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Nest architecture in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson)

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Summary

The structure and thermal environment produced by the nest cones of the western harvester ant, *Pogonomyrmex occidentalis*, are investigated. The nest cone is oriented so that the longest slope faces towards the southeast ad the nest entrance faces the southeast. The temperature of the soil was monitored at thirty-six locations within the nest in order to measure the daily temperature change as a function of depth, aspect and radial distance from the center of peak of the cone. The occupancy of the nest cone by workers and by brood was assessed by core samples taken at different times of day in different portions of the cone. The brood are only present during the midmorning sample and are present in greatest numbers on the eastern side of the cone. The adult workers are present in the cone in highest numbers during the midmorning, virtually absent from the cone during mid-afternoon and returning in smaller numbers at dusk, apparently spending the night near the surface on the eastern side of the mound. The eastern and southern portions of the cone are occupied most frequently while the western side of the cone is nearly vacant. The nest cone is an adaptation which magnifies the amplitude of daily temperature fluctation. By moving to appropriate areas of the nest cone, the ants can take advantage of the increased range of temperature.

Introduction

A problem commonly faced by desert-dwelling arthropods is the extreme daily temperature variation. Daytime temperatures often exceed 60° at the ground surface, while nighttime temperature can fall to near freezing. Rapid heating has the effect of limiting to a narrow time window the time available for activities such as foraging (Wehner et al. 1992). A number of desert ants have behavioral adaptations for dealing with extremely high temperatures (e.g. seasonal shifts to nocturnality: Dlussky 1981, Hölldobler 1976) and they also retreat into the nest during the hottest parts of the day. At the other extreme adaptations to increase the rate at which warming occurs can increase the size of the foraging window. In this paper I shall examine the role of the nest cones of the western harvester ant, *Pogonomyrmex occidentalis* as a test of the hypothesis that the nest cone functions as an adaptation to increase the rate at which the ants increase their temperature on cool mornings.

The conical nest cones of *P. occidentalis* are one of the most conspicuous and characteristic features of deserts and grasslands in western North America. These nest sites can be occupied for long periods of time. Nest sites are visible in aerial photographs at least for decades. Young colonies are known to move into older, abandoned nest sites (Wheeler and Wheeler 1986) suggesting that the nest structure itself represents a resource of considerable importance to the colony. In the closely related species *P. owyheei* (Lavigne 1969) the nest consists of a central tunnel system to a depth of about two meters which is ramified into several vertical tunnels in larger nests. The queen is found in chambers near the bottom of the tunnel system. The nest is surmounted with a conical mound. It has frequently been noted that the entrance to the nest is usually towards the southeast (an observation that goes back at least to McCook 1881) and this has led to speculation that the nest architecture, especially the cleared area surrounding the nest of this species allows workers, in the chambers immediately beneath the soil to warm up more quickly in the morning (Wheeler and Wheeler 1986).

The temperature within the nests of other mound-building ants, e.g. *Formica polyctena*, (Coenen-Stass et al. 1983, Horstmann and Schmid 1986) is known to be affected by the presence and structure of the mound. Covering the surface of the mound with pebbles has been suggested as a design feature which results in trapping heat (see Hölldobler and Wilson 1990, page). I wish to make a distinction between those features of design which dampen environmental fluctuations in an adaptive fashion (homeostatic) and those which magnify environmental fluctations in an adaptive fashion which I refer to as heterodynamic. By this term I refer to a design which incorporates positive feedback or which exaggerates structural characteristics in order to increase the dynamic range of environmental change in an adaptive manner.

Materials and methods

This study was done on Bureau of Land Management land approximately 15 km northwest of Fruita (Mesa Co.), Colo. (39° 16′ N, 108° 45′ W) at 1470 m elevation. The study site is dominated by saltbush (*Atriplex* spp.) and greasewood (*Sarcobatus vermiculatus*). The dimensions of fifty mounds were measured to establish the physical characteristics of typical mounds. The height of the mound at the peak, the length on the north-south axis and the length on the east-west axis was measured. The bearing of the nest entrance from the peak of the nest cone was determined. The volume of the nest cone was estimated as if the nest cone was a regular elliptical cone. This was not always the case because the peak of the cone was generally offset from the center of the mound, however, the estimate of nest cone volume is accurate to the extent that the mounds have similar shapes. The angle of the slope from the entrance to the peak is calculated by knowing the offset of the peak from the center of the cone, the height of the cone and assuming that the angle of the nest cone is constant across the nest surface.

