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Notes on Ground Temperatures at Nesting Sites of the Maleo *Macrocephalon maleo* (Megapodiidae)

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Literature on temperature and temperature fluctuations in mounds and pits of megapodes is scarce and often incomplete. Few papers give detailed descriptions (Crome & Brown 1979; Seymour & Ackerman 1980; Todd 1983; Booth & Seymour 1984; Seymour 1985; Seymour, Vleck & Vleck 1986). Apart from Todd (1983), all articles refer to megapodes that build mounds of leaf litter where heat is produced by microbial decomposition. These mound-building megapodes spend much time and energy in constructing the mound and in the regulation of its inner temperature (Baltin 1969; Seymour 1985; Seymour, Vleck & Vleck 1986). Non-mound-building megapodes like the Maleo *Macrocephalon maleo* and several *Megapodius* spp. bury their eggs in excavations (pits) in sand on beaches or inland where the sun or volcanism heats the ground, and do not spend any time in regulating the incubation temperature. Records of ground temperatures at nesting sites of the Polynesian Scrubfowl *Megapodius pritchardii* (Todd 1983) are the only detailed data for any non-mound-building megapode. The present study provides data on ground temperatures at nesting sites of the Maleo.

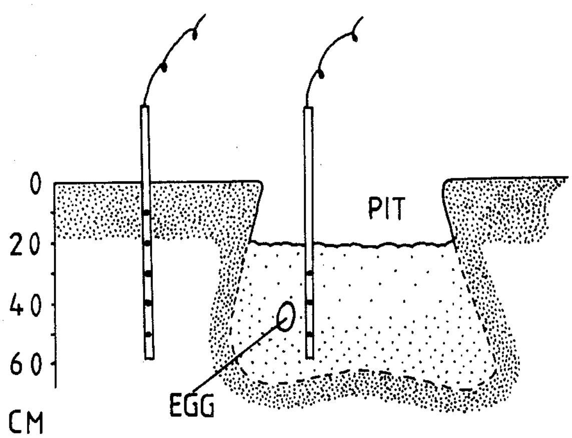

FIGURE 1 Maleo pit with egg. Temperature sensors shown inside and outside pit (1), Tambun inland nesting ground, Dumoga-Bone National Park, North Sulawesi, Indonesia.

Materials and methods

Temperature measurements were made at three different Maleo nesting grounds in North Sulawesi, Indonesia, during 1985 and 1986: (1) Tambun, Dumoga-Bone National Park: this nesting ground (1.6 ha) is heated by a hot water stream and several hot water wells. The lowland tropical rainforest at this site was recently felled and it is now overrun by *Lantana camara* and other secondary vegetation. The soil is dense and stony. (2) Tiwo, Tangkoko-Batuangus Nature Reserve: this nesting ground, situated in the lowland tropical rainforest, consists of several small bare spots. It is heated by subterranean hot water and the sun. The soil is a loose volcanic rubble. (3) Batu Putih, Tangkoko-Batuangus Nature Reserve: this black volcanic gravel beach, where the sun acts as a heat source, is now abandoned by the Maleos. It was historically an important nesting ground, but has been out of use since 1913 due to over exploitation of the eggs by man (MacKinnon 1978).

The ground temperature at Tambun and Tiwo was measured at the bottom of the pits in which the Maleos bury their eggs (Fig. 1). Depths at which temperatures were recorded inside pits, were measured from the floor of these pits. On two occasions the temperature was measured just next to an egg. At the Tambun nesting ground, temperature recordings were also made outside pits, with depth measured from the actual surface level. Thus, depths measured inside and outside pits are not directly comparable. Ground temperature at Batu Putih beach was recorded above the high-tide line at the location where the Maleos used to bury their eggs according to Wallace (1860) and Guillemard (1886).

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Temperatures were recorded with a digital 5-channel thermometer connected to five sensors buried at any desired depth. This thermometer had an accuracy of 0.1°C and a maximum variation of 0.2°C between the sensors.

At Tambun temperatures were recorded from 7 September-18 October 1985, 24 January-5 April 1986 and 7 April-13 May 1986, with a single recording between 0900 and 1200 h whenever the nesting ground was visited. These data show variations in temperatures between different days, mainly influenced by the weather. Temperatures were also recorded during day-night experiments, lasting 24-31 h, with recordings at least once every two hours during the day and several times during the night. As these data were recorded on days with calm dry weather, they show the differences in ground temperatures, mainly caused by day-night air temperatures.

