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The biology of the Moluccan megapode *Eulipoa wallacei* (Aves, Galliformes, Megapodiidae) on Haruku and other Moluccan Islands; part 2: final report

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The Moluccan megapode *Eulipoa wallacei* inhabits forests of several Moluccan Islands (Indonesia). The birds only leave this habitat for the purpose of egg-laying in self-dug burrows on sandy beaches, where solar heat incubates the eggs. The eggs are collected, sold and consumed by local people, a tradition that is said to threaten the species' existence. An intensive study was carried out in the periods June 1994 - June 1995 and January - May 1996 at one of the largest known communal nesting grounds, 'Tanjung Maleo' near Kailolo Village on Haruku Island and at nesting grounds on other islands. In close collaboration with the local people, reproduction data were obtained by daily counts of the number of collected eggs and fledged chicks. Experiments were carried out to establish the incubation period. Egg-laying behaviour was studied with nightvision equipment. The egg-laying interval, home range, inland habitat and provenance of the female birds were established by radio-tracking of nine individuals. Of the 36.263 eggs that were harvested in the 94/95 season (1 April-31 March) peak numbers (max. 211 eggs per night) were found in the dry season (October-March) when 68.4% of the total egg production is laid. 13.7 % of the total egg production was not found by the collectors. Of those eggs, 1.7% got lost otherwise and 12% resulted in fledglings. This apparently ensures (for the time being) enough offspring to keep the population in balance. The total egg-laying population of Tanjung Maleo was estimated at 4200 females. The average egg-laying interval was 13 days. Chicks fledged after an average incubation period of 74.2 days. A fledging percentage of 92.6 for reburied freshly laid eggs indicates good prospects for re-introduction of the species. Female birds were tracked down to South Seram and also appeared to be resident in the secondary forest and neglected cultivated areas of Central Haruku. Surveys to check the status of other known nesting grounds showed many old sites abandoned (e.g. Meti off Halmahera) or diminished numbers of egg-laying birds. Tanjung Maleo (Haruku) and Galela (NE-Halmahera) appeared to be the two remaining large nesting grounds, although on almost all Moluccan islands within the range of the species, medium sized nesting grounds, where substantial numbers of eggs are being laid, were found. New nesting localities were discovered on Buru (scattered along the north coast) and along the northern and southeastern coasts of Seram.

Het Wallace grootpoothoen *Eulipoa wallacei* is een bewoner van (berg)bossen op verschillende Molukse eilanden (Indonesië). De vogels verlaten deze habitat uitsluitend om eieren te leggen in zelf gegraven holen op zandstranden, waar zonnewarmte de eieren uitbroedt. De lokale bevolking verzamelt, verkoopt en consumeert de eieren op grote schaal. Deze traditie schijnt het voortbestaan van de soort te bedreigen. Een uitvoerige studie van deze vogel vond plaats in de perioden juni 1994 - juni 1995 en januari - mei 1996 op één van de grootste bekende legplaatsen, 'Tanjung Maleo' bij het dorpje Kailolo op het eiland Haruku. In nauwe samenwerking met de locale bevolking werden gegevens verzameld van het dagelijks aantal geoogste en uitgekomen eieren. Middels experimenten werd de broedduur vastgesteld. Het nachtelijk eileg-gedrag werd bestudeerd met nachtzicht apparatuur. De eileg-interval, home-range, habitat en de herkomst van de vrouwtjes werden vastgesteld aan de hand van negen gezenderde vogels. Van de 36.263 eieren die in het oogstjaar 94/95 (1 april-31 maart) werden verzameld, werd het maximum aantal van 211 per nacht vastgesteld in februari (droge tijd). In de droge tijd (oktober-maart) werd 68.4% van de totale jaarlijkse eiproductie gelegd. 13.7 % van de gelegde eieren ontsnapte aan de oogst, daarvan ging nog eens 1.7% anderszins verloren en resulteerde 12% in uitgevlogen jongen. Dat percentage is klaarblijkelijk voorlopig voldoende om de populatie in evenwicht te houden. De gemiddelde eileg-interval bleek 13 dagen te bedragen en de gemiddelde broedduur was 74.2 dagen. Een uitkomst-percentage van 92.6 van geoogste en weer herbegraven vers gelegde eieren, geeft goede vooruitzichten voor het verplaatsen van eieren met het oog op de (her)introductie van de vogel. Gezenderde vogels werden teruggevonden in Zuid-Seram en bleken ook het centrale heuvelland van Haruku als leefgebied te hebben. Zoektochten naar legplaatsen op andere eilanden, toonden aan dat veel vanouds bekende legplaatsen verlaten zijn (bv. Meti bij Halmahera) of dat het aantal eieren dat er gelegd wordt, sterk is teruggelopen. Tanjung Maleo (Haruku) en Galela (Halmahera) blijken de enige twee grote legplaatsen te zijn, maar op bijna alle Molukse eilanden binnen het verspreidingsgebied van de soort blijken toch ook nog middelgrote legplaatsen, waar behoorlijke aantallen eieren worden gelegd, voor te komen. Nieuwe legplaatsen werden ontdekt langs de noordkust van Buru en langs de noord- en zuidoostkust van Seram.

Selama periode bulan Juni 1994 - Juni 1995 dan Januari - Mei 1996 di Pulau Haruku, Maluku, telah diteliti biologi dan cara bertelur burung momoa Maluku (*Eulipoa wallacei*). Telah dipastikan lama perkembagan telur beserta pengaruh luar yang mempengaruhinya. Tempat bertelur lama di Maluku diperiksa dan telah ditemukan tempat-tempat bertelur baru. Dalam penelitan ini termasuk cara pengumplan telur oleh pendukuk Kailolo dan adat isiadat yang berkaitan dengan hal tsb. Dicantumkan pula rekomendasi untuk pelestarian dan penglolaan spesies ini.

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CONTENTS

'There are small hens in the jungle, who lay such large eggs, much bigger than duck eggs, that it would be quite a task if you had to eat two of them. I have seen them. These hens, a species of Megapode, lay their eggs into the soft soil at a depth of about one metres or into the sand. After a few days the chicks hatch and dig themselves up from the soil and then run off very fast, like young partridges, so fast in fact, that no one or nothing can catch up with them. It is almost unbelievable, unless you see it for yourself like I and my companions did when we were there on the spot. I have even eaten these hens, they taste allright, although the meat is a bit tough'.

from: Nuñes 1576 (in Jacobs 1974), the first known written report about *Eulipoa wallacei*

1 INTRODUCTION

The megapodes (Megapodiidae) form one of the most peculiar families of birds. This is largely due to their breeding biology which is unique among birds: they use external heat sources for incubation. Microbial respiration, geothermal energy or solar radiation generate heat that causes the eggs, laid in mounds of leaflitter or burrows in the soil, to hatch. Consequently, chicks of megapodes are the most precocial of all bird species: newly hatched chicks are immediately able to fly, are fully self supporting and receive no parental care. Currently, the family comprises 22 species that occur on the Nicobar Islands (India), in eastern Indonesia, Australia, on New Guinea, the Philippines, on Niuafo'ou Island (Tonga) and the Mariana Islands (Southwest Pacific). The center of their distribution lies in the Indo-Australian region, east of Wallace's Line, where the birds generally inhabit tropical forests. Current knowledge of the megapodes is summarized by Del Hoyo et al. (1994) and Jones et al. (1995).

This article concerns the Moluccan megapode, a species discovered by A.R. Wallace in 1858 on the island of Halmahera (Wallace 1860, 1869). It was described by Gray (1860), based on the specimens collected by Wallace[1], as *Megapodius wallacei*, but later workers (Ogilvie-Grant 1893 and, more recently, Roselaar 1994) placed the taxon in a distinct genus, *Eulipoa*, based on colouration and structural characteristics differing clearly from those of *Megapodius*. The species inhabits the Moluccan Islands of Halmahera, Bacan, Seram, Buru, Ambon and Haruku, and the Western Papuan Island of Misool, all within the boundaries of the Indonesian Republic.

Eulipoa wallacei is a forest bird that only leaves its habitat to lay eggs in self-dug burrows at communal nesting grounds situated on sun-exposed beaches or in forest-clearings at sea-level. It is the only megapode that lays eggs at night: one at a time after which the birds return to their inland habitat, in general before dawn. The species' existence is currently believed to be seriously threatened due to the large scale harvesting of eggs at their communal nesting grounds (Collar et al. 1994), a habit that has a history of at least a century (Van Hoëvell 1875; Martin 1894) and is therefore deeply rooted in local human communities which reside close to the birds' nesting grounds (Heij 1995a; Argeloo & Dekker 1996). The breeding biology, population-dynamics, behaviour and other aspects of the birds' life history and ecology are virtually unknown. Most basic data were gathered by early naturalists of the Malay Archipelago (Wallace 1869; Martin 1894). Bird-collectors of the 20th century (Stresemann 1914a, 1914b; Siebers 1930; Heinrich 1956 and Ripley 1960) only added to the understanding of the bird's distribution and taxonomy. The few recent data on the breeding biology, population dynamics and behaviour of *Eulipoa wallacei* result from rather short encounters with the birds and the local human population on communal nesting grounds (De Wiljes-Hissink 1953; Dekker 1991; Dekker et al. 1995). This recent information points at two major communal nesting grounds, one on the island of Halmahera (north of Galela Town) and one on the island of Haruku (Tanjung Maleo near Kailolo Village). There, more than half the species' estimated world population is expected to lay their eggs.

This article reports on the intensive study of *Eulipoa wallacei* carried out at the Tanjung Maleo nesting grounds near Kailolo Village on Haruku Island (Moluccas, Indonesia) during the periods June 1994 - June 1995, January - May 1996 and March-April 1997. Additional data were gathered on other islands within the species' range. Heij (1995a) summarised the scope of this study and presented preliminary results. An Indonesian translation of the first draft of this article was privately published by the first author (Heij & Rompas 1997a). Other publications that resulted from this study are Heij (1995b), Heij (1996) and Heij & Rompas (1997b, 1997c).

Authorship and credits

Within the framework of this study and this article that reports on it, dr Heij is the senior author. He prepared and organised everything: obtained the permits and institutional feedback in Indonesia, raised the necessary funds and made the contacts with the local community of Kailolo Village. The fieldwork was also conducted and lead by him. Rompas took part in this project as an Indonesian counterpart and studied the morphology, karyology and eggwhite-pattern of *Eulipoa wallacei* which resulted in her 'Magister of Sains'-thesis (Rompas 1996, see Appendices 3 & 4). Besides, she carried out incubation experiments in the laboratory and assisted in the field during October -December 1994, March-April 1995, and January 1996. Moeliker acted as the contact back home at the museum in Rotterdam, carried out fieldwork at the nesting grounds and during surveys to other islands in October/November 1994 (Moeliker 1995), worked on the interpretation of the data and was responsible for the editing of the text, tables and figures. Here, Moeliker wants to stress that, although this publication is a multi-authored one, Heij deserves all credits: without his perseverance in the field, his careful collecting of data and his courteous cooperation with local villagers, this investigation would not have taken place.

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[1] Although Warren (1966) listed the presence of three syntypes of *Megapodius wallacei* G.R. Gray 1860 in the BMHN-collection, Robert P. Prys-Jones (in litt. 1996) stated that only two skins, both unsexed specimens collected by Wallace in East Gilolo in 1858, can be considered syntypes. The third skin, a female that Wallace collected on Buru in 1861, does not have the type status as it was obtained after the original description of *Megapodius wallacei* was published.

2 STUDY AREA AND METHODS

STUDY AREA

Tanjung Maleo

The study area is located on the island of Haruku, which together with its neighbouring islands Saparua and Nusa Laut belongs to the Lease Islands of the Maluku (Moluccan) province of Indonesia. This archipelago is situated just south of the much larger island of Seram and east of Ambon Island (Fig. 1A). Haruku (total surface 138 km ^{2}), is located south of West Seram and east of Ambon in the Banda Sea between 128º 24' 30'' E and 128º 32' E and between 3º 30' S and 3º 35' S (de Graaff & Stibbe 1918). The main study area is located on the northwest coast of Haruku, just south of Kailolo Village, on a cape called Tanjung Maleo (Figs. 1B, 1C, 2). It is an area of approximately 12.5 ha (500x250m) where sun-drenched beaches are bordered by a dense coastal forest that changes towards the east into an area with scattered trees (*Plumeria acuminata*) and bushes where the local islamic graveyard is situated. The parts of Tanjung Maleo that are used as nesting grounds by *Eulipoa wallacei* are four open fields (total surface 5450 m ^{2}, 0.545 ha) with a substrate of fine white sand (Fig. 2). Field 1 (the largest: 3000 m^2) is bordered by the southernmost houses of Kailolo, the graveyard to the east and the forest to the south (Fig. 1 C). It has been in use as the local soccer field. Field 2 (1300 m ^{2}) lies directly south of field 1 and is almost completely surrounded by forest. Here a shed was built, from which we carried out nocturnal observations. Field 3 (250 m ^{2}) lies just outside the forest, next to field 2, in the half-open graveyard area. Field 4 (900 m^2) is located about 10 m from the beach, completely surrounded by forest at the southern end of Tanjung Maleo (PLATE I, Appendix 6), close to the site (the 'harbour') where small speedboats leave for Ambon. Here a second shed was built from which most of our nocturnal observations were done. Compared to the other fields, field 4 has a somewhat higher elevation and hence the soil is dryer. Field 4 is the particular nesting ground described by Martin (1894).

From the 'harbour' a narrow road runs south towards Haruku Village and north, along the cemetery, towards Pelauw Village and into Kailolo Village. East of the road that runs into Kailolo there are some old high trees, foodcrop-gardens and fields grown with alang-alang grass *Imperata nucifera* after which a high limestone plateau rizes steeply. On the plateau densely vegetated, neglected gardens predominate and the area slowly rises to a height of about 500 m: Mount Huruano, being the highest point of Haruku.

Vegetation around the nesting grounds

The forest that surrounds the Tanjung Maleo nesting grounds appeared to be of great importance to the Moluccan megapodes. Birds flying in from their inland habitats on Haruku and Seram, stay in the treetops for a while before laying eggs. Birds that could not lay eggs due to late arrival or disturbance, spend the day in the forest (see: chapter 4). For newly fledged chicks it forms the first hide-away (see: chapter 7). Local custom strictly forbids cutting trees for firewood or other uses, although collecting fruit is allowed. The forest mainly consists of trees bearing edible or medicinal fruits. Other, non-useful trees are left alone. Together they form a rather dense, 100-150 m wide stretch of bushes and high trees. Old trees are often overgrown with epiphytes like ferns and orchids. Table 1 lists the most abundant trees, shrubs and (non-grassy) plants that we encountered in the forest.

Kailolo Village

Kailolo is one of the twelve villages of Haruku. Formerly, lots of trees were felled and at present in these open areas there are many gardens with banana, kasbi, vegetables, nutmeg and some sagopalms. The local human population mainly consumes fish and local garden products. The *Eulipoa* eggs form an important source of food, work and income for the community. At least five to seven families earn their living from egg-collecting. Chauvel (1990) judged the socio-economic situation as follows: 'Kailolo is

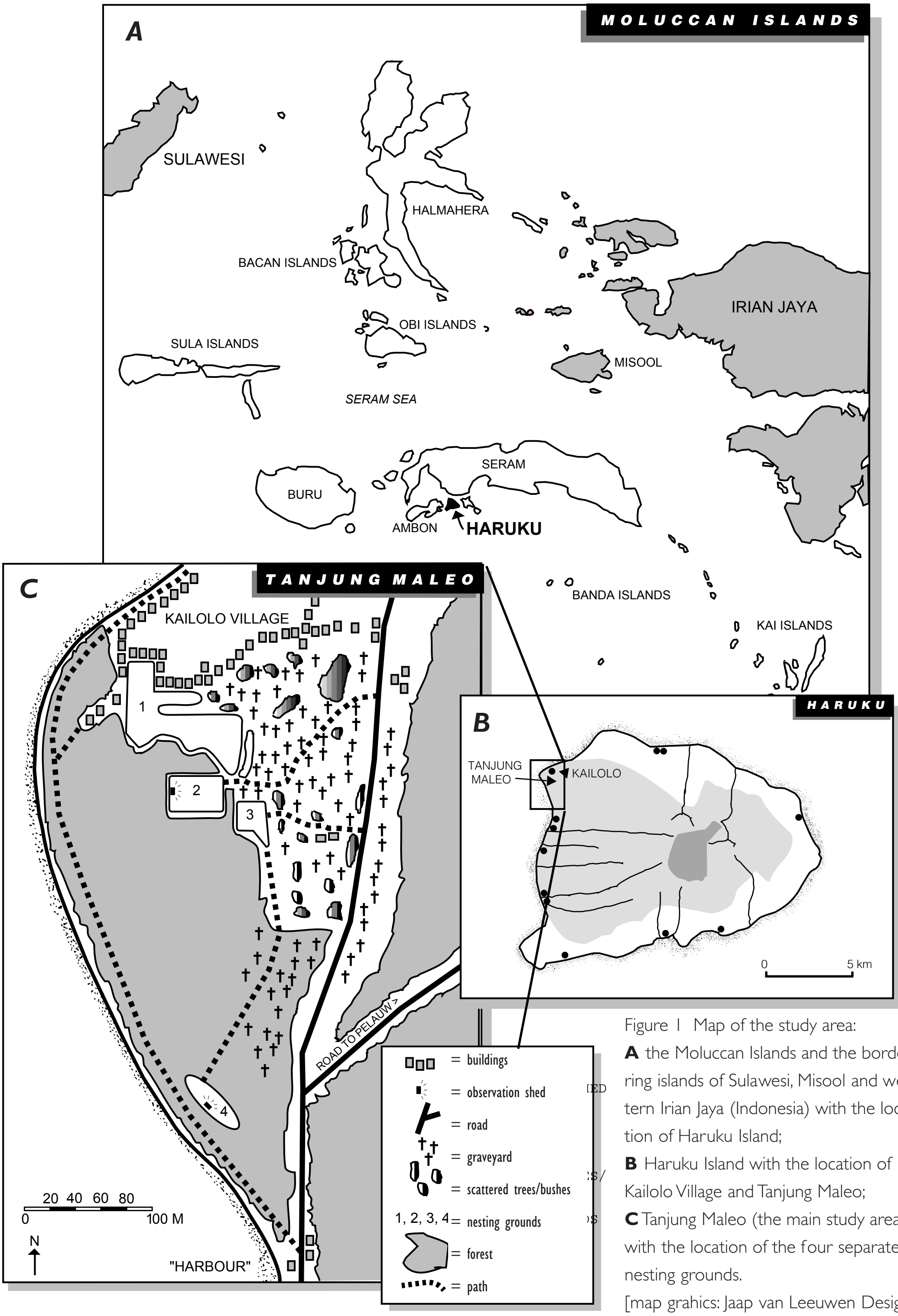

Figure 1 Map of the study area:
A the Moluccan Islands and the bordering islands of Sulawesi, Misool and western Irian Jaya (Indonesia) with the location of Haruku Island;
B Haruku Island with the location of Kailolo Village and Tanjung Maleo;
C Tanjung Maleo (the main study area) with the location of the four separate nesting grounds.
[map grahics: Jaap van Leeuwen Design]

poor in food resources. as n ecessary for their very existence. Motivation and necessity are high and they are quick to seize upon new ideas'.This attitude surely has had a positive influence on the close cooperation we had with the people of Kailolo during this study.

In the Islamic community of Kailolo the women do the hard work. They cut wood in the hills, fetch water from the wells, do the washing and cooking: in short they look after the entire family. Some of the men work as porters in the Ambon harbour and some work in the mountain gardens or are involved in the egg-harvest, but lots are jobless. In 1982 and 1983, respectively , 20 and 30 families transmigrated from Kailolo to Seram. There are a great many children in this village. Family planning has hardly been heard of. In 1994 the total human population was 2508 (1398 men and 1110 women).