I obtained a daily temperature curve from a mound on May 24, 1988 (a day with clear skies during the entire day) in order to describe the effects of depth and aspect within the mound on temperature fluctuation. Temperatures from a number of locations within a mound have never been measured before. Temperature was recorded at three depths, from each of twelve locations within the nest cone. Measurement at the three depths, 5 cm, 10 cm and 15 cm below soil surface were taken at 5 cm horizontally from the peak of the cone (on the E, S, W and N facing slopes of the nest cone), 20 cm from the peak of the cone (E, S, W and N facing slopes of the nest cone), 35 cm from the peak of the cone (E, S and N facing slopes) and 50 cm E of the peak of the cone (i.e. the nest cone did not extend 50 cm to the S). The asymmetry in temperature collecting locations was due to asymmetry in the nest cone itself. Plastic soda straws were inserted into the nest cone to the proper depth and left there for subsequent measurements. Two cm of the straw protruded above the surface at each of the thirty-six measurement sites. The end of each straw was plugged with foam rubber to reduce airflow. Temperature was measured nineteen times at each depth and position every 45 minutes from approximately 6:00 am to 9:00 pm. Temperature was measured with a Wescor TH-65 thermocouple and was recorded to the nearest 0.1 °C.

To determine the position of the adults and brood within the nest cone, throughout the day, a series of core samples were taken of nest cones. Core samples were taken at four times during the day, 6–6:30 am, 10–10:30 am, 2–2:30 pm and 7–8 pm. Each series consisted of cores of sixteen nests, four cores each from east, south, west and north-facing mound slopes. Three sets of nest cores were taken at dawn and mid-afternoon and four sets of nest cores were taken at mid-morning and dusk. A total of 224 nest cones were cored; a nest cone provided a single core sample to control for the effects of damage to the nest. Each core sample consisted of the material from a 5 cm diameter core driven 10 cm into the nest halfway up the appropriate slope of the cone. The numbers of adults and of brood were recorded, and the data square root transformed for analysis of variance.

Results

The fifty nest cones of *P. occidentalis* averaged 83 ± 21 cm (= 1 standard deviation) on the north-south axis, 81 ± 22 cm on the east-west axis, and 19 ± 5.2 cm in height. Not surprisingly, the lengths of the two axes are correlated with one another (Fig. 1a), as is the height of the mound and the diameter (Fig. 1b). The height of the mound scales linearly with the diameter. Furthermore, the angle between the ground surface and the slope of the nest toward the entrance (mean = 21°) is not a function of the size of the nest cone (Fig. 1c). Apparently, there is isometric scaling of the nest mound; nests do not vary in shape as a function of size. A frequency histogram of the estimated nest volume is given in Fig. 2. The mean volume is 39.2 liters and the distribution is roughly lognormal. The nest entrance is oriented towards the southeast (Fig. 3, mean direction 120°, mean vector length 0.74, $p < 0.001$).

In Fig. 4, I summarize the diurnal temperature changes in the nest cone as a function of depth (Fig. 4a), aspect (Fig. 4b) and distance from the peak of the cone

