Volcanic heat incubation in *Megapodius freycinet eremita* Hartl.

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(*Med et dansk resumé: Udrugning ved vulkanvarme hos* Megapodius freycinet eremita Hartl.)

The Megapodidae (Megapodes, Incubator Birds, Temperature Birds, Jungle-Fowl) are the only certain instance of birds which hatch their eggs through means other than body heating. The majority utilize the fermentation heat in scratched-together mounds of decaying vegetable matter (e.g. *Talegalla cuvieri*, *Aepypodius arfakianus*, and *Megapodius freycinet duperryi* in New Guinea and *Alectura lathami* and *Megapodius freycinet yorki* in Queensland, Australia).

A combination of fermentation and solar heat is used by the Mallee Fowl *(Leipoa ocellata)* of Australia.

A third group of Megapodes seems to be quite independent of fermentation heat, viz. the Maleo, *Megacephalon maleo* and *Eulipoa wallacei* in Indonesia which lay their eggs in black, soft lava sand near the beach, thus utilizing the solar heat (SARASIN & SARASIN 1894, p. 13, DE RUITER 1930, RIPLEY 1960). FRITH (1955) recorded two rare instances of *Leipoa ocellata* incubating entirely by solar heat.

1. MEGAPODIUS FREYCINET EREMITA

This third group also includes a single subspecies of the widespread species *Megapodius freycinet*, viz. *M. f. eremita* HARTL. While the other subspecies practically always[1] build mounds of leaf-mould or sand and seaweed, utilizing the fermentation heat, there are no convincing records of *M. f. eremita* acting in the

1. BANFIELD (1913) recorded that *M. freycinet* (probably *M. f. castononotus)* on Dunk Isl. south of Cairns, Queensland, not only built the usual mounds in the jungle but also laid single eggs in small holes on the sandy flats. FRITH (1956) referred to BANFIELD and found that the birds "depended apparently entirely on the heat from the sun to incubate them". This is not necessarily so. BANFIELD stated that on the sandy flat (not beach as FRITH wrote) "there is a fair amount of shade" and that the egg in the 6 or 8 inches deep pit is covered with leaves. He also stated that there can be little doubt that the egg deposited in such a pit is occassionally hatched. According to FRITH (l.c.), "some individuals even dispensed with digging holes in the sand and the egg was laid in a deep fissure between two flat rocks warmed by the sun and insulated by a layer of leaves". There is no such statement in BANFIELD 1913.

same way[2]. Instead, it incubates the eggs by means of inorganic heat sources, viz. solar and volcanic heat.

A. Solar heat incubation

Woodford (1888) (not Lister (1911), as stated by Frith (1956)) mentioned that the Megapodes on Savo Island north of Guadalcanal in the Solomons "lay their eggs on two large cleared sandy spaces, and nowhere else on the island". No weeds or grass can grow there as the sand is constantly turned over by the digging birds or by the natives in search of eggs. This is probably an instance of sun-heating, as also believed by Woodford who wrote (l.c.): "An open space being of course essential to allow the rays of the sun to warm the ground". However, as Savo is an active volcano, which had its latest eruption in the 1840's, it cannot be excluded that volcanic heating of the underground is involved.

Sibley (1946) reported that a few birds of *M. f. eremita* nested in sun-warmed sand on a small islet near Simbo Isl. in the Central Solomon Islands. This *may* be the same site as that referred to by Grover who in his description of the geology of Simbo Island and Islet (1955) wrote: "The southern end of Simbo Islet is a nesting area for megapode birds, who bury their eggs about 4 ft. down in the loose soil, which is warmed by local thermal effect".

B. Volcanic heat incubation

Previous records

Prior to my own observations there seem to be only three reliable records of volcanicly heated soil being utilized by *M. f. eremita*.

Two years before the violent eruption in 1937 of the volcano Tavurvur a few km south of Rabaul, Pockley (1937) found several Megapode nesting sites on the slopes of the volcano. Some were located in "hollow-sounding, flat, hard bottom, which, over an area of several square yards, was studded with deep holes about a foot in diameter". Some looked like well-defined post-holes, filled with loose sand up to about a foot from the top, others slanted down at an angle, with the hole between the sand and the upper wall passing out of sight. The sites were in groups, surrounded by thick bush. However, one nesting site was on a steep land slide, about a hundred metres long. The many holes here were more ragged as there was no firm surface soil (l.c., photograph on pl. 9). Natives produced several eggs and a couple of newly hatched birds from the holes. Pockley suggested that the "volcanic heat is a big factor in assisting incubation and in determining the habitat of the birds".

