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TEMPERATURE REGULATION IN THE INCUBATION MOUNDS OF THE AUSTRALIAN BRUSH-TURKEY[1]

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Abstract. The Australian Brush-turkey, *Alectura lathami,* constructs incubation mounds of decomposing forest litter in which many large eggs are incubated by microbial heat generation. On Kangaroo Island, the average mound is about 12.7 m^3 and weighs about 6,800 kg. It maintains an incubation temperature of 33°C in an average ambient air temperature of 18°C. When eggs are in the mound, the rate of heat production is estimated to be about 100 Watts, a value more than 20 times the heat production of the resting adult. Thus, the mound can incubate many more eggs than would be possible in a normal nest.

Core temperature is stable due to mound size and biophysical homeothermy. Mounds tend to reach a stable "equilibrium temperature" at which the rate of microbial heat production equals the rate of heat loss to the environment. The bird adjusts equilibrium temperature by adding or removing litter as required. A numerical computer model, incorporating experimental data on mound size, ambient temperature, and the mound material's rate of heat production, water content, dry density, and thermal conductivity, predicts that as little as 1 cm of litter added to the mound will raise core temperature about 1.5°C.

Experimental manipulation of artificial and natural mounds uphold the model and indicate that functional mounds require (1) a critical mass of fresh litter (ca. 3,000 kg), (2) sufficient water content (>0.2 ml/g dry material), and (3) occasional mixing of the litter. Once constructed and adjusted, natural mounds require little attention, and larger ones can stay warm for several weeks without the bird. The mound characteristics appear to minimize the work required for maintenance. The bird maintains water content of the mound at a level ($\bar{x}$ = 0.3 ml/g) that minimizes thermal conductivity and microbial heat production. Therefore, heat is retained in the mound and decomposition occurs slowly, reducing the requirement to collect fresh litter. Kangaroo Island mounds are larger than those in sub-tropical rainforest, probably because rates of decomposition of mound material are lower, not because of differences in either thermal conductivity of the material or ambient temperature.

Key words: Megapode; incubation; incubation mound; thermoregulation; egg; thermodynamics.

INTRODUCTION

The nesting habits of birds are diverse, but practically all groups share the common feature that an adult provides the heat for incubation and regulates egg temperature (Skutch 1976). An exception to this rule is the Family Megapodiidae, the megapode birds of Australia and adjacent Pacific islands. Megapode eggs are incubated underground where the heat comes principally from solar, geothermal or microbial heat production (Frith 1956b). Some species insert eggs in warm soil, but others build incubation mounds of decomposing plant litter. Because close contact between the eggs and adult has been lost, regulation of incubation temperature is less direct, and it relies either on the thermal stability of the nesting sites or on active manipulation of the sites by the birds.

There are nineteen species of megapode birds, three of which construct mounds in Australia: Mallee Fowl (*Leipoa ocellata*), Orange-footed Scrubfowl (*Megapodius reinwardt*), and Australian Brush-turkey (*Alectura lathami*). H. J. Frith has produced a detailed study of thermoregulation in the sandy incubation mounds of the Mallee Fowl (Frith 1962 and references therein). This classic work shows that the core mound temperature remains near 34°C throughout the nine-month breeding season, because the bird manipulates the mound size and shape according to the intensity of solar and microbial heat input. In spring, the mounds are heated mainly by decomposition of mallee litter situated just below the eggs. In summer, decomposition diminishes and the bird prevents overheating of the eggs by keeping the mound piled high with sand. Solar heat

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decreases in autumn, but the bird is able to keep the eggs warm by spreading the sand to warm in the sun during the day and piling it over the eggs at night. Frith (1956a, 1957) experimentally altered heat production and heat loss in natural mounds and confirmed that the bird's behavior is instrumental in thermoregulation. He also made artificial mounds and observed the factors important in maintaining incubation temperature.

We wished to analyze the biophysical factors of the megapode incubation mound and account for the remarkable temperature stability. However heat transfer through Mallee Fowl mounds is complicated by the ever-changing heat sources, which makes quantitative analysis of mound thermoregulation quite difficult. Therefore we analyzed heat flux in another mound-builder, the Australian Brush-turkey, which manipulates heat input from only one source. The male builds incubation mounds consisting almost entirely of forest litter, usually in shaded situations (Jones 1988a). The major heat source is microbial respiration (Seymour et al. 1986). Moreover, the temperature distribution in the mounds is reasonably symmetrical (Seymour and Ackerman 1980), unlike the case of the Orange-footed Scrubfowl which nest in large communal mounds that heat unevenly (Crome and Brown 1979).

Seymour (1985) proposed that Brush-turkey mounds are stable homeotherms. That is, the core temperature approaches a stable "equilibrium temperature" at which the rate of heat production in the mound is equal to the rate of heat loss. If the mound is cooled (say, by opening it to deposit an egg and then closing it again), the rate of heat loss becomes less than the rate of heat production, and the mound rewarms toward the equilibrium temperature. On the other hand, if the mound somehow becomes warmer than the equilibrium temperature, heat loss exceeds heat production, and the mound cools to equilibrium temperature. Heat production depends on the rate of microbial respiration which in turn depends on the temperature and water content of the mound material. Heat loss depends on mound size, thermal conductivity of the material, and ambient temperature. To investigate the importance of these factors, we constructed a numerical computer model that calculates the equilibrium core temperature in a volume of mound material bounded by a constant surface temperature. We quantified the variables of the model with measurements from natural mounds in the field.

METHODS

NATURAL MOUNDS

Brush-turkey mounds were studied during five breeding seasons (1979–1984) on Kangaroo Island, near Adelaide, South Australia. Although not native to the island, a population has flourished in Flinders Chase National Park since the introduction of a pair in 1948 (Ford 1979).

Temperature distribution was measured within natural mounds at selected times by inserting a 1.5 m Fiberglas fishing rod blank that had copper-constantan thermocouples placed in it at 10 cm intervals. After temperature stabilized, the outputs were read to the nearest 0.1°C with either Comark or Wescor electronic thermometers. A single vertical transect was always made in the center, but when necessary, a complete section was made by inserting the probe at intervals across the mound. Isotherms were drawn on a cross-sectional profile by interpolation. Continuous records of temperature were also made with Grant analog recorders and thermistors positioned at selected depths in the mound center. The thermistors were introduced without disturbing mounds by inserting them with a rod from the edge of the mound base.

Because the mounds were rarely on level ground, positions in the mound were measured with reference to a horizontal "ground level" line that was chosen to pass through the mound center and two points on bare ground that were at the same elevation, as determined with an optical surveyor's level. A measuring tape was strung above the mound, parallel to "ground level," and vertical distances were measured down from it. Mound diameters and circumferences were measured to the nearest 10 cm, and vertical distances were accurate to 5 cm. Volume and surface area of the mound were calculated assuming the mound was a segment of a sphere protruding from the ground. The radius of the sphere was calculated from the base diameter and height of the mound (see Fig. 1).

