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Calorimetric investigations on mound-building birds [☆,1]

Roger S. Seymour

Department of Zoology, University of Adelaide, Adelaide, S.A. 5005, Australia

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Abstract

Megapodes, and mound-building birds of the Pacific, incubate their eggs underground where the heat is supplied by organic decomposition, solar radiation, or geothermal sources. The incubation biology of the Australian mound builders has been examined from the standpoints of (1) the energetic requirements of malleefowl (*Leipoa ocellata*) to construct and maintain incubation mounds and (2) the physics, physiology, and behavior concerning mound thermoregulation of the brush turkey (*Alectura lathami*).

The energetic cost of mound tending in malleefowl is estimated by indirect calorimetry. The power required for digging into the mound to reach the eggs is approximately 20 W, or 3.8 times the basal metabolic rate of the bird. About 850 kg of sand has to be removed and replaced on the mound every time it is opened, a task requiring about 5 h. The overall energy investment for incubation for the entire 9 month season is 2.5 times that expected in similarly sized birds.

Brush turkey mounds become homeothermic because of (1) the high thermal inertia of their 3–11 t mass and (2) a stable equilibrium that is reached between heat production and heat loss. The mound tends to seek the equilibrium, but the bird adjusts the temperature by subtle manipulation of the mound. At an equilibrium temperature of 33°C, the mound produces about 110 W. Empirical data from natural mounds, set in the context of a numerical model of heat production and heat flux in the mound, indicate that equilibrium temperature is extremely sensitive to ambient temperature and mound size, but not water content. Wet or dry mounds can maintain appropriate incubation temperature, but the dry ones have low thermal conductivity, retain the heat well, and minimize the amount of forest litter collected during the incubation season.

Keywords: Bird; Homeothermy; Incubation; Megapode

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1. Introduction

The incubation biology of the megapode birds of Australia and the adjacent Pacific Islands is unusual because they bury their eggs underground where heat is supplied by microbial decomposition, solar radiation, volcanism, or a combination of these sources. Most of the 19 species incorporate plant litter in incubation mounds, and accordingly, the group is often called the "mound builders."

There are three species of Australian mound builders that occur in many regions of the continent (Fig. 1). The scrub fowl (*Megapodius reinwardt*) occurs in coastal northern tropics where it constructs enormous communal mounds, reaching 4 m high and 20 m diameter [1]. The Australian brush turkey (*Alectura lathami*) is distributed in forests along the eastern coast of Queensland and New South Wales where individual males construct smaller mounds of forest litter [2]. The malleefowl (*Leipoa ocellata*) is widespread in arid mallee woodland across a south-central band in the continent [3]. Organic decomposition of plant litter is the major source of heat in the mounds of all three species. Forest litter is collected by the birds, wetted by rain, and decomposed aerobically by microorganisms, mainly thermophilic fungi. Organic heat is supplemented by solar radiation only in the malleefowl.

The energetics of mound building are of interest to calorimetrists for at least two reasons. First, mound tending behavior appears to have an enormous energetic cost. With manipulation of mounds that weigh several tonnes, throughout an extended breeding season of many months, these chicken-sized birds apparently expend prodigious amounts of energy for reproduction. Second, the mound builders are the only birds to incubate the eggs underground, apart from the thermoregulatory systems of the adult bird. In normal birds, regulation of egg temperature is

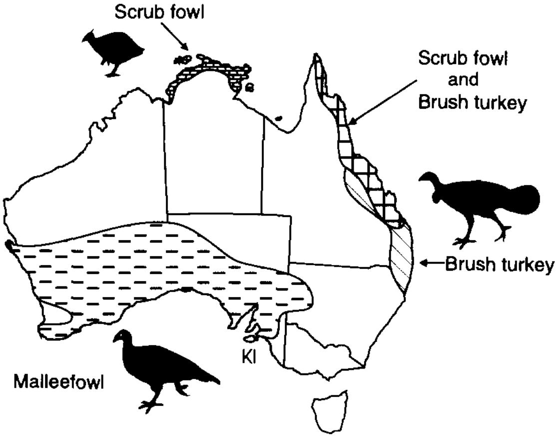

Fig. 1. Distributions of the Australian megapode birds. The brush turkey is also introduced to Kangaroo Island, off of the south-central coast.