Sibley (1946) described a nesting site on the densely vegetated north slope of the active volcano on Simbo Isl. in the New Georgia group, Central Solomon Islands. The soil was deep, although rocky, and there was no surface evidence of volcanism. Within an area of about 5000 square yards there were at least 200 separate nest burrows. A similar nesting site was said to be located on the opposite side of the volcano. The burrows varied in

2. Frith (1956) stated that in the Solomon Islands (according to Mayr 1930) "the typical type of mound, on a small scale was found inland, but nearer to the coast eggs were laid between the buttressed roots of trees and covered over by heaps of decaying leaves". No such statement on the Solomon Islands Megapodes was made by Mayr (cf. below, p. 82). Frith (l.c.) also reported that he had been informed by Australian troops that in Bougainville they had found the two types of mounds described in the above citation. Moreover, he stated that "in the Wide Bay area of New Britain, in 1943, the "normal" type of organic-matter mound was found in the jungle", but gives no reference as to the source of this observation.

diameter from 10 inches to 3 feet, and in depth from 1 to 3 feet. In spite of the humid climate the soil was found to be dry and crumbled owing to heat dehydration. The bottom soil of the burrows was appreciably warmer to the touch than was the exposed surface of the earth. About a dozen eggs were excavated. SIBLEY suggested that the concentration of Megapode nests on this particular hill was directly correlated with the heat supplied by the volcano. There are many hills on Simbo which superficially resemble the volcanic hill but which, according to the natives, have no Megapode nests. The few Megapodes nesting in the sun-warmed sand on a near-by islet were referred to above.

Before joining the Noona Dan Expedition in 1962 I was told by Dr. CARL J. KREBS that in the course of a geological expedition to New Britain in 1960 he came across a Megapode nesting site near a volcanic area at Cape Hoskins, on the north coast of the island. He later published a short account of his observations (KREBS 1963).

Own observations

In May 1962 the Noona Dan Expedition worked for three weeks in the mountains of New Britain. It was then decided that a lowland area on the same island should be investigated for comparison. Cape Hoskins was chosen, first and foremost because the volcanic soil of the area suggested both a rich vegetation and an abundant animal life, but also because we were interested in confirming KREBS'