CHARACTERISTICS OF MOUND MATERIAL

Samples of natural mound material were collected and analyzed for dry density (g dry material/cm^3), water content (ml/g dry material) and air-filled porosity (cm^3 air/cm^3) as described ear-

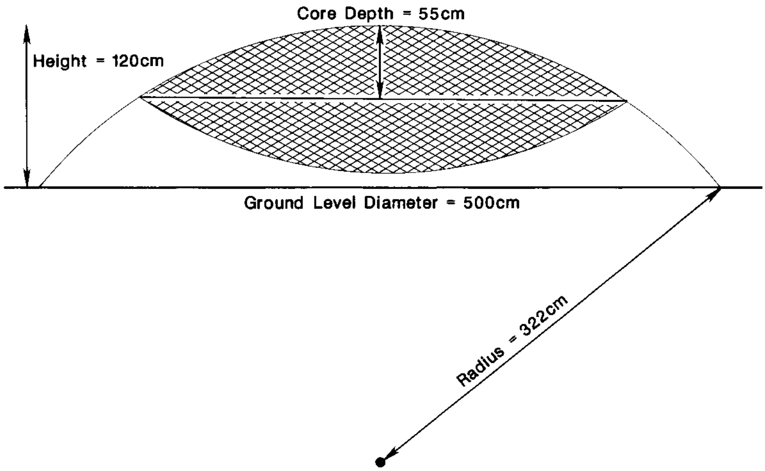

FIGURE 1. Model of an average Brush-turkey mound on Kangaroo Island. A sphere of 322 cm radius is superimposed on the mound of 500 cm base diameter and 120 cm height. Equilibrium heat production, radial heat flux, and temperature are computed at 0.4 cm increments in radius assuming heat production occurs only in the outer 55 cm of the entire sphere. To provide a more realistic estimate for total heat production in the mound that occupies only part of the sphere, heat production is also computed assuming it occurs only in the lens-shaped region with a center at 55 cm depth (see text).

lier (Seymour et al. 1986, 1987). In addition, some of the dried mound samples were burnt in a muffle furnace at 600°C and the ash content (g/g dry material) determined. The complement of ash content is the organic content. All mass-specific measurements refer to dry mass.

Thermal conductivity of mound material was measured in a custom-built apparatus consisting of three concentric copper tubes, 1.5 m long and with radii of 0.42, 6.15, and 7.43 cm. The outer tubes were sealed together to form a water jacket that was perfused by a thermocirculator. A second thermocirculator pumped water at a different temperature through the thin central tube. Mound material was placed between the central tube and the water jacket, and heat flowed radially through it, outward or inward, depending on the temperature gradient. The ends of the instrument were plugged with 10 cm thick discs of expanded styrene to prevent heat loss, and sealed with thick latex diaphragms so that the gas space within the litter could be flushed with pure nitrogen to prevent respiratory heat production by microorganisms (Seymour et al. 1986). The water jacket was surrounded by foam insulation. Because this apparatus resembled an Australian sausage roll, we called it the sausage roll machine (SRM).

The temperature gradient across the mound material was maintained at about 30°C (about 40°C on the outside and 10°C on the inside or vice versa) and was measured with a Comark thermometer from two sets of parallel thermocouples that indicated average temperature. One set of two junctions was on the outside of the inner copper tube, 60 cm apart, and another set of six junctions was distributed on the inside of the water jacket, also 60 cm apart. The radial distance between the outer and inner thermocouples was 5.73 cm. To avoid non-radial heat flux at the ends, we considered heat flux in the central 57 cm of the 131 cm cylinder of material.

Heat flux was measured from the change in the temperature of the water as it flowed through the inner tube. This was measured with thermopile consisting of eleven pairs of fine, insulated copper-constantan thermocouples that were placed inside the inner tube so that the two sets of junctions were exactly 57 cm apart. The thermopile was calibrated to 0.02°C against a certified mercury thermometer and its output was measured with a Perkin-Elmer model 165 chart recorder. The rate of water flow was measured to 1 ml/min with a calibrated Gilson flowmeter and it was controlled so that the temperature change was about 1–2°C along the test section.

Radial heat flux ($\dot{Q}$) through a single layer cylinder with specified boundary temperatures was calculated by the equation (Chapman 1974, p. 49):

$$\dot{Q} = \frac{2\pi KL(T_1 - T_2)}{\ln(r_2/r_1)} \quad (1)$$

where $\dot{Q}$ was the heat flux rate (Watts), K was the thermal conductivity (W cm^{-1} $°C^{-1}$), L was length of the cylinder (57 cm), T_1 and T_2 were the inner and outer temperatures (°C), r_1 was the inner radius (0.417 cm) and r_2 was outer radius (6.15 cm).

The rate of heat flux to or from the central tube was calculated by the equation:

$$\dot{Q} = \dot{V}\Delta H \quad (2)$$

where $\dot{V}$ was the rate of water flow (ml/sec) and ΔH was the change in the water's heat content across the 57 cm test section. ΔH was calculated from the heat capacity of water (4.18–4.20 J ml^{-1} $°C^{-1}$), and the water temperature difference along the tube. Substituting Eq. (2) into Eq. (1) and solving for K:

$$K = \frac{\dot{V}\Delta H \ln(r_2/r_1)}{2\pi L(T_1 - T_2)} \quad (3)$$

A large sample of dry mound material was collected from several sites in two natural mounds. It was thoroughly mixed and sieved through a 1 cm wire mesh to remove larger pieces. Approximately 9.3 kg of the mixed material was sprinkled into the SRM without packing. The SRM was sealed and flushed with nitrogen (ca. 500 ml/min) for 30 min. The thermocirculators were attached and left for at least 6 hr, the time required for equilibrium, as demonstrated in pilot experiments. Flow rates and temperatures were then recorded at least three times, 30–60 min apart, to confirm stability. Then the temperature gradient was reversed by exchanging the thermocirculators and the procedure repeated.

The initial water content was 0.063 ml/g dry material, but water was added sequentially to bring the water content up through selected levels. The dry density remained constant at 0.54 g dry/cm^3 and the ash content was 0.59 g/g dry material. After each measurement at a given water content, the material was removed from the SRM and weighed in total. Three subsamples (ca. 400 g) of well-mixed material were weighed, dried at 100°C, and reweighed to determine water content. Water content was used to calculate the amount of water to be added to the material to bring it up to the next saturation level. The dried subsamples were returned to the material along with the required water, and the whole was thoroughly mixed in a plastic bag. All of the material was repacked into the SRM for the next run on the following day. As the water content increased, the material expanded and it required compression to repack it. Care was taken to repack the SRM evenly; if more than 100 g of material remained after packing, the entire amount was removed and repacked evenly.

Rates of microbial heat production in mound samples were measured as oxygen consumption (Seymour et al. 1986), assuming that 20 kJ is released when 1 liter of oxygen is consumed (Bartholomew 1982).

EXPERIMENTS ON MOUNDS

We constructed artificial mounds by raking forest litter and remains of old mounds into heaps resembling natural mounds. We manipulated mound size and water content in artificial and natural mounds to determine their effects on core temperature.

RESULTS

CHARACTERISTICS OF NATURAL MOUNDS

Jones (1988a) documents two phases of active mound life, the "construction phase" and the "maintenance phase." During the construction phase, most of the material is collected, the mound warms, often to temperatures above incubation levels, and no eggs are laid. In the maintenance phase, core temperature is closely regulated around 33°C and eggs are introduced at intervals. In this paper, we use Jones' terminology.

The shapes of the mounds on Kangaroo Island closely approximated spherical sections (Table 1; Fig. 1). In the construction phase, they were convex on top, but in the maintenance phase, they often had a plateau of about 1 m diameter. The mounds were usually constructed at the sites of older mounds and the material at depths greater than about 70 cm was usually invaded and solidified by roots and occasionally by termite galleries. The material above this level was kept soft, uniform and friable by the activities of the male bird. The surface of the mound consisted of a layer of coarse sticks, twigs and leaves. Greater detail of mound construction can be found in Fleay (1937), Baltin (1969), Seymour et al. (1986) and Jones (1988a, 1988b).

Litter from principally *Eucalyptus diversifolia*, *E. landsdowneana*, and *Acacia retinoides* com-

TABLE 1. Characteristics of maintenance phase Brush-turkey mounds that contained eggs. The two diameters are measured perpendicularly across the center of the mound. Statistics are grand means, 95% confidence intervals (CI), and number of individual mounds (n). Comparable data from Mount Tamborine, Queensland, are from Jones (1988a).