Climate and weather

The climate of the Moluccas is very wet, like all mountainous islands around the equator . According to De Graaf f & Stibbe (1918) the coastal areas of the islands around Ambon are among the wettest of the archipelago. The islands are influenced by the monsoon, with mainly southeastern winds from April to November and northwestern winds from December till March. The southeast monsoon causes the presence of cold water from the Banda Sea in coastal areas, whilst the northwest monsoon is strongly guided by the position of the mountainous island of Seram (Fig. 1A). On Haruku, in general, the rainy season lasts from April till September and the dry season lasts from October till March. The average temperature during the year on Ambon Island is 26.3ºC. The average rainfall per year is 1775 mm, of which 1241 mm falls during the rainy season

Table 1 The 20 most noticeab le trees, shrubs and non-gr assy plants in the coastal f orest that sur rounds the Tanjung Maleo nesting ground at Har uku Island, based on: Balick & Mendelsohn (1992); Bell & van Houten (in: Edwards et al. 1993); Hildebrand (1951); Peters et al. (1989); Phillips & Dahlen (1985); Pulle (1952); Sahulata (1984) and van Steenis (1949).

species	local name	type	height (m)	use
Cerbera manghas	Mangga brabu	a	1 - 17	1
Garsinia dulcis	Manggis hutan	a	5 - 20	1
Ficus septica	Siripopar	b	1 - 5	2
Calophyllum inophyllum	Bitanggur	a	10 - 20	3
Ficus benjamini	Beringin	a	3 - 40	3
Canarium commune	Kenari	a	10 - 30	1
Hibiscus tilliacus	Baru	a	5 - 15	3
Plumeria acuminata	Kamboja	a	1.5 - 6	2
Pterocarpus indicus	Lenggua	a	10 - 40	2
Terminalia catappa	Ketapang	a	10 - 35	1
Erithrina variegata	Kayu galala	a	12 - 25	3
Pandanus tectorius	Pandan	a/b	3 - 7	2
Myristica fragrans	Pala	a	5 - 18	1
Scaevola fructescens	Papaceda	b	1 - 3	3
Cassytha filiformes	Tali putri	c	3 - 8	3
Polyscias nodosa	Patatulan	a	5 - 8	3
Lantana camara	Solasi bangke	b	0.5 - 5	3
Mangifera indica	Mangga	a	8 - 30	1
Canavalia maritima	Katang-katang	c	2 - 6	2
Stachytarpeta jamaicensis	Alosa	b	1 - 2	2

1 edible fruit; 2 used for medicine; 3 not used in Kailolo; a tree; b shrub; c creeper

Figure 2 Tanjung Maleo and Kailolo Village (Haruku Island) seen from the air and from the south (the sandy f ields used for nesting by *Eulipoa wallacei* are indicated by the numbers 1, 2, 3 and 4). [photo: C.J. Heij, December 1994)]

Table 2 Weather-parameters obtained at Pattimura-airport, Ambon Island in 1986 (unpublished data, locally obtained).

	temperature °C max.	temperature °C min.	rainfall (mm)	number of rainy days	relative humidity (%)
rainy season					
April	31.9	23.1	143	20	86
May	31.3	21.6	216	21	86
June	31.2	21.6	208	22	88
July	30.0	21.0	273	21	86
August	29.6	21.2	187	17	86
September	31.3	21.3	214	16	84
total rainy season			1241	117	
dry season					
October	31.9	22.1	54	16	85
November	32.4	22.7	94	9	83
December	33.2	22.0	21	11	78
January	33.2	22.4	139	22	81
February	32.3	22.4	135	20	83
March	32.3	22.4	91	20	86
total dry season			545	98	
yearly total			1775	215	

Figure 3 The egg-harvest administration was accurately kept by the lease holders. As the harvest year begins on 1 April, the month of March has no notes on egg n umbers.

(April-September) and 545 mm during the dry season (October-March). The number of rainy days per year on Ambon is 215 (rainy season 117, dry season 98 days) and the average relative air-humidity is 84.3%: rainy season 86% (84-88%), dry season 82.7% (78-86%). See also Table 2. Because of its protected location (embraced by Seram) Haruku receives less rainfall than the figures given above (Whitten & Whitten 1992).

METHODS

For a general outline of the methods, we refer to Heij (1995a). In addition to this, the period Januari - May 1996 was used to obtain data onthe provenance of birds and the egg-laying interval by radio-tracking of individuals provided with a radio transmitter (see: chapter 8). In March-April 1997 Haruku Island was visited to prepare a re-introduction project and, in addition, a survey on Misool Island was conducted. Specific information on methods used are presented in each chapter.

Time spent at the nesting g round

In order to obtain data on the egg-laying behaviour, the flying in, the predators and the numbers of collected eggs and fledged chicks, a total of 742 hours was spent on the Tanjung Maleo nesting grounds during June 1994 - June 1995 (Table 3). Many hours were also spent together with the villagers of Kailolo and especially with the leaseholder of the Tanjung Maleo nesting grounds, his family and his egg-collecting team in order to obtain data on the local habits and traditions concerning the egg-harvest. Through carefully established contacts with former leaseholders we obtained the daily egg-harvest results, accurately kept on calendars (Fig. 3), dating back to the 1987 lease. During June 1994 - June 1995, egg-harvest data and data on the numbers of fledged chicks were obtained daily by counts carried out in the field by the author(s). Data from the period after 30 June 1995 were obtained through monthly correspondence with the leaseholder(s).

Table 3 Time spent to obtain field-data on the Tanjung Maleo nesting grounds (Har uku Island) dur ing the period 1 June 1994 - 30 June 1995.

period	time	hours spend
mornings	06.00 - 08.00	224
afternoons	13.00 - 14.00	26
evenings	17.00 - 19.00	106
nights	20.00 - 06.00	385
total		741

When not present at Kailolo, most time was spent to visit other Moluccan Islands in search of *Eulipoa* nesting grounds. Then, basic data, such as the number of harvested eggs and fledged chicks and temperature readings were noted on standard forms by the leaseholder or by members of his collecting team. Surveys to other islands were always planned in a way that assured our presence at the Tanjung Maleo nesting grounds during the full-moon period, when most egg-laying birds appeared to be present.

Equipment

The following standard equipment was used throughout the study periods:

- 5 digital thermometers (Thermo-electric, Syntech Original Instruments, Hilversum, the Netherlands)
- thermometer (Veterinar)
- pesola springbalances 100 g, 300 g, 1000 g (the pesola's were regulary gauged at Harapan Goldsmith, Ambon)
- vernier callipers
- altimeter (Barigo, Germany)
- compass (Silva System, Sweden)
- passive night-vision scope PM 5 FG (Delft Instruments Electro-optics, Delft, The Netherlands)
- 10x40 binoculars (Leitz Trinovid, Wetzlar, Germany)
- mini-cassette recorder RQ-350 (National)
- photo camera (Canon Epoca-caption, 35-105 mm)
- naturalist's colour guide (Smithe 1975)

3 THE TRADITION OF EGG-COLLECTING ON TANJUNG

The legend of origin

Although Martin (1894) was the first to describe the nesting grounds and the collecting of *Eulipoa* eggs for human consumption at Tanjung Maleo, the tradition dates back much further. This is witnessed by the legend of origin which is being told in Kailolo and in Piru (West Seram). It was explained to us on many occasions and by many persons. The legend indicates how the birds have come to use the tanjung (cape) with its sandy fields as a nesting ground.

At the heart of the story lies the fact that a man from Kailolo married a woman from Waai (Ambon). In Piru it is said to have been a woman from Piru from the Manupasso family. They had four children who were being teased by the children of Waai. The children asked their mother where their father had come from and she mentioned the village of Kailolo. Soon after, they decided to go there. They walked to the beach near Waai[2] and drew a boat in the sand. The drawing then became a real boat [3]. They arrived in Kailolo with a present from their mother, a golden ball. As soon as they arrived, they started to play with the ball. However, suddenly the ball disappeared into the sand, and they left it for their grandchildren to play with. Almost immediately after these events the 'maleo birds' (*Eulipoa wallacei*) arrived from Pombo, Kasa, Babi, Seram and other islands, to lay their eggs on the beach.

The lease of harvest rights

As a consequence of this legend, Tanjung Maleo is considered to be a miraculous ancestral gift, and thus to belong to the village community. The village feels responsible for the protection of the nesting grounds and the birds and, in return, claims the right to harvest the eggs. In order to have some regulations governing the harvest, a 'sasi' has been established [4]. According to the Kepala Desa (village chief) there has always been a 'sasi' on Tanjung Maleo. However, it seems to have been re-established after the political turmoils in the 1960's. Essential to the 'sasi' is an auction ('lelang') which is held annually on 31 March under the guidance of the village chief (Fig. 4). The highest bidder obtains the right to harvest the eggs from 1 April to 31 March of the following year. The lease period thus begins when the rainy season starts and ends when the dry season has come to an end. No one else, except the people who are employed by the tenant, is allowed to collect even a single egg, a rule that is strictly followed[5].

According to the Kepala Desa, who in 1994 had been chief for a year, only inhabitants of Kailolo are allowed to take part in the auction. However, the present (94/95 and 95/96) tenant Parit Tuanaya (PeDe) stated that everybody, outsiders included, are allowed to lease the harvest rights. The new Kepala Desa managed to almost double the lease price for the 1994/95 season to 6.105.000 Rupees (then circa US$ 3000) (Table 4). As the nesting grounds are considered communal property, the amount benefits the

Figure 4 The auction ('lelang') for the harvest-rights of 1995/1996, Kailolo Village 31 March 1995. [photo: C.J. Heij]

Table 4 Lease price of harvest rights at Tanjung Maleo and the price of a single *Eulipoa* egg on the local market. Amounts in Indonesian Rp (Rp 1000 = US$ 0.4).

harvest year(s)	lease price	egg price
1992/1993	3.275.000	250
1993/1994	3.670.000	250
1994/1995	6.105.000	300
1995/1996	5.500.000	300
1996/1997	6.300.000	300
1997/1999*	13.000.000	300

* price for two years (see page 101).

village community and is not to be used forother purposes: 25% goes to the Kepala Desa and to the staff of village elders and 75% is to be used for renovation and maintenance of the mosque.

Besides the right to harvest the eggs which is granted to the highest bidder, the 'sasi' forbids to cut wood from the forest that surrounds the nesting grounds and also forbids any hunting. As a consequence, the adults and chicks of *Eulipoa wallacei* are not consumed. Predators of the bird and its eggs - other than man - are poisoned or killed otherwise (Fig. 5). Because of the 'sasi', the support and strong influence of the mosque, and of the high penalty for breaking the rules (the fine is similar to the lease price), hardly any irregularities occur: nobody else collects eggs or takes wood from the forest. Even so, the nesting grounds are under surveillance by the tenant and his collectors, locally known as 'the maleo team'. The only public use of Tanjung Maleo is a path that runs from the village through the coastal forest bordering the nesting grounds. Locals use this as a shortcut to the harbour (Fig. 1C). In July 1996 the island authorities (Camat) placed a fence around Tanjung Maleo, in an apparent attempt to give the area some kind of of ficial protective status (P. Tuanaya, personal communication). The path was, however, still in use. The only other natural resource of Kailolo that is also ruled by 'sasi' are the coconut palms and nutmeg trees. The forest and gardens surrounding the village are divided into three parts and a manager is appointed for each part (kewang). This person receives 10% of each harvest. The sea is not governed by 'sasi'. Fishing by means of home made explosives goes on almost daily. Although commonly condemned, every villager continues to eat fish killed that way.

Figure 5 The lease holder injects poison into an *Eulipoa* egg in order to kill egg predators. [photo: C.J. Heij]

Egg price

The maximum price for which the tenant is allowed to sell an egg is established by the village council and, as a consequence of the communal ownership of the nesting grounds, is being kept at reasonable height. For years an egg was sold for Rp 250 and but after the increase of the lease price in 94/95 by almost 100%, an egg costs Rp 300, an increase of a mere 20% (Table 4).

Economic necessity: mor e eggs

The high lease price forces the tenant to harvest as many eggs as possible. He not only looks after his own family of five children, but also six men are employed, who also have to maintain their families. To get even (i.e. to earn back the lease price) a simple calculation shows that during the 94/95 season at least 20.350 eggs had to be collected and sold. In order to get some profit, many more eggs have to be harvested. The assumption that the local rules make sure that about 20% of the eggs are deliberately left untouched in order to keep the *Eulipoa* population in balance (Dekker 1991, see also: Del Hoyo et al. 1994; Monk et al. 1997), proved to be wrong. Every morning and even during the night the tenant and his collectors unearth as many eggs as possible with just one purpose: their own survival. The observation of Monk *et al.* (1997) that eggs which are laid deeper than the length of the lower arm of the collector are not harvested, is a myth: we have often seen half the body length of collectors immersed in the sand in an effort to unearth an egg. The lack of interest in the survival of the bird is also shown by their habit of destroying collected eggs that are already hard-set (missed during earlier collecting activities) and not suitable for

Figure 6 Local villagers buy their *Eulipoa* eggs for breakfast on the Tanjung Maleo nesting ground. [photo: C.J. Heij]

consumption. Religious belief rather than insight into the dynamics of the bird population ensures the tenant that Tanjung Maleo and *Eulipoa wallacei* will remain a source of income and food for the village community. The protection, governed by 'sasi', of the nesting grounds and surrounding forest against human activity (other than collecting eggs), surely is advantageous to the bird. Without this measure their nesting habitat would have been lost long time ago.

The eggs are mostly sold locally. In the early morning, when most of the eggs have been harvested, the villagers come to the nesting grounds to buy fresh eggs (Fig. 6). They form an important part of their daily diet. The demand is high, especially during religious festivities and weddings. During the dry season, when the number of collected eggs can reach peaks of more than 200 eggs per day, the surplus is sold on the neighbouring island of Ambon. Argeloo & Dekker (1996) reported eggs from Kailolo being sold in Masohi, South Seram, but we saw eggs from small local nesting grounds being sold there. In Ambon, where the demand for *Eulipoa* eggs is high, the housewives of Haruku sell the eggs through the intermediary of PeDe's brother who works in the Government Office.

The egg-collecting practice

The four to six men employed by the tenant start their daily routine in the late afternoon. Then they work to keep the nesting grounds devoid of any vegetation and plant debris. The fast growing grass (alang-alang) is being removed. They also keep an eye if any illegal activities (e.g. woodcutting) occur. After dinner (at sunset) they congregate in the shed at the edge of field 2 or at the beach and sleep. Every now and then the nesting grounds are checked for digging birds, using torches. They especially disturb birds that are digging early because - in their opinion - the burrows that are dug during the hours close to sunrise, will not be as deep, thus easing the collecting of eggs. Burrows that are believed to contain eggs (for which they have a trained eye) are covered with fresh twigs (Fig. 7). This is to prevent other birds to dig and lay in the same burrow, which, in case it would happen, means a lot of digging and searching (for more than one egg) next morning. In case they encounter a bird in a burrow during a nightly round, they catch it and press the egg out of the body (Fig. 8). The bird is then released. At clear, full-moon nights during the dry season - when most of the eggs are laid - collecting begins already during the night, causing a massive disturbance of the regular

Figure 7 Fresh twigs, placed on the burrows at night, indicate the presence of an egg. The twig prevents the multiple use of the burrow. [photo: C.J. Heij]

laying strategy of the bird (see chapter 4) and casualties among hatchlings reaching the surface. In general, the collecting activities begin at sunrise when the birds have disappeared. The beach of Tanjung Maleo is also checked for burrows. Among the men, there are two so called 'engineers' who are well trained in knowing whether or not there are eggs in a pit. The others assist in digging, filling and tamping the holes (Fig. 9). After about two hours of work (depending on the amount of burrows) the nesting grounds that looked like exploded minefields are smooth

Figure 8 When a Moluccan megapode is encountered in the burrow by the egg collectors, she is caught and her egg is squeezed out. [photo: C.J. Heij]

Figure 9 Early morning collecting activities at Tanjung Maleo (field 1): digging for eggs. [photo: C.W. Moeliker]

Figure 10 After the harvest the collectors take breakfast and count the eggs. For counting, the eggs are always placed in triangular shapes, containing 10 eggs. [photo: C.J. Heij]

again and ready for the next night. The habit of smoothing the nesting grounds after collecting the eggs eases finding new burrows and was not observed at nesting grounds on other islands, e.g. Buru and Halmahera. There, the burrows are not filled after the eggs have been unearthed. It should be stressed that in a natural, undisturbed situation, nesting grounds never look smooth as the birds themselves do not completely fill the burrow after the eggs have been laid.

The team takes breakfast (*Eulipoa* omelettes and rice) at the nesting ground, during which the tenant carefully counts the harvest and makes notes of the numbers (Fig. 10). For the purpose of counting, the eggs are placed in the sand in triangles containing ten eggs each. This triangular shape is present on earthenware plates in possesion of Kailolo's village chief (Fig. 11).

Figure 11 The Kepala Dessa (village chief) of Kailolo showing an earthenware plate with triangular egg motives. [photo: C.J. Heij]

Allah and *Eulipoa*: the influence of Islam

Three times a year the Imam (religious leader of the village) and his staff members ('umat') hold an early morning prayer meeting at the nesting grounds to ask Allah to protect the birds and

Figure 12 While the imam and his staff pray for more eggs, the egg-collecting continues. [photo: C.J. Heij]

make them lay many eggs (Fig. 12). For this ceremony, for which the tenant prepares himself all night, mats are spread out on the sandy fields. On the mats small bowls are laid out, each containing 1000 Rupees, one bowl for each high functionary. Apart from this, everybody receives some *Eulipoa*-eggs, the number depending on the harvest results. In August 1994, each official received two eggs. During the prayers and the monotonous singing of 'La Ila Ha Illauallah' in various rhythms, the egg-collectors simply continue to dig for the eggs (Fig. 12). At the end of the praying session the Imam walks over the nesting grounds, throwing rice grains for the birds to grant them fertility.

During private conversations with the tenant PeDe (the first author is fortunate in that he is considered to be one of his family) he kept saying that the high lease price is not very important because he is convinced that the bird will therefore lay more eggs. In addition, a high price is of course profitable for the mosque. On the question 'Does the bird not get angry when every time more is demanded of her?', his answer was that Allah looks after the bird. Even the first author was considered to be a gift of Allah because of his donation of a refrigerator.

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2 From Kailolo, Waai on Ambon can be clearly seen (the distance is about 6 km).

3 Every year, during the 'Adat' festivities, a miniature version of the boat ('rasulan') is being built and carried around.

4 'Sasi' in the Moluccas is a right, granted to village communities, that governs the ownership of natural resources and agricultural crops from wilderness areas and that regulates the harvest and its finances. It was described, while Indonesia was still under Dutch rule, inArticle 71 of the Internal Government Regulations and of the Finance Department on Amboina and subjected islands (Ind. Stb. 1824 No. 19a). Before govenor J.C.F. Riedel ruled this part of the Dutch East Indies, great use was made of this right. However, as Riedel was against it, 'sasi' has henceforeward hardly been applied (van Hoëvell 1875; Sachse 1907; de Graaff & Stibbe 1918; Volker 1925). Sasi forms part of the 'adat', the customary law which is still deeply rooted in the Moluccan society despite the fact that, in 1967, 'sasi' and all other aspects of the 'adat' were being subjected to Indonesian law.

5 In March 1990 there were problems amongst the different 'dusuns' (areas in which a village is divided) of Kailolo. Because of these problems, that year no auction was held. Some people did harvest eggs though, but nothing was registered.

4 BEHAVIOUR AT THE NESTING GROUND

Nightly observations at the nesting grounds of Tanjung Maleo and at the bordering beach have revealed the following stages in behavioural patterns connected with egg-laying:

1 flying in
2 exploring and burrowing
3 laying, post-laying and departing
4 returning

There appeared to be a marked difference in behaviour between clear nights and dark nights. Clear nights are common during the dry season (October - March) around the full moon period: the sky is cloudless, the nesting grounds are well lit and there is good vision; observation can also be done using normal binoculars, although with the night-vision scope the view over the nesting ground is perfect. Dark nights are characteristic of the rainy season (April - September): the sky is clouded, the nesting grounds are dark and there is almost no vision; observations can only be done using the night-vision scope. It should be noted though that in the dry season during the new-moon period or during cloudy weather, nights can also be dark. A full-moon during a cloudless night during the wet season also deviates from the average picture (Table 5).

Egg-laying behaviour will be described for both the average clear night and the average dark night. It is the result of the analysis of 25 tape recorded nightly observation sessions (21.00 - 06.00 hours), mostly executed from the shed at field 4 and the bordering beach.

Table 5 Visibility for the human eye at Tanjung Maleo during different weather conditions and different moon stages.

sky	full moon	new moon
clear	++	+-
clouded	-	--

(++ = good; +- = reasonable; - almost no; -- = no).

Clear night situation (see Table 7)

1 Flying in - Observations to establish the number and direction of in-flying birds were carried out during 33 clear nights and lasted from 19.00/20.00 p.m. till 24.00/01.00 p.m. Observation sites were situated along the beach next to the nesting grounds and north of Kailolo, the hills just northeast of Kailolo and at at sea off the northwest coast of the island. Observations were carried out simultaneously from two or three sites. Despite these efforts, only few birds were actually seen flying in (Table 6), however egg-collecting activities proved that large numbers of birds had been present at the nesting grounds. On nights with e.g. 200 egg-laying birds, we were only able to observe about five birds flying in, indicating that the vast majority arrived out of our sight or (unlikely) during the late night hours. Most of the birds we saw flying in, arrived from a northerly direction, although birds were also observed flying in from the south and southeast, and from the west (over the sea) (Table 6). All birds arrived solitarily. Flying-in started about 15-30 minutes after dusk and lasted all night. At the site northeast of Kailolo we did not observe any arriving bird, although at the nesting grounds we did see (and mostly heard) birds flying in from the east. Victims of the electricity wires that run along the road just east of the nesting grounds and birds that collided with motorcycles on that road indicate that birds arrive from easterly directions as well.

Table 6 Direction from which birds (*Eulipoa wallacei*) arrived at the Tanjung Maleo nesting ground, based on observations during 33 nights along the beach, at sea and in the hills east of Kailolo.

direction	number of birds	number of nights	average per night
N / NW	30	9	3.3
W	5	4	1.3
S / SE	25	24	1.0
E / NE	-	-	-
total	60	33	1.8

We expect birds arriving from northerly directions to originate from South Seram, situated just opposite of North Haruku. Birds that reach the nesting grounds from southerly and easterly directions probably belong to two populations: (1) birds that reside in Central Haruku (see: chapter 8) and (2) birds originating from the Elpaputih Bay region and more easterly areas of Seram. They cross inland Haruku to reach Tanjung Maleo. Birds arriving from a westerly direction, may originate from the population that is expected to inhabit mount Salahutu on Northeast Ambon (Dekker et al. 1995; Jones et al. 1995), though we believe they more likely belong to the population that resides in the Piru Bay area of Seram. These birds probably cross via Kasa Island and turn left in an easterly direction once they reach Northeast Ambon or Pombo Island. In general, the birds fly in at tree-top height. Into headwinds, coming from northerly and westerly directions, they first land on the beach north of, or next to, Tanjung Maleo. Burrowing movements occur at the beach. Especially on windy, clear nights many burrows are found on the beach. Eggs are also laid on the beach when the birds have been disturbed at the nesting grounds during full moon nights. As a consequence, regular egg collecting on the beach takes place. Birds have only been seen or heard to arrive solitarily, one at least some minutes after the other.