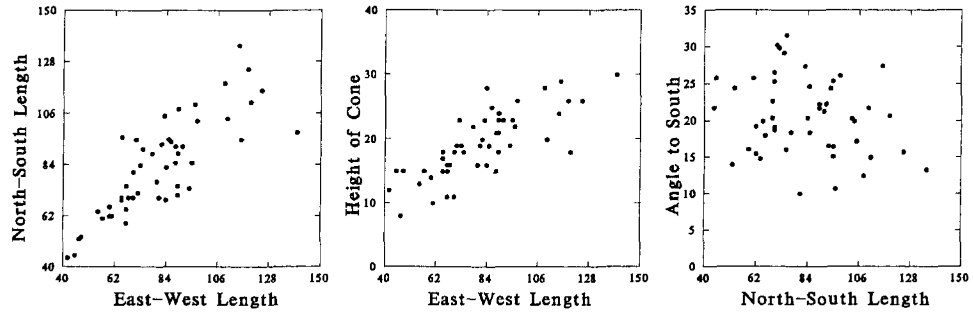

Figure 1. The lengths of the north-south and east-west axes (in cm) of the nest cones of *Pogonomyrmex occidentalis*. The correlation (0.82) is highly significant ($p < 0.001$). B. The height of the nest cone as a function of its east-west diameter. The correlation (0.78) is highly significant ($p < 0.001$). C. The angle of the southern slope of the nest cone as a function of the size of the cone. There is no correlation between the two quantities ($r = -0.21$, $p = 0.14$)

(Fig. 4c). Depth has the expected effect on diurnal temperature variation. Temperature fluctuation is greatest at the shallowest soil depths (hottest during midday and coldest at dawn). Temperature fluctuation at shallow depth precedes the fluctuations deeper in the soil. The aspect and the distance from the peak of the mound also have an effect on temperature fluctuations. As might be expected, the eastern side of the mound heats more rapidly in the morning than the western side of the

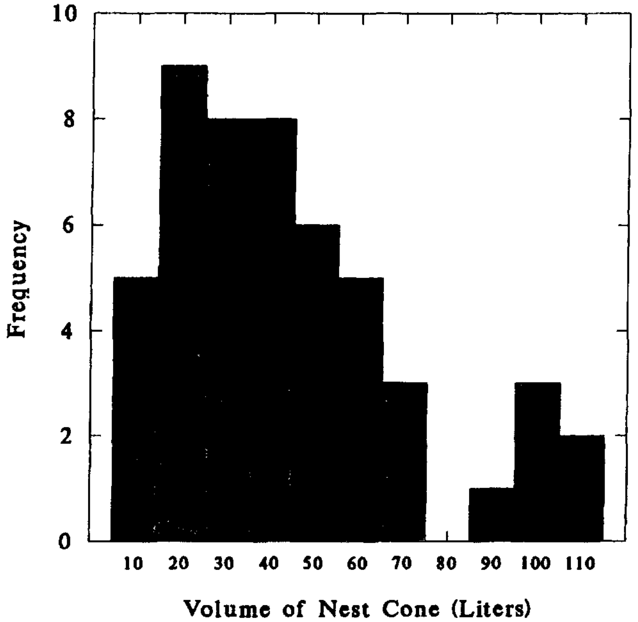

Figure 2. A frequency distribution of the estimated volume of the nest cone. The mean is 39 liters

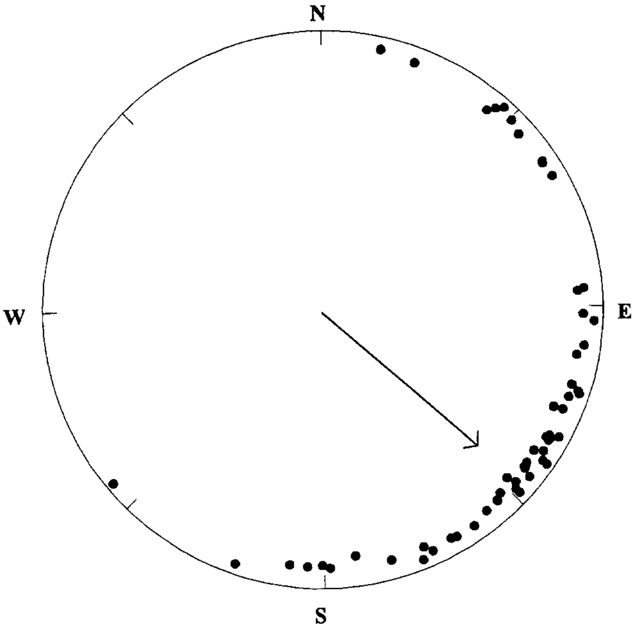

Figure 3. The location of the nest entrances of the mounds and the mean vector. The length of the mean vector is highly significantly different from zero

mound (Fig. 4b). At 10:30 am the temperature difference between east and west was approximately 7°C. The maximum temperature was the highest on the southern exposure, at approximately 4 pm. The lowest maximum temperature was reached on the northern side of the nest. The radial distance from the peak of the nest also affects daily temperature variation. In general, the temperature near the fringe of the nest cone was higher through mid-morning but higher maximum temperatures were reached as one approached the peak of the nest cone.