Variable	Kangaroo Island			Mount Tamborine		
	Mean	CI	n	Mean	CI	n
Height (m)	1.20	0.11	14	0.85	0.07	25
Diameter a (m)	4.89	0.44	14	3.59	0.29	25
Diameter b (m)	5.03	0.37	14	4.10	0.36	25
Temperature (°C)						
Surface (day)	21.56	1.27	16	19.56	1.54	22
Core	32.95	0.74	16	33.3	0.3	50
Depth of core (cm)	55.4	3.1	16			

prised the mounds. The largest component of microbial activity in maintenance phase mounds was fungal (10^7 colonies/g at 22°C and 35°C), with the most abundant organisms being *Penicillium* sp. However there were at least seven other genera of fungi present. Bacteria and actinomycetes were also present, but in lower proportion (10^6 colonies/g). Many of these organisms are common components of soil (Ellis and Keane 1981).

After the construction phase, the litter added during the maintenance phase offset mound subsidence, and the mound volume remained constant. In nine mounds followed throughout the breeding season, the changes in mean height (+3 cm) and circumference (+19 cm) were not significantly different from zero.

The average volume of 14 maintenance mounds was 12.7 m^3, assuming they were spherical sections (Table 1). At a mean dry density of 0.41 g/cm^3 and water content of 0.30 ml/g dry mass (Seymour et al. 1986), this represents about 6,800 kg of material. The minimum volume was 6 m^3 (3,200 kg) and the maximum was 20 m^3 (10,700 kg).

Ambient temperatures recorded continuously throughout the heart of the breeding season (4 November 1981–31 January 1982) rose from about 15°C to 20°C, but averaged 17.8°C (SD = 5.6, n = 314). The mean minimum and maximum were 13.4°C and 22.7°C and the absolute minimum and maximum were 5°C and 35°C.

The mean core temperature (i.e., the warmest point in the center) of maintenance mounds was 33°C (Table 1). In each of five mounds that were followed between November and February, core temperature varied only 0.9 to 2.0°C (mean 1.52°C). However, different mounds appeared to be regulated at temperatures varying up to 3.9°C. There were practically no diurnal changes in core temperature, but mounds tended to be warmer shortly after the construction phase at the beginning of the season, and they tended to cool slightly starting in February, after the last eggs were laid. There was no relationship between core temperature and water content in 21 mounds during November to February, 1979–1982.

On 13 December 1979 we discovered a cold heap of damp litter that had been recently assembled into an incipient mound about 0.5 m high. On subsequent visits we found it abandoned and cold throughout the breeding season. However, when a Brush-turkey added more material to it in the 1980–1981 season, it increased to 1.0 m high and 3.6 m in diameter and it warmed to 40.6°C by 7 November 1980. After that it cooled to incubation temperatures around 33°C and eventually contained 14 eggs.

Long term temperature stability was demonstrated by a large mound (#2B, ca. 5 m diameter, 1.2 m high) that we discovered on 13 December 1979. It was apparent that the mound had not been worked since the previous season because small herbs were growing over its entire surface, tree rootlets had invaded up to a level of 25 cm below the surface, live beetle larvae were present in the litter, and only broken egg shells occurred at egg level. Nevertheless, the temperature was 33.8–34.3°C between 60 and 80 cm deep. On 15 December 1979, another long-abandoned mound was 28.3°C inside, when the surface temperature was 19.4°C.

CHARACTERISTICS OF MOUND MATERIAL

Data on water content, air content, dry density and oxygen consumption of mound material have been given by Seymour et al. (1986, 1987). The mean ash content of core samples from eight mounds was 0.47 g/g dry material (SD = 0.13). Therefore the organic material represented 0.53 g/g dry.

The thermal conductivity (K) of the mound material increased with increasing water content of the material (Fig. 2). There was a considerable difference in apparent K depending on whether the heat moved outward or inward through the SRM. This resulted from the fact that heat moved through the material by conduction along a temperature gradient and by evaporation and condensation along a water vapor pressure gradient. Westcot and Wierenga (1974) estimated that up to about half of the heat flux through warm moist soil could occur by water vapor flux. These mechanisms interacted in a complex way because vapor pressure was not linearly related to temperature. K was apparently higher when the heat was moving in, because the average temperature and total vapor density in the system was higher, and the amount of latent heat transported was greater. Assuming that the temperature profile across the SRM was proportional to $\ln(r_2/r_1)$ (Chapman 1974), the volume-weighted average temperature was 34°C when heat moved in whereas it was only 13°C when heat moved out. Therefore K depended somewhat on temperature. We estimated the boundary values of K by comparing the apparent values when heat moved inward and outward in the SRM. Because 34 and 13°C correspond roughly to the range of temperatures occurring in different parts of natural mounds, the curves shown in Figure 2 approximate the upper and lower limits of K.

The average water content of natural mounds on Kangaroo Island was about 0.3 ml/g dry material (Seymour et al. 1987) which places conductivity in the region of 1.6–3.3 mW cm^{-1} °C^{-1} (Fig. 2). For comparison, the conductivity of pure unstirred water is 6.3 mW cm^{-1} °C^{-1}, dry sand is 3.2 mW cm^{-1} °C^{-1} (General Electric 1981), dry soils are about 2.4 mW cm^{-1} °C^{-1} and dry peat is about 0.6 mW cm^{-1} °C^{-1} (De Vries 1966).

Thermal conductivity was also calculated from the volume-fractional composition of the mound and published values of thermal conductivity of soil components (De Vries 1966). In field mounds with a mean dry density of 0.41 g/ml, a water content of 0.30 ml/g, and an ash content of 0.47 g/g, K became 2.5 mW cm^{-1} °C^{-1}. For SRM material with a water content of 0.30 ml/g, the calculated value was 2.7 mW cm^{-1} °C^{-1}. These values were close to the mean value of 2.4 mW cm^{-1} °C^{-1} measured in the SRM at a water content of 0.30 ml/g.

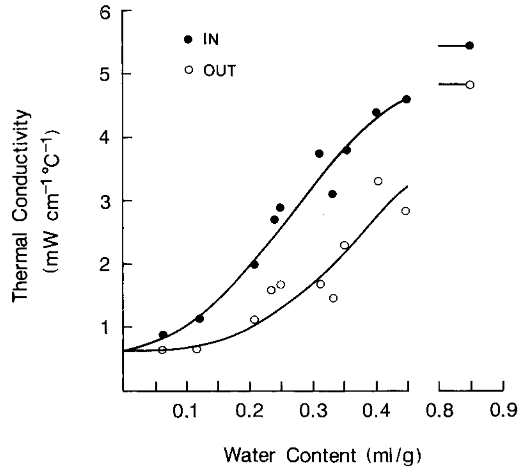

FIGURE 2. Thermal conductivity (mW cm^{-1} °C^{-1}) of Brush-turkey mound material as a function of water content (ml/g dry material). The two curves were fitted by eye to data obtained when heat was moving inward (●) or outward (○) through a cylinder of the material.

MANIPULATION OF NATURAL MOUNDS

We altered two natural mounds to determine the effect of adding or removing mound material. Mound #17 was incubating eggs on 7 January 1984 with a peak core temperature of about 34.9°C at about 50 cm depth (Figs. 3, 4). Three days later we added a layer of material taken from disused mounds and increased the height of the mound from 1.2 to 1.4 m; there was no change in the diameter (6 m). The eggs were initially below 55 cm, so adding the litter placed them below 75 cm. On 19 January, the temperature at egg level increased to 44°C, and the new temperature at what was now 55 cm depth had increased to 45°C. The bird apparently excavated the mound on 19 January and 24 January when the temperature dropped quickly (Fig. 4). The bird continued to work until 1 February, but had abandoned the mound by the time we examined it on 25 February. We discovered two dead eggs and a dead chick, apparently killed by the heat, at the original egg level. There were no new eggs, despite the fact that the incubation temperature of 32°C prevailed at 60 cm depth. The two shallower thermistors had been displaced and rested at 35 and 40 cm depth.