As soon as an adult bird (hereafter called 'she') arrives on Tanjung Maleo, she clumsily lands in the trees, making a lot of noise in the foliage with her flapping wings. She especially prefers to sit on thick parallel branches where she can also walk up and down. After some time in the tree (a maximum of 30 minutes was observed, but it might take longer), she flies down towards the nesting ground.

2 Exploring and burrowing - Now there are two scenario's: either the recently landed bird is the first one at the nesting ground (solitary), or several birds are already active there (group).

Solitary - When the bird is the first to arrive on the nesting ground, the exploration starts at the edge, close to the forest. She observes the area while standing stock still for five to fifteen minutes with her neck stretched and tail hanging down (PLATE II). Then, often, she takes a few (mostly five) steps to the right and to the left, then stops and looks around. She repeats this display two to five times. Every now and then she makes burrowing movements by scratching the sand four to five times with left and right foot, followed by a few halting steps to the left and to the right. She then turns 180º and walks back a few metres. This display is regularly repeated. At every stop the neck is stretched. If the bird remains alone, she will eventually dig her burrow at the dark, shady edge of the field. Within two minutes she may totally disappear under the surface. During burrowing, she continuously changes direction or she might start again at a different place. This may last for hours: several birds were observed exploring and burrowing for two to three hours before they had started the next stage, laying the egg. To summarize: on clear nights, solitary birds have trouble starting, they take a long time to burrow several pits which lead to different directions. This hesitating behaviour is probably influenced by uncertainty and fear: a solitary bird is more vulnerable than a group.

Group - When other birds are already present on the nesting ground, the bird lands (mostly in the vicinity of the other birds) and upon arrival, familiarizes herself with the surroundings and rather promptly walks haltingly, neck stretched, in the direction of the others. She looks at the burrowed pits and is often chased off by the 'owner' with excited 'kek-kek-kek' calls. Depending on the hour and the quietness (no human disturbance) of the night, she will start to burrow her own pit within three to five minutes after arrival. This common, clear-night situation is given below:

23.06-23.10 h: Full moon, clear sky. After a brief human disturbance, nine birds are active. Bird 1 lands in the centre of the nesting ground, does not move for about two minutes, looking around and stretching her neck, then walks about 5 metres, looks left, right and back. Then she walks in the direction of bird 2 while making burrowing movements with her feet. The two birds meet at

a distance of about one metre, both with necks stretched, jerkingly looking to the left and to the right. They both utter calls like 'kek-kek-kek' and 'kew-kew-kew'. Birds 1 and 2 observe the burrowing movements made by bird 3, which then chases them away . Birds 1 and 2 walk around attentively, necks stretched, now and then away from each other , always looking around. Now bird 1 starts to burrow and bird 2 continues her way , looking left and right, making burrowing movements and walking over the field in hairpin patterns, tail hanging down, neck stretched. Bird 3 stops burrowing where she was and starts all over again at a different spot: within one minute she totally disappears under the surface, every so often peeping over the edge of the pit. Birds 1 and 2 burrow at a distance of two metres from each other, emerge from the pits, approach each other and start to fight by pecking, kicking and fluttering like two domestic cocks *Gallus domesticus*. They return to their own pits. The only thing we see now is sand being thrown up out of two pits in all directions. Every now and then a bird peeps over the edge of the pit.
23.10 - 23.15 h: Birds 1 and 2 emerge from their pits and start digging somewhere else. Bird 1 returns to her first pit, stays under ground and throws up sand in all directions. Bird 1 comes out of her pit and walks over to bird 2, which has also started to dig at a different spot. This new burrow is abour one metre from bird 1's pit, so that by throwing up the sand, they partly refill each other's pits again. Bird 2 comes out of her pit, has a look at bird 1 and is chased off. From the direction in which the sand is thrown up out of the burrow, it is evident that under the surface bird 1 has turned 180º and is burrowing in a different direction. Birds 1 and 2 emerge from their burrows and look at bird 3. Bird 4 joins in. They all start kicking and fluttering. At one instance four birds are burrowing within four square metres. Bird 1 emerges from her pit, chases off bird 3 which moves away and starts digging somewhere else. Seeing the shadow of a bird flying over, bird 3 presses herself against the ground. There are now five birds burrowing within four to five square metres. Many 'kek-kek-kek' and 'kew-kew-kew' sounds are heard. Now bird 2 leaves her burrow and starts all over again in a different spot. A critical distance during digging appears to be essential. This is expressed by flapping of wings and kicking. More time is now spent displaying this agressive behaviour. Two 'new' birds closely pass our shed while making soft grumbling noises ('grr - rrr, greeee').
23.15 - 23.25 h: Now six birds are burrowing within four to six square metres. Birds clearly seek each other's company. Everywhere on the field, groups of birds are burrowing (Fig. 13). There is much walking about between groups. Their 'kek-kek-kek' calls fill the night, sometimes deafened by the loud wailing cries of Forstens

Figure 13 About twelve Moluccan megapodes during nightly digging activities at field 4 of Tanjung Maleo. The white vent is clearly visible in most birds. [photo: C.J. Heij]

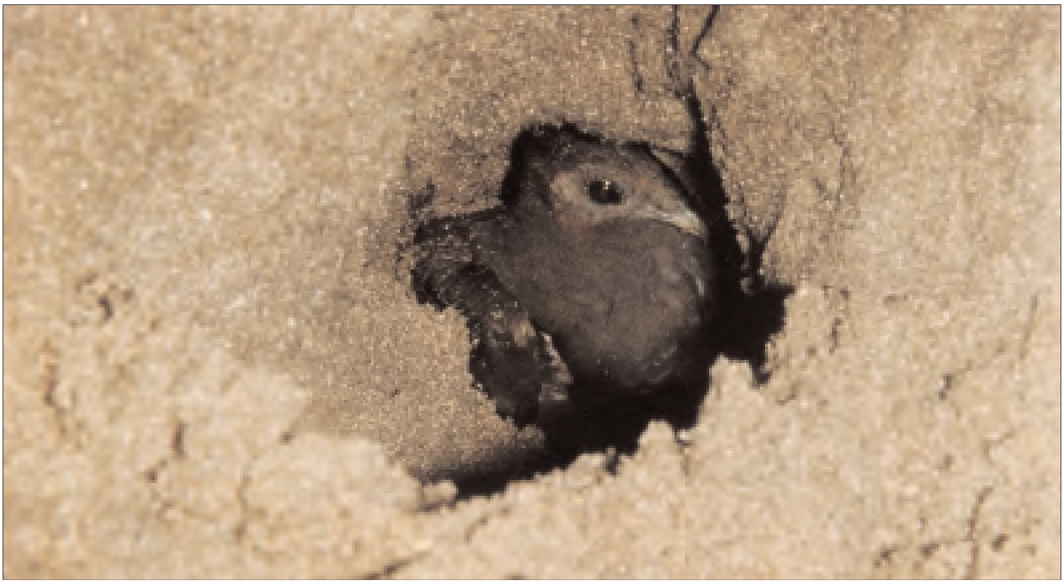

Figure 14 A Moluccan megapode in her burrow, in the egg-laying position, at Tanjung Maleo. [photo: C.J. Heij]

megapode *Megapodius forstenii forstenii*. Birds do not display the behavioural patterns of the exploring phase.
23.25 - 24.00 h: A total of 43 birds is burrowing in five groups that are more or less evenly spread over the field. Newly arrived birds do not display the exploring behaviour, but start burrowing immediately.
24.05 h: Now 53 Birds are active in six groups.

3 Egg laying, post-laying and departing - After having dug three or four pits, the female disappears for several minutes into one of the burrows. She enters head-first in order to turn around at the bottom so that she will be looking upward (Fig. 14). The egg is laid within a few minutes. After having laid her egg, she emerges, shakes her feathers and scrapes a little sand into the pit. She then digs a little more around the pit into various directions and chases off neigbouring birds. Sometimes she digs a few small pits in another area and then returns to the burrow that contains her egg, scraping some more sand into it (post-laying behaviour). When the bird flaps her wings and stretches her legs, it is a clear sign that she will leave the nesting ground. Sometimes a bird will run some metres before flying to a tree at medium height, but mostly she takes off directly. During clear nights, after displaying the post-laying behaviour, birds were always observed to fly into the trees first before they depart from Tanjung Maleo and return to their forest habitat on Haruku, Seram or other islands (returning behaviour).

4 Returning - The birds returning to their habitat, mostly first fly across the beach bordering Tanjung Maleo and continue flying to the west in the direction of Ambon. Then, at a distance of 50 to 100 m from the coast, they seem to re-orientate and choose a more definite direction. In most cases birds were seen to fly back over Tanjung Maleo just above treetop height in an easterly direction or more to the north over the trees parallel to the coastline. The initial returning direction of nine birds fitted with transmitters (see chapter 8, Table 26) was approximately SE (n=7) and NE (n=2).

Dark-night situation (see Table 7)

1 Flying in - This stage is basically similar to the clear-night situation. Landing in the trees and finding a suitable branche is even more noisy.

2/3 Exploring, burrowing and laying - The birds that have been present all day in the forest surrounding the nesting grounds and have not been able to lay their eggs during the preceding night (see below), already start to burrow along the edges of the nesting ground even before dusk. Before it gets really dark (between 18.00-19.00 p.m.) the burrows dug by the early birds may already contain eggs. These pits are always situated at the edge of the field close to the forest. The early birds fly off and leave Tanjung Maleo immediately after having laid their eggs. The newly arrived birds wait in the trees, exploring the field. They do not become active before the sky becomes clear. Then they descend from the trees and start to burrow rapidly, displaying little exploring behaviour. When there are regular clear moments, most birds have become active by 04.00 and at 06.15 a.m. all behavourial patterns, including egg-laying, have been carried out. When the entire night is very dark or when there has been a lot of disturbance (mostly human: the collectors), the burrowing and egg-laying procedure is concentrated around dawn, between 05.30 and 06.30 a.m. Then, they walk and dig in a noisy way, almost as if hurrying each other up. They regularly use existing burrows. In one case we even observed a bird burrowing a new pit and laying her egg within 13 minutes. As a consequence, dark-night pits are less deep than clear-night pits (see: chapter 5). During these early morning hours, the collectors do not disturb the birds since the eggs will be easily found.

3/4 Departing and r eturning - Birds having laid their eggs at dawn and those who have not been able to lay at all, do not fly into the trees but simply walk into the forest. Before they really get out of sight, they congregate at the edge of the forest (Fig. 15) and walk through dry fallen leaves. This behaviour resembles foraging, but picking food has never been observed. It is during this stage that agressive interactions between *Eulipoa wallacei* and *Megapodius forstenii forstenii* are common. There are several mounds of the latter species at the edge of the nesting grounds and *Eulipoa* was regulary observed near them. They were even seen burrowing in the mounds (Fig. 16). Those burrows were not finished and did not contain eggs. Toxopeus (1922) and Siebers (1930) mentioned the (same) find of an *Eulipoa* egg in the mound of *Megapodius forstenii buruensis* on Buru and judged it as parasitic behaviour. This was considered highly unlikely by Jones et al. (1995) since the eggs of both species are indistinguishable. Our observations indicate that *Eulipoa* does dig burrows in the mounds of *Megapodius forstenii*, though not as a parasitic egg-laying strategy but accidentally, when the mounds are located at the pheriphery of the nesting grounds.

Figure 15 A Moluccan megapode close to the forest edge at Tanjung Maleo. [photo: C.J. Heij, March 1996]

Figure 16 A mound of *Megapodius forstenii* at Tanjung Maleo showing burrows of *Eulipoa wallacei.* [photo: C.J. Heij]

At (or just before) dawn *M. forstenii* becomes active around their mounds. Fighting, like the intraspecific aggresive display, resembles two fighting domestic cocks: lifting the body by wing flapping and kicking with both feet. *M. forstenii* is the aggressor and clearly dominant: when approached by a running *Megapodius*, *Eulipoa* runs away. It seldom comes to fighting as described above. At first sunlight all birds have disappeared into the forest. There they flock together all day, staying low and running around like partridges *Perdix perdix*. They utter the 'kek-kek-kek' or 'kuk-kuk-kuk' calls almost continuously. Because these noisy calls, we could easily locate them in the forest. Only when we approached them within five metres, or when we persistingly chased the groups, they would clumsily fly into the trees while making a lot of noise. During the morning, groups from all four fields join together in the forest. The largest congregation that we observed consisted of 40 birds. They were never seen to leave Tanjung Maleo on the wing during hours of daylight. Probably they will do so during the following night. It should be noted that birds that manage to lay their eggs during a clear moment before dawn, do depart from Tanjung Maleo on the wing and return to their habitat. Also nightly burrowing in the forest on sandy patches has regulary been observed (during dark nights), but there the soil temperature is expected to be low and eggs will probably not hatch. This might be subject to future research.

Males: present or absent at the nesting grounds?

Males and females of *Eulipoa wallacei* are indistinghuisable in the field, and even museum-skins are hardly separable on basis of plumage characters (Jones et al. 1995; Rompas 1996). The presence or absence of males at the nesting grounds is therefore difficult to establish and should be based on differences in behaviour of the sexes and/or gonadal/cloacal inspection of captured birds. Dekker (1991), Dekker et al. (1995) and Jones et al. (1995) suggested, based on incidental observations of two individuals remaining close together while digging and egg laying at the Tanjung Maleo nesting grounds, that male and female visit the site together. Our observations do not support this. We did regulary see birds, while digging burrows, behave differently e.g. more upright stance, more aggressive towards neighbouring birds. However, close observations with the night-vision scope revealed that those birds (n=33) in the end had dug a

Table 7 Summary of the activities of *Eulipoa wallacei* during clear nights and dark nights at Tanjung Maleo, Haruku Island. See text for explanation.

activity	exploring	burrowing/laying	departure	return
clear night	on field prolonged	all night prolonged deep	flying via trees	same night
dark night	from trees	clear moments or dusk/dawn fast less deep	walking forest floor	next night*

* only in case of egg-laying at dawn

full-depth burrow and when caught, appeared to have laid an egg (n=13, estabished by cloacal inspection and/or the find of the egg) or still had the full size egg in the body (n=29; local collectors habitually collect the egg by pressing it out). Furthermore, we did not observe any behaviour that indicated both sexes to be present: no courtship or copulation was seen.

In addition to this, during 38 nights the totalnumber of digging birds at Field 4 was established by nightly counts and compared with the total number of burrows and the number of eggs laid (harvested eggs, established during the early morning hours, together with the number of eggs not found by the collectors established by a calculation based on counts of fledged chicks, see chapter 9). In total, 1419 birds present at field 4 dug 3384 burrows which yielded 1410 eggs (1 egg per 2.4 burrow , on average 37.3 birds and 37.1 eggs per night). These figures indicate that all birds that visit the nesting grounds actually lay eggs and hence are females. The fact that there are more burrows than eggs, does not mean that the surplus is dug by males. Why these 'mockpits' are not used is not clear . Temperature or humidity might not be favourable, although most mockpits are found in clusters of burrows, indicating the abiotical factors to be good. Mockpits are no doubt a nuisance to predators of eggs (including humans), so there might be an anti-predator strategy involved.

Dekker et al. (1995) and Jones et al. (1995) did, however, not supply conclusive evidence for the male presence at the nesting grounds, and mentioned that four birds they caught at Tanjung Maleo and five birds collected at a nesting beach on Buru by Siebers (1930) were all females. A worldwide inventory among 33 institutions shows that in natural history collections, adult male specimens are underrepresented: of 33 sexed specimens, only 21.2% are males (Table 8). When these specimens of known sex are correlated to the habitat from which they were collected, a clear picture emerges (Table 9): all 15 specimens known to be collected on nesting grounds (Tanjung Maleo [Haruku], Wa'kasi and Wai Pate [Buru], Galela and Sidangole [Halmahera]) are females. Dekker et al. (1995) argued that the method likely to be used mostly to collect *Eulipoa* at nesting grounds - trapping while inside the burrow - might favour females being caught. The seven adult birds we collected (Table 8), however, were all victims of electricity wires and, after checking their gonads, also appeared to be females. Of nine specimens from an inland habitat (mount Sibela [Bacan], Fakal [Buru], Hatu Sake [Seram] and Tamulol [Misool], seven (77.8%) are males. With females regulary being away for egg-laying purposes, there appears to be a greater chance to collect males in the inland habitat. For specimens of which the habitat could not be retrieved from the labels, the sex ratio is not so heavily biased. When chicks are concerned, the sex ratio of specimens in museum collections is also more or less even (Table 10). In this analysis we assume that all museum-specimens, of which the label indicated the sex, were sexed anatomically and trustworthy. In the case of three out of three specimens collected on Misool by Ripley (Table 8) being males, we have some doubt. Sexing these specimens using DNA-techniques would be the solution.

As there is no conclusive evidence of males being present at the nesting grounds, both from field observations and specimens in museum collections, we conclude that nesting grounds are only visited by females. In other burrow-nesting species, the Polynesian megapode *Megapodius pritchardii* and Melanesian megapode *Megapodius eremita*, the female also has no male company while digging and laying (Jones et al. 1995). Vogel (1996) concluded from the study of colour-ringed Polynesian megapodes that territorial behaviour of males is restricted to feeding territories and that the male stays behind when the female leaves for egg-laying.

Voice

Eulipoa wallacei is a noisy bird during egg-laying activities. They almost constantly uttered sharp 'kek-kek-kek' or 'kuk-kuk-kuk' calls. The same voice was heard while groups of birds reside in the forest surrounding the nesting grounds during the day , indicating that it is a contact-call. Besides, at night on the nesting grounds, the birds regulary produce a grumbling sound 'grgrgrgrgrgrgr' that was only audible from close distances (< 4 m). Dekker et al. (1995) also mentioned the 'kuk-kuk-kuk' calls and added 'ki-ouw kouw' and 'kou-kouw-kouw-kouw'. The latter two calls were never heard by us. Wallace (1869) attributed 'loud wailing cries' to the species and De Wiljes-Hissink (1953) mentioned 'noisy crowing at the beach'. We believe both authors were wrong. No loud cries uttered by *Eulipoa* were ever heard by us at the nesting grounds, although we commonly heard nightly cries of *Megapodius forstenii* (at Haruku and Buru) and *Megapodius freycinet* (at Halmahera) that deafened all other sounds. The 'crying and crowing' mentioned by Wallace and De Wiljes-Hissink most probably refer to (one of) these species, whose mounds are often found near nesting grounds of *Eulipoa*. The voice *Eulipoa* produces while in its inland habitat, and the call of the male are not known to us.

Table 8 Numbers, sex and provenance of adult specimens of *Eulipoa wallacei* in the collections of thirteen Natural History Museums, based on a world wide inventory (n=33). Localities of male specimens are underlined, those of females are in italics; combinations do occur. [ANWC Canberra, HLMD Darmstadt, MCML Liverpool, MNHN Paris, MZST Turin, NFSR Frankfurt, NHMV Vienna, NMB Basel, UMMZ Ann Arbor, UZMC Copenhagen, ZFMK Bonn, ZMH Hamburg, ZMZ Zürich and ZSM München have no holdings of *Eulipoa wallacei*; KBIN Brussels, MGD Genova and MBL Lisbon did not respond; abbreviations of institutions according to White & Bruce (1986)]

collection	total number of adult specimens	number of sexed specimens	number of male specimens	provenance
AMNH New York	8	5	3	*Bacan*[1], Seram[2], *Ternate*
BMNH Tring	3	1	-	Halmahera[3], *Buru*[4]
FMNH Chicago	1	-	-	Seram
MCZ Cambridge (USA)	2	1	-	Seram, *Ternate*
MZB Bogor	7	7	1	*Halmahera*[5], *Buru*[6]
NMR Rotterdam	7	7	-	*Haruku*[7]
PMNH New Haven	4	3	3	Misool[8], Bacan[9]
RMNH Leiden	6	4	2	Seram, Halmahera, *Ternate*
SMTD Dresden	1	-	-	Ternate
UMB Bremen	1	-	-	Halmahera
USNM Washington	8	3	1	*Halmahera*[10], Misool[8]
ZMA Amsterdam	3	1	-	Halmahera, *Buru*, Ternate
ZMB Berlin	1	1	1	Bacan[1]
totals	52	33	11 (21.2%)	

1 Mount Sibela, altitude 1500 m, collected by Heinrich (1956).
2 Hatu Sake, altitude 1000 m, one male collected by Stresemann (1914a).
3 two syntypes, collected by Wallace (Gray 1860; Warren 1966).
4 Wai Pate nesting ground, one female collected by Wallace (1863).
5 one female from Sidangole nesting ground (collected by Vorderman) and one male from an unknown habitat, collected by De Haan.
6 of five females, four are from the Wa Kasi nesting grounds (collected by Toxopeus) and one is from the inland habitat near Fakal (Siebers 1930).
7 all victims of electricity wires or traffic at the Tanjung Maleo nesting ground, collected by Heij during this study.
8 Tamulol, altitude 100 - 300 m, collected by Ripley (1960, 1964).
9 Mount Sibela, one male collected by Ripley (1960).
10 Pasir Putih village near Galela nesting grounds, two females collected by Taylor.