achieved by a complex physical and physiological interaction between the parent, the egg, and the nest. Because the egg and the parents are separated in the mound builders, these normal feedback control mechanisms are impossible, and thermoregulation must occur by a new interaction involving microbial heat production, the physics of heat transfer through the mound, and mound tending behavior of the parent. Insight into these two aspects of megapode biology can be gained through calorimetry, and consequently this review emphasizes our work on energetics of the birds and their mounds.

2. Thermoregulation and energetics of mound tending by malleefowl

Frith's [4,5] classical studies of malleefowl mounds showed that incubation temperture remained within a degree or so of 34°C throughout a 9 month breeding period, an accomplishment that led him to call the animal "the thermometer bird" [3]. Frith found that thermal stability is achieved by behavioral modification of the mound according to the heat source and the season (Fig. 2). In winter, the male digs a hole in the sand, by kicking it backward with his feet, and fills it with dry litter. When the litter is dampened by winter and spring rains, it begins to decompose, whereupon he covers it with sand and the female begins to lay eggs. She lays one egg every 5–7 days, depositing it in the center of the mound, about 50–60 cm below the surface. Microbial decomposition supplies most of the heat during spring. During summer, the litter dries out, diminishing organic heat production, but solar radiation becomes intense, so the mound is covered with a deep layer of sand to prevent the eggs from overheating. In autumn, total solar radiation begins to wane, so the bird's behavior shifts to opening the mound in the morning, allowing the daytime sun to warm the sand, and then heaping the warm sand over the eggs to keep them warm throughout the night.

The question of how much energy is expended in mound tending was first raised for malleefowl (Fig. 3). Each time the bird digs down to egg level, to check the temperature or to allow the female to lay an egg, the 1.8 kg bird must remove and replace about 850 kg of sand [6]. Scaling the task up to human size for comparison, the work would be equivalent to a human moving 34 t of loose sand with a garden fork. The bird's task requires over 5 h and is performed nearly every day, except for about 2 months during the summer, when the mound is opened weekly, and 3 months during the winter, between breeding seasons.

We have estimated the energy cost of mound tending in malleefowl, for comparison with birds with normal incubation behavior [7]. The measurement was indirect and relied on the assumption that equivalent work results in equivalent rates of heat production. We noticed that malleefowl males worked continuously during excavation and often became heat stressed because of the buildup of metabolic heat. After a period of digging, the bird began to gular flutter, a thermoregulatory behavior functionally similar to panting, and after a short time he retreated into the shade to rest and eliminate the excess body heat. We

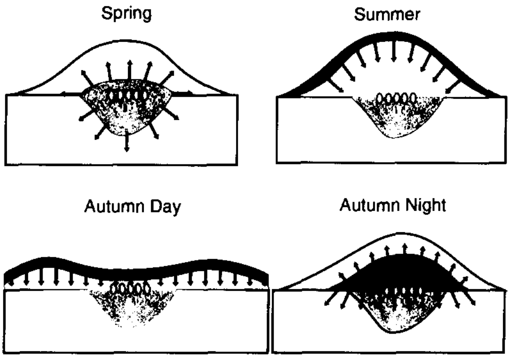

Fig. 2. Diagrammatic cross-section of the malleefowl incubation mound during the three seasons when eggs are present. Organic decomposition of litter prevails during spring. In summer, the litter dries out and stops producing heat. Then the mound is piled high to prevent solar radiation from overheating the eggs. In autumn, the sand is spread out in the morning to warm in the sun and heaped over the mound in the evening to keep the eggs warm overnight.