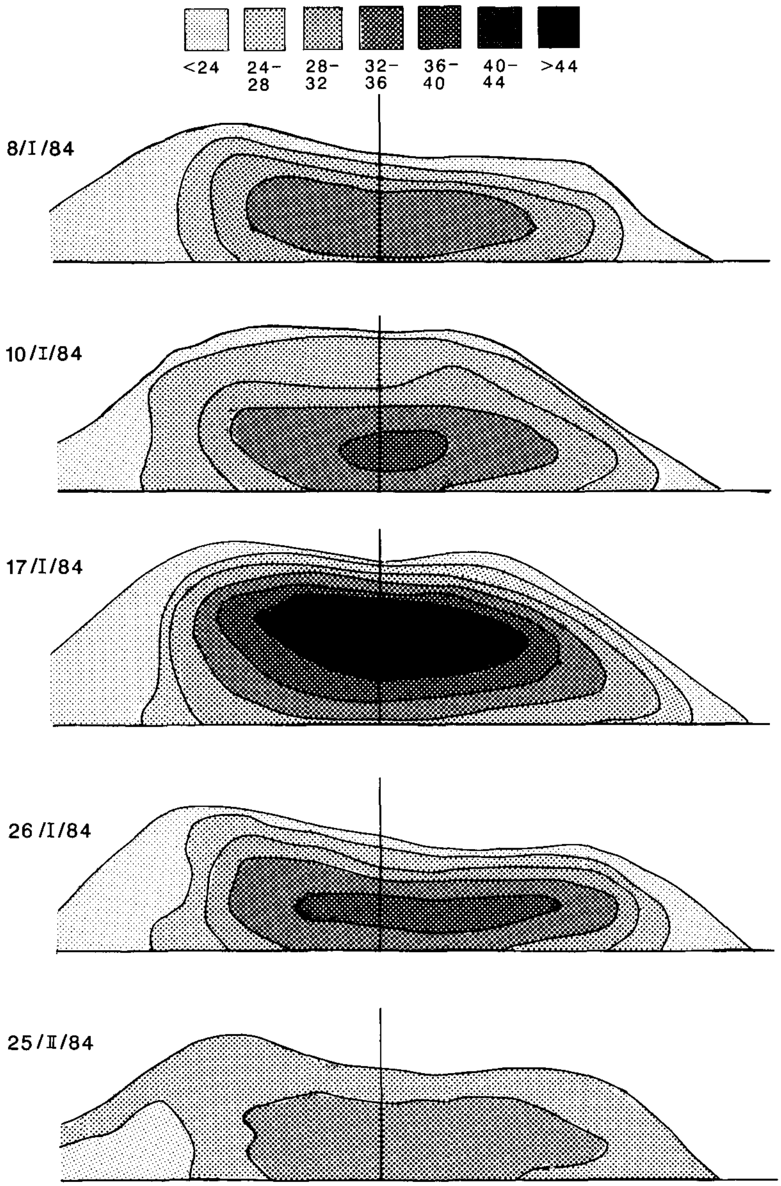

FIGURE 3. Temperature profiles within a natural Brush-turkey mound (#17) before and after adding 20 cm of extra litter. The isotherms are at 4°C intervals and the vertical line is 1.5 m. Changes in central temperature are given in Figure 4.

Mound #20 was about 1.1 m high, 5.9 m in diameter, and had a core temperature of 34.5°C on 7 January 1984 (Fig. 5). On 11 January, we removed about 15 cm of friable material from just underneath the coarse surface layer and distributed it into the forest up to about 10 m away. The new height was 95 cm (Fig. 5). Seven days after remodeling (18 January), approximately 5–10 cm of material had been returned to the mound by the bird. The bird collected old and fresh litter that had been wetted by a recent rain. Nevertheless the temperature had dropped to 30.5°C. By the sixteenth day (27 January), it had dropped to 27.7°C despite continued work by the bird.

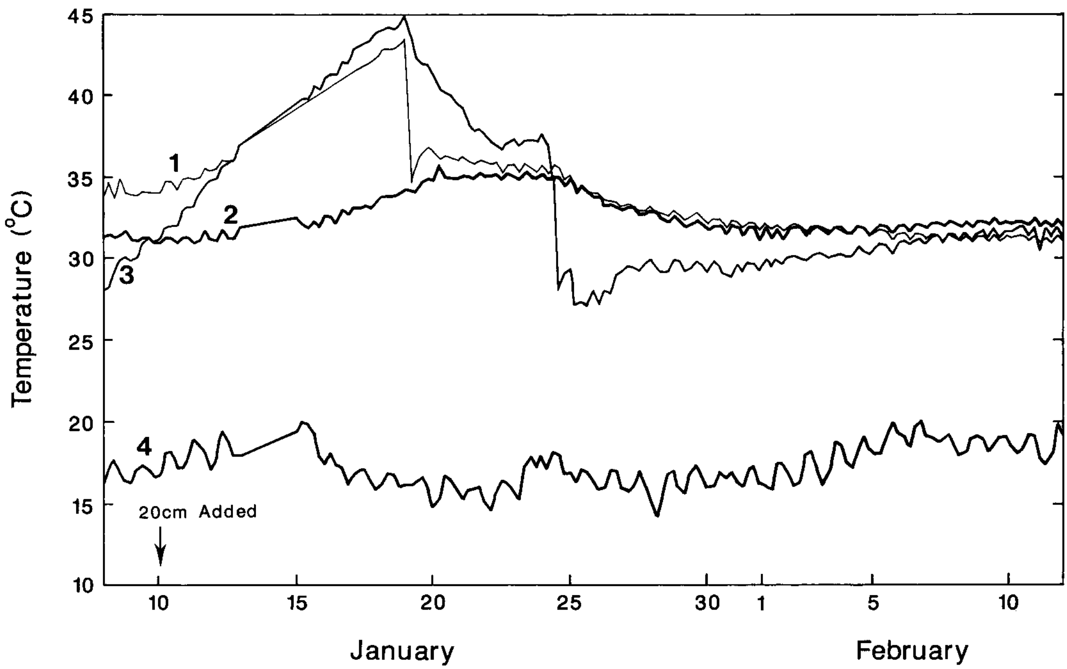

FIGURE 4. Changes in mound and ambient temperature before and after adding 20 cm of extra litter to a natural Brush-turkey mound (#17). Lines 1, 2, and 3 represent respective depths of 35, 50 (egg level) and 70 cm in the original mound. Line 4 is ambient temperature taken 5–10 cm deep in soil adjacent to the mound.

Interestingly, the bird cleared previously worked areas immediately around the mound rather than venturing farther to obtain material from new patches of ground. In fact, we removed large sticks that had prevented collection of litter near the mound, but the bird did not take the opportunity to collect there. Work ended on the mound shortly before 27 January. On 29 January, and again on 1 February, we interceded and added litter to the mound, eventually increasing the depth by about 25 cm, causing a slight temperature rise, but not to incubation level. We found two eggs and four hatching sites.

MANIPULATION OF ARTIFICIAL MOUNDS

On 4 November 1981 (Fig. 6, Point A), we used a construction phase mound as a primary source of material to construct three artificial mounds of selected sizes. Our aim was to use fresh material as would be collected by the bird. The natural mound was 1.3 m high, 4.6 m in diameter and had a volume of approximately 7.2 m^3. At the time, there were no eggs and the temperature at 40 cm depth was 48.6°C. Old eggshells in the deeper parts of the mound and other evidence indicated that this mound had been used in previous years. We spread the mound material on the ground to cool, and added more fresh litter from the forest floor. After preparing a uniform base consisting of a 25 cm layer of decomposed material from under the original mound, we constructed three mounds (#1, 2, 3) by throwing the fresh material into heaps until the diameters reached 1, 2, and 3 m. The heights at construction were 0.75, 0.98 and 1.26 m, respectively, and the volumes were 0.7, 1.9 and 5.1 m^3. The initial water content was 0.45 ml/g dry matter and the temperature was uniform at about 19°C. Thermistors on wooden stakes recorded temperature for 106 days.