Soil moisture content around the probes was measured at the beginning and end of each session from a sample of 300 g of soil, which was sun-dried. Soil moisture content (%H_2O) was calculated as $(M_w - M_d)/M_w \times 100$, where M_w is wet mass and M_d is dry mass of the soil sample. Additional data on soil moisture content were recorded at the inland nesting grounds of Tumokang, Pusian and Molibagu and at the nesting beaches of Buntalo and Pinolosean.

TABLE 1 Minimum and maximum ground temperatures (°C) at different depths. Single measurements between 0900 and 1200 h. Tambun nesting ground, North Sulawesi, Indonesia.

	Inside pit	**Outside pit**	
Duration	7 April-13 May	7 Sept.-18 Oct	24 Jan.-5 April
No. recordings	10	18	21
Depth (cm)			
20	29.4-31.0	32.1-34.6	31.3-35.7
30	30.9-32.7	34.2-36.4	33.0-37.6
40	32.1-34.3	35.8-37.8	35.1-39.2
50	33.8-36.0	37.5-39.3	37.4-41.0
% H_2O	6.3-11.0	—	—

Results

Table 1 shows the minimum and maximum ground temperatures at Tambun recorded over three periods of several weeks. The differences between minimum and maximum ground temperatures at one particular depth, when recorded outside a pit in undisturbed soil, never exceeded 4.6°C. From 7 September until 18 October, when the temperature was measured at the same spot, the maximum temperature difference was only 2.5°C. Inside an often used pit the maximum difference between minimum and maximum temperature at egg depth (30-50 cm) was 2.2°C.

The data in Table 2 show the minimum and maximum ground temperatures during day-night experiments of 24-31 h. The maximum temperature difference is 1.8°C at a depth of 10 cm at Tambun, 1.6°C at 20 cm at Tiwo and 4.3°C at 20 cm at Batu Putih. The temperature difference is almost negligible at a depth of 30 cm or more at all three locations. The air temperature on Sulawesi fluctuates between the low twenties during the night and the low to mid-thirties in the shade during the day. The effect of these fluctuations on the ground temperature is smaller than caused by the weather (see Table 1). Table 2 also shows the differences between the Tambun and Tiwo nesting grounds, with hot springs as the main heat source, and Batu Putih, where the sun provides the ground heat. At Tambun

TABLE 2 Minimum and maximum ground temperatures (°C) at different depths during day-night measurements at three Maleo nesting sites, North Sulawesi, Indonesia. Pit 1 contains a 10 cm long egg, buried with its upper end at a depth of 20 cm. Pit 2 contains an egg with its upper end buried at a depth of 30 cm.

	Tambun		**Tiwo**	**Batu Putih**
Heat source	hot springs		hot springs + sun	sun
	pit 1	pit 2		
Duration	19-20 March	26-27 March	13-14 Aug	15-16 Aug
No. recordings	13	17	25	25
Depth (cm)				
10	28.6-30.2	29.5-31.3	—	—
20	30.9-31.6	31.6-32.5	31.2-32.8	34.1-38.4
30	32.6-33.1	33.6-33.9	31.8-32.4	34.9-36.4
40	—	—	32.2-32.5	34.7-35.2
50	—	—	32.8-33.0	34.3-34.5
% H_2O	9.0-9.0	11.0-8.3	11.6-11.6	10.6-10.6

and Tiwo the ground temperature increases with depth while at Batu Putih it decreases.

Soil moisture content of Maleo nesting grounds measured on ten occasions during the temperature experiments, varied between 6.3-11.6%. Additional data from other nesting grounds during the egg-laying season show different percentages: Molibagu 36.3-45.0% (n = 5); Tumokang 12.6-20.0% (n = 5); Pusian 12.0% (n = 2); Buntalo 4.0% (n = 1); and Pinolosean 1.6% (n = 1). So, the soil moisture content at different Maleo nesting grounds during the egg-laying season varies extremely, from dry dusty sand at Pinolosean (1.6%) to a clayish soil at Molibagu (45.0%).

Discussion

The pits in which Maleos lay their eggs can be of various size and depth. At Tambun they are approximately 40-150 cm in diameter and 10-50 cm to the floor of pit. Size and depth depend on the distance of the pit to the heat source, the frequency of use by the birds and the age of the pit. The temperature of the soil inside and outside these pits increases during dry weather and decreases after rain. The effect of rain is not only direct through absence of the sun and the addition of cool water, but also indirect by dilution of the hot springs. One day after heavy rains, the temperature of the hot water wells and streams at Tambun was 1-5°C cooler than before (Zieren 1985). The highest ground temperatures between 24 January and 5 April were recorded after a dry period of nearly two weeks, while heavy rains were responsible for the minimum temperatures. From 7 September until 18 October, when the difference between minimum and maximum ground temperature was smaller, the weather showed no extreme fluctuations.