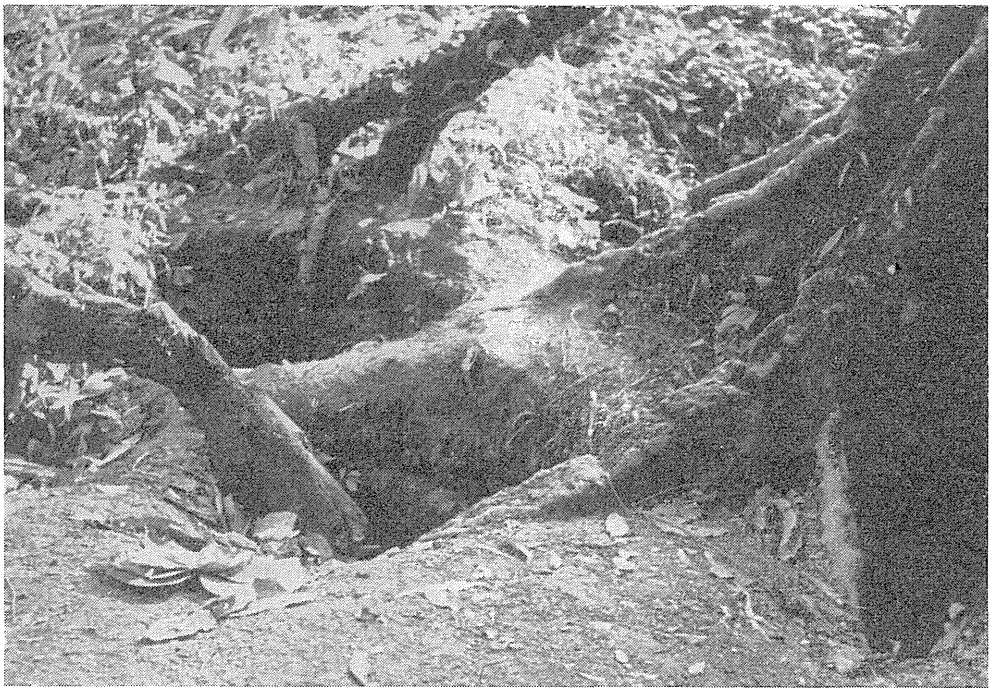

Fig. 1. Burrows of *Megapodius freycinet eremita* at the foot of Mt. Bango, Cape Hoskins, New Britain. Three burrows to the left, two or three to the right, behind the tree. (T.W. phot.).
Redehuller af Megapodius freycinet eremita ved foden af Mt. Bango, Cape Hoskins, New Britain. Tre redehuller til venstre og to eller tre til højre bag træet.

Fig. 2. Same nesting site as in Fig. 1. Native egg collector. (H. DISSING phot.).
Samme redested som på fig. 1. Indfødt ægsamler.

interesting observations on the Megapode breeding habits.

The expedition members worked at Valoka, Cape Hoskins, from 4.—13. July 1962. On three occasions the nesting area of *M. f. eremita* was visited, although only for short periods. It is known locally as the Kiau-(egg)land.

The site is situated at the northern foot of the impressive volcano Mt. Bango. A few hundred metres south of the site is an open area in the forest, measuring about 3 ha (7 acres), with several hot springs, boiling ponds, mudpots, and steaming fissures. A similar volcanic area was mentioned by SIBLEY (l.c.) not far from the nests on Simbo.

The nesting site itself is in a more open forest than elsewhere in the area, consisting of low trees, about 20 m high, with some undergrowth. The yellowish, loose tuff soil is in places entirely undermined by burrows which closely resemble fox dens (Figs. 1—2); these are 20 to 75 cm in diameter, and sometimes stretch several metres in an oblique direction from the opening. The wide entrance is probably caused by native egg-hunting activities. On our arrival only a few birds were observed, and these were moving on the ground in the usual Megapode way. Occasionally, the loud harsh call was heard. It was not until a gun was fired that we realized that a great many birds were hiding in the tree-tops. Some of the birds shot contained eggs ready to be laid.

According to information of several local inhabitants the nesting site covers an area of 2—3 km² (0.7—1 sq. mile). I estimated the density of nest holes to be at least one per 10 m², and the natives claimed that the density of the rest of the site equalled that of the area seen by us. If these figures are correct (unfortunately we had no time to confirm them), the number of nesting birds must run into hundreds of thousands as each burrow is probably used by more than a single female. (WOODFORD (1890, p. 100), speaking of the Megapode nesting sites in Guadalcanal (Solomon Islands) stated: "Many thousands of these birds congregate at the same place, the laying-yards being often some acres in extent"). These large numbers are in accordance with the fact that, according to local information, the total population of Megapodes within the Cape Hoskins area (between the rivers Kapiura and Dagi, which are never crossed by these birds) utilize this site. The area between the rivers covers approximately 900 km² (300 sq.-miles), the greater part of which is covered by primary forest.

On one occasion I measured the temperature in a burrow. Air temp.: 31° C.; temp. of the soil where an egg was placed,

depth about 1.2 m: 36°; temp. of soil about 15 cm below the egg: 37°.

The few eggs collected seem to be smaller than eggs from Vuatom near New Britain (MEYER 1930a) and eggs recorded by HEINROTH (1902) from various islands in the Bismarck Archipelago:

Cape Hoskins		Vuatom (MEYER)		(HEINROTH)
85 g	47×77 mm	84.5 g	46×75 mm	89 g
91 g	46×79.5 mm	102.0 g	47×81 mm	90 g
93 g	49×78.5 mm	103.5 g	48×83 mm	93 g
		103.5 g	47×84 mm	95 g
		105.5 g	50×76 mm	97 g
		106.5 g	50×76 mm	100 g
		107.8 g	49×82 mm	101 g
				107 g
				116 g
Average				
89 g	47×78 mm	102 g	48×80 mm	99 g

Like ours, most of the Vuatom eggs were collected in the beginning of July. REICHENOW (1899) gave the egg weight as 67—86.4 g and the size as 47—50× 71—81 mm.

