Effect of temperature on brood relocation in *Pogonomyrmex salinus* (Hymenopteria: Formicidae)

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Recommended Citation

EFFECT OF TEMPERATURE ON BROOD RELOCATION
IN *POGONOMYRMEX SALINUS* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT.—Brood movement in response to temperature by *Pogonomyrmex salinus* (seed-harvester ant) nurse workers was examined in the sagebrush steppe of southeast Idaho. Shading the mound surface of *P. salinus* colonies at dawn caused a decrease in mound temperature and led to significantly less brood accumulation near the surface. In a related experiment, a lab colony of *P. salinus* was offered an artificial thermal gradient during the cool/dark portion of the daily cycle. Nurse workers removed brood from the 21°–22°C range to soils with temperatures between 29°C and 36°C. Daily brood relocation by *P. salinus* nurse workers is a highly flexible behavior, capable of immediate response to temperature, and does not appear to follow a strict endogenous rhythm.

Key words: thermoregulation, endogenous, rhythm, circadian, Pogonomyrmex salinus, *harvester ant, Hymenoptera, Great Basin.*

Nearly all organisms show predictable daily cycles of activity. Although some cycles are a response to environmental cues, most are controlled by an internal biological clock known as an endogenous circadian (daily) rhythm. An endogenous rhythm persists in the absence of environmental time cues and will "free-run," thereby revealing its own natural period (Saunders 1976). An endogenous rhythm allows an organism to anticipate and exploit predictable environmental variation, whereas a direct response to environmental cues allows an organism to escape from or exploit unpredictable environmental variation. Some insects possess strict endogenous rhythms (Alpatov et al. 1999); others are largely dependent on environmental cues (Odhiambo 1966). Most investigations thus far have shown a mixture of strong endogenous components modified by exogenous components (Saunders 1976, McCluskey and Soong 1979, Roces and Nunez 1996).

In ant colonies internal nest temperatures directly influence nurse worker activity and the rate of brood development (MacKay 1985, Porter and Tschinkel 1993). Bushinger (1973) reported that 5 temperate species not only tolerate daily nest temperature variations, but require them for larval development. Temperature selection for brood depends on the behavior of nurse workers (Roces and Nunez 1989). The temperate species *Camponotus mus*

follows a strict endogenous rhythm where nurse workers relocate brood at 2 critical times of the day, when environmental temperature is expected to reach its maximum and minimum values (Roces 1995). Nurse workers of *Pogonomyrmex salinus* and *P. occidentalis* also transport brood throughout the nest chambers, but this behavior seems highly dependent on hourly temperature cues (Anderson and Munger personal observation). Extensive chamber area is present near the nest surface of many harvester ant species (Cole 1994, Tschinkel 1999) and may have functional value in brood thermoregulation.

The northernmost species of *Pogonomyrmex* are *P. salinus* and *P. occidentalis.* These species are ecologically similar; both inhabit temperate climates, exhibit a daily cycle of brood relocation during the warm season, and construct a nest surmounted by a conical mound. Cole (1994) considered the nest-cone of *P. occidentalis* to be a morning solar collector. Brood individuals are taken into the nest-cone in the morning as the nest-cone warms, and then moved to lower portions of the nest as the nest-cone attains overly high temperatures. At dusk, brood individuals remain in lower portions of the nest while workers return to the chambers in the nest-cone and presumably remain there until dawn, perhaps in anticipation of warming. Cole (1994) noted

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that those workers in the nest-cone chambers before dawn are concentrated on the eastern side of the nest-cone, although that portion of the nest-cone is not any warmer at that time of day. This apparent anticipatory behavior in *P. occidentalis* suggests the presence of an endogenous rhythm, but also could be explained by exogenous factors.

Is the brood-tending behavior of *P. salinus* capable of exogenous control, showing immediate response to temperature, or is it under strict endogenous control, entrained by daily cycles of light and/or temperature? In the present study we disrupted the typical daily cycle of environmental cues to determine the extent of endogenous control. Because brood-tending behavior is normally performed in the dark, we manipulated the environmental cue of temperature. Specifically, we examined how brood relocation in *P. salinus* is affected by a shade-induced disruption of the natural morning warming of nest-cones in the field, and a heat-induced disruption of the normally cool/dark period in a laboratory nest.