The two larger mounds (#2, #3) warmed to above 50°C, the limit of our recorder. The rate of temperature rise was higher in the largest mound and it maintained a higher temperature longer. After about 50 days, temperatures in these mounds returned to ambient. The smallest mound (#1) warmed only slightly, maintaining a small temperature excess (6–10°C) above the environment for about 40 days. On 24 January 1982 (Fig. 6, Point D), we thoroughly mixed and

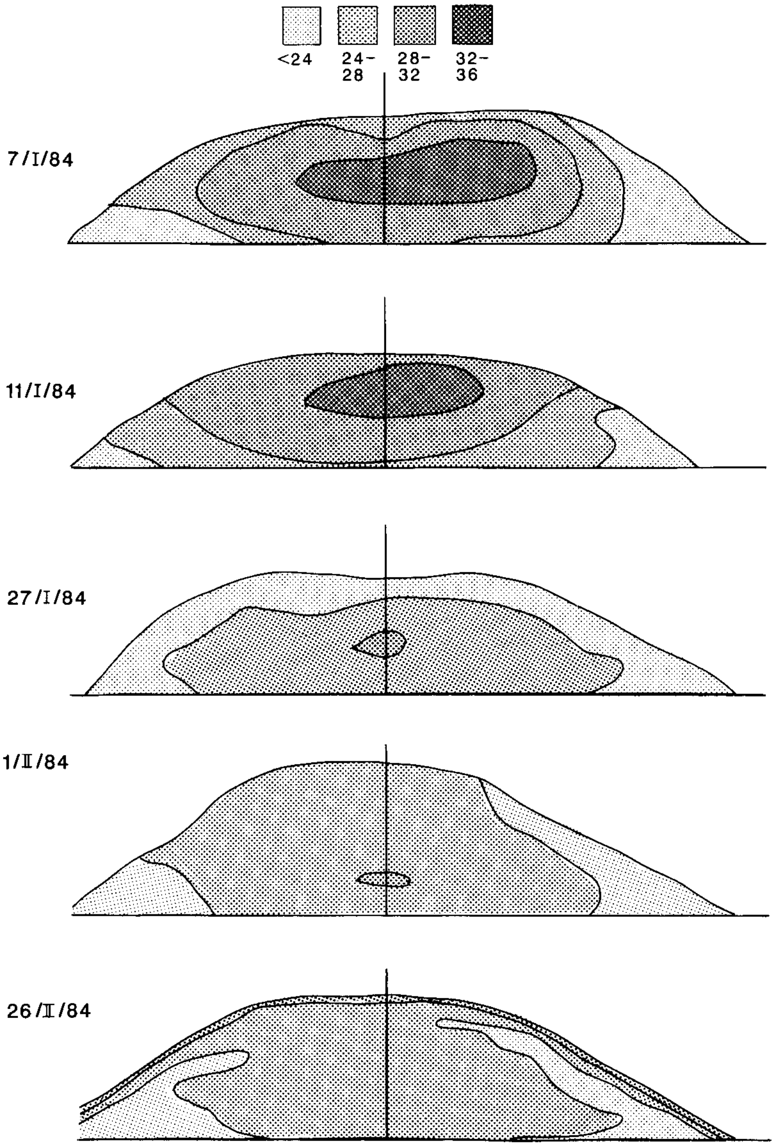

FIGURE 5. Temperature profiles within a natural Brush-turkey mound (#20) before and after removing 15 cm of litter from under the surface. The scale is the same as Figure 3.

rebuilt mound #3, without adding fresh material or water. Although it had a water content of about 0.36 g/g shortly after rebuilding, it failed to warm appreciably. On the same day, we added about 90 liters of water into a crater on mound #2 without otherwise disturbing it. Water contents ranging from 0.40 to 0.54 g/g prevailed for the next 26 days, but the mound warmed only 6°C above ambient.

We built another artificial mound (#4) on 2 February 1981 (Fig. 6, Point B) from a disused mound that had apparently been abandoned for at least two years. We dug up the mound and reassembled it on the original site, but covered it with a thin layer of fresh sticks and leaves from the forest floor. The water content of the material was 0.29 g/g dry. The mound warmed about 4°C above the environment (Fig. 6). When we intro-

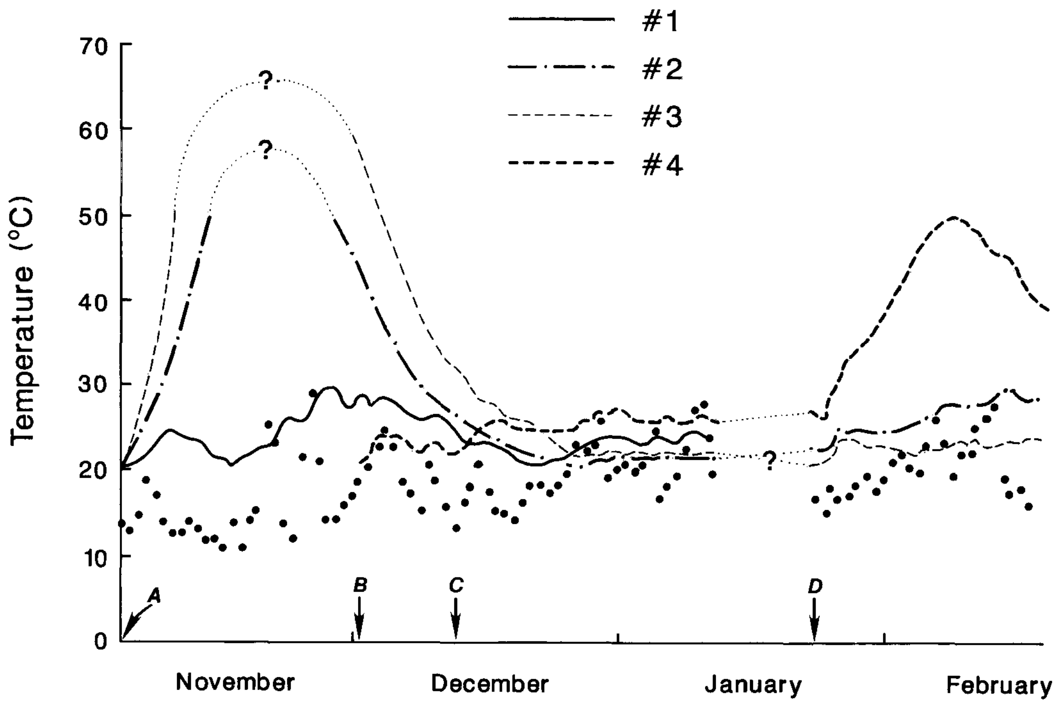

FIGURE 6. Changes in core temperature in four artificial mounds after experimental manipulation. Daily mean ambient air temperatures are given by dots. Activities at times A–D are described in the text.

duced a core of fresh material with 0.52 g/g water content into the mound on 13 December 1981 (Fig. 6, Point C), the excess increased to about 6°C where it remained until 24 January 1982 (Fig. 6, Point D). On this day we shoveled the mound aside and rebuilt it while spraying 270 liters of water into it. After three days, the water content was 0.43 g/g and the temperature had begun to rise. The temperature reached 50°C before starting to decline.