HEINROTH recorded the weight of adult birds (both sexes) as 570—660 g; MEYER gave no weights. Adult females from the Noona Dan Expedition weighed as follows:

Cape Hoskins	555 g	
	565 g	
	580 g	
Dyaul Isl.	550 g	Weighed after deep-freezing.
Credner Isl.	550 g	
New Hanover Isl.	600 g	
Average	570 g	

Thus, it appears that the egg weight amounts to about one sixth of the total body weight.

Fig. 3. Women on their way home from the nesting site, carrying packed and piled Megapode eggs. (T.W. phot.).
Kvinder på vej hjem fra rugepladsen med æg af tallegallahøns.

It is a well known fact that probably wherever the Megapodes occur their eggs are exploited by the local natives. For example, STRESEMANN (1941) mentions that the local government takes a lease of the nesting sites of *Megacephalon* on Celebes, and WOODFORD (1888) states that on Savo in the Salomon Islands "the sandy spaces are fenced off into plots which belong to different owners". Similarly, "the dangerous Sepiks in the interior of New Guinea know each owner of the 30 to 50 nest mounds located within a radius of five miles of the village of Kanganaman; they do not rob nests owned by other members of the tribe. The nest mounds are often within a hundred yards of villages" (GILLIARD 1958).

As far as *M. f. eremita* is concerned, STUDER (1877), LAYARD (1880), WOODFORD (1888), MEYER & STRESEMANN (1928) and KREBS (1963) report that the natives collect and eat the eggs. We found that they came to the nesting area from the entire Cape Hoskins area, covering distances of 30—40 km to get there. We saw no division of the nest holes, as referred to above.

The eggs are neatly packed two by two in small baskets made of the fresh young leaves of cane *(Calamus)* and furnished with a small handle. They are stacked on flat trays and transported on the head (Fig. 3).

During our stay in Rabaul later in July I had the opportunity to pay a short visit to the still active volcano Tavurvur, a few km south of Rabaul, on the east bank of Blanche Bay. Its most recent eruption occurred in 1937, and the temperature of the crater is measured once or twice a week by collaborators of the Volcanological Observatory. I joined an inspection trip, and on inquiring whether the Megapode was present was shown several burrows under low trees and bushes at the foot of Tavurvur, only about 30 m from the shore line (Figs. 4—5). They closely resembled those on Cape Hoskins, and although time did not permit temperature measurements there can hardly be any doubt that volcanic heat was also used at this site. The beach in front of the site consisted of black sand which would appear very suitable for incubation by solar heat (cf. STUDER 1877). No nest holes were, however, found here.

I saw no nesting holes on the vegetation-free slopes of Tavurvur corresponding to those described by POCKLEY (1937) before the eruption. However, at a later date Mr. STEVEN SIMPSON of Rabaul took me on a short drive to the forest covering the land behind the volcano. Time permitted a

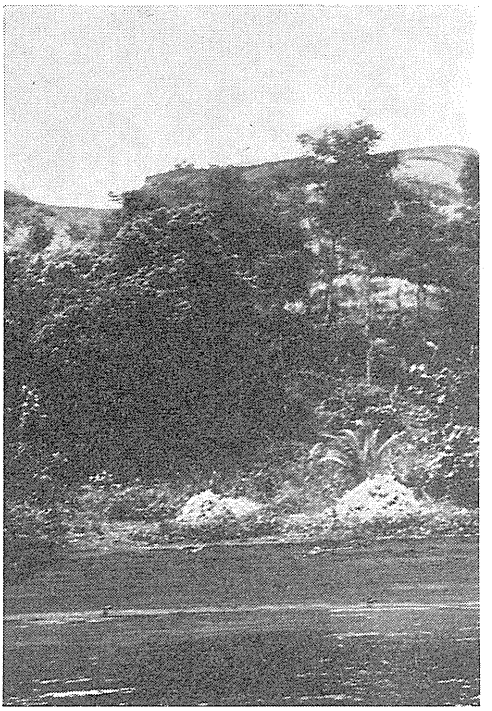

Fig. 4. Nesting site is in the centre thicket. In the background, the active volcano Tavurvur south of Rabaul; in the foreground, beach with black sand. (T.W. phot.).
Yngleplads en findes i tykningen i midten. I baggrunden ses den aktive vulkan Tavurvur syd for Rabaul, i forgrunden strandbredden med sort sand.