MATERIALS AND METHODS

Field Study

This study was performed on 23 July 1996 in an area of mixed sagebrush (*Artemisia tridentata*) and cheatgrass (*Bromus tectorum*) south of Kuna, Idaho. The terrain is predominantly flat, and soils are of moderately deep gravelly loam. Twenty-five *Pogonomyrmex salinus* colonies along a roadside were selected for study. All colonies had the same slope and aspect and were surmounted by a well-formed nest-cone. All colonies were mature, active, and received about the same daily solar exposure.

Just before sunrise, 13 of the nest-cones were shielded from the sun with stiff cardboard (approximately 1 m square) supported at a 45° angle by 3 wooden stakes. The 12 control colonies were disturbed in the same manner but not shaded. Nonshaded colonies alternated spatially with shaded colonies. Shade construction began at 0615 hours and was completed by 0730; sunrise was at 0633 hours.

A mature harvester ant nest may extend several feet below the surface, but only the uppermost portions of the nests are affected by daily temperature cycles. Between 0829 and 1130 hours, all 25 colonies were excavated

to a depth of 20 cm, alternating between shaded and nonshaded colonies. The excavation procedure was as follows: a shallow groove was etched east to west across the surface of each nest-cone to divide the colony into halves. Then, one-half of the nest-cone was removed in layers to expose brood chambers, while the other half of the nest-cone was used to measure chamber depth, with the first detected chamber representing 0 cm. The number and depth of brood individuals and the temperature of chambers containing brood were recorded. The total number of brood individuals above 20 cm in shaded vs. nonshaded colonies was analyzed using an independent-samples t test. For graphing purposes brood were classified as (<5) per chamber, ($5-10$) per chamber, ($10-20$) per chamber, and (>20) per chamber. Temperature was recorded from the surface substrate of each nest-cone prior to excavation and at depths of 2.5 cm, 5 cm, and 10 cm. Soil temperature was measured using a 40-gauge Cu-CuNi thermocouple (response time <5 seconds) read by an Omega HH25TC digital thermocouple reader.

Lab Study

A colony consisting of a queen, approximately 250 workers, and 80 brood (mostly pupae and final instars) was excavated from the field site. The colony, including nest soil, was placed in a vertical glass enclosure that measured 50 × 65 × 1 cm, and topped horizontally with a 20 × 30 × 8-cm foraging area. The soil within the enclosure was equipped with 7 Cu-CuNi thermocouple wires at depths of 2.5, 5, 10, 20, 30, 40, and 50 cm. The lower 40 cm of the vertical glass enclosure was covered from the outside with a 1-foot-thick soil/sand mixture packed firmly against the outside. This soil layer was moistened and shaded with cardboard to simulate the stability of natural ground temperature. The foraging area was filled with a 2-cm-deep layer of soil and exposed to the solar cycle to maintain natural light and temperature fluctuations and any endogenous rhythm present in *P. salinus.* The colony was allowed to reestablish its nest structure with the foraging area and upper 10 cm of the glass enclosure exposed to natural outdoor conditions: LD 16:8 cycle and naturally occurring July/August climate. Stored seed caches from the natural nest were transferred to the laboratory

nest, and the colony was given additional seed (*Lepidium perfoliatum*) to harvest from the foraging area.

After 3 days the colony had established an extensive network of chambers and tunnels in the soil. The nest had a 2-dimensional morphology resembling a 1-cm slice of naturally occurring nests, and the colony had resumed normal daily foraging cycles. The brood was tended by about 50 nurse workers and was concentrated near the queen in 1 medium and 3 large chambers at depths of 35, 40, 45, and 47 cm.

On the 4th day, the colony was offered an artificial thermal gradient during the middle of the dark cycle. A 30-cm-square heating pad was attached to one side of the glass at the top of the nest. We created a thermal gradient by placing cardboard of varying thickness between the heating pad and the glass of the nest. Temperatures in this gradient ranged from 39°C at 2.5 cm to 21°C at 50 cm. Brood individuals were initially concentrated 5–17 cm below the heat source. Heat was applied at 2330 hours, and a stable thermal gradient was achieved within 30 minutes. Brood location and related observations were recorded every 30 minutes between 2330 and 0400.