Table 9 Habitat type where 33 adult specimens of *Eulipoa wallacei* of known sex were collected. Sex ratio for each habitat is given (see Table 8).

habitat type	nesting ground			inland/mountainous			unknown		
sex	male	(%)	female	male	(%)	female	male	(%)	female
n = 33	–	(0.0%)	15	7	(77.8%)	2	4	(44.4%)	5

Table 10 Numbers, sex and provenance of juveniles (chicks) of *Eulipoa wallacei* in the collections of four Natural History Museums, based on a world wide inventory. See Table 8.

collection	total number of chicks	number of sexed chicks	number of male chicks	provenance
MZB Bogor	1	1	1	Buru[1]
NMR Rotterdam	13	13	6	Haruku[2]
RMNH Leiden	5	2	2	Halmahera[3], Ambon
USNM Washington	2	2	1	Halmahera[4]
totals	21	18	10 (55.6%)	

1 Wa'Kasi nesting ground.

2 found dead by Heij at the surface or in the soil of the Tanjung Maleo nesting grounds.

3 males are from the Galela nesting grounds, specimens with unknown sex are from Halmahera (with no more precise locality) and Ambon.

4 Pasir Putih village near Galela nesting grounds.

Food

Hardly anything is known of the food choise of *Eulipoa wallacei*. Siebers (1930) noticed that a newly hatched chick kept in captivity ate the insects he offered. Toxopeus (1922) and Siebers (1930) mentioned that five adult female specimens (carrying a mature egg) had only a small lump of green coloured sand in the stomach. Section on seven adult females, found dead at Tanjung Maleo during this study (now in the collection of the Natural History Museum Rotterdam, see Table 8), revealed that all but one had the stomach empty. One specimen (NMR 9997-00265) had a few hard seeds (2 x 2 mm) and the remains of scarab-beetles (Coleoptera: Scarabaeidae) and ants (Hymenoptera: Formicidae) in the stomach. The omnivorous food choise as supposed by Jones et al. (1995) could thus be confirmed.

We never actually observed *Eulipoa* to forage at the nesting grounds or in the surrounding forest. Remnants of termite nests found regulary below trees where the birds generally arrive and reside before they start their egg-laying activities, indicate that they do feed on termites. We have, however, no proof.

5 BURROWS

Most of the burrows at Tanjung Maleo are dug on the four fields that consist of fine white silicaceous sand and that are devoid of any vegetation. A small percentage (< 5%) is dug on the bordering beach, in the forest surrounding the fields and in sandy spots on the graveyard, sometimes even in the graves themselves. The four fields have a similar soil (sand) structure, although field 4 is situated about 20 cm higher and as a consequence, measured over a year, the soil is dryer.

Size

Direct observations already suggested that the surface size of the opening and the depth of the burrow depend on the humidity and the related structure of the soil. Often the colour of the soil, thrown up from the burrow, indicates the depth at which the egg has been laid. The sand at a depth of 100 cm is noticeably dryer and therefore of a much lighter colour. To quantify the difference in laying-depth, burrows were measured both in the dry season and in the rainy season during the early morning hours before the collecting of eggs had started as well as during the collecting activities. The length and width of the entrance was noted as well as the depth of the tunnel that leads to the spot where the egg has been laid. Two depths were measured: (1) 'burrow-depth': the depth at which the bird has left the burrow (with sand thrown and fallen in) and, (2) 'egg-depth': the depth at which the egg has been laid, measured after the egg has been unearthed (Fig. 17). The angle at which the birds dig their burrows was estimated by eye and appeared to be very constant at 45º in both dry and wet circumstances. Table 11 gives the results of the measurements. A clear difference exists between the dry season and the rainy season. In the rainy season the eggs are laid at an average depth of 79 cm (Type 1A, Fig. 17), which is over 30 cm deeper than during the dry season (Type 1B, Fig. 17). Schönwetter (1961) mentioned a general average depth of 60-75 cm. Also the dimensions of the burrow differ considerably. Especially during the dry season the surface of the opening of the tunnel can be extremely large due to inflowing sand (Type 1B, Fig 18). During the rainy season, the humid soil has a firm structure and as a consequence the burrow-opening is just wide enough for the bird to pass (Type 1A, Fig. 19). Apart from these seasonal differences in the average laying-depth, which appear to be adaptive to both humidity and temperature of the soil (see below), the range of measurements also points at the ability of the bird to adapt to specific nightly circumstances like clearness (full moon/new moon, cloudy/clear). For example on clear nights and in humid soil the eggs appear to be laid deeply into the ground, whereas on dark nights in dry soil the eggs are laid less deeply and sometimes the burrows cannot even be found (Table 12). Disturbance, especially when repeated during the course of the night, also influences the laying-depth.

Burrow types

All burrows are dug at an angle of about 45º and enter the soil in a straight line. Once the bird has reached a certain depth the egg is laid at the end of the tunnel (Type 1A and 1B, Fig. 17) or the bird diverts and continues to dig horizontally (every direction is possible) and lays the egg at the end of the horizontal tunnel (Type 2, Fig. 20). Normally, the bird then leaves the burrow through the same tunnel. Burrow-type 2 is mostly (not exclusively) found during the

Table 11 Dimension in cm (surface in cm ^{2}) of the burrow and laying depth during both the rainy and the dry season (n = number of burrows measured, range between brackets). See also Fig 17.

season	length	width	surface	burrow-depth	egg-depth	n
rainy	23(10-38)	15(10-25)	345(100-950)	44(25-90)	79(60-125)	201
dry	62(25-120)	48(20-90)	2976(500-10800)	28(10-65)	48(30-65)	228

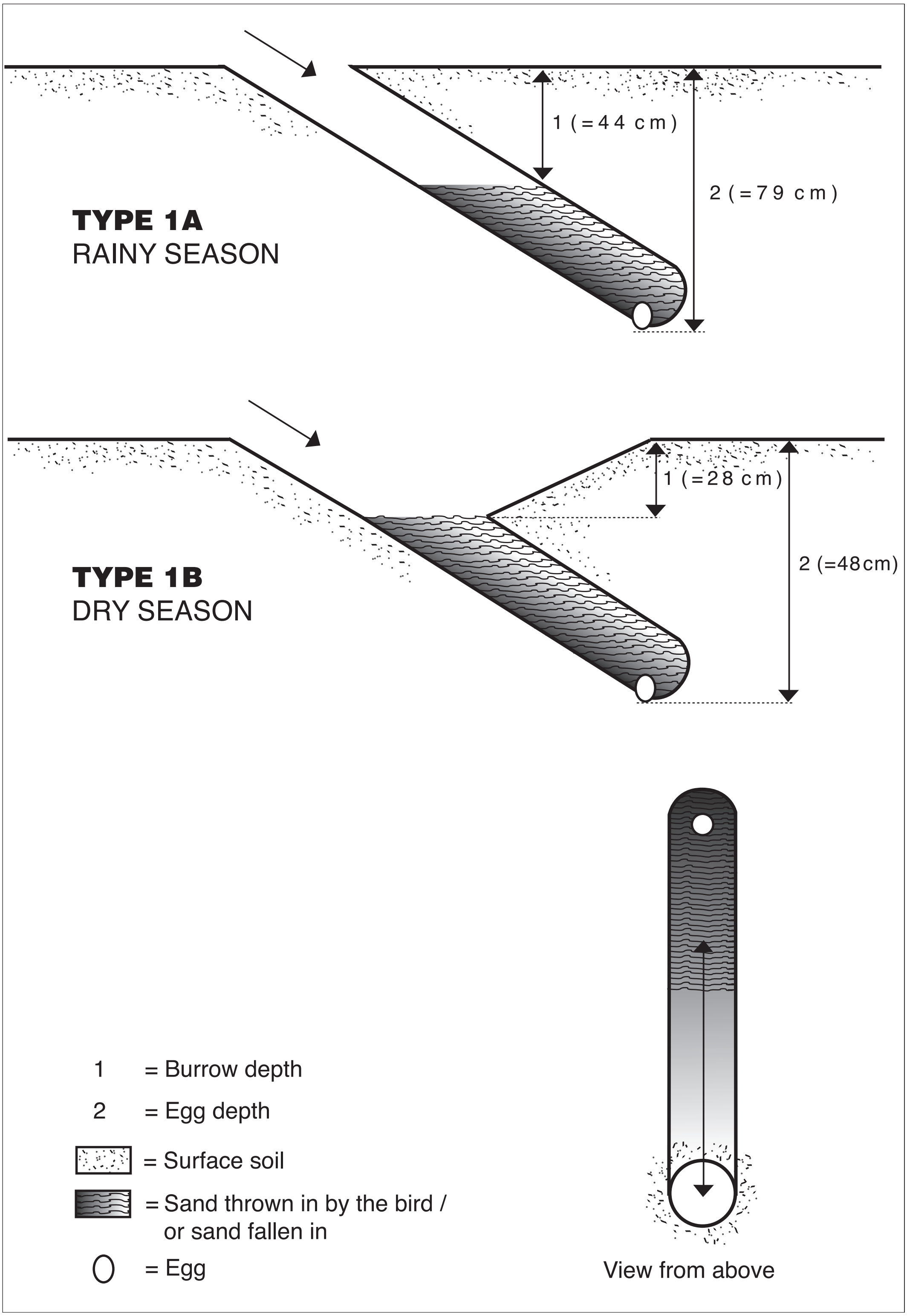

Figure 17 Burrow type 1: the most common type at Tanjung Maleo. The bird lays at the end of the tunnel. [illustration: Jaap van Leeuwen Design]

Table 12 Matr ix showing relative egg-laying depths at Tanjung Maleo under diff erent soil conditions and clearness situations.

situation	dry	humid
clear	+	++
dark	--	-

(++ = deepest; + = deep; - less deep; -- = minimum depth)

Figure 18 A typical dry season burrow. [photo: C.J. Heij]

rainy season and both egg-depth and burrow depth are the same as for burrow-type 1A. Occasionally, we observed a third type of burrow during the rainy season in humid soil: after digging in a straight line at the normal angle to a depth of 80 to 100 cm, the bird diverts and continues to dig horizonally (like in Type 2) for at least one metre. Somewhere on the horizontal track the egg is laid. Then the bird perpendiculary digs its way up. Just under the surface she stops digging and remains sitting like newly hatched chicks do, forming a cavity in the soil (‘internal exit-cavity’). After a while (1-5 minutes) she emerges, leaving a small exit-burrow, which has a form similar to that of a newly fledged chick, but is lar ger (Type 3, Fig. 21, Table 13). Burrows of type 3 are very misleading to predators, even to humans.

Mostly during dark nights, existing burrows may be used by more than one bird, although in cases like that the second bird only uses the entrance and digs her own tunnel. This kind of laying-strategy annoys the egg-collectors. They respond by marking single-entry burrows with fresh twigs, which prevents a multiple use of the burrow (see: chapter 3, Fig. 7).

Figure 19 Typical rainy season burrows. *Eulipoa* footprints are clearly visible. [photo: C.J. Heij]

Table 13 Average dimensions of the exit of burrow-type 3 in cm (surface in cm^2), range between brackets (n = number of burrows measured). See also Fig. 21.

	length	width	surface	n
exit-opening (A)	14(9-20)	12(11-19)	168(70-460)	28
internal-cavity (B)	19(13-25)	18(14-25)	342(182-420)	28

Use of the fields
In the morning after a clear night the nesting grounds resemble a crater landscape or an exploded mine field. All over the field there are clusters of burrows. The entire field seems to have been used. However, when the amount of displaced sand per (collected) egg is calculated, it appears that the birds have only used part of the available surface for egg-laying purposes. In order to ascertain this, the average amount of displaced soil per egg was calculated (from Table 11) and compared with the total available quantity of soil at Field 4 (considering the maximum laying depth of 1.25 m). On the average a single bird displaces 40 dm^3 sand for the laying of an egg (burrows which do not contain eggs [mockpits] have been included). On Field 4, calculated over a year, all egg-laying birds combined appear to have displaced 57.6% of the available soil.

As was noted earlier (see: chapter 3), the burrows are refilled and the fields are completely flattened each morning by the local people after the eggs have been collected. Tanjung Maleo is the only *Eulipoa* nesting ground where this is done. It is unknown if or how the flattened nesting grounds influence the behaviour of the birds. Perhaps it explains the high number of birds using a relative small area (Heij 1995a). Nesting grounds at which many burrows are still visible, might trigger the birds to lay elsewhere. Further study is needed to test this hypothesis.

Clusters of burrows
As became clear after nightly observations at the nesting grounds, the birds tend to dig their burrows in groups during both the dry and the rainy season. Every morning on each field the burrows were found in a number of clusters (Fig. 22). On Field 4, which at our request suffered no or very few nightly disturbances, the clustering pattern was studied in detail. Clusters appeared to be evenly spread over the field. Based on 36 early-morning counts, the average number of clusters was 4 (range 2-6) and the average number of burrows per cluster was 8.5 (range 4-13).

Number of eggs per burrow
Not all burrows appeared to contain eggs ('mockpits') and not all eggs were found by the collectors. In order to quantify this, 162 early-morning counts of the total number of burrows on all four fields were made and compared with the total harvest (number of eggs) of the day: an average of 1 egg per 2.5 burrow was collected. In Halmahera (Gamkonora and Galela nesting grounds) 1 egg per 4 or 5 burrows was being collected in the period 30 January - 3 February 1995. This difference might be caused by the total absence of nightly human disturbance at the Gamkonora and Galela nesting grounds. At Tanjung Maleo disturbances occur frequently, which prevents the birds from digging all night and forces them to lay their eggs rather in a hurry at dawn (see: chapter 4). Occasionally, during dark nights, two or three eggs were found in (what appears to be) one burrow, although closer examination revealed that, in such cases, birds indeed used one entrance but had dug separate tunnels.

Temperature in the burrow
Two abiotic factors are essential for the development of the embryo: temperature and humidity. The temperature of the soil could be monitored permanently with sensors placed at the surface (0 cm) and at depths of 20, 40 and 80 cm in a part of field 2 that was used for

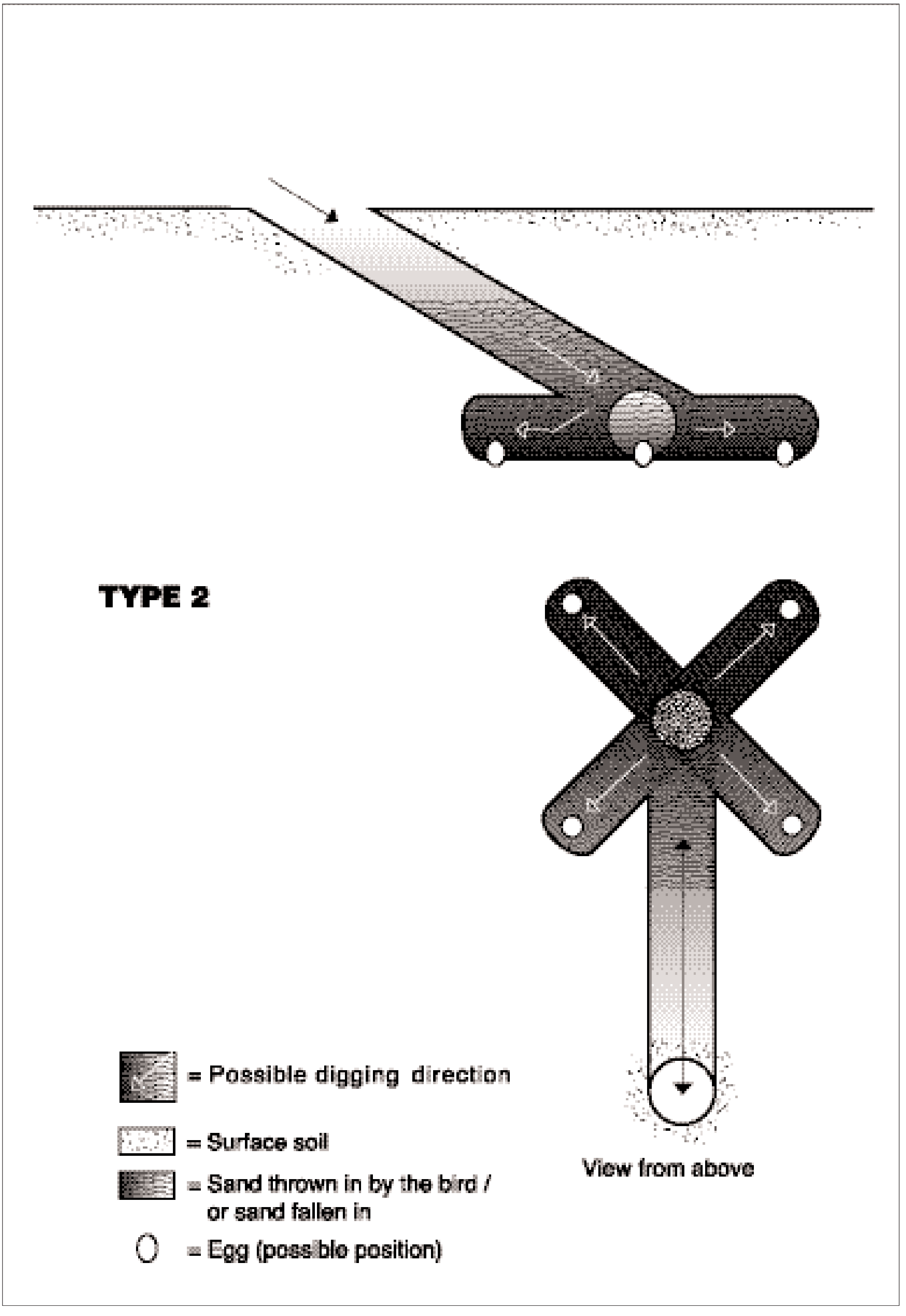

Figure 20 Burrow type 2: commonly found at Tanjung Maleo. At the end of the tunnel the bird contin ues to dig horizontally, in every possible direction and subsequently lays her egg at the end of the hor izontal track. [illustration: Jaap van Leeuwen Design]

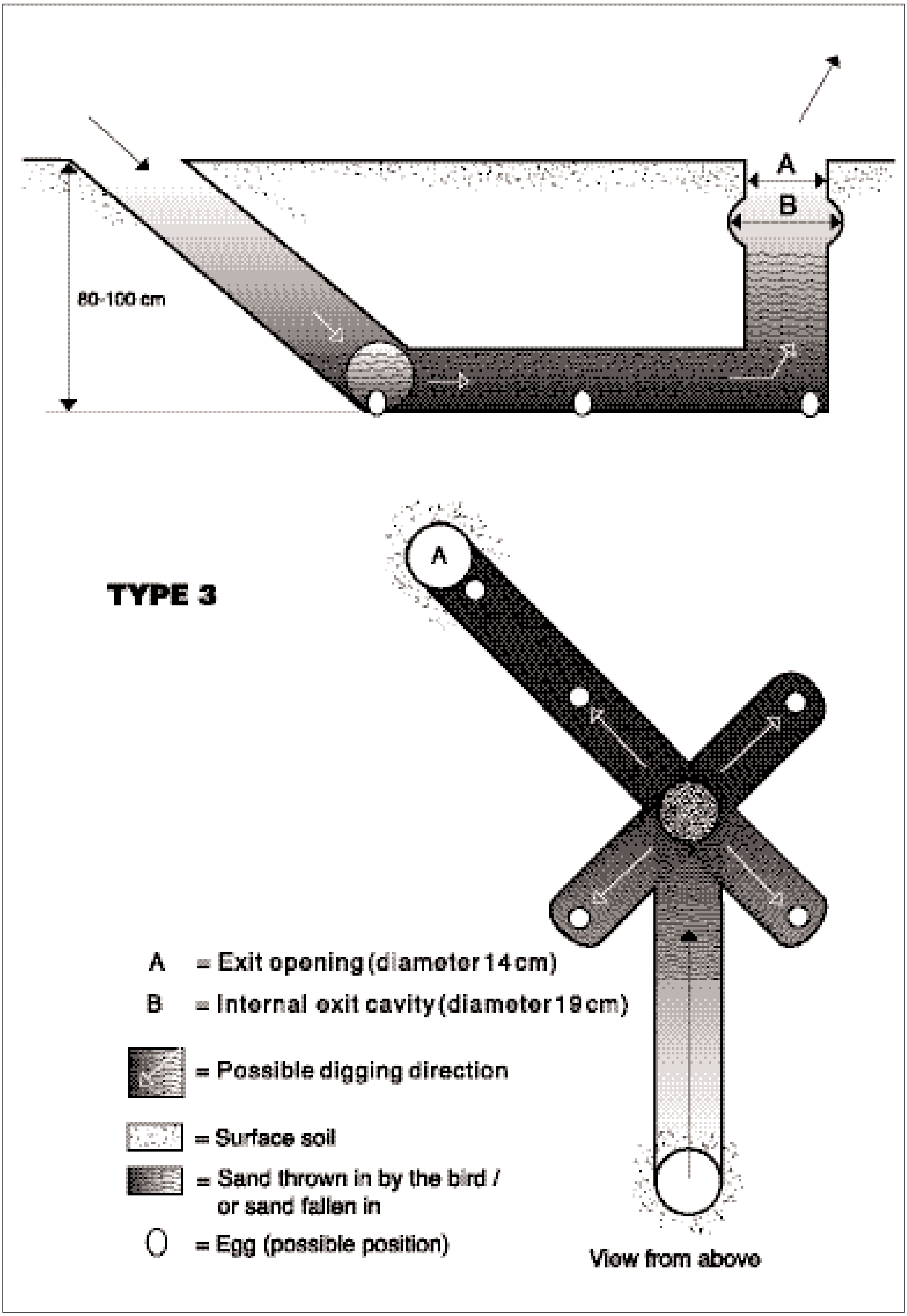

Figure 21 Burrow type 3: occasionally encountered at Tanjung Maleo. For explanation see text.
[illustration: Jaap van Leeuwen Design]

Figure 22 A typical cluster of *Eulipoa* burrows at Tanjung Maleo. [photo: C.J. Heij]

incubation-experiments and that was protected for this reason by a wooden frame (105 x 90 x 25 cm) covered with wire netting (Fig. 23). Readings were done almost daily during the 1994/1995 study period at three standard moments: 06.30-07.30 a.m., 12.30-13.30 p.m. and 18.00-19.00 p.m. The shortest continuously monitored period was 68 days. The total number of temperature readings at each of the four depths was 288 in the rainy season and 255 in the dry season. Table 14 gives the results and in Figure 24 the average soil temperature is plotted against a 24 hour time scale.