The effect of insulation on mound temperature was shown by artificial mound #6 that we constructed by raking forest litter into a pile on 9 December 1983. By 10 January 1984 it had gone through the initial heating phase and had cooled to 28.5°C. On this day we insulated the mound by covering it with a layer of old artificial mound material (from #1–4), increasing the height from 0.75 m to 1.22 m and the diameter from 3.5 m to 3.8 m. After an initial cooling of 2 days, when the temperature dropped a degree, the artificial mound warmed to 35.1°C in 8 days following insulation, and eventually reached 43.8°C in 16 days. Meanwhile, a nearby natural mound (#19), that had been abandoned earlier in the season, dropped from 28.5°C to 25.7°C between 10–26 February 1984.

Manipulation of two other natural mounds and four artificial mounds provided qualitatively similar results.

THE MODEL AND ITS RESULTS

The numerical model is based on a sphere superimposed on the average Kangaroo Island maintenance phase mound (height = 120 cm, diameter = 500 cm; Table 1). The radius of the sphere is therefore 322 cm (Fig. 1), and it is divided up into 805 concentric shells, each 0.4 cm thick. The model calculates the heat production, net outward heat flux, and temperature at equilibrium in each of the 138 outer shells, from a maximum depth of 55 cm. Because 55 cm is the depth of maximum temperature in real mounds (Table 1), any heat produced below this level moves downward rather than through the outer shells. Heat production below 55 cm is therefore assumed to be zero.

The details of the model program are too extensive to present here. In brief, however, the model consists of an equation in which outward heat loss from any shell is equivalent to the heat produced in the shell itself plus all of the heat produced from deeper shells. Equilibrium core temperature (a stable temperature at a depth of 55 cm) is arrived at by solving the equation iteratively until (1) total heat production in all active shells equals total heat loss from the outermost shell, and (2) the temperature on the surface of the mound is equal to ambient temperature.

Heat production and loss are calculated from the mass-specific rate of heat production (HP, J kg^{-1} hr^{-1}), the thermal conductivity of the mound material (K, W cm^{-1} $°C^{-1}$), its dry density (ρ, g/cm^3), water content (w, ml/g dry), shell volume and temperature. Seymour et al. (1986) showed that heat production depends on temperature according to the equation: $HP = 10^{(aT+b)}$ where a and b are constants and T is the temperature of the material. With values from the present study and Seymour et al. (1986), we assume $a = 0.0243$ and $b = 1.63$, $K = 0.0024$, $\rho = 0.41$, $w = 0.30$, and ambient temperature = 18°C. These values represent "standard conditions" for our average mound and yield a core temperature of 33°C. Parameters of the model may be varied individually to view their effects.

HEAT PRODUCTION IN THE MOUND

Although the model is useful in assessing the importance of mound parameters, the value of total heat production at equilibrium is unrealistically high because the model represents an entire sphere, whereas the mound occupies only a fraction of it. A better representation of the active part of the mound is a lens-shaped space the center of which lies at a depth of 55 cm (Fig. 1). The lens is divided into two half-lenses by a horizontal plane, and heat production in each shell of a half-lens is calculated according to the fraction it occupies in the entire shell of the spherical model described above. The total heat production of the entire lens is then taken to be twice the sum of all of the shells in the upper lens. Because heat produced in the upper half-lens moves up while that produced in the lower one moves down, the model isotherms correspond reasonably well with measured ones (Figs. 3, 5). Below the lens, the mound is considered inert because the material is a year or more old and is not worked by the bird (Baltin 1969).

Under the standard conditions of the model, these calculations indicate that a mound with an equilibrium core temperature of 33°C in an ambient temperature of 18°C would produce about 111 Watts.

EFFECTS OF MODEL VARIABLES ON EQUILIBRIUM CORE TEMPERATURE (T_c)

Radius (r). It is important to understand that "radius" refers to the radius of the sphere on which the mound model is based (Fig. 1), not the radius of the mound at ground level. Small changes in radius have pronounced effects on T_c (Fig. 7). T_c rises from 33 to 34.5°C if 1 cm is added to the radius, or it drops to 31.8°C if 1 cm is removed.

Ambient air temperature (T_a). T_c is also very sensitive to T_a (Fig. 7). A drop in T_a from 18 to 17°C results in a 3°C decrease in T_c. Increasing T_a 1°C results in a 5°C increase in T_c. It should be emphasized that these are equilibrium values; there would be little change in T_c in response to short-term (e.g., daily) changes in T_a, because of the mound's high thermal inertia (discussed below).

Heat production coefficient (HP_b). In the equation for heat production, coefficient b represents the elevation of the log-log plot of heat production versus temperature. Assuming a constant coefficient a which represents the slope of the line, changing b changes the level of heat production. Again, in the region of normal mound temperatures, small changes in heat production have large effects on T_c (Fig. 7).

Thermal conductivity (K). T_c is profoundly affected by relatively small changes in K (Fig. 7). For example, decreasing K from 2.4 to 2.3 mW cm^{-1} $°C^{-1}$, results in T_c rising from 33 to 36°C. Because water content is a major factor determining K (Fig. 2), changes in mound water would greatly change mound temperatures were it not for the antagonistic effect water has on heat production.

Water content. The effect of water content is complex because it affects both heat production (Seymour et al. 1986) and thermal conductivity (Fig. 2). If we keep all other factors constant and vary water content, the model results in very low T_c at contents less than 0.2 ml/g, a peak at 0.3 ml/g and then moderately high values prevailing above 0.3 ml/g (Fig. 8). This points to the fact that mounds can maintain incubation temperatures throughout a wide range of water content.

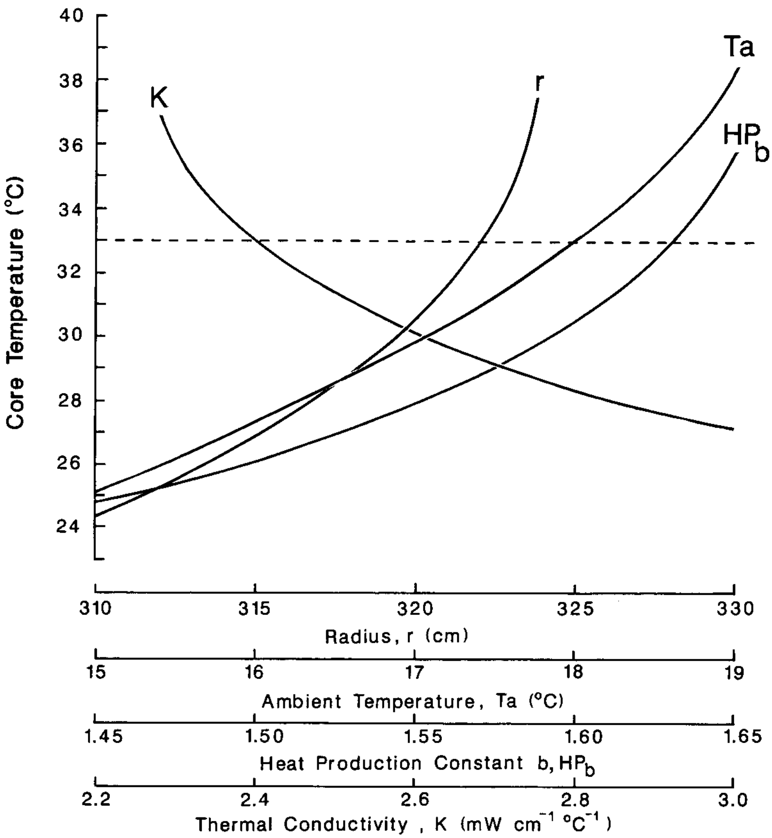

FIGURE 7. Effect of changing selected parameters on equilibrium core temperature in the numerical model of a Brush-turkey mound. All parameters are fixed at "standard conditions" except those under investigation (see text). Dashed line represents observed average core temperature of 33°C.

However, the rate of heat production increases steadily at water contents above 0.3 ml/g (Fig. 8).