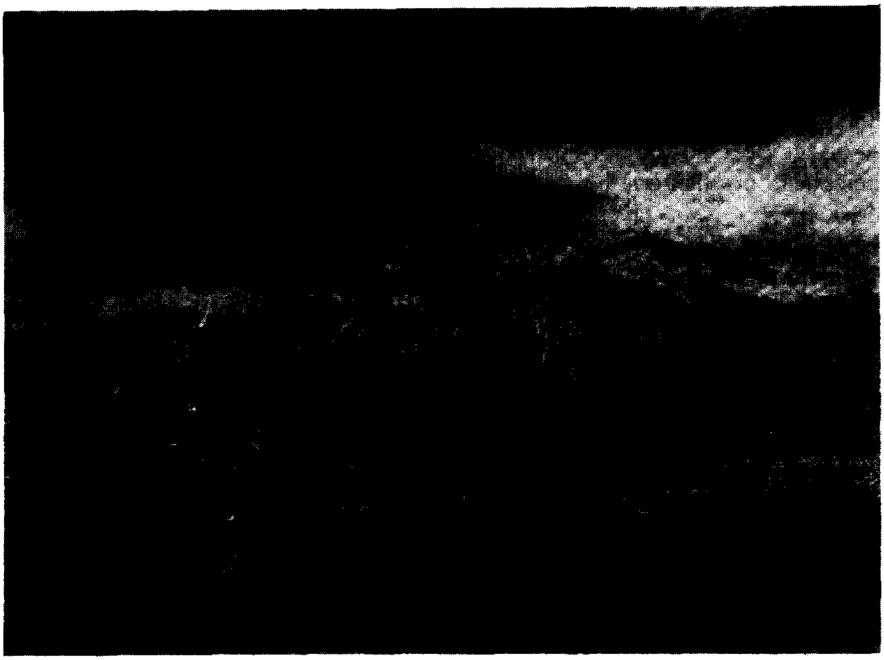

Fig. 3. Male malleefowl removing sand from his mound by backward kicking with the feet.

assumed that the time between the beginning of work and the onset of gular flutter indicated an increment in body heat content caused by the exercise period. The same increment could be duplicated in the laboratory by running birds on a treadmill under the same operative temperature and humidity regimes as measured in the field. We measured the rate of oxygen consumption of treadmill birds with a flow-through mask, and therefore we were able to relate the rate of heat production to the time period to onset of gular flutter. Accordingly, we estimated that the rate of energy expenditure during mound work was about 20 W in a 1.8 kg bird, or about 3.8 times the basal metabolic rate. When the length of the breeding seasons and the daily proportion of incubation behavior are taken into account, we conclude that the energetic cost of incubation in malleefowl is about 2.5 times that of typical birds that sit on a nest and supply body heat to their eggs. The evolutionary compensation for this cost is that many more, extremely precocial, offspring can be produced from a mound than from a conventional nest.

3. Temperature regulation in the brush turkey mound

The complexity of heat sources and configurations of the malleefowl mound complicates analysis of the physics of heat balance in the mound. However, analysis of the brush turkey mound is facilitated by the uniform size, shape and composition, and also its single heat source (decomposition). Brush turkey mounds on Kangaroo Island are impressive structures (Fig. 4). With a mean height of 1.2 m and a diameter of 5 m, they weigh from 3 to 11 t [8]. The mounds are worked by the male bird in two phases [9]. The construction phase occurs during 1–2 months in spring when the bird collects a mound of forest litter. Microbial respiration becomes significant when the mound reaches a critical size, about 3 t of fresh material. Initially the core temperature is unstable and can reach temperatures well above 40°C due to rapid decomposition of fresh material. In the maintenance phase, however, respiration rates drop to nearly constant levels and the core temperature stabilizes.

Brush turkey mounds maintain temperature of about 33°C at egg level throughout the subsequent 5–7 month period when eggs are present. A constant core temperature results from a balance between the rate of heat production and the rate of heat loss. To analyze the determinants of core temperature, therefore, it is necessary to quantify the factors affecting these rates. Because it is impossible to measure the heat production of an entire mound directly, it is necessary to construct a numerical heat flux model and apply to it empirical values derived from natural mounds in the field.