Fig. 5. About twenty burrows of various sizes in the same nesting site as in Fig. 4. (T.W. phot.).
Omkring 20 redehuller af forskellig størrelse i den samme rugeplads som på fig. 4.

visit to only one of the nesting sites, but Mr. SIMPSON knew of at least 30 more in the area.

The site visited was located on a slope, shaded by a clump of large bamboo and by low trees (Fig. 6). It covered about 40 × 25 m and contained about 30 burrows. These were excavated in the loose brownish tuff soil (Fig. 7) and varied in size from about 25 to 60 cm. The soil of the burrows felt warmer than the surroundings but no temperature measurements were made. The whole area is volcanic; not far from the site visited, the Japanese troops used to obtain salt by boiling sea-water in oil-drums dug into the hot soil. Thus, I feel certain that here, again, the Megapodes utilize volcanic heat.

As at Cape Hoskins, the native name for the egg is kiau; the Megapode is termed ngiok.

C. UNCERTAIN INCUBATION METHODS

STUDER (1877) described a nesting site of *M. f. eremita* near the port of Rabaul, New Britain, where the species was found in considerable numbers. The female was reported to dig 30—60 cm deep holes in the black sand where the eggs were laid. Measurements of the sand showed a temperature of 38—40° C. and only insignificant cooling during the night. STUDER said nothing about the source of heat. In the early days the Germans used two bays as a harbour, viz. the innermost part of Blanche Bay where the present-day Rabaul is located, and also what is now known as Greet Bay just north of Tavurvur. If STUDER's "Rabaul Hafen" refers to the first-mentioned locality the heat in the nesting site would probably have originated from the sun as there has never been any volcanic activity in that part of

the Blanche Bay area. This site would later have been abandoned owing to the expansion of the town.

However, in my opinion it is much more likely that STUDER talked about Greet Bay. According to STEVEN SIMPSON many Megapode nests are still to be found in the sand along the shore of this bay. As volcanic activity is notable along this entire section of the coast, the sea-water being heated locally to boiling point, there can be little doubt that here the sand-nesting Megapodes utilize volcanic heat for the incubation. Actually, Mr. SIMPSON knew of several similar sites in sand along the shores of Blanche Bay and felt sure that volcanic heat was involved in each case. He could think of no place where the sun may have been utilized.

Also LAYARD (1880) described a nesting site somewhere near Rabaul. It was located in a steep ravine, the slopes of which were covered with dense bushes; an open space of about 20 square yards with small round volcanic pebbles contained several Megapode hollows. LAYARD does not mention any volcanic activity in the neighbourhood which may have produced an increased ground temperature.

MEYER reported (MEYER & STRESEMANN 1928) that on Vuatom Isl. near New Britain the nest sites of *M. f. eremita* are always found in shaded forests where the birds either make use of natural holes or dig extensive burrows in the loose soil; here the eggs are laid and covered with soil. The natives hunt for the eggs and claim that these are only to be found in niches which are warm to the touch as the eggs heat the surrounding soil. Based on these and other similar observations STRESEMANN (l. c.) suggested that when buried in loose, dry soil the original heat from the mother hen combined with the heat production of the embryonic metabolism was sufficient to secure the incubation of the eggs. MEYER (1930a) gave a more detailed description of the nesting site. He also recorded temperature measurements of the soil close to buried eggs. In one case he found 30.5°, in three cases 31° and in two cases 31.5° C. He claimed to be able to rear an egg at room temperature (25—30° C.) (MEYER 1930b).