INTERACTION OF MODEL VARIABLES

Regulation of equilibrium temperature is accomplished by the bird changing the size of the mound. The model can be used to estimate how mound radius must be changed to compensate for a given change in a certain variable. For example, if a mound of model radius 322 cm is at equilibrium at 33°C at a T_a of 18°C, we can estimate how much the radius would have to increase if T_a decreased to 17°C. The new equilibrium T_c would be 29.8°C (Fig. 7), and the radius would have to increase 2.2 cm to re-establish 33°C. Similarly increasing K from 2.4 to 2.5 mW cm^{-1} $°C^{-1}$ requires an increase in radius of 1.2 cm; decreasing HP_b from 1.63 to 1.58 or increasing water content from 0.3 to 0.4 ml/g both require a 3.5 cm increase in radius. The model predicts that a mound at T_a = 28°C, such as in the tropics, would have a radius of 298 cm, that is, a mound only 96 cm high.

NON-EQUILIBRIUM RESULTS

The model determines T_c in equilibrium conditions, but it can be modified to demonstrate the concept of mound homeothermy by calculating heat production under non-equilibrium conditions. By changing the heat production coefficient *b* under standard conditions, the model equilibrates at different levels of core temperatures and rates of heat loss (heat loss line, Fig. 9). For example, the standard mound in equilibrium at 33°C produces (and loses) 111 Watts. If

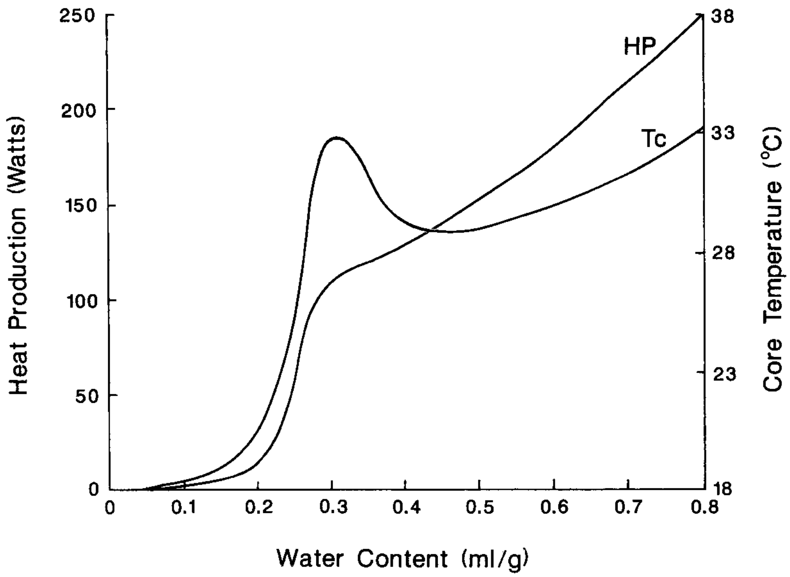

FIGURE 8. Effect of water content (ml/g dry material) on equilibrium core temperature (T_c), and total rate of heat production (HP), in the lens-shaped active zone of our model Brush-turkey mound (Figure 1).

T_c were changed by excavation of the mound and subsequent reconstruction, T_c would no longer be at equilibrium. We can calculate the transient, non-equilibrium, rate of heat production from the heat production coefficient *b* and the new temperature distribution in the mound. This rate of heat production is the sum of production in all shells, assuming a linear temperature profile from the surface to the core (heat production line, Fig. 9). As an example, say the mound were cooled to 25°C at the core. Upon reconstruction, heat production would be 94 Watts, which is considerably above the rate (57 Watts) required for equilibrium at 25°C, and the mound temperature would continue to rise toward equilibrium at 33°C. If the core somehow exceeded 33°C, heat production would be less than heat loss and the mound would cool.

APPLICATION OF THE MODEL

According to the model, adding 20 cm of mound material would cause the mound to heat above the limiting temperature of the microorganisms (>60°C). When we did this to the natural mound, T_c began a steady rise that was interrupted at 45°C when the bird opened and cooled the mound (Fig. 4). Taking 15 cm away from another natural mound should have caused T_c to drop to about 28°C. Removal caused a dramatic drop in T_c slightly lower, and it never rose again, despite the efforts of the bird and us at rebuilding the mound (Fig. 5). We do not know why T_c did not rise. Possibly the added material was too dry or we did not wait long enough for the microorganisms to become established.

DISCUSSION

REQUIREMENTS FOR A FUNCTIONAL MOUND

Active mounds require a combination of three factors: (1) a critical mass of fresh litter, (2) sufficient water content, and (3) occasional mixing. The experiments involving artificial mounds demonstrate that all three are required (Fig. 6). When three artificial mounds (#1, 2, 3) were made of the same fresh material, but of different sizes, only the largest two warmed above 30°C. Apparently the smallest mound (#1), initially 0.7 m^3 in volume, was near the critical mass, because it warmed a few degrees. The smallest natural mound on Kangaroo Island that warmed to incubation temperature had a volume of about 6 m^3, or a mass of about 3,200 kg. A minimum water content above about 0.2 ml/g is required to produce significant heat production in mound material (Fig. 8). Low water content never was the single cause of failure for artificial mounds to remain warm, because all of them had water contents above 0.29 ml/g. Turning the material

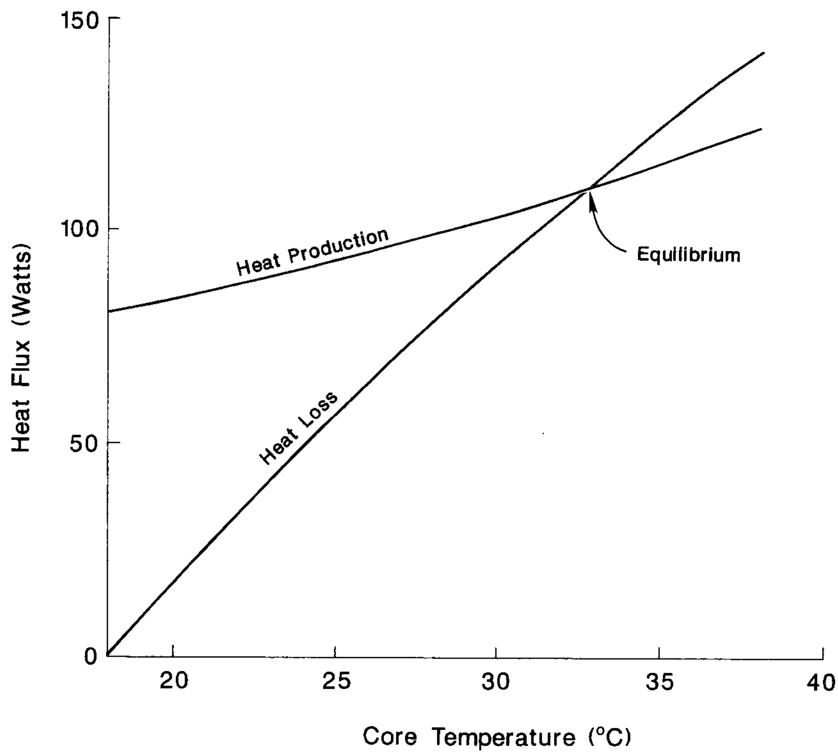

FIGURE 9. Model calculations of rates of heat production and heat loss as functions of core mound temperature at an ambient temperature of 18°C. The line for heat loss applies to a mound at a stable equilibrium core temperature and is calculated from "standard conditions" except for changes in heat production coefficient *b*. The line for heat production is calculated under non-equilibrium, transient conditions, as described in the text.

breaks it up, prevents compaction and reduces thermal conductivity. Our artificial mounds were not mixed frequently and probably had higher than normal thermal conductivity. They lost a great deal of energy shortly after construction and were unable to remain warm for very long. Neither mixing the old material alone (#3, #4), nor adding a small amount of fresh material to the core of an old mound (#4), nor adding water alone (#2), was sufficient to cause a substantial temperature rise. However, extensive mixing as well as adding water did trigger warming (#4).