The surface-temperature of the soil is between 3.5 and 4.0 ºC lower during the rainy season compared to the dry season. The 24 hour temperature-curve shows that the surface has accumulated most of the heat at 18.00 p.m. and that at 06.00 a.m. the temperature is lowest (Fig. 24). This pattern, together with the difference between both seasons, is predictable and in accordance with the ambient air-temperature (Table 2). At a depth of 20 cm the difference in temperature is even greater: an average of 4.2 - 5.5ºC higher during the dry season (Table 14). During the rainy season the average temperature at 20 cm is rather low and very constant (26.9-27.3ºC) throughout day and night. This is probably effected by water that saturates the soil and subdues a high amplitude. At greater depth temperatures are higher, and differences between both seasons are slight. During the dry season there is almost no difference in temperature between depths of 40 and 80 cm (the averages range between 32.8/32.9 and 35.0ºC at both depths), although during the rainy season the average temperature is 0.7 - 1.8ºC higher at a depth of 80 cm. At 40 cm the rainy season

Figure 23 The installation of the wooden frames used for incubation experiments and temperature readings at Tanjung Maleo, field 2. [photo: A.G. Heij-Ruuls]

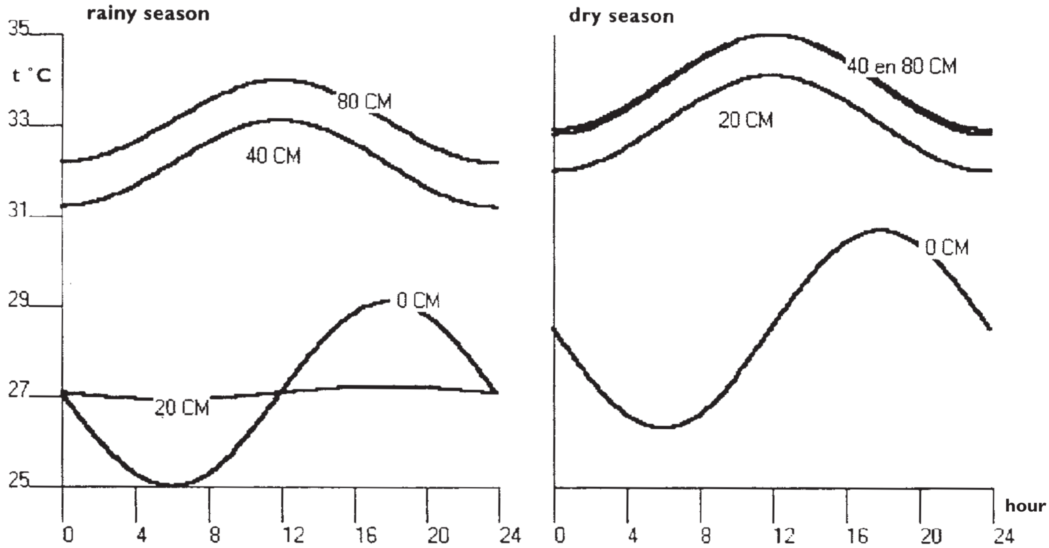

Figure 24 The 24 hour path of the average soil temperature, measured at the surface (0 cm) and at different depths (20, 40 and 80 cm) at field 2, Tanjung Maleo, during the rainy season and the dry season. Measurements were taken daily at standard times during the period July 1994 - June 1995.

soil-temperature averages from 31.2 to 33.1ºC. Knowing these temperature data, the laying-depth during the rainy season is expected as no less than 40 cm to be energetically profitable as the eggs of burrow-nesting megapode species are usually incubated at temperatures of 32-35ºC (see: Dekker 1988), with 34ºC being the optimal temperature (Jones et al. 1995). Such appeared to be the case: during the rainy season the birds lay their eggs at greater depth (average 79 cm, range 60-125 cm, Table 11), where the average temperature ranges between 32.9 and 34.7ºC (Table 14). During the dry season the eggs are laid at a considerably lesser depth: 48 cm (range 30-65 cm), though still at average temperatures ranging from 32.9 to 35.0ºC. As the soil temperature is equal at depths of 40 and 80 cm during the dry season (Fig. 24, see above) there is apparently no need to bury eggs deeper, indicating that the laying-depth is adapted to the temperature of the soil. However, incubation-experiments executed during both the dry and the rainy season (see: chapter 6) showed that freshly laid eggs, reburied at depths of 20, 40, 60 and 80 cm had an equal chance to hatch. The duration of the incubation period – likely to be related to soil temperature (Jones et al. 1995) – appeared to vary considerably and was longer during the rainy season (see: chapter 6). As was noted earlier, laying-depth is also influenced by the clearness of the night and the occurrence of prolonged nightly disturbances.

Humidity in the burrow

To establish the humidity of the soil of the Tanjung Maleo nesting grounds, sand samples of 300 g each, were taken from depths of 0 cm (surface), 20 cm, 50 cm and 100 cm. Per depth three samples were taken, a total of 48 samples evenly spread over the dry season and the rainy season. After drying in the sun, the water percentage was calculated as follows:

$$\frac{(Mw - Md) \times 100}{Mw}$$

Mw = wet mass;
Md = dry mass of the soil sample.

It appeared during our studies that drying in the sun was not sufficient to completely remove the water. Therefore the samples were once more dried for 24 hours in an oven at a temperature of 60ºC, after which the percentage of water was again calculated. Table 15 gives the results.

Table 14 Average temperature of the soil at different depths in field 2 of the Tanjung Maleo nesting grounds during the rainy and the dry season (ranges between brackets; n = total number of temperature readings at each of the four depths).

depth (cm)		rainy season (n=288)	dry season (n=255)
	time	temp. °C	temp. °C
0	06:30 - 07:30	25.0 (24.0 - 28.3)	28.5 (26.1 - 35.8)
	12:30 - 13:30	27.7 (24.9 - 35.3)	31.7 (30.0 - 36.9)
	18:00 - 19:00	29.1 (22.8 - 38.4)	32.9 (28.0 - 45.4)
20	06:30 - 07:30	27.1 (25.0 - 29.1)	32.0 (29.3 -35.6)
	12:30 - 13:30	26.9 (24.5 - 29.4)	34.1 (30.1 - 39.9)
	18:00 - 19:00	27.3 (25.2 - 29.1)	32.8 (30.0 - 37.1)
40	06:30 - 07:30	31.2 (30.0 - 35.2)	32.9 (29.3 - 35.8)
	12:30 - 13:30	33.1 (31.6 - 38.5)	35.0 (30.4 - 39.5)
	18:00 - 19:00	32.2 (30.1 - 36.2)	33.2 (30.3 - 35.9)
80	06:30 - 07:30	33.0 (30.0 - 34.9)	32.8 (30.2 - 35.6)
	12:30 - 13:30	34.7 (31.1 - 37.4)	35.0 (32.5 - 39.6)
	18:00 - 19:00	32.9 (29.9 - 35.5)	33.6 (30.2 - 36.7)

The humidity in the soil proved to be very important for the development of the egg. Laboratory-experiments we conducted both at Kailolo and in Bogor, proved that at low (< 3%) humidity of the soil an embryo could develop to a mature chick, but would eventually dry up totally, not being able to hatch. The minimum water content of the soil allowing eggs to develop and chicks to hatch is, however, not known. In burrows of *Macrocephalon maleo*, Dekker (1988) found a moisture content at different nesting grounds that varied from 1.6 - 45%, although in one monitored burrow the range was 6.3 - 11.6%. Upon digging we noted that, especially when the surface is cooler than the underlying soil, a warm vapour escapes from the sample, showing the humidity of the sand. Table 15 gives the percentage of water during dry and wet season at various depths. Moisture content increases with the depth, the highest water-percentage was found at 100 cm in both seasons: 4.9 % during the rainy season, 5.5% during the dry season. In general the humidity of the soil was higher during the dry season, the difference is however slight: 3.4% rainy season and 3.8% dry season. This is rather surprising and might be due to accumulation of water in the course of the rainy season, being measured at the start of the dry season. The surface soil was, however, much dryer during the dry season (Table 15).

Tabel 15 Water contents (humidity), established by both drying in the sun and in an oven at 60°C, of the soil at Tanjung Maleo at various depths during the dry season and the rainy season.

depth/cm	dry season		rainy season	
	water contents in samples of 300 g		water contents in samples of 300 g	
	g	%	g	%
0	1.5	0.5	6.2	2.1
20	12.6	4.2	10.4	3.5
50	14.8	4.9	9.9	3.3
100	16.5	5.5	14.8	4.9
depths combined	45.4	3.8	41.3	3.4

6 EGGS

Here we will report on weight, measurements, colour, contents and temperature of the *Eulipoa* egg. Data were taken on site, immediately after the eggs had been unearthed (Fig. 25). The results of two field-experiments are also given. It concerns experiments to establish the duration of the incubation period and to test the ability of hard-set eggs and freshly laid eggs to hatch after being replaced and reburied.

Figure 25 An early morning routine at Tanjung Maleo: the first author weighing eggs. On the background some burrows are clearly visible. [photo: P. Rehatta]

Size

Measurements of eggs are given in Table 16. The form of the egg is quantified by dividing length by width (L/W). The higher the L/W ratio, the longer the egg (Schönwetter 1985).

Table 16 Measurements (in mm) of *Eulipoa* eggs collected at Tanjung Maleo (ranges between brackets). Data collected year round.

length	width	l/w ratio	n
78.1 (74.1-85.5)	48.9 (42.0-51.8)	1.6	299

An average egg measured 78.1 x 48.9 mm, with the L/W ratio being 1.6. Dekker's sample of 19 eggs from Haruku measured 80.0 x 49.0 mm (Dekker et al. 1995; Jones et al. 1995). Our sample of 299 eggs ends up having slightly lower averages, but shows a wider range of extremes, the difference between the lowest and higest values being about 10 mm (Table 16).

Weight

The average weight of the *Eulipoa* egg at Tanjung Maleo is 101.7 g. Eggs being laid during the rainy season are on average 2.7 g heavier than those from the dry season (Table 17). While computing these data, eggs laid during the full-moon period appeared to be the heaviest, though more data is needed to to provide conclusive evidence on this matter. The average weight we calculated from a sample of 433 eggs is almost 5 g lower than the weight given by Jones et al. (1995): 106.4 g based on a sample of 42 collected in October at Tanjung Maleo. This difference is influenced by the presence of two extremely light eggs (each 59 g) in our sample, an inevitable result of the large number of eggs we weighed. Another sample of 57 eggs from January/February listed by Dekker et al. (1995) had an average weight of 102.8 g and comes much closer to our values. West et al. (1981) had clearly been sent a batch of small eggs (average 94.1 g; n=20). Eggs we collected at other nesting

Table 17 Weight (in g) of freshly laid eggs of *Eulipoa* at Tanjung Maleo.

	average weight	(range)	n
rainy season	103.6	(86 - 120)	130
dry season	100.9[1]	(59 - 124)	303
year round	101.7	(59 - 124)	433

[1] The average weight for eggs collected during the dry season was incorrectly printed in the preliminary report of this study (Heij 1995a). It should read 100.9 g instead of 109 g. The conclusion that 'eggs are less heavy during the wet season' should therefore be 'eggs are less heavy during the dry season'.

Table 18 Average weight of the egg relative to the average weight of the body in 29 captured *Eulipoa* females at Tanjung Maleo (ranges between brackets).

body weight without egg	egg weight	relative egg weight	n
517.5 g (456-605)	105.8 g (95-119)	20.5 % (18.0-22.2)	29

grounds weighed 103 g (90-120 g, Buru, September, n=19); 103 g (98-105 g, Seram, November, n=9); 110 g (105-115 g, Kasa, November, n=2) and 100 g (95-103 g, Halmahera, February, n=4). The Halmahera sample was biased, as the largest eggs had already been sold. To avoid this, eggs should always be weighed at the nesting sites, directly after unearthing, before the sale has started.

Relative weight

The weight of the egg relative to the body weight of the female was established by pressing the egg out of the body of 29 captured birds and weighing both egg and bird (Table 18). The average weight of the birds just after extracting the egg was 517.5 g, the egg taking account of 20.5 % of the body weight. Relative egg weight measured from three females caught at Tanjung Maleo as given by Dekker et al. (1995) and Jones et al. (1995) ranged between 18.4 and 20.6%.

Colour

There is a marked difference in the colour of freshly laid and hard-set eggs. The longer an egg has been in the soil, the more the colour deepens to rusty brown and chocolate colours (PLATE III). The coloured outer layer (a kind of powder) loosens after some time so that a patchy pattern emerges: the underlaying white shell becomes clearly visible. In order to ascertain the colour of the egg, Smithe (1975) was used as a standard. Freshly laid eggs are coloured light flesh to dark salmon (PLATE IV) (Smithe Guide notation: R. 7.0/6.0; YR 7.0/6.0; Swatch notation 0.8 YR 6.95/5.9; YR 6.90/6.0). Hard-set eggs are, according to this method, antique brown (Smithe Guide notation: 7.5 YR 4.5/5.0; Swatch notation 6.9 YR 4.40/5.6).

Yolk percentage

Megapode eggs contain an extremely large amount of yolk in comparison with the eggs of other birds, ranging from 48 to 69 % of the weight of the egg (Jones et al. 1995). In order to ascertain the yolk percentage for *Eulipoa wallacei*, a total of 50 eggs were weighed and boiled (PLATE V). Afterwards, the yolk, the eggwhite (albumen) and shell were weighed separately, so that the percentage per item could be calculated (Table 19). During boiling the eggs became, on average, three grammes (2.9%) heavier through water absorption. This water dissipated when the egg was dissected and was of no influence to the results. The average yolk percentage appeared to be 66.3. Jones et al. (1995) listed 65-67% for the species, though no sample size was given. Nine eggs analysed by Dekker et al. (1995) had an average yolk percentage of 67.6 (range 65.0-71.4%).

Table 19 Average yolk percentage in 50 eggs of *Eulipoa wallacei* collected at Tanjung Maleo in November 1994 (during full-moon), and the average weight of the three major components (weights in g, range between brackets). The average yolk percentage was calculated from the total weight of the sample (50 eggs): 5355 (egg) - 440.2 (shell) = 4914.8 [3256.6 yolk = 66.26%].

egg weight (not boiled)[1]	shell weight[2]	albumen weight	yolk weight	% yolk	n
107.1 (99-124)	8.8 (7.0-11.0)	32.2 (25.5-39.0)	66.7 (56.0-81.0)	66.3 %	50

1 freshly boiled eggs weighed 110.3 (99-138), not used to calculate yolk percentage

2 average thickness of the shell is 0.07 mm (0.04-0.12 mm); the heaviest eggs have the thinnest shell.

Table 20 Temperature just around the egg during incubation and at similar depth in the soil at 55 cm in the dry season (79 days, 237 readings) and the rainy season (81 days, 243 readings) at Tanjung Maleo.

	dry season		rainy season	
time	temperature around egg	temperature at similar depth	temperature around egg	temperature at similar depth
06:30 - 07:30	32.5°C	31.4°C	31.9°C	31.5°C
12:30 - 13:30	33.3°C	32.3°C	33.7°C	33.2°C
18:00 - 19:00	32.1°C	31.2°C	31.9°C	32.5°C
average	32.6°C	31.6°C	32.5°C	32.4°C

Temperature
Just after the egg has been laid, it has a temperature of 41.5ºC, equal to the body temperature of the bird (measured in four cases). Subsequently, the temperature of the egg was measured constantly (next to the shell) during incubation at a depth of 55 cm for 79 days in the dry season and 81 days in the rainy season. Besides, the temperature of the soil at the same depth and at the same site was monitored (Table 20). During the dry season the temperature of the developing egg was, on average, 1ºC higher (32.6ºC) than the temperature of the soil (31.6ºC) at the same depth. During the rainy season this difference was just 0.1ºC: egg 32.5ºC, soil 32.4ºC (Table 20), but still the developing egg does produce measurable heat. Compared to the average temperature of 35-36ºC at which birds eggs are generally incubated (Kendeigh et al. 1977), these temperatures are rather low. Artificially incubated eggs of the malleefowl *Leipoa ocellata* (a mound-breeding megapode) had the highest chance of hatching at 34ºC, but the embryos survived a temperature range of 28-38ºC (Jones et al. 1995).

Incubation period: observations and experiments
Methods - The duration of the incubation period (i.e. the amount of time between the laying of the egg and the fledging of the chick) was monitored in the field by both incidental observations and experiments. Freshly laid eggs were carefully reburied in their original position and depth, and also in different positions and at different depths. In the latter way it was established whether a change in the original position of the egg has a negative influence on the development, as was argued by several authors (Fleay 1937, Dekker 1990, Jones et al. 1995). For these experiments, five protective frames were placed at the nesting grounds. These wooden frames, 105 cm long, 90 cm wide, 25 cm high, were sunk to a depth of 10 cm in the soil in the middle of field 2 (Fig. 23). Eggs were reburied within the boundaries of the frames. The frame could be covered with a net to prevent predation and to prevent unwanted eggs to be laid. The moment of fledging could easily be established by the appearance of little round cavities from which the chicks had emerged (Fig. 26) and/or chicks trapped in the frame. During the dry season these emergence craters are less conspicuous due to the loose structure

Figure 26 In the breeding experiments the moment of fledging could easily be established by the appearance of little round craters in the soil from where the chicks had emerged. [photo: C.J. Heij]

of the dry soil (see: chapter 7). In addition to these experiments to establish the duration of the incubation period, it was also investigated whether already developed (hard-set) eggs (that are normally destroyed by the local collectors), which we reburied in a different position as laid by the bird, had any chance of further development. Laboratory experiments were carried out both in Kailolo and Bogor.

Laboratory results - In 75% (n=8) of the eggs placed in sand-filled glass jars and kept on a kitchen shelf in Kailolo, an embryo came to full developement. However, after 104 days the chicks had died since they had not been able to break the egg-membranes. Of 15 freshly laid eggs placed in an incubator at the Bogor laboratory, where the temperature was kept between 31.5ºC - 32.0ºC at a relative humidity of 70% , all the embryo's died after a few weeks. In the incubator at the same conditions, 10 already hard-set eggs containing embryo's, produced three hatchlings which lived for respectively 5, 14 and 15 days. West et al. (1981) also experimented with artificial incubation of *Eulipoa*-eggs: their hatchlings also died very soon. Valentijn (1726) already indicated that this bird cannot be tamed or kept in captivity.

Table 21 Average duration of the incubation period of *Eulipoa wallacei* at the Tanjung Maleo nesting grounds (extremes between brackets; n = number of monitored eggs). The incubation period includes the time needed for the chick to reach the surface.

	incubation period in days	n
year round	74.2 (49-99)	63
dry season	73.2 (49-99)	53
rainy season	79.6 (70-85)	10

Field observation - On 23 August 1994, a freshly laid egg was left in the burrow by a local collector because the tunnel ran under the concrete edge of a human grave and the collector feared 'revenge'. The burrow was refilled and patted and the date was written on the grave with a felt pen. During the night of 28/29 November 1994 a small round hole in the grave indicated that the chick had hatched and had fledged. The incubation period took 98 days.

Results of field experiments - The average duration of the incubation period throughout the year, based on the monitoring of 63 freshly laid eggs, is 74.2 days. This includes the time it takes the chick to reach the surface (1-4 days, see chapter 7). During the dry season it is 73.2 days and during the rainy season it takes an average of 79.6 days before a chick emerges from the soil (Table 21). Three eggs had an extremely long incubation period. They were from a sample of five freshly laid eggs that were reburied at the usual protected experiment-site. After 92 days no chick had appeared so the eggs were unearthed and checked. All five eggs appeared to contain embryo's and were in good condition. They were subsequently buried again at the same site and depth (55 cm) and kept under constant surveillance. After an other 72 days two healthy chicks emerged from the soil: their total incubation period amounted 164 days, more than twice the average. It should be noted that these two hatched eggs are not included in the sample that resulted in the average incubation period of 74.2 days.

Tables 22 & 23 give the results of the reburying experiments of freshly laid eggs. Of the 68 eggs reburied at various depths, 92.6% produced hatchlings (that fledged). The actual depth at which the egg had been reburied (20-80 cm),

Table 22 Results of reburying experiments at different depths with a total of 68 freshly laid *Eulipoa* eggs carried out at Tanjung Maleo (eggs reburied in their original position).

depth	number of reburied eggs	number hatched	%
20 cm	19	17	89.5
40 cm	37	35	94.6
60 cm	5	5	100
80 cm	7	6	85.7
totals	68	63	92.6

Table 23 Results of several types of reburying experiments with freshly laid *Eulipoa* eggs carried out at the Tanjung Maleo nesting grounds.

type of experiment	number of reburied eggs	number hatched	%
original position (year round)	68	63	92.6
original position (dry season)	57	53	91.4
original position (rainy season)	11	10	90.9
changed position (upside down)	10	10	100
changed position (horizontally)	10	10	100

did not seem to be of any significance to the results (Table 22). The season and the position in which the eggs were reburied did not influence this result either (Table 23): even eggs that were reburied in a reversed position (upside down or horizontally) all hatched.