This incubation by specific warmth was strongly opposed by FRITH (1956) who found that MEYER's observation that the soil temperature in holes containing eggs was higher than in holes not containing eggs was built on very slender evidence. FRITH did not suggest any other incubation method. In my opinion, it seems probable that volcanic heat is involved. This might also explain why the soil of the site is so dry and loose. However, the extraordinary difference between MEYER's temperature records, and those of STUDER (1877) and my own is hard to explain.

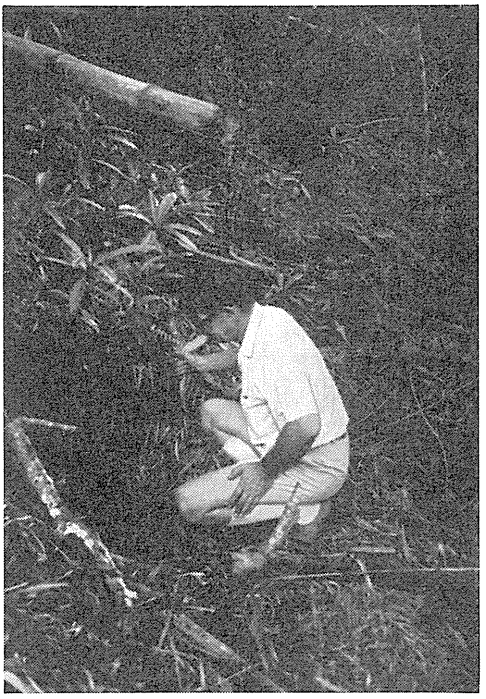

Fig. 6. Part of the nesting site N.E. of Tavurvur. (T.W. phot.).
En del af rugepladsen NØ for Tavurvur.

Very different from the two said biotopes at Rabaul and on Vuatom is that described by MAYR (1930). In the Solomon Islands (Choiseul, San Christoval and Malaita) he found the eggs of *M. f. eremita* buried at the foot of giant buttressed trees, in places as far inland as 10 km from the coast. Incubation by solar and (probably also) volcanic heat is excluded. MAYR stated that the method used is in strong contrast to the usual mound-building, and did not mention whether decaying leaves were involved.

2. OTHER SPECIES

Volcanic heat is probably also utilized by *Megapodius pritchardi* G. R. GRAY which is restricted to the very actively volcanic island Niuafo'ou between Fiji and Samoa. According to FRIEDLÄNDER (1899) the eggs are laid in hollows in tuff-like soil. Nest holes containing eggs could be distinguished from abandoned nest holes by remarkable heat. MEYER & STRESEMANN (1928) referred to this observation as support for their theory on incubation by specific heat in Megapodes, but there is no evidence that so-called abandoned nest holes had actually contained eggs. FRIEDLÄNDER himself suggested that the heat might be of volcanic origin, as in the vicinity of active fumaroles all kinds of different temperatures are to be found. He therefore regarded it very likely that the birds select places where they find temperatures suitable for incubation.

Fig. 7. Flash photograph of one of the larger burrows in the same nesting site as in Fig. 6. (T.W. phot.).
Kunstlys fotografi af et af de store redehuller i den ugeplads som er vist på fig. 6.

Obvious incubation by volcanic heat in the Maleo *(Megacephalon maleo* HARTL.) was recorded as early as 1894 by P. and F. SARASIN (1894, pp. 388 and 396). On two occasions in the Bone Mountains, North Celebes, and on one occasion at an altitude of 1200 m on the volcano Embung, Minahissa (SARASIN 1905, p. 13), they found Maleo nest holes in the close vicinity of hot springs (about 50—60° or more). One site was located at Bone River on a sandy bank overgrown by bamboo. In the same place was a hot spring resembling a tiny geyser (SARASIN 1905, p. 150, fig. 47). The authors have no doubt that in shaded localities in the cool mountains the Maleo has turned to this breeding method instead of the ordinary incubation in sun-heated sand near the sea.

Although there can be no doubt that *Megapodius freycinet eremita* incubates the eggs by either solar or volcanic heat, careful observations on its behaviour at the nesting site are still badly needed. Transfer of hens from sun-heated beaches to volcanic areas and vice versa might also prove very interesting. It also remains to be stated with certainty whether or not

this subspecies can adopt a breeding method resembling that of the other subspecies in places where solar or volcanic heat is not available and whether these other, closely related subspecies always depend on organic heat even in places where inorganic heat is easily available.