To get a dynamic view of the use of the nest cone during the day, I used the core samples of nests at different times of day and on different sides of the nest. The results are summarized in Fig. 5 which shows the mean number of adults (5a) and brood (5b) per sample at the four times of day and in the four directions. The data were analyzed using a two way analysis of variance (Table 1). The brood were only recorded from the mid-morning sample indicating that they must be taken up into the nest cone during the morning as the cone warms and are taken out of the cone, into the nest proper, as the cone reaches very high temperatures. For the brood there is a significant effect of the time of day, but no effect of the direction of exposure.

The pattern of adult occupancy is more complicated. Again, the highest frequency of workers in the cone occurs at mid-morning. There are many fewer present in the cone at dawn and at dusk, while the cone is almost completely unoccupied during mid-day. Furthermore, there is a significant direction effect. The workers, when present, are most likely to be found in the eastern portion of the

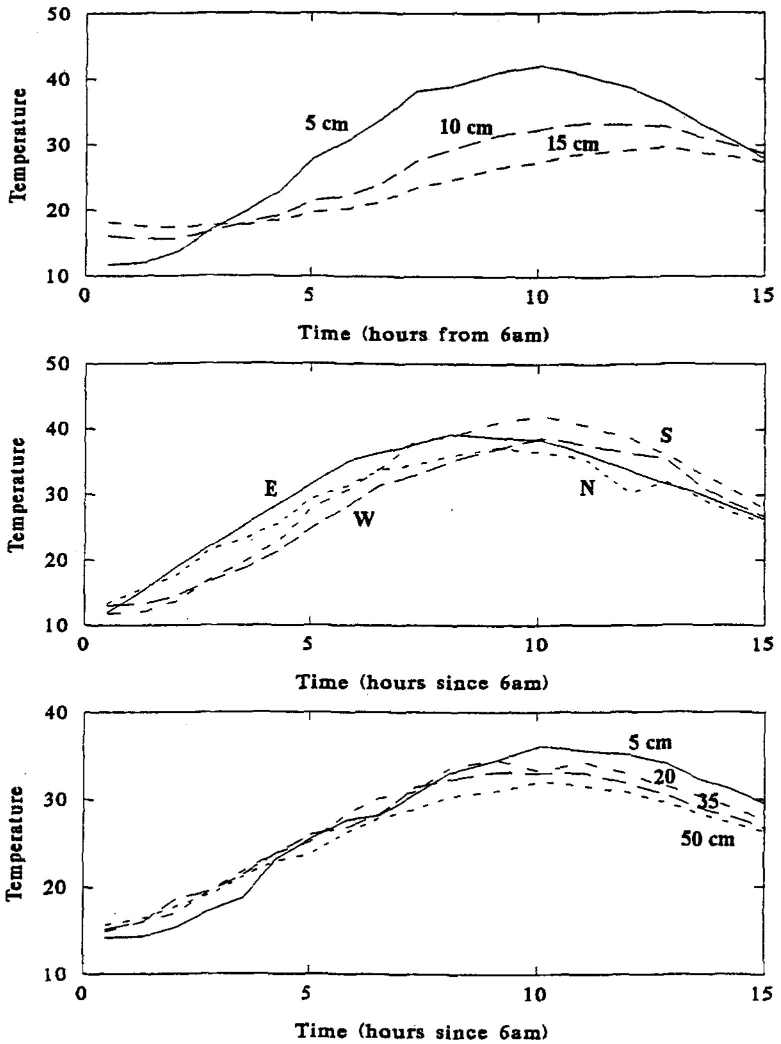

Figure 4. Daily temperature curves from within the nest mound. A. The effect of depth on daily temperature variation. The temperature measurements are taken from the southern slope, 20 cm from the peak of the mound, at three depths, 5 cm, 10 cm and 15 cm. B. The effect of direction of exposure on temperature variation. The temperature measurements are taken from a depth of 5 cm, 20 cm from the peak of the nest cone. The temperature is nearly identical at dawn, but increase most rapidly on the eastern and southern side of the mound. C. The effect of distance from the peak of the mound on daily temperature variation. The depth of all temperature measurements is 5 cm and all were taken on the eastern side of the mound. The temperature at 5 cm from the mound peak was the lowest in the morning; in the evening, the temperature decreased with the distance from the peak of the nest cone.

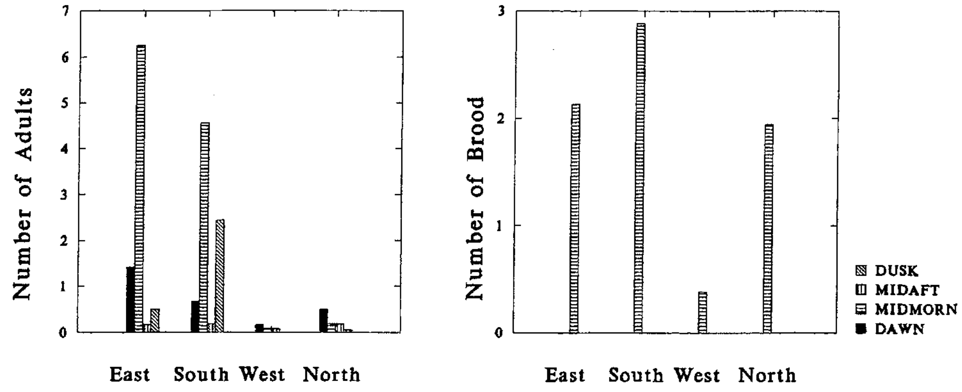

Figure 5. A. The average number of workers captured in core samples taken from the nest cone as a function of aspect and time of day. The number of workers taken was relatively high during the dawn sample, reached a maximum at the mid-morning sample, and a minimum during the mid-afternoon sample. Workers were virtually absent at all times from the western portion of the nest cone. B. The average number of brood (of all stages) taken in core samples from the nest cone as a function of aspect and time of day. Brood were only taken during the mid-morning sample and were least abundant on the western side of the nest cone