Discussion - Compared to the (few) data on the duration of incubation in other megapode species, summarized by Jones et al. (1995), the average incubation period of *Eulipoa* eggs at Tanjung Maleo is within the range of absolute extremes (44-99 days) listed for the family (mound breeders and burrow nesters combined). The normal range is, however, 49-65 days. For the burrow nesting *Megapodius pritchardii*, *M. eremita* and *Macrocephalon maleo* the range is 47-67, 42-70 and 62-85 days respectively. One egg of *M. cummingii* (also a burrow-nester) hatched after 63 days (Jones et al. 1995). The two *Eulipoa*-eggs that hatched after 164 days (see above) had the longest incubation period ever recorded for a megapode, and indicate the extreme flexibily of the species' breeding-biology. This flexibility is also shown by the 100% hatching-rate of eggs that were reburied upside down and horizontally (*contra* Dekker 1990) and by the burrow and egg temperatures that were, at Tanjung Maleo, - on average - below the optimal incubation temperature of 34ºC as given by Jones et al. (1995).

Reburying hard-set eggs

During collecting activities, eggs that had been in the soil for a longer period and consequently were in various stages of development, are regulary unearthed. They are easily recognised by their darker colour and the loose and partially missing outer skin. In case of doubt they are held up against the light. These hard-set eggs must have been overlooked during previous collecting activities and - as only freshly laid egg have commercial value - are either destroyed by the collectors, or , in case of lightly hard-set eggs, are taken home and fried. Occasionally hard-set eggs are injected with poison and left out in the open as a bait to kill egg-predators like monitor lizards (Fig. 5).

Methods - During our presence at the Tanjung Maleo nesting grounds we tried to prevent the unearthed eggs from being destroyed. A total of 202 hard-set eggs could be rescued and were reburied at safe locations at the edges of the fields at depths between 15 and 50 cm. The exact location of each egg was indicated with a plastic label showing the reburying date (PLATE III). Reburying locations were checked daily as the eggs could hatch any moment. In case there was no indication of fledging 2.5 months after reburying, the location was excavated to check the fate of the egg. The remnants of the eggs clearly showed whether a chick had hatched or not: clean egg shells indicated an hatched egg (Fig. 27) whereas egg shells grown with roots of plants and with fungi (Fig. 28) indicated that the egg did not hatch; plants and fungi having used the egg contents as a rich substrate.

Results - These experiments resulted in 67.8% fledged chicks (n=202); 23.3% of the reburied eggs did not hatch and 8.9% of the eggs could not be checked since the labels got lost. During the first months when these experiments were carried out, the fledging-rate of reburied hard-set eggs was 50% (n=45). This rather low percentage was probably caused by the fact that the depth at which the eggs had been reburied (15-20 cm) was not favourable. Later on, the eggs were reburied at depths between 35 and 50 cm and the percentage that produced fledged chicks increased to 72.6 (n=157), whereas 16.0%

Figure 27 Unearthed remnants of a sucessfully hatched *Eulipoa* egg. [photo: C.J. Heij]

of the eggs did not hatch and 1 1.5% could not be retrieved due to lost labels. In contrast to these findings, the hatching-rate of reburied freshly-laid eggs was equal at depths between 20 and 80 cm (see above and Table 22).

In the laboratory-incubator, 33.3 % (n=10) of the hard-set eggs hatched, although the survival of the chicks in captivity was very low . Earlier attemps to experiment with artificial breeding of hard-set *Eulipoa* eggs (De Wiljes-Hissink 1953) failed, as on Ambon and Halmahera only freshly laid eggs were sold for consumption, and hard-set eggs were not available.

The positive results of the field-experiments with hard-set and freshly laid eggs give good prospects for reburying as a measure to increase the survival of the *Eulipoa* population. Although the local egg-collectors of Tanjung Maleo always seemed very enthousiastic when reburied hard-set eggs hatch, they are not motivated to keep hard-set eggs and only reburied them under our supervision. In general the local interest and insight in the survival of the species is totally absent (see also: chapter 3). We believe, however, that through guidance and education, the villagers of Kailolo can continue collecting eggs and still give *Eulipoa* a chance to survive (see: chapter 12).

Figure 28 Unearthed remnants of *Eulipoa* eggs that did not hatch: roots of plants and fungi used the egg contents as a substrate. [photo: C.J. Heij]

7 HATCHLINGS AND FLEDGLINGS

We define a 'hatchling' as an *Eulipoa* chick working its way out of the egg and up to the surface. Once at the surface and out in the open, we call it a 'fledgling'. A 'chick' refers to both hatchlings and fledglings. The term 'juvenile' is not used here, despite the fact that megapode fledglings already have a feathered (juvenile) plumage rather than a downy plumage. We regard birds having obtained a second generation of feathers through post-juvenile moult a few weeks after hatching (Jones et al. 1995), as true juveniles. Birds in that (immature) plumage were, however, not encountered during this study.

Hatching: breaking the egg shell

The behaviour of the *Eulipoa* chick during hatching is virtually unknown. Campbell (1903) mentioned that megapodes hatch by kicking their way out of the shell. Siebers (1930) considered the way the *Eulipoa* chick frees itself from the egg shell, to be an enigma. He noticed that the egg is surrounded by sand that - due to penetrating rain - is compressed and firm. So indeed it is quite a job for the chick just to emerge from the egg, let alone to struggle its way up to the surface. As megapodes are known to loose their egg-tooth before hatching (Del Hoyo et al. 1994, Jones et al. 1995) the chick has to push in order to break the egg shell (instead of picking). From dissection of 35 hard-set eggs in various stages of development (damaged during collecting-activities at Tanjung Maleo), we established that the chick looses its (vestigial) egg-tooth a few days before hatching. Both in the field and the laboratory we established from direct observations that at hatching the chick pushes violenty, creating a lengthwise crack in the shell (Fig. 29) after which the egg breaks open along the crack within a few minutes. We witnessed that if the egg shell does not immediately break completely (and the chick is not able to hatch), pulmonary respiration does not start, causing the chick to die. Unearthed eggs, showing the lengthwise crack, always contained a fully developed (dead) chick. In many cases, we observed these eggs, while still buried in the soil, to be invaded by ants (*Solenopsis* sp.) which had entered the egg through the crack and were scavenging on the chick. So, in case a chick, unable to free itsef from the egg shell, does not suffocate immediately, the ants surely will cause its death.

Figure 29 At the moment of hatching the *Eulipoa* egg shows a lengthwise crack. [photo: C.J. Heij]

The upward struggle

After breaking the egg shell (hatching), the chick struggles up to the surface, a journey of 30-125 cm (see chapter 5, Table 11). Immediately after hatching, while still deeply buried, the chick has a complete, feathered plumage although both the flight feathers and contour feathers are still packed in waxlike sheaths. During the upward struggle the sheaths gradually wear of f. While digging for eggs, the collectors accidentally came across chicks on their way to the surface. These 'premature' fledglings were released at the forest edge. Their condition, depending on the depth at which they were found, was generally bad. They were inactive, had their feathers still packed in sheaths (thus unable to fly), made squeaking noises and were soon to die. Dissection of these chicks (n=15) established the presence of a thick layer of subcutaneous fat on the breast, thighs and behind the coccyx. Their pectoral muscles were strongly developed and the presence of a lar ge provision of yolk was striking. Fledglings that had reached the surface on their own (n=17), however, appeared to have no subcutaneous fat, but still had a good amout of yolk in their yolk sac. The weight of chicks working their way up and the weight of those that had reached the surface differs accordingly (Table 24): 69.1 g while in the soil and 57.0 g when at the surface.

Table 24 Weight of *Eulipoa* chicks during their upward struggle (hatchlings) at an average depth of 50 cm and weight of chicks (fledglings) that reached the surface. All at Tanjung Maleo nesting grounds, Haruku Island, both in dry and rainy season.

depth (cm)		weight (g)		
average	range	average	range	n
50	10-80	69.1	59-92	15
0	surface	57.0	48-79	35

Emergence time
To monitor the time a hatchling needs to cover the distance to the surface (emergence time), 'premature' fledglings were reburied at the depth at which they were found and their activities were closely watched. It appeared, during the dry season, that it takes a hatchling an average of 24 hours to cover an upward distance of 20 cm (0.83 cm per hour, range 0.60 - 1.1 cm; n = 32). Twelve chicks had an exceptional average speed of 2 cm per hour (range: 1.7 - 2.4 cm). It should be noted that hatchlings did not dig continuously, but had moments of activity interspersed with periods of rest (see also: Jones et al. 1995), consequently the emergence speed per hour as given here are calculated averages. The experiments were not conducted during the rainy season, but we then expect the emergence time to be longer as the soil is damp, heavier and firm. As eggs are laid at an average depth of 48 cm during the dry season (see chapter 5, Table 11) it takes a chick 24-58 hours to reach the surface. In case of the average rainy season egg-depth of 79 cm (Table 11) a chick needs at least 39-95 hours to surface. For *Eulipoa* there are no data to compare. For mound-breeders, Jones et al. (1995) listed 2 - 15 hours for the malleefowl *Leipoa ocellata* and 1 - 2.5 days for the Australian brush-turkey *Alectura lathami*. For the burrow nesting maleo *Macrocephalon maleo*, they mentioned 'very slowly , often remaining within the material for several days'.

Fledging: emerging from the soil
Upon arrival at the surface, the soil surface breaks open and the chick pokes its head into the air and waits, breathing heavily (PLATE VI). We noted an average of 128 breathing movements per minute (n=17). While still with its body under the surface, the chick makes pumping movements with its wings, creating a cavity. In this 'exit-cavity' the chick is very vigilant. After a while the chick turns around and looks at its surroundings. Especially at daytime, it can wait for many hours, just sitting in the cavity, breathing heavily. Then, suddenly it jumps out and flutters into the direction of the forest that surrounds the nesting ground. In 95% of the cases, chicks emerged and fledged during hours of darkness.

It appeared that the upward journey and the time spent in the exit-cavity is of vital importance to loose the feather sheaths and develop the ability to fly. Premature fledglings were not able to fly. Chicks we bred in incubators could not fly till 2-3 days after hatching, having lost the feather sheaths. Siebers (1930) mentioned that an *Eulipoa* chick, unearthed too early and therefore not fully developed, was able to flutter after three days and fly off after a week. Clark (1960, 1964) noted that 'young megapodes can fly weakly on their hatching-day and are able to forage successfully within a day or so after hatching'.

After fledging, especially when the surface is wet (rainy season), a small round or oval pit is clearly visible in the soil (Fig. 30). When these 'exit-pits' are excavated, the internal cavity ('exit-cavity'), where the chick resided for some hours becomes visible (Fig. 31). Dimensions are given in Table 25.

Early morning counts of exit-pits proved to be a trustworthy method to establish the number of fledglings. During the rainy season and after

Table 25 Dimensions (in mm) of 181 exit-pits and exit-cavities of *Eulipoa* chicks, measured at the Tanjung Maleo nesting grounds, Haruku Island during the rainy season. (see Fig. 31)

	average	minimum	maximum	n
exit-pit (P)	55 x 56	40 x 40	80 x 93	181
exit-cavity (C)	81 x 81	65 x 65	100 x 115	181

Figure 30 Exit pits of *Eulipoa* fledglings seen from above (average dimensions are 55 x 56 mm, see Table 25). [photo C.J. Heij]

rainy nights in general, the pits were easy to locate. During the dry season the pits were less well marked due to inflowing sand, but could still be recognised by the trained eye. However, especially during the dry season, some exit-pits might be overlooked. We estimate that, on average per year, we missed about 10% of the fledglings. After the nesting grounds had been trodden on by the egg-collectors, no reliable counts of exit-pits could be made. Counts were therefore always executed before egg-collecting had started.

Behaviour after fledging

Once it has reached the forest, the fledgling presses itself flat against the forest floor and due to the cryptic plumage, can hardly be detected again (PLATE VII). Despite serious efforts during the entire study period, we only discovered about 10 fledglings in the forest. We noticed that they were passive at daytime, hiding between dry leaves on the forest floor. At night they became active and foraged. The same activity pattern was observed in captivity: chicks mainly passed the day asleep and at night they fed on the food we offered: locusts, millepedes, ants, termites, flies, beetles, worms, slugs, fruit (papaya, apple, melon) and seeds (maize, rice and poultry-food). In addition to foraging, captive chicks dug, jumped and fluttered continuously, often damaging themselves. In most cases captive chicks collapsed within a few days. Siebers (1930) also noticed the nightly activity of captive *Eulipoa* chicks and was not able to keep them alive for more than a few weeks.

The life and whereabouts of fledglings and juveniles of *Eulipoa wallacei* remains unknown. The fact that we hardly observed any fledglings in the forest of Tanjung Maleo indicates that they soon leave the area, otherwise the accumulation of chicks should have resulted in more sightings. When and how they leave is unknown. To answer questions such as ‘are they able to fly across the sea to Ambon and Seram while not fully grown?’, ‘do they remain on Haruku and move about on foot?’ and ‘when do they return to the nesting grounds to lay their first egg?’, further study is needed.

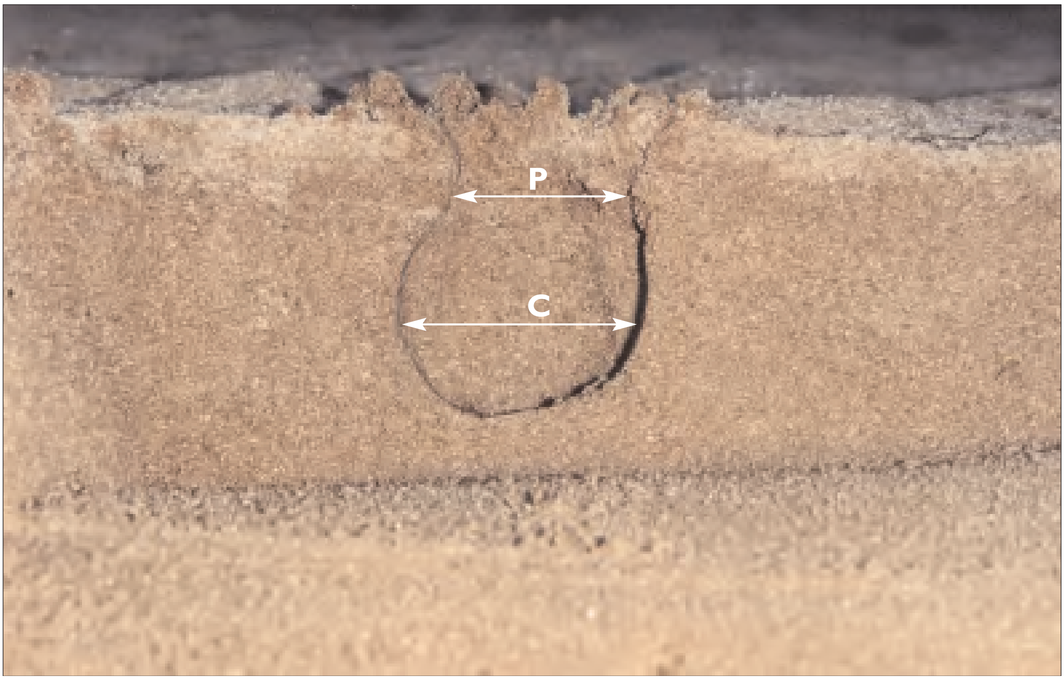

Figure 31 Lateral view of an excavated exit-pit (**P**) of an Eulipoa fledgling. The exit-cavity (**C**) is now visible (average dimensions of the cavity are 81 x 81 mm, see Table 25). [photo C.J. Heij]

8 HABITAT, HOME RANGE AND EGG-LAYING INTERVAL

Away from the sun-exposed beaches that are used as nesting grounds, the habitat of *Eulipoa wallacei* is generally described as 'mountain forest' (Ogilvie-Grant 1897; van Balen 1926; White & Bruce 1986; Sibley & Monroe 1990; Del Hoyo et al. 1994). Jones et al. (1995) added 'hill-forest' to this. Wallace (1869) called it 'forest of the interior' and Ripley (1960), for Bacan Island, described the habitat as 'evergreen rainforest' and 'subtropical wet moss forest' at a height of 750 - 1650 m. On the Western Papuan Island of Misool, though, two[6] male specimens were collected at altitudes of 100 and 300 m (Ripley 1960). Still, direct observations of the birds in their habitat are rare: Stresemann (1914a) encountered a small group in the forest of Hatu Sake (North Seram) at 1000 m and Heinrich (1956) collected the bird at 1500 m at Mount Sibela on Bacan Island. More recently the species was also observed on Seram both in coastal scrub (Bowler & Taylor (1989) and in disturbed primary forest close to cultivation at 230 m (Dekker et al. 1995).

We also observed several Moluccan megapodes away from their nesting grounds in coastal secondary forest and cultivated areas (gardens) in South Seram (Piru Bay, Amahai), North Seram (Wahai) and along the east and west coast of Haruku. Once even a bird was seen in the middle of a village. The question remains whether the birds use these lowland areas as their main habitat or as a transient between their nesting grounds and the mountain forests were they are supposed to occur.

The provenance of the birds that lay their eggs on Tanjung Maleo is not sufficiently known. Dekker (1991) and Dekker et al. (1995) argue that the total population that uses the area as a nesting ground is too large for Haruku, which has even no primary mountain forest. Therefore, the birds are expected to come from neighbouring Seram and Mount Salahutu on Northeast Ambon (Dekker et al. 1995; Jones et al. 1995). At Tanjung Maleo, the birds we saw flying in from the sea (see: chapter 4) do indeed indicate Seram and Ambon to be important source areas. There is, however, no proof.

Methods

In order to find out the origin and habitat of the Moluccan megapodes that use Tanjung Maleo as a nesting ground, a total of nine female birds were fitted with transmitters and immediately released on 11, 12 and 13 February 1996. Their whereabouts were monitored until 28 April 1996. The birds were caught in their burrow while, or just after, laying an egg and consequently were adult females. Bird and egg were weighed separately. Four birds got a transmitter fitted on the leg (tarsus) and five birds got the transmitter fitted on the back by means of a harness. The total weight of transmitter and attachment-kit was 15 g for the leg-type and 20 g for the harness-type (Table 26). Transmitter parts and battery were sealed in a waterproof PVC-tube. The nine transmitters and two universal transceivers (FT 290 R11, 150 MhZ) with two types of direction-sensitive antennas were obtained from IBN/DLO (Institute for Foresty and Nature Research), Wageningen, The Netherlands. To check the transceiver a test-transmitter was available. Each transmitter had its own programmed frequency and accompanying sound, hence the nine transmittered birds could be traced individually. Batteries were guaranteed to work for at least three months. The maximum distance between transmitter and transceiver should be 30 km, provided they were protected from extremely high temperatures and relative humidity. In the field however, at an average temperature of 30ºC and relative humidity of 85%, the maximum distance at which signals could be picked up by the transceiver, was 10 km in favourable circumstances (i.e. at night, clear weather, dry, plain terrain, open sea). Mountain forests appeared to be a

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[6] Although Ripley (1960, 1964) specifically mentioned two male specimens, our inventory of *Eulipoa* specimens in museum collections (see chapter 4, Table 8) revealed the presence of three male skins, all collected by Ripley on Misool in 1954: two in PMNH Newhaven (07341, 23-XI-1954; 073042, 19-XI-1954) and one in USNM Washington (518921, 19-XI-1954).

hindrance to receive signals. Even from an air - craft at an altitude of 700 m, the study area (Fig. 32A) could only be covered partly . The maximum period during which signals were received was 51 days for birds 1 and 9. Of the other transmittered birds, signals were received during a shorter period (T able 27). It is not known whether this is due to malfunctioning transmitters or the birds being out of reach.

To track the transmittered birds, one transceiver was permanently stationed at Tanjung Maleo and one was taken out to survey the entire study area which emcompassed Haruku, Pombo, Northeast Ambon, Saparua and the western, southwestern and southern part of Seram east to Amhahai (Fig. 32A). Tanjung Maleo was monitored every night to establish the period of time between visits of the individual females (the egg-laying interval).

The inland area of Haruku was monitored at least five times a week during daylight hours. This was done by motorbike and by foot (Mount Huruano was climbed on several occasions). On Northeast Ambon, Mount Salahutu was climbed twice, the rest of this area was covered by car and motorbike. A speedboat was used to monitor coastal South Seram and to track birds from the sea between Ambon, Seram and Haruku. Inland Seram was monitored by motorbike and car from the road that runs between Latu in the south and Kawa in the northwest. Entering this mountainous area was almost impossible. Therefore on 2 April a small aircraft was chartered to cover the traject Pattimura airport (Ambon) - Elpaputih Bay / Amahai (Seram). Figure 32A gives the total area covered by our surveys.