Freshly constructed mounds can overheat because the rate of heat production always exceeds heat loss, and the mounds can warm to temperatures above 60°C where heat production by the thermophilic organisms becomes inhibited. Brush-turkeys commonly open the top of the mound during the construction phase and allow heat to escape (Frith 1956b). This behavior prevents the wave of high temperatures that we observed in artificial mounds (Fig. 6). Indeed the highest temperatures we and Jones (1988a) ever recorded in natural mounds were below 49°C during the construction phase. Preventing high temperatures not only makes the mound suitable for incubation earlier, but also conserves the energy in the litter.

MOUND HOMEOTHERMY

With data from real mounds, our model demonstrates that stable equilibrium temperatures are possible in the maintenance phase of mound life (Fig. 9). Not only are the mounds physiologically homeothermic, they are also inertially homeothermic. With a mean mass of 6,800 kg, they are essentially independent of diurnal changes in ambient temperature. Furthermore mounds are slow to reach the new equilibrium temperature if the mound or its environment is altered. For example, when 20 cm of material was added to mound #17, core temperature changed 1.5°C per day (Fig. 4). When 15 cm of material was taken from mound #20, it changed only 0.35°C per day. Thermal stability is also aided by the slow change in the rate of heat production in natural mounds. There was no measurable change in oxygen consumption in unstirred material for 25 days, but there was a 40% drop over 63 days (Seymour et al. 1986). Once a mound has passed into the maintenance phase, it can remain warm for long periods of time without much work by the bird. Jones (1988a) found that the rate of incorporation of new material into mounds decreased sharply during this phase. Large mounds on Kangaroo Island are so stable, they can remain near incubation temperature for several weeks without attendance by the bird. The most striking example is mound #2B that was apparently abandoned all winter and spring. Although it may have cooled due to low ambient temperatures during these months, by summer, it had rewarmed to incubation temperatures all by itself.

Whereas most species of incubating birds are tied to the nest, megapodes can leave the mound for long periods to undertake other activities such as foraging and breeding behavior. In Queensland, male Brush-turkeys work the mound for about 30 min each day (Jones 1990), but on Kangaroo Island, time-lapse cameras revealed that mounds could be ignored for several days at a time (unpubl. data). It is probable that the mounds were excavated only when eggs were laid during the maintenance phase.

REGULATION OF EQUILIBRIUM TEMPERATURE

Our model indicates that incubation temperature is quite sensitive to changes in mound size. Addition of 1 cm of litter to a mound would change the temperature about 1.5°C. It is not surprising, therefore, that we noticed no changes in mound size throughout the breeding season, because our measurements of natural mounds were accurate only to 5 cm. In a fairly constant ambient temperature, a stable mound size is expected, and fresh material compensates for mound subsidence. After the breeding season, disused mounds gradually decrease in size over several years.

EFFECT OF WATER ON MOUND TEMPERATURE

The mean water content of Brush-turkey mounds on Kangaroo Island decreases from about 0.35 ml/g in October to about 0.25 ml/g in February (Seymour et al. 1987), resulting in a 43% decrease in heat production (Seymour et al. 1986). The effect of decreased heat production is practically counterbalanced by a decrease in thermal conductivity of about 37% (Fig. 2). It is reasonable, therefore, to observe absolutely no correlation between core mound temperature and water content throughout three breeding seasons. The model shows that the temperature can be similar in wet and dry mounds, but wet ones consume stored energy faster (Fig. 8) and require more work by the bird to collect fresh litter. At a mean water content of natural mounds (0.30 ml/g), the total rate of heat production (111 Watts) is about half of the value (240 Watts) that would be required at 0.78 ml/g. The other advantage of having a relatively dry mound is that it promotes diffusion of gases through the material and assures that the embryos are exposed to gas tensions similar to those of other species of birds (Seymour et al. 1986).

MOUND ENERGETICS

How much energy is incorporated into a mound each season? Jones (1988a) estimated that the bird collects about 780 g of dry leaf litter each day during the maintenance phase at Mt. Tamborine, in Queensland. Assuming the dry leaves yield 22 kJ/g if fully combusted (Pompe and Vines 1966), this represents a potential rate of heat production of 200 Watts. Calculated this way, heat production in the maintenance phase is 80% higher than the estimate from our model (111 Watts), but the difference may be due to failure to combust the material completely, substantiated by a low respiratory exchange ratio of microorganism metabolism (Seymour et al. 1986), or to differences in mound characteristics (see below). In either case, the rate of heat production is more than 20 times that of a resting 1.8 kg megapode bird (Booth 1985), which demonstrates that the mound is capable of incubating many more eggs than could be incubated in a normal nest under the adult bird.

MOUNDS IN OTHER CLIMATES

The natural distribution of Brush-turkeys ranges from the tip of York Peninsula (11°S latitude), mostly along the coastal slopes of the Great Dividing Range, south to approximately Sydney (34°S), spilling over in some places into areas slightly west of the Range (Pizzey 1980). The latitude of Kangaroo Island (34°S) is at the southern end of the natural distribution. However, there is no reason to think that breeding is limited by cold environments. Successful mounds have been constructed in zoos in Melbourne (38°S) (Fleay 1937) and even in Frankfort (50°N) (Baltin 1969). Compost heaps can be made in all climates, provided the heaps are large enough.

All other things being equal, one would expect to see larger mounds at higher (cooler) latitudes. The mounds on Kangaroo Island are generally larger, higher and rounder than those studied by Jones (1988a) at Mt. Tamborine (Table 1). However, the difference in mound size between Kangaroo Island and Mt. Tamborine is not apparently related to differences in ambient temperature. Although Mt. Tamborine is at a lower latitude (28°S), it is at a higher elevation, and the average daytime surface temperatures are similar (19.6°C at Mt. Tamborine and 21.6°C at Kangaroo Island). Because the incubation temperatures in the two locations are almost identical, either the conductivity of Mt. Tamborine mounds is lower or their volume-specific heat production is higher. Low conductivity is probably not the cause, because the mounds have similar damp density. Assuming that the volume of Mt. Tamborine mounds is 4.6 m^3 and that 2,270 kg of material is collected, the damp density becomes 0.49 g/cm^3 (Jones 1988a). On Kangaroo Island, the damp density averages 0.53 g/cm^3 (Seymour et al. 1986). Higher rates of heat production in Mt. Tamborine mounds (calculated above) are consistent with smaller mounds. Rapid respiration may be due to different microorganisms or plant litter in the mound. Jones (1988b) noticed that Brush-turkeys avoid *Eucalyptus* at Mt. Tamborine, possibly because the leaves are more resistant to decay than are rainforest species. On Kangaroo Island, *Eucalyptus* and *Acacia* are the only litter available and therefore the mounds may need to be larger to compensate for lower rates of heat production.

OPTIMIZING THE MOUND

With knowledge of the factors affecting heat production and loss in the Brush-turkey mound, we are amazed how well the bird's behavior is adapted to minimize the work required to maintain incubation conditions. The optimum mound is well insulated so that the rate of heat production is minimal and less work is required to collect litter. The bird is selective about the materials incorporated in the mound that affect thermal conductivity. They minimize dry density by preferring litter rather than soil, and tossing it into the mound without compaction. By keeping water content fairly low, possibly by manipulating mound shape (Fleay 1937), they minimize heat production and maximize heat retention, while facilitating adequate oxygenation of the eggs (Seymour et al. 1986). They often make mounds over old mounds that provide good insulation from the ground. They create a boundary layer of still air on the surface of the mound by kicking a layer of coarse sticks on the surface, and they tend to position mounds near thickets that reduce convective heat loss from the surface (Jones 1988b). Finally, they may steal mounds constructed by other Brush-turkeys or even use domestic compost heaps (Jones 1989).

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