RESULTS

Field Study

No brood individuals were present above 20 cm in either shaded or nonshaded colonies excavated between 0830 and 0900 hours. From 0900 to 1130, shaded colonies contained significantly less brood in chambers above 20 cm than nonshaded colonies, t (15) = 6.93; P < 0.0001. Sample means were 6.3 for shaded colonies and 104.3 for nonshaded colonies. From 0900 to 1130 hours, brood were present at a depth of 0–2.5 cm in all nonshaded colonies, while brood were present at this same depth in the shaded colonies on only 2 occasions, and in far fewer numbers (Fig. 1). One of these occasions represents the highest surface temperature attained by a shaded colony (29.8°C at 1058 hours).

Shading reduced the surface temperature of the nest-cone and brood chambers 2.5 cm deep, but differences were not as great at depths of 5 and 10 cm. Surface temperatures of shaded colonies ranged from 20.9°C to 29.8°C, and increased at a rate of 2.5°C per hour, while surface temperatures of nonshaded colonies ranged from 22.8°C to 48.8°C, and increased at a rate of 7°C per hour.

Lab Study

Location of brood in the artificial nest shifted markedly in response to the thermal gradient (Fig. 2). Temperatures in the 35–50 cm region of the nest were relatively unaffected by the addition of the thermal gradient: 20.5°–21.3°C before heat was applied and 20.9°–22.5°C during the experiment. Two hours after the gradient became stable, only 20% of brood remained in the region (35–50 cm) where all brood had been located prior to presentation of the gradient.

At 2400 hours very few brood individuals had changed position relative to temperature, and approximately 40% of brood were being carried by nurse workers. No net pattern of brood movement was evident. By 0130, approximately 25% of brood were stationary in warmer locations, nurse workers were carrying 65% of brood, and the entire colony was very active. By 0230, most brood individuals were concentrated at a depth of 20–30 cm in 4 large chambers with temperatures in the 29.2°–36.4°C range (Fig. 2). Also at 0230, worker movement in the 39.5°C chambers at a depth of 10 cm was most transient, and brood individuals were not deposited there but were quickly transported through that region of the gradient.

The artificial temperature gradient unexpectedly and differentially dried the soil within the artificial nest, creating drier soil patches within the walls of the warmest chambers. At 0300 hours lines were drawn on the glass to delineate dry from moist soil. By 0330, the moist soil had been reduced from 45% to 35% of the total chamber area. All but a few stray brood individuals had been crowded into the moist patches of the 29.2°–36.4°C chambers.