Our model considers the average mound to be spherical section, 1.2 m high and 5 m in diameter at ground level, being the mean values from Kangaroo Island mounds (Fig. 5). The active part of the mound is a biconvex-shaped lens which corresponds to the material that is renewed each year and occasionally excavated by the bird for temperature sensing and egg laying. Deeper parts of the mound are not worked [10], and have very little thermogenic activity. The lens weighs about 3 t and has a volume of 6 m^3. Heat is produced throughout the lens, according to local temperature conditions, and it flows out through the lens along radial paths, both upward and downward. Core temperature is that occurring at the center of the lens, 55 cm below the surface of the mound. Equilibrium core temperature depends on

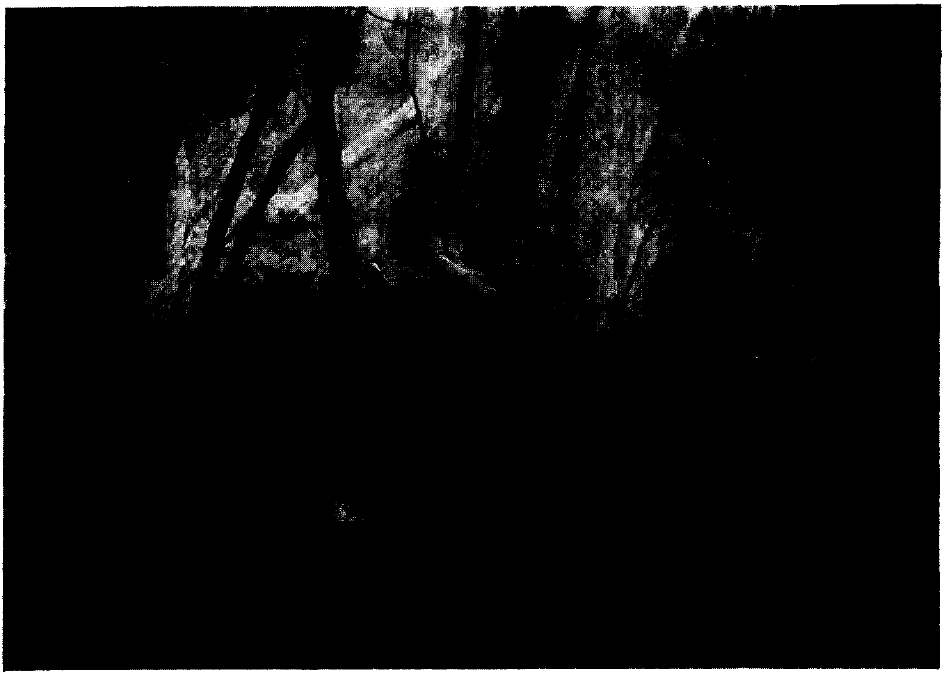

Fig. 4. Brush turkey mound on Kangaroo Island in comparison with the author (left) and David Vleck (right).

a complex interrelationship between the factors affecting heat production and heat flux through the mound material.

We introduced into the model empirical data derived from natural mounds in the field. Heat production by the microorganisms was found to be entirely aerobic, so we measured it indirectly by open- and closed-system respirometry [11], assuming

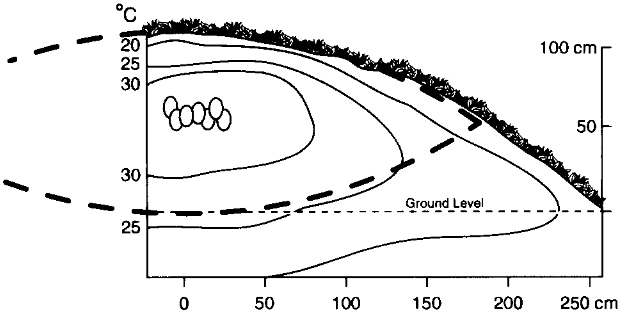

Fig. 5. Natural brush turkey mound in cross-section, showing isotherms and the location of the eggs. The lens-shaped volume assumed for the model is superimposed on the mound.

that 20 kJ was released for each liter of oxygen consumed. We collected large samples of mound material and measured the effects of temperature, water content, oxygen partial pressure, and age on respiration rate. The first two factors were dominant. The results showed that heat production increased with temperature according to an exponential equation $\phi = 10^{(aT+b)}$, where a and b are constants and T is temperature. Heat production was also greatly affected by water content: below 0.2 l per/kg of dry material, practically no heat was produced; between 0.2 and 0.6 l per/kg of dry material, heat production increased almost linearly and then plateaued. Natural mounds had a mean water content of 0.3 l per/kg of dry material and produced about 90 mW per kg of dry material, or 70 mW per kg of wet material, at 32°C.