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SUMMARY

The scattered literature on volcanic heat incubation in *Megacephalon maleo* and (probably) *Megapodius pritchardi* and the solar and volcanic heat incubation in *M. f. eremita* is reviewed and discussed.

The large nesting site in the vicinity of a fumarole area at Cape Hoskins, New Britain, is described. Temperature measurements, size and weight of eggs and weight of adult females are given and compared to other records, and exploitation of the eggs by natives is recorded. Two other nesting sites at the volcano Tavurvur south of Rabaul are briefly described.

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DANSK RESUME

Udrugning ved vulkanvarme hos *Megapodius freycinet eremita* Hartl.

Langt de fleste tallegallahøns *(Megapodiidae)* lader deres æg udruge ved hjælp af gæringsvarmen i sammenskrabede høje af muld og vissent løv. En kombination af gæringsvarme og solvarme benyttes af den australske Malleehøne *(Leipoa ocellata)*, den eneste art, hvis ynglebiologi er grundigt studeret.

Enkelte arter, som Hammerhønen *Megacephalon maleo* og *Eulipoa wallacei* i Indonesien, bruger udelukkende uorganiske varmekilder, først og fremmest solvarme. Det samme synes at være tilfældet med en enkelt underart af den vidtudbredte art *Megapodius freycinet*, nemlig *M. f. eremita*, der forekommer på Bismarck- og Salomonsøerne.

Den sporadiske litteratur om denne underarts ynglebiologi omfatter to ret sikre angivelser af brug af solvarme (WOODFORD 1888 og SIBLEY 1946). Der foreligger tre korte beskrivelser af, at *M. f. eremita* lader æggene udruge i vulkansk ophedet jord (POCKLEY 1937, SIBLEY 1946 og KREBS 1963).

Under min deltagelse i Noona Dan ekspeditionen i 1962 havde jeg lejlighed til at gøre en del iagttagelser af *eremita*'s ynglebiologi på New Britain, Bismarckøerne.

Ved Cape Hoskins på øens nordkyst besøgtes et yngleområde, der lå i umiddelbar nærhed af et felt med kogende kilder m.m. ved foden af vulkanen Mt. Bango. Området fandtes i skov og dækkede efter sigende 2—3 km². Den løse tuf-jord var delvis undermineret af talrige rævegrave-lignende huller, der tjente som ynglepladser for hundred-tusinder af fugle fra et meget vidtstrakt skovområde (på sandsynligvis 900 km²). Talrige fugle sås i træerne.

Måling af temperaturen viste 31° C ved hullets indgang, 36° hvor æg lå begravet og en stigning på yderligere 1° kun 15 cm herunder.

Måling af æg viste mindre gennemsnitsstørrelse end tidligere angivelser i litteraturen. Vægten af det uforholdsmæssigt store æg udgør 1/6 af hunnens vægt.

Ligesom andetsteds udnyttes æggene af de indfødte, der kommer langvejsfra, opgraver æggene og transporterer dem hjem indpakket to og to i palmeblade og opstablet på flade bakker.

Under ophold i hovedstaden Rabaul i nordøstenden af New Britain aflagde jeg besøg ved to tilsvarende men meget mindre yngleområder ved foden af den stadigt aktive vulkan Tavurvur, der havde sit seneste udbrud i 1937. Det ene område lå ganske nær kysten, det andet, der omfattede ca. 30 huller, på en skrænt i skoven. Jeg fik oplyst, at der var mindst 30 lignende yngleområder omkring Tavurvur.

Nogle ældre beskrivelser i litteraturen af *eremita*'s yngleområder refereres og diskuteres.

Medens der ikke kan herske tvivl om, at også *Megacephalon maleo* foruden solvarme benytter vulkansk varm jord (P. & F. SARASIN 1894), er ynglemetoden for *Megapodius pritchardi*, der kun findes på den lille vulkanske ø Niuafo'ou ved Fiji, ikke med sikkerhed fastslået. Ligeledes kræves der fortsatte undersøgelser for at konstatere, om *M. f. eremita* foruden ovennævnte uorganiske varmekilder tillige kan anvende gæringsvarme under en eller anden form.

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