Table 1. Analysis of variance of adult worker occupancy of the nest as a function of the time of day and the direction in the mound

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
time	36.886	3	12.295	16.822	0.000
direction	11.211	3	3.737	5.113	0.002
time · direction	18.228	9	2.025	2.771	0.004
Error	152.025	208	0.731		

Analysis of variance of brood occupancy of the nest cone as a function of the time of day and the direction in the mound

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
time	15.939	3	5.313	12.323	0.000
direction	1.072	3	0.357	0.829	0.479
time · direction	3.575	9	0.397	0.921	0.508
Error	89.681	208	0.431		

cone. Finally, the time-direction interaction effect is also significant. This latter is less surprising since workers are almost never found on the west side of the cone; it is then almost inevitable that the effect of time of day would be different between the east and west. In summary, adults flux into the nest cone during the morning, move out during mid-day and move back in, in smaller numbers, at dusk.

Discussion

The nest cone of *Pogonomyrmex occidentalis* seems to act as a solar collector by increasing the interception of morning sunlight at a low angle in accord with previous suggestions (Wheeler and Wheeler 1986). The mound slopes more to the south and east than would be expected because the peak of the mound is displaced to the north and west from the center of the cone. The nest entrance is oriented toward the southeast, which would allow any workers gathered at the nest entrance to take advantage of the southeastern slope. The workers take advantage of the nest morphology by gathering before dawn, perhaps by dusk the previous day, in chambers near the nest entrance. Those workers that are in nest cone before dawn are concentrated on the eastern side of the cone although at that time of day the nest cone is not any warmer on the eastern side. The workers gather on the eastern side in anticipation of warming. At dawn and at mid-morning the eastern portion of the nest cone is occupied, while the other parts of the nest cone are relatively unoccupied as is the entire nest cone during mid-afternoon.