The factors affecting heat flux through mound material were ambient temperature outside the mound, the size of the mound (measured by radius of the spherical section), and its thermal conductivity. Of course changes in ambient temperature effected heat loss, but not in direct proportion. For example, a change in ambient temperature of 1°C caused a 3–5°C change in core temperature in the same direction. This effect was caused by the exponential relationship between microbial heat production and temperature. A rise in ambient temperature caused the mound to warm up which increased the rate of heat production until a new equilibrium was reached. Paradoxically, therefore, a rise in ambient temperature actually increased the rate of heat loss from the mound.

Although larger mounds produced, and therefore lost, heat at a higher rate, heat flux from the core of the mound (the volume of material immediately containing eggs) decreased in larger mounds because of a thicker layer of insulating, thermogenic material around the core. Core temperature was very sensitive to mound size. If mound radius increased 1 cm, core temperature rose about 1.5°C. This sensitivity explained why we never detected any changes in size of natural mounds throughout the breeding season; our measurements were only accurate to 5 cm. When we removed 15 cm of material from a natural mound, its core temperature dropped from 34.5 to 27.7°C over several days. When we added 20 cm to another mound, its temperature rose from 34.9 to 45°C before the bird interceded and removed the material. Although a new equilibrium temperature was not established in either case, these coarse experiments on natural mounds, and others on artificially constructed mounds, confirmed that core temperature was quite sensitive to changes in mound size.

Thermal conductivity of the mound material was also an important factor in heat flux, but it was also the most difficult parameter to measure. An apparatus was designed which measured the radial heat flux between two concentric 1.5 m tubes, perfused with thermostatted water and separated by a 58 mm thick cylinder of material [8]. Heat flux depended on the temperatures of water in the tubes, and it was measured by the flow rate of water in the central tube and the change in temperature along a medial test section. Heat production by the material was prevented by sealing it in an atmosphere of pure nitrogen. Apparent thermal conductivity depended on density and water content of the material, but averaged 2.4 mW cm^{-1} K^{-1} in material of average composition from field mounds. Up to half of the conductivity was attributed to evaporation and condensation of water vapor along a temperature gradient through the material.

When all of the empirical information was entered into the model and core temperature adjusted to 33°C, the total rate of heat production by the whole mound was 110 W at the average ambient temperature of 18°C. Approaching quantification of heat production from another direction, we noted that brush turkeys in Queensland incorporate about 780 g of dry leaf litter each day [9]. If dry leaves yield 22 kJ g^{-1} if fully combusted [12], this represents about 200 W. However, low respiratory quotients and acid products in the mound indicate that biological combustion is not complete, so actual heat flux must be somewhat less. There is also evidence that rainforest litter in Queensland breaks down more quickly than the dry sclerophyll litter from Kangaroo Island. Regardless of the value accepted, heat production between 100 and 200 W represents at least 20 times the metabolic heat production in the adult bird, demonstrating that much more heat is available to incubate many more eggs that would be possible in a typical bird's nest.