Tracking results

After being fitted with a transmitter and released, three birds left Tanjung Maleo within 30 minutes, two birds birds left after 1-2 hours and two birds stayed until dawn. Two birds kept within 1-2 km from Tanjung Maleo until the next

Table 26 Basic data on nine Moluccan megapodes *Eulipoa wallacei* (adult females) captured at the Tanjung Maleo nesting grounds and fitted with radio-transmitters (weights in g).

transmitter/ bird nr.	capture date & time	transmitter type	body weight	departure direction	notes
1	11 Febr 1996 (02.00 a.m.)	leg	477	SE	left Tanjung Maleo after 15 minutes
2	13 Febr 1996 (03.00 a.m.)	harness	526	SE	stayed at Tanjung Maleo till 16.00 p.m.
3	13 Febr 1996 (02.30 a.m.)	harness	527	ESE	left Tanjung Maleo after 30 minutes
4	11 Febr 1996 (02.20 a.m.)	leg	527	SE	stayed at Tanjung Maleo till 07.00 a.m.
5	12 Febr 1996 (01.30 a.m.)	leg	511	NE	stayed at Tanjung Maleo till 0.700 a.m.
6	12 Febr 1996 (02.00 a.m.)	leg	511	SE	stayed at Tanjung Maleo till 04.00 a.m.
7	13 Febr 1996 (03.30 a.m.)	harness	546	SSE	stayed 1-2 km SSE from Tanjung Maleo till 14 Febr, 02.00 a.m.
8	13 Febr 1996 (02.00 a.m.)	harness	500	NE	stayed at Tanjung Maleo till 03.15 a.m.
9	13 Febr 1996 (03.15 a.m.)	harness	536	SE	left Tanjung Maleo after 20 minutes

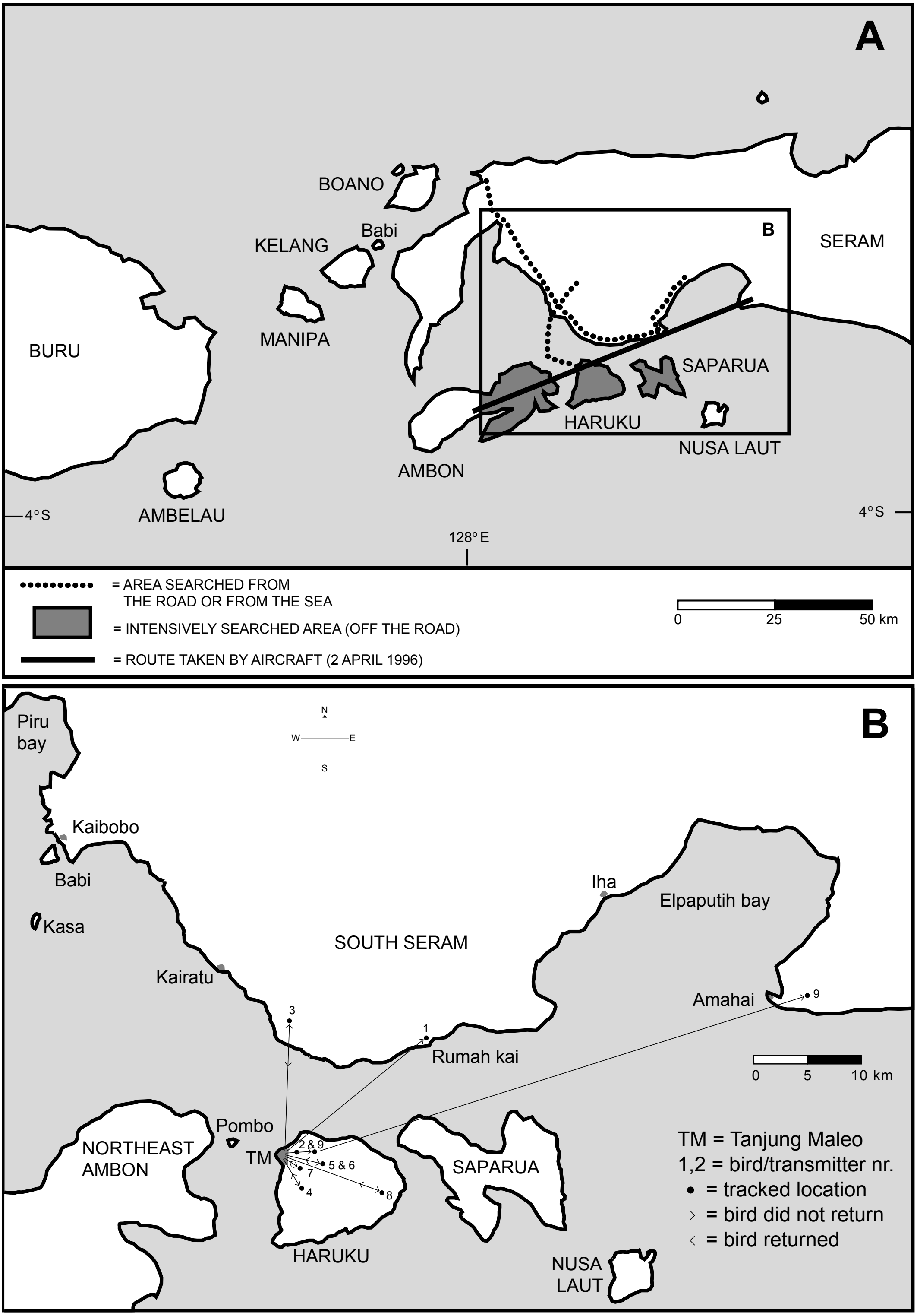


Figure 32 Buru and the Seram Island-group; **A** The area covered to trace nine radio-transmittered Moluccan megapodes; **B** tracking results (see also Table 27). [map graphics: Jaap van Leeuwen Design]

Table 27 Tracking results of nine adult female Moluccan megapodes *Eulipoa wallacei* fitted with radio-transmitters. (see Table 26)

bird number	transmitter-fitting date	returning date(s) at nesting ground	time-interval	tracked locations other than Tanjung Maleo	date(s)	distance from Tanjung Maleo
1	11 Febr	--	--	South Seram (Rumah Kai[1])	2 Apr	20 km
2	13 Febr	--	--	Central Haruku	13 Febr[2]	3-5 km
3	13 Febr	23 Febr 10 March	10 days 16 days	South Seram (12 km E of Kairatu[3])	4-23 March	15-20 km
4	11 Febr	26 Febr	15 days	Central Haruku	11-13 Febr, 23 Febr	4-6 km
5	12 Febr	--	--	Central Haruku	13 Febr	2-4 km
6	12 Febr	26 Febr	14 days	Central Haruku	13-14 Febr	3-5 km
7	13 Febr	25 Febr	12 days	Central Haruku	14 Febr[5]	1-2 km
8	13 Febr	24 Febr 7 March 19 March	11 days 12 days 12 days	Central Haruku	13 Feb - 25 Mar[4]	4-10 km
9	13 Febr	--	--	Central Haruku South Seram (Amahai[1])	13 Febr[2] 2 Apr	3-5 km 50 km

[1] tracked from an aircraft at 2000 ft.
[2] till 16.00 p.m.
[3] tracked from the beach north of Tanjung Maleo and from Pombo Island
[4] almost daily during that period
[5] till 02.00 a.m.

evening/night (Table 26). The next two days, four birds were tracked down on the high plateau of Haruku between altitudes of 100 and 300 m. Of these four birds one was never found again, two returned to Tanjung Maleo on 25 and 26 February and one bird (number 9) was tracked down on 2 April near Amahai on South Seram at a distance of 50 km from Tanjung Maleo (Table 27, Fig. 32B). The signals of bird 4 and 8 were heard for a longer period. Number 4 was present on the Haruku plateau from 11 till 13 February and on the 23rd of that month; on the 26th she laid an egg on Tanjung Maleo. Number 8 was constantly present on the Haruku plateau between 13 February and 25 March, and returned three times in that period to Tanjung Maleo for egg-laying purposes. Bird number 3 appeared to have left for Seram. She was tracked down in the hills east of Kairatu and her signal could even be heard almost contantly between 4 and 23 March from the beach north of Kailolo and from Pombo island. She returned twice (23 February and 10 March) to Tanjung Maleo. The distance covered was 15-20 km. One bird (number 1) of which the signal was only heard for 15 minutes after she was released, was found in the hills near Rumah Kai on South Seram on 2 April. She never returned to Tanjung Maleo during the period she was monitored (Table 27, Fig. 32B).

Inland habitat

Of the nine birds fitted with a transmitter, six lingered for a shorter or longer period on the high plateau of Haruku. Bird 9 used it as a transient area on her way to Seram. Probably for birds 4 and 6, and certainly for bird 8, this area forms a permanent inland habitat. The plateau rises straight up from the sea to a height of 100 m. It features hills of mostly 200 - 500 m altitude. The highest point is Mount Huruanu, which reaches 500 m. A number of rivers runs from southern, western and northern directions into the sea. The area consists of tertiary (Miocene) formations with mountain ridges of limestone and coral (Riedel 1886). The plateau is mainly overgrown with neglected plantations. It is wild parkland with age-old trees like the 'kenari' *Canarium commune* and 'durian' *Durio zibethinus* which serve as shadow trees for coconut-palm *Cocos nucifera*, nutmeg *Myristica fragrans*, cloves *Eugenia aromatica* and in the lower areas and along the rivers banana *Musa* sp. and sago palm *Metroxylon* sp. These plantations have been very badly maintained during the past few years, which has created a thick shrub layer consisting of grasses, ferns and seedlings of plantation trees. The vegetation is lush and the soil very humid: it houses a rich fauna both on the forest floor and in the soil. This apparently plentiful food supply in the hills of Central Haruku could be the incentive for the birds, after having laid their eggs and having an empty stomach (Toxopeus 1922; Siebers 1930), to forage there for a while before they cross to Seram. Still, the area must be the inland habitat for a good part of the Tanjung Maleo breeding-population.

The secondary forest with limestone formations of Central Haruku as described above, is similar to the coastal hill-vegetation of South Seram where we found three transmittered birds. Near the village of Latu, South Seram, which we visited on 24-26 February 1996, a local professional birdcatcher knew *Eulipoa* well from the inland habitat (PLATE VIII) and described how small groups run through the dense vegetation and even claimed to have observed courtship behaviour. His description is similar to that of the local egg collectors of Tanjung Maleo, regarding their observations of small *Eulipoa* groups on the Haruku plateau and also resembles the behaviour of the groups we observed after darks nights in the forest that surround the Tanjung Maleo nesting grounds (see: chapter 4). Stresemann (1914a) encountered similar behaviour in the forest of Hatu Saku, a mountain pass at 1000 m in North Seram.

In conclusion, the fact that *Eulipoa wallacei* regulary occurs in degraded secondary forest at rather low altitudes and even in neglected cultivated areas, may indicate that the species has adapted to the loss of primary mountain-forest habitats where they were encountered by the early explorers. If this is the case throughout its range, the chances of survival of the species might increase considerably.

Egg-laying interval

Of the nine transmittered birds, five (55%) returned to the nesting grounds, supposedly for the purpose of egg laying. Of these five birds, three returned once, one returned twice, and one returned three times, so the total number of return-cases was eight. From these data (Table 27) the average egg-laying interval (i.e. the period of time between two consecutive visits to the nesting ground) was established at 13 days (range 10-16 days, calculated average is 12.75, for convenience put at 13). It should be noted though that the birds were transmittered in February, about two months before the end of the dry season. As the number of eggs collected on Tanjung Maleo cleary increases from the end of the rainy season (in August/September) onwards and reaches a maximum in the dry season, after which the numbers decrease to a minumum in July (Heij 1995a, see also: chapter 9, Fig. 34), some of the birds probably had laid their last egg of the season on the night they were fitted with a transmitter and could be expectednot to return before August/September. This explains the absence on the nesting grounds of birds 1 and 9 that were eventually tracked down in Seram. The lack of observations of birds 2 and 5 (which disappeared after 1-2 days) might be due to a malfunctioning transmitter.

The average egg-laying interval of 13 days established by radio-telemetry applies to birds visiting the nesting grounds at the end of the dry season (February-March). The question remains whether individual birds lay at constant intervals throughout the year, or concentrate their egg-laying activities in the dry season. The latter seems to be the case as peak numbers of eggs are found in the dry season (Heij 1995a): the number of eggs laid during the rainy season is only about one third (31.6%) of the total egg production (see: chapter 9, Table 28). The fact that still quite a number of eggs are laid during the rainy season is probably caused by individual birds starting their laying-period already in the rainy season and birds that start in the course of the dry season and continue into the rainy season. In case birds do spread their laying activities over the year (both seasons), the calculated interval during the rainy season (based on the egg-production ratio of 1/3 rainy season, 2/3 dry season: 100/68.4 x 12.75) is expected to be about 19 days. We do not regard this possibility as likely.

Data on the egg-laying interval of other megapode species are rare. Jones et al. (1995) give 2-9 days for the Australian brush-turkey *Alectura lathami* and 13 for the orange-footed megapode *Megapodius reinwardt*, both mound-breeding species. For burrow-nesters there is no information on the interval, but their egg-laying season is said to start after the end of the rainy season when the substrates have warmed.

9 NUMBERS: EGGS, FLEDGLINGS AND ADULTS

During the periods 1 June 1994 - 30 June 1995 and 1 February - 30 April 1996 the numbers of harvested eggs and fledged chicks were established by the author(s) through direct counts carried out in the field. For the preceding period (dating back to the 1987/1988 harvest year) the egg numbers were kindly supplied by the former lease holders who each had kept an accurate administration (Fig. 3). As the lease holders only had registered the numbers of eggs available for sale, we had to add approximately five eggs to the daily numbers exceeding 30 and approximately ten eggs to the daily numbers exceeding 100. This addition relates to the remuneration (in eggs) received by the collectors. Each lease holder, however, had his own key to calculate the actual number of collected eggs. These corrected egg numbers apply to the harvest years 1987/1988, 1988/1989, 1989/1990, 1991/1992, 1992/1993, 1993/1994 and the first two months of the 1994/1995 harvest year. With the exception of the period 1 February - 30April 1996, the data of the harvest years 1995/1996 (after 30 June 1995) and 1996/1997 were obtained through monthly correspondence with the lease holder(s) and needed no corrections. Appendices 1 and 2 list the basic data on egg and fledgling numbers.

Numbers of harvested eggs

Figure 33 shows the numbers of eggs harvested at Tanjung Maleo from 1987/1988 till 1996/1997. In the course of the years, an increase is clearly visible: from 1987/1988 till 1994/1995 the harvest almost doubled, whereas afterwards the numbers stabilized close to 37000 - 38000 eggs. We expect that now (1996/1997) the maximum harvest is reached: the capacity of the birds, the area and the collectors has come to an end. The increasing numbers of harvested eggs are, however, not the result of more birds visiting Tanjung Maleo for egg-laying, but are caused by increasing and more intensive egg-collecting activities. The higher lease price (see: chapter 3, Table 4) and the increasing demand for eggs, forced the lease holder to act like any other entrepreneur would do: hire more personnel and intensify the activities. As many eggs as possible are collected. Local egg-collectors and elderly villagers reported that 'in the past' (probably a few decades ago), many more egg-laying birds visited the Tanjung Maleo nesting grounds.

Table 28 Numbers of harvested *Eulipoa* eggs at the Tanjung Maleo nesting grounds in the harvest years 1987/1988 - 1996/1997, divided in rainy season (April - September) and dry season (October - March). A harvest year runs from 1 April till 31 March. Based on data listed in Appendix 1.

	number of harvested eggs			
harvest year	total	rainy season	dry season	% dry season
1987/1988	18260	6085	12175	66.7
1988/1989	27978	9655	18323	65.5
1989/1990	22934	7898	15036	65.6
1990/1991	no data			
1991/1992	27648	8796	18852	68.2
1992/1993	26886	9981	16905	62.9
1993/1994	32722	11185	21537	65.8
1994/1995	36263	11253	25010	69.0
1995/1996	36618	10095	26523	72.4
1996/1997	37712	9425	28287	75.0
total/average	267021	84373	182648	68.4

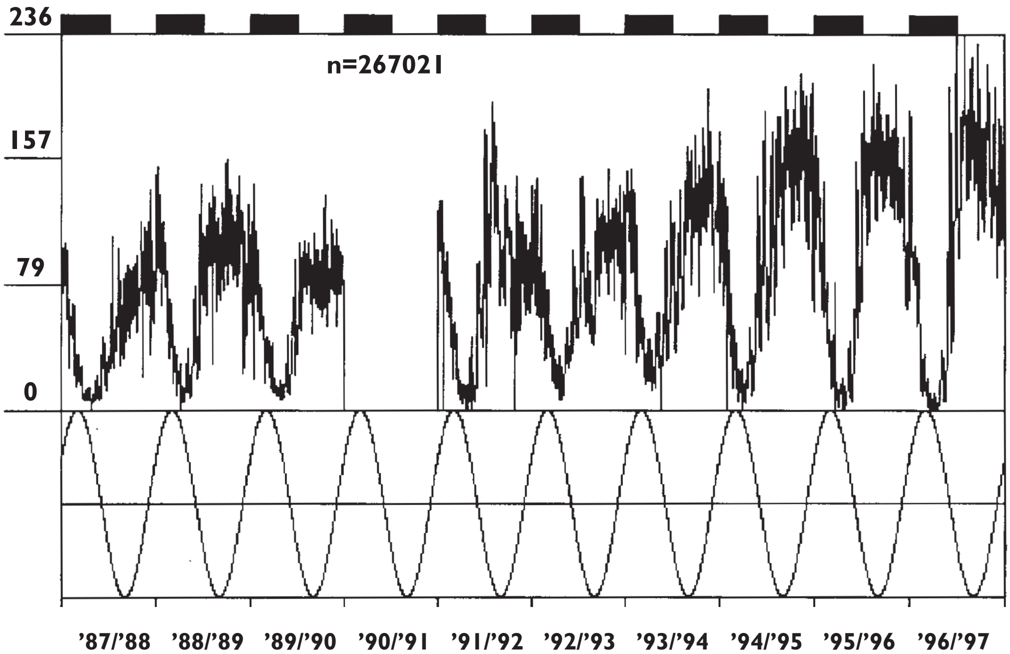


Figure 33 Numbers of collected eggs of *Eulipoa wallacei* at Tanjung Maleo in the course of the period 1 April 1987 - 31 March 1997 (see Table 28 and Appendix 1) together with course of the solar cycle (sinusoid line) and indications of the rainy season (black bars). Data from the 1990/1991 harvest year are lacking.

Then, apparently with little effort, daily numbers of harvested eggs regulary reached 300 or more, while nowadays numbers exceeding 200 per day are seldomly collected (see: Table 30). The effort is, however, much greater.

Table 28 lists the total numbers of collected eggs per harvest year and separates the numbers found in the rainy season and the dry season. On average 68,4% (range 62.9-75.0%) of the eggs are found during the dry season (October - March), meaning a dry : rainy ratio of about 2:1. This seasonal pattern is not biased by more or less collecting activities (pers. observations), but clearly caused by low numbers of birds visiting the area during the rainy season. To some extent, this pattern is known for other burrow-nesting megapodes such as *Megapodius eremita* and *Macrocephalon maleo*, and is generally believed to be an adaptation to the temperature of the substrate (Jones et al. 1995). For *Macrocephalon maleo*, Dekker (1988) found that coastal (sandy) nesting sites were mainly used during the dry season, whereas inland geothermal incubation sites were used all year round. The sun, regulary absent during the rainy season, apparently could not heat up the wet soil of the coastal nesting grounds. Temperature readings in nesting burrows at Tanjung Maleo (see: chapter 5, Table 11) did indeed reveal lower temperatures during the rainy season. At greater depths (where eggs are laid), differences between both seasons were, however, slight and temperatures remained at values suitable for year-round incubation.

Despite the clear seasonal pattern, eggs are laid all the year round. In nine years (3285 days) only 14 days did not yield a single egg (Table 29). From the basic data on the egg-harvest listed per day and month in Appendix 1 and the graphs computed from that data-base (Fig. 34), it appears that the lowest numbers of eggs are found in the midst of the rainy season, in the months of June, July and August. The month of July features, without exception, the mininum egg-numbers: on average 1.7% (range 0.4-2.5%) of the total harvest (Table 29). As Jones et al. (1995) already

Table 29 Monthly distribution of the lowest numbers of harvested *Eulipoa* eggs at Tanjung Maleo per harvest year. Data from Appendix 1. See also Figure 34.

