ant mounds in south Florida (where temperatures are always high) are often sprawling and low to the ground (Tschinkel, 2006).

When the mounds were shaded to mimic cloudy conditions there was no tendency to aggregate the brood on one side or the other (Fig. 4). This suggests that there is no behavioral habit to choose a side, and this is the common behavior observed in the field under cloudy conditions. Fire ants are opportunists when it comes to foraging, and they display the same behavior when it comes to thermoregulation—they will aggregate wherever they find the most favorable temperature. Because the mound has a lower specific heat than the surrounding ground, it still offers a thermal advantage when there is no direct heat source (like on cloudy days), and ants respond to this by spreading brood evenly under the surface of the mound without preference to any side.

Fire ants are capable of making even more complex choices concerning thermoregulation. Porter and Tschinkel (1993) showed that fire ants chose temperatures that exceeded optimal more often when given a choice between increasingly higher temperatures and lower temperatures. Thermal preferences also vary with food consumption, and a starved colony will choose to aggregate at lower temperatures than a satiated colony (Porter and Tschinkel, 1993). Fire ant thermal preferences are more complex than a simple on/off switch, and ants are capable of choosing temperatures that maximize their growth with the least amount of metabolic costs.

Although circadian rhythms play a role in thermoregulation of other ant species (Roces and Núñez, 1989), this was not observed in *S. invicta*. Fire ants responded to heating of mounds during the night at the same rate they would respond to heating in the morning with sunrise. Periods of day or night have little effect on temperature tracking, and have little to do with activity levels of fire ants in other aspects. Like temperature tracking within the nest, foraging rates of *S. invicta* are not affected by photoperiod and correlate closely with soil temperature at 2 cm (Porter and Tschinkel, 1987).

Factors other than temperature affect brood placement, among them, humidity and soil moisture. Workers alone do not show a humidity preference in lab colonies, but when brood is added, brood-tending workers show a preference for saturated atmospheres (Potts et al., 1984). In field observations, pupae are often located in galleries just below the surface of the mound while larvae are

found a few centimeters deeper where soil moisture is high. Separation of brood stages between humidity gradients has not been studied fully in *S. invicta*, and should be looked into further. In other species of ants, separate humidity preferences have been shown to exist between the larvae and pupae, with pupae generally aggregated in dryer regions (Hölldobler and Wilson, 1990).

Optimal temperature was assumed to be 32 °C for this study. Cokendolpher and Francke (1985) reported that the preferred temperature of *S. invicta* was 28.3 °C, which is 2.7 °C lower than the median temperature preference reported by Porter and Tschinkel (1993). The explanation given for this difference is that Cokendolpher and Francke tested temperature preferences of *S. invicta* outside of their familiar nests without the presence of a queen, while Porter and Tschinkel tested thermal preferences of entire colonies within their familiar lab nests (Porter and Tschinkel, 1993). Testing temperature preferences in the field would be the most meaningful measure, and might well show the preferred temperature to be 32 °C, the temperature determined as optimal for brood rearing in the lab (O'Neal and Markin, 1975; Porter and Tschinkel, 1993). Collecting temperature data from field colonies in this study was an initial step towards understanding thermoregulation in *S. invicta* within their natural settings.

Fire ants invest a lot of energy into thermoregulation, and as shown through experiments in which colonies were heated during the night, temperature tracking within the nest is a constant task. Very little is known about how this is carried out—is there a specific caste of workers responsible for temperature tracking? Is the task carried out only by nest workers? Also, little is known about how brood-tending workers make thermoregulatory choices. Do they receive feedback from larvae and pupae, or are these decisions left solely up to brood-tending workers? When temperatures are manipulated in laboratory colonies, a minority of workers transport brood, often to areas that are not at the preferred temperature (pers. obs.). Eventually, the brood is transported to the region with approximately optimal temperature, possibly as a result of feedback from brood at various temperatures.

The response to temperature changes in the field is impressively quick. When heating was reversed in field colonies after brood had already been brought up into the mound on the south side, brood was found in samples from the north side within 10–15 minutes (unpubl. data). After the region of optimal temperature has been located, what tells other brood-tending workers to move their brood in mass to the new location? It is obvious that some level of recruitment is involved, but the mechanism is unknown.

The mound structure provides a heating advantage, and it has been shown that lower temperatures can trigger the ants to build taller and larger mounds (Vogt and Smith, 2007). The thermal advantage of these mounds combined with temperature tracking behavior has an

estimated benefit of a 13–30% increase in brood production over a colony that either keeps their brood in the mound at a 2 cm depth or 40 cm underground without tracking temperature (Tschinkel, 2006). The advantage of building a mound has been estimated to give a 23% annual thermal benefit over a colony that only tracks temperature underground without a mound (the cost of building a mound has not been estimated), and this would greatly affect competition with other colonies when brood production rates count (Tschinkel, 2006).

Colonies of *S. invicta* reach maximum size during midwinter, and raise their first sexual brood on worker fat reserves when outside temperatures are still too low for foraging (Tschinkel, 1993), and it is the mound's ability to capture morning heat during this crucial time in sexual production that creates the right temperature to raise brood when air temperatures are too low (Tschinkel, 1993, 2006). Combining the thermal properties of the mound with temperature tracking behavior is strongly involved in the timing and production of sexual brood and contributes a great deal to the fecundity of a colony and to colony fitness. An understanding of the basic principles that control thermoregulation within a social insect colony can help elucidate properties that lead to the evolution of these behaviors and expand our knowledge of organization within insect societies.

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