The pattern of movement of workers and brood into and out of the nest cone during the day is an interesting one. During mid-morning, when there is a great deal of nest activity by foragers, the occupancy of the nest cone is also high. Although the nest cone is completely deserted during the mid-afternoon, workers return by dusk. Presumably those workers that occupy the nest cone during the evening are those who occupy the nest cone at dawn the next day. The movement of brood into the nest cone, in moderate numbers, at mid-morning may allow the colony to take advantage of the higher temperatures to increase the rate of brood development. An alternative explanation, that does not require the brood movement to be adaptive, is that the greater overall activity of workers in the nest cone at mid-morning results in incidental transport of brood into the nest cone. The brood are then actively transported out during the hot afternoons. The data do not allow me to explicitly distinguish these alternatives, however indirect evidence favors the former explanation. The volume of a core sample represents less than 1% of the volume of the nest cone (Fig. 2). Since a core sample averages 1.8 pieces of brood, the total amount of brood in the nest cone is probably over 300. In the closely related *P. owyheei* (Lavigne 1969) a nest contains approximately 1000–3000 brood depending on the time of year. Since a substantial fraction of the total brood may be in the nest cone during the mid-morning, the hypothesis of active transport seems plausible.

The temperature variation within nest of other ants, including the mound building *Formica* (Coenen-Stass, et al. 1980, Horstmann and Schmid 1986, Rosengen et al. 1986, MacKay and MacKay 1984) and *Pogonomyrmex montanus* (MacKay and MacKay 1985) has been studied. The nest cones of *F. polyctena* which slope towards the south represent a convergence in the nest architecture of organisms which depend on reaching a critical body temperature for foraging in a cool climate. The species of *Pogonomyrmex* which build cone shaped nests without entrance craters are *P. occidentalis* and the closely related *P. owyheei*. These are the two species of *Pogonomyrmex* which have the most northerly distribution (*P. owyheei* is found well into Canada and *P. occidentalis* found as far north as North Dakota) and it seems reasonable to speculate that the structure of the nest cone contributes to the ability of these species for rapid diurnal warming. For completeness it must be noted that there are sympatric species of *Pogonomyrmex* which produce nest structures that do not have a conical shape or which do not appear to be designed to capture sunlight more effectively. *P. rugosus*, for example, which creates a flat gravel disc over its nest is also near the northern limit of its distribution.

The architecture of the nest of *Pogonomyrmex occidentalis* seems to be adaptive. For *P. occidentalis* the functional characteristics of the nest are heterodynamic, magnifying environmental variation for the apparent adaptation of extending the time available for foraging or to increase the amount of time favorable for the development of brood. While they produce a microenvironment that warms more quickly in the morning, it also produces a microenvironment that heats more during the midday. The range of temperature variation 5 cm below the ground surface was a low of 12.9° and a high of 41.8°, while the range of temperature fluctuation at a depth of 5 cm, near the peak of the nest cone was from 10.7° to 43.3°. These heterodynamic features of nest architecture stand in contrast to nest design features that result in homeostasis within the nest. The use of insulation (as in *Formica haemorrhoidalis*, MacKay and MacKay 1984), production of ventilation tunnels to maintain a constant thermal environment, or for the exchange of gases (e.g. in termites, Gay and Calaby 1970, Noirot 1970), behavioral adaptations to maintain constant temperature such as movement within the nest (e.g. Gay and Calaby 1970 for *Apicotermes meridionalis*) and the more elaborate temperature regulation mechanisms of honeybees (e.g. Seeley 1985) are examples of homeostatic adaptations.

Typically we think of environmental fluctuation as deleterious, disruptive to the maintenance of optimal conditions and something to be overcome through a homeostatic adaptation. However, under some circumstances one can imaging that environmental fluctuations could be exaggerated in an adaptive fashion. Amplifying environmental fluctuations could increase the amount of time available for foraging by allowing earlier onset provided the organisms are capable of later heat avoidance. Such heterodynamic adaptations may be common in small, mobile poikilotherms that must utilize a narrow window in environmental conditions.

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