4. Mound homeothermy

Any structure that produces heat tends to warm itself until the rate of heat production equals the rate of heat loss, whereupon the temperature of the structure stabilizes. This "equilibrium temperature" may be a stable equilibrium if the temperature returns to it after a temporary disturbance. I have previously proposed that the core temperature of brush turkey mounds results from a stable equilibrium that depends on the biological and physical nature of the mound [13]. The mound is homeothermic in the sense that once it is constructed, it seeks the equilibrium temperature. Unfortunately, the mound does not necessarily stabilize at a temperature suitable for incubation of eggs. The bird assumes the thermostatic role of adjusting the equilibrium point by adding or removing mound material as appropriate. Our new model and empirical data support this idea and permit quantitative assessment of mound homeothermy [8]. It is now possible to view the effects of transient cooling and spontaneous rewarming of the mound, for example, after the bird excavates the mound to deposit an egg or check temperature (Fig. 6). The model predicts that, if core temperature drops from 33°C to 30°C as a result of excavation, once the mound is reformed, the rate of heat production becomes 104 W, which is above the rate of 92 W required for equilibrium at 30°C. This imbalance prevails until the mound warms to equilibrium at 33°C again.

Thermal stability of the mound is also aided by its immense size. With a mass of 7 t and a specific heat capacity of 1.7 J g^{-1} K^{-1} [14], the temperature of a brush turkey mound would decrease less than 1°C in a day if all heat production ceased entirely. This thermal inertia and the low thermal conductivity of the material isolate the core from daily changes in ambient temperature. However, long-term changes in ambient temperature would be magnified as larger changes in core temperature, so occasional manipulation by the bird is necessary.

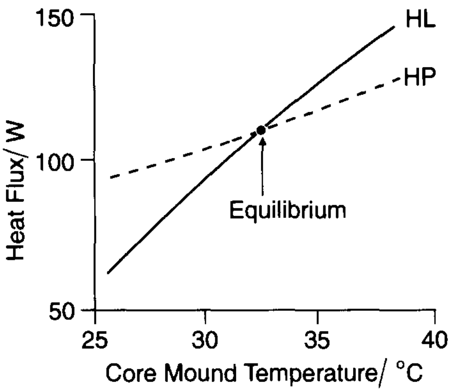

Fig. 6. Model results demonstrating equilibrium temperature in the brush turkey mound. The solid line represents the rate of heat loss (HL) from the entire mound at a given equilibrium core temperature. The dashed line represents heat production (HP) in a mound with a core temperature temporarily cooled (or warmed) away from an equilibrium temperature 33°C. Any deviation results in conditions that drive the temperature toward equilibrium. Assumptions are given in Ref. [8].

Compared to the 5 h of work carried out on a daily basis by malleefowl, however, the brush turkey does little work on the mound, after he has collected the material and core temperature has reached equilibrium. In Queensland, the bird spends only about a half hour each day tending the mound during the maintenance phase [2], and less time is spent on Kangaroo Island. We have found appropriate incubation temperatures inside island mounds that had been abandoned for as long as 6 months, and time-lapse photography practically never showed the bird working the mound [14]. Such little activity on island mounds is attributed to low water content of the mound material. The mean water content of 0.3 l per kg of dry material is just above the level (0.2 l per kg of dry material) where microbial heat production effectively ceases, and the relatively dry material has a low thermal conductivity. Therefore the rate of heat production is low, but the heat is retained in the mound and appropriate incubation temperature is possible. Wet mound material would produce more heat, but it would be lost faster due to higher thermal conductivity. Both dry and wet mounds can achieve proper incubation temperature, but the dry one requires less input of fresh litter and therefore less work by the bird. Fleay [15] suggests that brush turkey could control the amount of water in its mound by appropriately adjusting its contour. Mounds that are too dry often have a crater in the top which tends to direct rainwater into the material, while wet mounds usually have a convex top which directs rain away, in the manner of a haystack.

A dry mound not only has the advantage of lessening the workload of the adult bird, it also favors adequate aeration of the mound and the eggs within it. Respiratory gases move through the mound by diffusion, and the microorganisms take up most of the oxygen and produce most of the carbon dioxide [11]. A dry mound not only limits microbial gas exchange, but also promotes diffusion by increasing the volume of gas-filled spaces between the particles of material. Both effects are beneficial to the buried eggs. Together with an abnormally high gas conductance of the eggshell, the atmosphere in a relatively dry mound assures that the megapode embryos are exposed to levels of gas that are within the range of normal birds.

Acknowledgment

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