DISCUSSION

Our results strongly indicate that brood relocation in *P. salinus* is highly sensitive to hourly temperature changes and is not a strict circadian rhythm. First, if a strict daily rhythm controlled brood relocation in *P. salinus,* brood in shaded colonies would be expected to occupy chambers close to the surface about the same time as brood in nonshaded colonies. However, we found that brood movement in
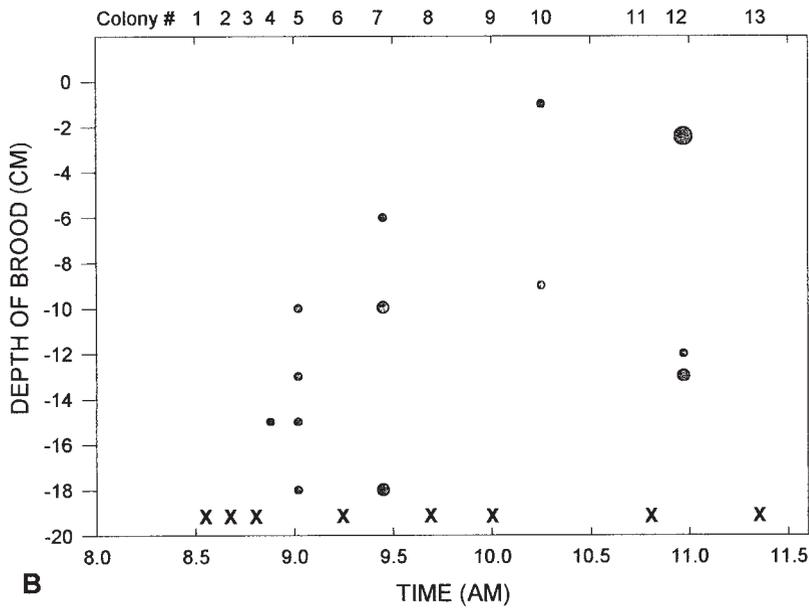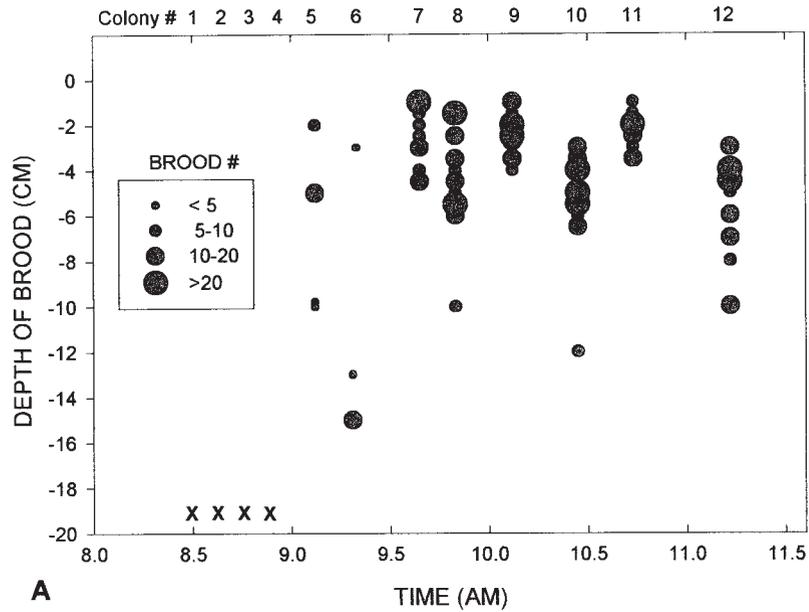
Fig. 1. Brood abundance and depth in 12 nonshaded (A) and 13 shaded (B) colonies. Data recorded between 0830 and 1130 hours, 23 July 1996, from 25 separate mounds with the same general substrate, shape, and solar exposure. An **X** indicates no brood detected in that colony to a depth of 20 cm.
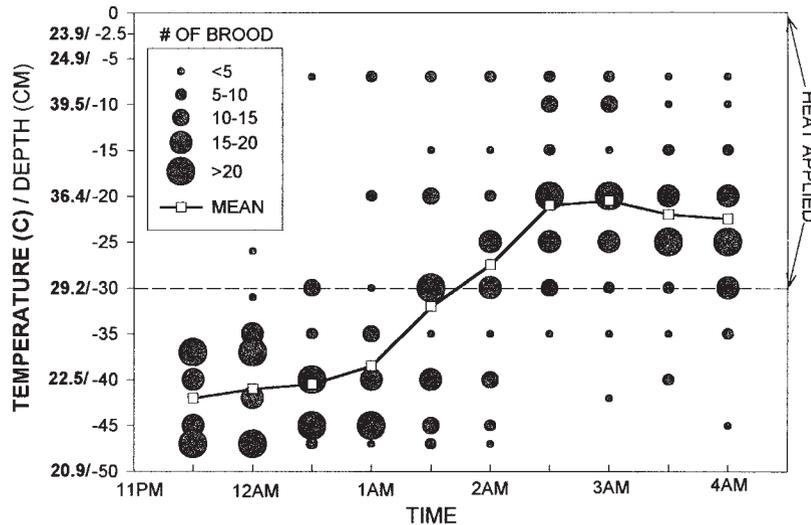
Fig. 2. Brood abundance and depth relative to temperature recorded every half hour from 2330 to 0400 hours following presentation of a thermal gradient. Heat was applied to the artificial nest between 0 cm and 30 cm (indicated by the dotted line) at 2330. The thermal gradient (temperatures in bold) became stable at 2400 hours and remained stable throughout the experiment. The bold line shows the change in mean brood depth over time.

shaded colonies did not occur at the time of day mounds are usually warmed by the sun, but instead depended on the temperature of the nest-cone. Second, if nurse workers were controlled by a strict endogenous rhythm, no immediate response would be expected to artificial heat applied at a time when the soil is normally cool. However, we found that artificial heat caused significant brood relocation 10 hours prior to the time brood are usually translocated in the field. In both experiments nurse workers of *P. salinus* were highly responsive to sudden changes in the normal temperature cycle.