In the course of 24 h the temperature drop caused by cool nights is first recorded in the upper layers. The cooling effect becomes smaller and occurs later at increasing depths. In fact, the lowest temperature at depths of 30, 40 and 50 cm was normally recorded in the afternoon, during the hottest time of the day. A higher ground temperature decreases the incubation period, which took 62-85 days during hatching experiments at Tambun (this study).

Eggs of the mound-building Australian Brush-turkey *Alectura lathami* and Malleefowl *Leipoa ocellata* are usually incubated at temperatures of 32-35°C (Frith 1956, 1962; Seymour & Ackerman 1980; Seymour 1985). Sixty-two percent of the eggs (n = 89) of the non-mound-building Polynesian Scrubfowl were found in pits at a temperature of 33-35°C (Todd 1983). At the Maleo nesting grounds this temperature is found over a considerable vertical range in the pits (Table 1 and 2). At Tambun, the Maleos bury their eggs between 20 and 85 cm, most frequently between 30 and 50 cm, measured from the floor of the pit. Eggs are laid deeper after heavy rains when the ground temperature has dropped and shallower after droughts. At inland nesting grounds egg depth is not only influenced by weather conditions but also by the distance of the pit to the hot springs. Eggs are buried less deeply and the pits are smaller and shallower when they are closer to the hot springs.

Other data on soil temperatures at nesting grounds of non-mound-building megapodes also show temperatures close to 32-35°C over a considerable vertical range. At a nesting beach of the Melanesian Scrubfowl *Megapodius eremita* on Savo, Solomon Islands, heated by the sun and subterranean volcanic activity, Roper (1983) recorded the ground temperature as 31.0°C at a depth of 15 cm, 31.5°C at 30 cm, 32.5 °C at 45 cm and 33°C at 1 m, measured at an air temperature of 32.0°C. The temperature difference over a vertical range of 50 cm, from a depth of 50 cm to 1 m, at five nesting grounds of the non-mound-building Polynesian Scrubfowl on Niuafo'ou, was only 2-4°C (Todd 1983).

During egg laying, male and female Maleo can be seen regularly with bills full of sand as has also been observed for the Malleefowl (Frith 1962) and Australian Brush-turkey (D. Jones pers. comm.). Experiments in which the temperature inside the mound was manipulated made Frith (1962) suggest that the tongue or interior of the bill of the Malleefowl is temperature-sensitive. Comparison of egg depths recorded at two different nesting grounds of the Polynesian Scrubfowl on Niuafo'ou (0.2-1.7 m) shows that eggs are laid deeper when the soil is cooler (Todd 1983). Also in this study the depth at which the eggs are buried at the Tambun nesting ground was observed to be related to weather conditions and distance from the heat source. This suggests that non-mound-building megapodes also monitor the temperature suitable for incubation and do not bury their eggs as deeply as they can, as assumed by MacKinnon (1978).

Without any care for the eggs and their environment, non-mound-building megapodes manage to incubate their eggs at similar temperatures as the hard-working mound-building species, who spend months in building, defence and maintenance of the mound.

The soil moisture content in pits at Tambun varied between 6.3% and 11.0% (n = 11), similar to that recorded in Malleefowl mounds and less than in Australian Brush-turkey mounds (Booth & Seymour 1984; Seymour, Vleck, Vleck & Booth 1987). The water in megapode mounds and pits eliminates the danger of dehydration of the eggs, which are among the dryest of avian eggs because of their large yolk and small albumen content (Vleck, Vleck & Seymour 1984). Excess water in the mounds and pits may, however, be detrimental. The soil moisture content during the egg-laying season varied between different nesting grounds from 1.6-45.0%. This suggests that the water content of the soil is not the key factor that determines the suitability of a certain site as a nesting ground.

Ten different Maleo nesting grounds on north Sulawesi, visited during this study, also showed considerable differences in soil structure, vegetation structure and density, level of disturbance and source of heat. At the Tambun and Tumokang inland nesting grounds, both heated by hot springs, egg-laying is year-round although a peak season can be recognised. At the coastal nesting grounds of Buntalo and Pinolosean, with the sun as the only heat source, egg-laying occurs only during the dry season (this study). During the wet season the sun is often absent and probably not capable of heating up the wet soil of these nesting beaches sufficiently. It therefore seems that the temperature is the key factor and that Maleos can and will use a site for egg laying as long as good incubation temperatures are present at depths that can be reached by the birds.

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