Our results contrast with those of Roces and Nunez (1996) for another temperate species, *Camponotus mus*. We found that *P. salinus* selected high temperatures for brood during the cool/dark phase of the diel cycle. However, *C. mus* did not tolerate a 3-hour advance in their natural temperature cycle. Instead, *C. mus* nurse workers responded to an advanced thermal cycle by removing brood from an area of unexpected warm temperature to an area with cooler temperature. It is apparent that *P. salinus* have a different mode of thermoregulatory behavior than that found in *C. mus*, in which an endogenous daily rhythm triggers a thermal-searching behavior in anticipation of

temperature extremes (Roces 1995). The present study does not exclude the possibility of an endogenous brood-relocation rhythm in *P. salinus*. However, it is clear that proximal temperature cues can modify or override any endogenous rhythm controlling brood care in *P. salinus*.

The ability to respond directly to proximal temperature cues would be adaptive for activities that rely on temperature, such as brood relocation (as has been shown in this study) and foraging. Harvester ant foragers show significant nonrhythmic activity in response to temperature. McClusky and Neal (1990) concluded that diversity between the foraging patterns of 6 species of desert ants could be explained by a circadian rhythm heavily modified by temperature response. Morton and Davidson (1988) found that the foraging of 4 of 10 harvester ant species was strictly nocturnal or diurnal, apparently under endogenous control, while foraging of the other 6 was highly responsive to temperature. In the genus *Pogonomyrmex*, an endogenous rhythm apparently aids the timing of foraging in *P. californicus* and *P. rugosus* (McCluskey and Soong 1979). Even when a rhythm is evident in harvester ants, it appears to be easily overridden or at least frame-shifted by unpredictable environ-

mental variation. *Pogonomyrmex salinus* forages during midday when clouds cover the sun or a tree casts a shadow across the mound surface (Willard and Crowell 1965). During abnormally hot summer conditions, many species of harvester ants will shift from diurnal to nocturnal foraging (Cole 1932, Tevis 1958, McCluskey 1963, Whitford and Ettershank 1975, Smith et al. 1987). These studies suggest that immediate response to temperature may be as influential as light or temperature cycles in coordinating the daily foraging activity of harvester ants.

Activity patterns in harvester ants are strongly affected by moisture, and many species of *Pogonomyrmex* will forage at odd times if the soil is wet (Whitford and Ettershank 1975, Gordon 1991). Brood individuals have a thin cuticle and are more sensitive than adults to conditions of low moisture. Moisture patterns in the nest soils provide an important humidity gradient that harvester ants can exploit to protect their brood from desiccation (MacKay 1981). The effect of humidity on larval development was dramatic in the fire ant *Solenopsis invicta.* Larvae in chambers with less than 100% humidity were not fed by workers, died of starvation, and were eventually cannibalized (Cassill and Tschinkel 2000). In the lab portion of the present study, nurse workers continually moved brood from dry to moist soil within the chambers, suggesting that brood relocation behavior in *P. salinus* is influenced directly by humidity.

In conclusion, *P. salinus* nurse workers are not strictly tied to an endogenous rhythm, but instead exhibit a high degree of behavioral flexibility in moving brood to temperatures and possibly humidity levels that facilitate brood development. Further investigations are required to determine the influence of temperature cycles and humidity on brood-relocation behavior. This short-term study addressed critical hours of the temperature cycle within a single day. To determine if an endogenous rhythm entrained by temperature is present in *P. salinus,* the brood relocation behavior of nurse workers should be recorded for several consecutive days in a fixed-temperature gradient void of usual environmental cues. Future studies should explore the interaction of temperature and moisture, as nurse workers appear to respond simultaneously to unexpected changes in these variables.

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