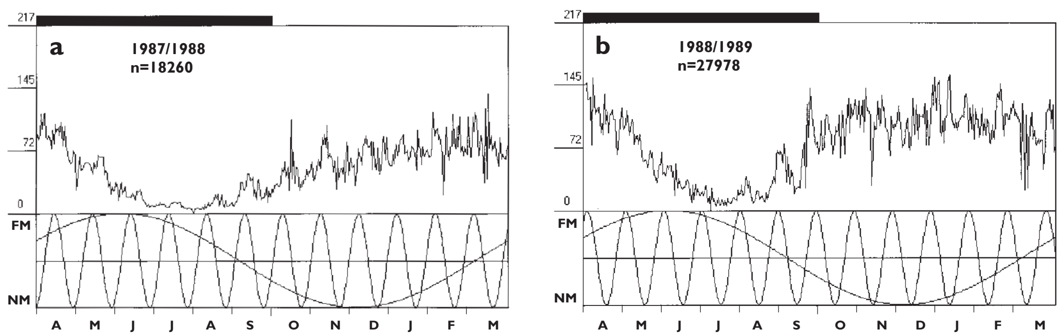
harvest year	lowest numbers in (minimum underlined)	% in July	no eggs on
1987/1988	June, July, August	1.5	July 31
1988/1989	June, July, August	1.5	July 8
1989/1990	June, July, August	1.9	--
1990/1991	no data		
1991/1992	June, July, August	1.1	August 1 & 15; January 31*
1992/1993	July, August	2.5	--
1993/1994	June,July, August	2.4	August 20
1994/1995	June, July	1.7	May 5*, June 28
1995/1996	June, July, August	0.7	June 22; July 23 & 28
1996/1997	June, July	0.4	June 30, July 8 & 18
	average percentage of eggs in July:	1.7	days without eggs 14 (0.4%)

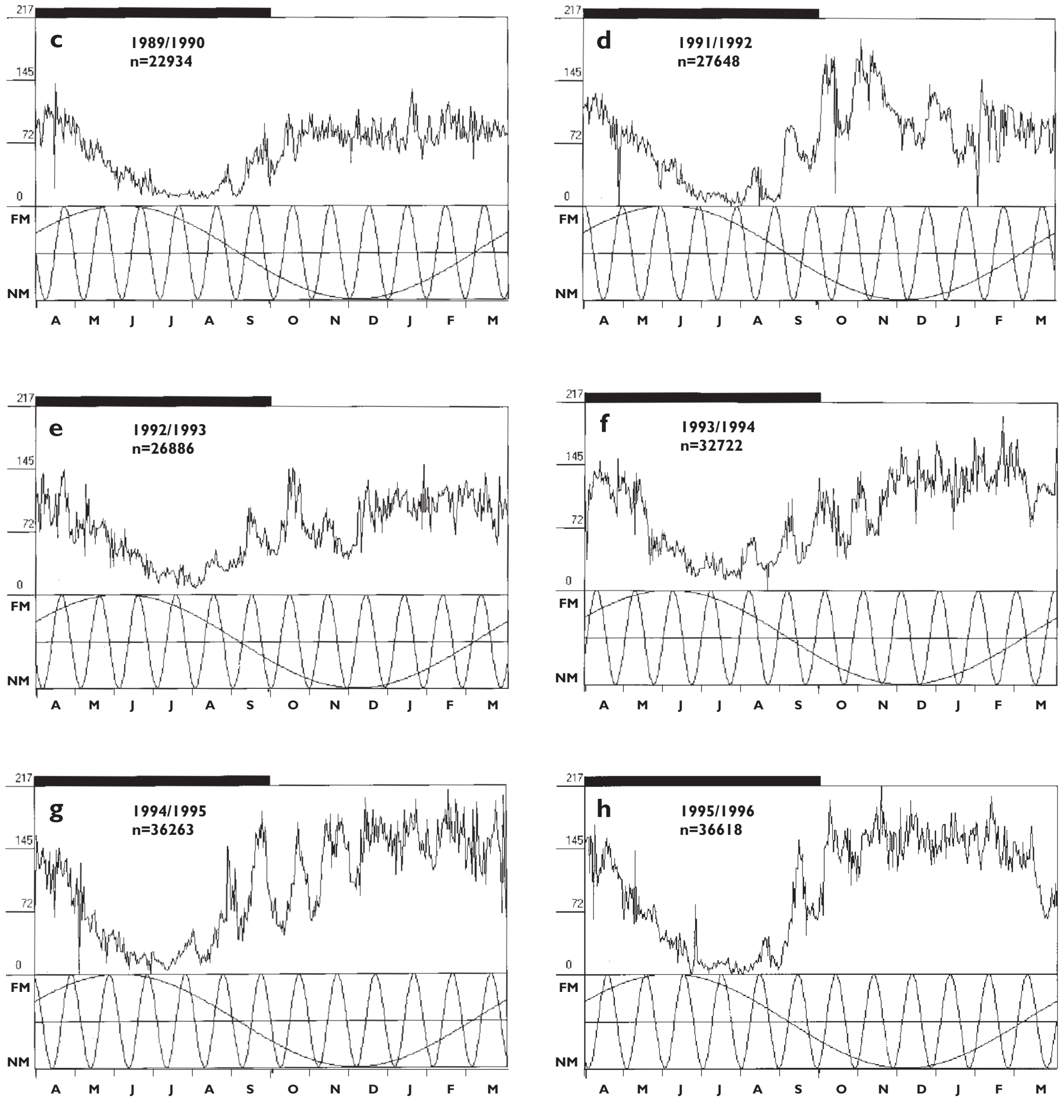
* neighbouring days yielded large numbers, there were probably no collecting activities due to social events.

emphasized for megapodes in general, it should be noted that prolonged patterns of egg laying do not mean that particular individuals produce eggs all the year round. Rather, these patterns result from the overlap of many birds using the nesting ground for short, irregular periods.

Still, most egg production at Tanjung Maleo (68.4%) is concentrated in the dry season. Fluctuations in the numbers of harvested egg are visible in Figure 34 and the occurrence of peak numbers is summarized in Table 30. Contrary to the lowest numbers (each year in July), the highest monthly totals of eggs are found in different months each year, but were mostly recorded in November (twice), December (twice) and January (three times), all in the midst of the dry season. March and April, bordering the change of seasons, each featured the highest monthly totals once. The average percentage of the total harvest found in the peak month is 13.2 and is, with a range of 12.2-15.1, remarkably constant in each year (Table 30). The maximum number of eggs collected during one day is also given in Table 30. Those numbers range from 113 in 1989/1990 to 236 in 1996/1997 and were recorded in four different dry season months (November, January, February, March).

The inclusion of the lunar cycle (29.53 days according to the synodic method [Bodifée 1983]) in Figure 34 clearly shows that throughout the





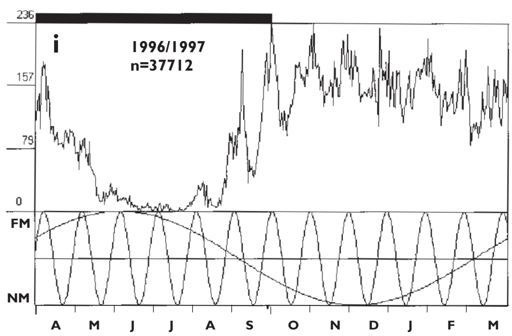


Figure 34 Numbers of collected eggs of *Eulipoa wallacei* in the course of nine separate harvest years (1 April - 31 March), together with the solar cycle (long sinusoid line), the lunar cycle (short sinusoid line; FM = full moon, NM = new moon) and an indication of the rainy season (black bar).

Table 30 Monthly distribution of the highest numbers of harvested *Eulipoa* eggs at Tanjung Maleo per harvest year. Data from Appendix 1. See also Figure 34.

harvest year	highest numbers in (peak-month underlined)	% in peak-month	maximum number of eggs (date)
1987/1988	Apr, Jan, Feb, Mar	14.2	138 (16 March)
1988/1989	Apr, Dec, Jan	12.2	156 (9 January)
1989/1990	Apr, Nov, Jan, Mar	12.5	113 (3 March)
1990/1991	no data		
1991/1992	Apr, Oct, Nov	15.1	193 (2 November)
1992/1993	Apr, Jan, Mar	12.1	150 (26 January)
1993/1994	Dec, Jan, Feb	12.8	201 (18 February)
1994/1995	Dec, Jan, Feb, Mar	13.4	211 (15 February)
1995/1996	Nov, Dec, Jan	13.4	217 (16 November)
1996/1997	Oct, Nov, Dec, Mar	13.6	236 (2 November)
average percentage of eggs in peak-month:		13.2	

year, peak numbers are found during full-moon periods (see also: Heij 1995a). To explain this phenomenon we can only speculate. Egg maturation might coincide with the lunar cycle, causing most birds to have an egg ready to be laid at full moon. The egg-laying interval (13 days) is, however, much shorter than the lunar cycle (see: chapter 8). A full moon in combination with a cloudless sky causes the nesting grounds to be well lit and might trigger birds to leave their inland habitat for egg-laying. Observations in the field (see: chapter 4) indeed revealed that during dark nights, birds were very reluctant to enter the nesting ground and hesitated to start digging burrows. Under such circumstances most digging and laying was done at daybreak. It should be noted that a full moon does not guarantee the nesting grounds to be well lit: a clouded sky still causes a pitch-dark night. This matter, therefore, needs to be studied more into detail.

Small-scale fluctuations in the number of harvested eggs are hard to explain. Direct observations in the field during 1994/1995, however, revealed that social events such as the nightly tv-broadcasting of the 1994 soccer worldchampionship, the annual muslim fasting (ramadan) and the absence for longer periods of the lease holder, causes less intensive ('lazy') or no egg-collecting activities and, as a consequence, a lower or no harvest, although the birds did lay eggs. We strongly believe that these circumstances are of great importance to the survival of the *Eulipoa* population: they account for the rather sudden peaks in the number of recorded fledglings (see below). Besides, the regular occurrence of fledglings and the finds of hard-set eggs proves that – despite their serious efforts – the collectors are not able to collect all eggs. A certain percentage (13.7 in 1994/1995, see below) is simply not found and has a chance to hatch.

Numbers of fledglings

The numbers of fledglings were established by counting the little round craters in the soil (exit-pits) from where they have emerged (see: chapter 7, Fig. 30). Figures 35, 36 and 37 show the fluctuations in the numbers in the course of three 'fledgling years' in the period 1 July 1994-31 March 1997. To ease comparison with data on the egg-numbers (Fig. 34), the 'fledgling year' runs from 1 July till 30 June. This three month shift in comparison with the 'harvest year' is necessary as the duration of the incubation period is about 2-3 months (see: chapter 6, Table 21). The total number of hatchlings that results from the eggs that have been laid in the harvest year (1 April - 31 March) is therefore expected to emerge from the soil in the period

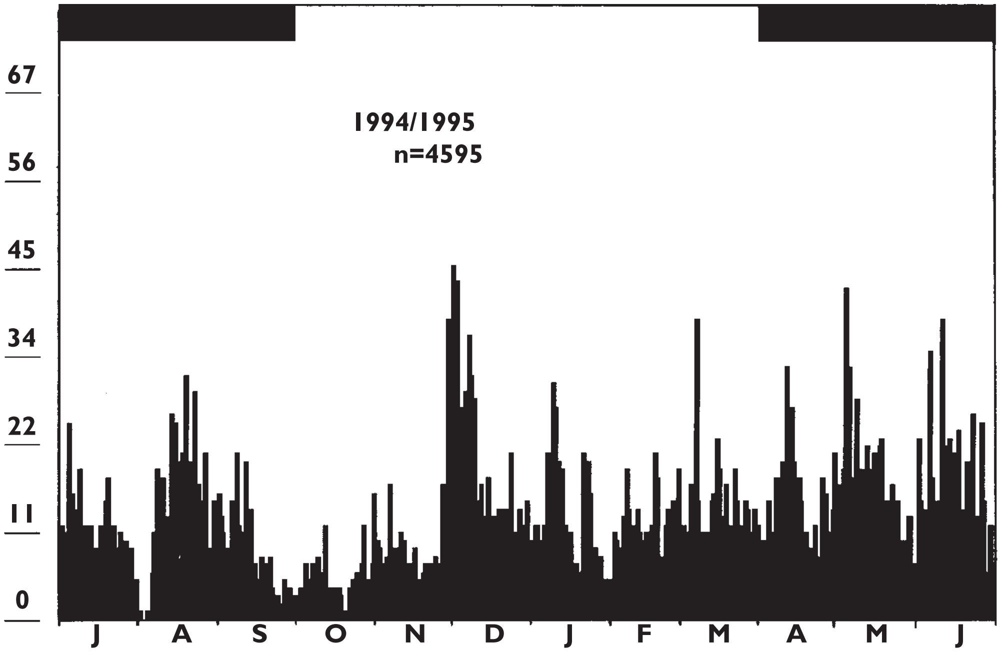


Figure 35 Numbers of fledged chicks of *Eulipoa wallacei* established by the presence of 'exit-pits' (see Fig. 30) at the Tanjung Maleo nesting grounds in the course of the period 1 July 1994 - 30 June 1995 (horizontal black bars indicate the rainy season).

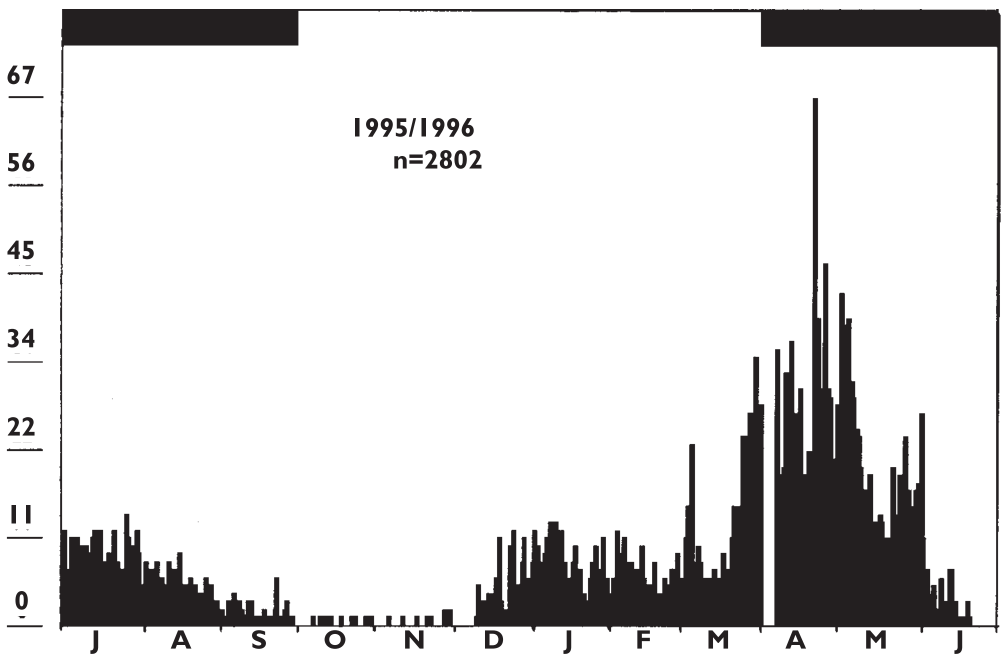


Figure 36 Numbers of fledged chicks of *Eulipoa wallacei* established by the presence of 'exit-pits' (see Fig. 30) at the Tanjung Maleo nesting grounds in the course of the period 1 July 1995 - 30 June 1996 (horizontal black bars indicate the rainy season).

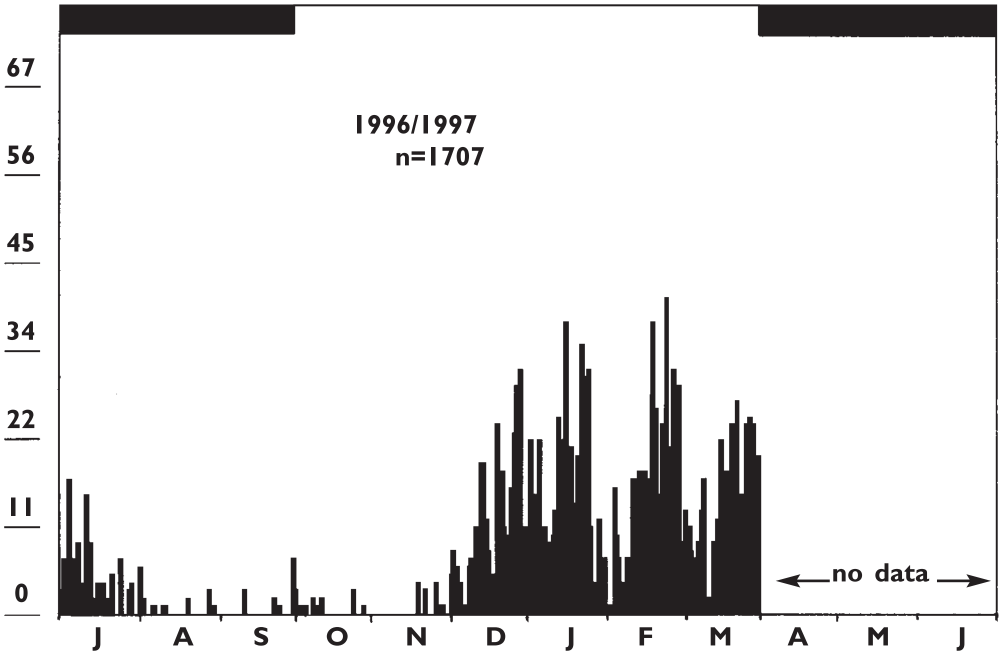


Figure 37 Numbers of fledged chicks of *Eulipoa wallacei* established by the presence of 'exit-pits' (see Fig. 30) at the Tanjung Maleo nesting grounds in the course of the period 1 July 1996 - 31 March 1997; data from April-June were not yet available (horizontal black bars indicate the rainy season).

1 July - 30 June (the fledgling year). When analysed on a monthly basis, we see the lowest numbers of fledglings (0.4-3.1 % of the yearly total) in the period September -November (Table 31). This pattern clearly reflects the lowest egg-production in the period June-August (*cf.* Table 29), being about 2-3 months earlier.

As with the peaks in egg production, the occurrence of peak numbers of fledglings does not show a well-marked pattern. Although, in 1994/1995, the maximum fledgling numbers in December 1994 (Table 32, Fig. 35) do mark the rather sudden dip in the egg-harvest during the first half of October 1994 (Fig. 34g). Here, we probably see the influcence of low egg-collecting activities. The high fledgling numbers in May-June 1995 (Fig. 35, Table 32) reflect the high egg-production during January-March (Table 30, Fig. 34g), when the chance of eggs being overlooked by the collectors is greater than in periods when egg numbers are low. In 1995/1996 the highest egg-production was recorded in November-January (Table 30, Fig. 34h) and, likewise, the numbers of fledglings

Table 31 Monthly distribution of the lowest numbers of *Eulipoa* fledglings at Tanjung Maleo per fledgling year. Data from Appendix 2. See also Figs. 35, 36 and 37.

fledgling year	lowest numbers in (minimum underlined)	% in minimum month(s)
1994/1995	September, <u>October</u>, November	3.1
1995/1996	September, <u>October</u>, <u>November</u>[1]	0.4
1996/1997	<u>September</u>, <u>October</u>, <u>November</u>[2]	0.4

[1] both underlined months yielded 10 fledlings each.

[2] underlined months yielded 13,14 and 13 fledglings respectively.

Table 32 Monthly distribution of the highest numbers of *Eulipoa* fledglings at Tanjung Maleo per fledgling year. Data from Appendix 2. See also Figs. 35, 36 and 37.

fledgling year	highest numbers in (peak month underlined)	% in peak month	maximum number of fledglings (date)
1994/1995	<u>December</u>, May, June	12.8	45 (2 December)
1995/1996	March, <u>April</u>, May	24.9	67 (21 April)
1996/1997	no complete data		

peaked in March-May (Fig. 36). The 67 hatchlings that emerged from the soil on 21 April 1996 form a distinct peak (Fig. 36), which should indicate low egg-collecting activities in early February. Figure 34h, indeed, shows relatively low harvest results during that period (see also Appendix 2). The fledgling numbers in 1996/1997 (Fig. 37) are not analysed as the data of the period April-June 1997 were not available at the moment of update and final editing of this paper.

Total egg production

The availability of both the numbers of collected eggs and the numbers of fledged chicks, enabled us to calculate the total egg production for the Tanjung Maleo nesting grounds. To these two parameters we add some corrections. (1) We estimate to have missed 10% of the fledglings (see: chapter 7) and add this percentage to the fledgling numbers. (2) We estimate the natural losses of eggs due to infertility and predators other than humans to be about 5 per week. (3) Additional losses of eggs and/or hatchlings due to collecting-activities are about 9 per week. The 1994/1995 harvest year is used for this calculation as the data were obtained by direct observations in the field. Table 33 lists the results. A total of 42039 eggs was produced. Of this total, 86.3% was collected, 1.7% was lost due to predation or damaged otherwise, and 12% resulted in fledged chicks.

Total egg-laying population

Knowing the total egg production of the Tanjung Maleo nesting grounds, the next step is to establish the number of egg-laying females involved. Basic to this are (1) the number of eggs produced per female (the 'clutch size') in a certain period, generally called the 'breeding season' (but in case of megapodes better called 'laying season'), and (2) the egg-laying interval.

As noted earlier, we have established that most eggs (68.4%) are laid in the dry season, which, for that reason, we may call the laying season. Nevertheless, a considerable percentage of the eggs (31.6) is laid during the rainy season which is of about the same length as the dry season. We can therefore state that at Tanjung Maleo, the moment a bird starts her laying season differs individually and does not necessarily coincide with the end of the rainy season (see: chapter 8). With a range of 10 to 16 days (average 13 days) the egg-laying interval appeared to be rather constant (Table 27).

For *Eulipoa wallacei* and most other (burrow-nesting) megapodes, the clutch size is not known or poorly understood (Jones et al. 1995). Dekker (1990) estimated the egg production of the burrow-nesting *Macrocephalon maleo* at 8-12 per season, and Jones et al. (1995) listed 15-24 eggs per year for the mound-breeding *Leipoa ocellata*. For *Megapodius reinwardt*, also a mound-breeder, Del Hoyo et al. (1994) mentioned a clutch size of 12-13 eggs.

We were not able to establish the average egg production of an individual *Eulipoa* through direct field observations. However, the study of the ovaries of four *Eulipoa* specimens that collided with electricity wires at Tanjung Maleo in April/May 1995, revealed the following information: in addition to a fully matured egg (ready to be laid), the ovaries each contained an average of 23 oocytes smaller than 1 mm in dia-

Table 33 A calculation of the total egg-production of *Eulipoa wallacei* at the Tanjung Maleo nesting grounds in the 1994/1995 harvest year (1 April 1994 - 31 March 1995).

collected eggs in 1994/1995 harvest year		36263	(86.3%)
fledged chicks recorded during 1 July 1994 - 30 June 1995	4595		
fledged chicks not noticed (10%)	459		
total offspring	5054	5054	(12.0%)
natural losses (estimated average 5 per week)*		260	(0.6%)
reburied hard-set eggs** (1 July 1994 - 30 June 1995)	202		
losses of hard-set eggs/hatchlings (average 5 per week)	260		
extra losses through collecting activities	462	462	(1.1%)
total egg production in 1994/1995 harvest year		42039	(100%)

* through infertility, predators other than humans etc; these eggs do not hatch and are not found either.

** we reburied undamaged hard-set eggs (75.6% hatched); normally they are destroyed by the collectors; therefore they are listed here as losses.

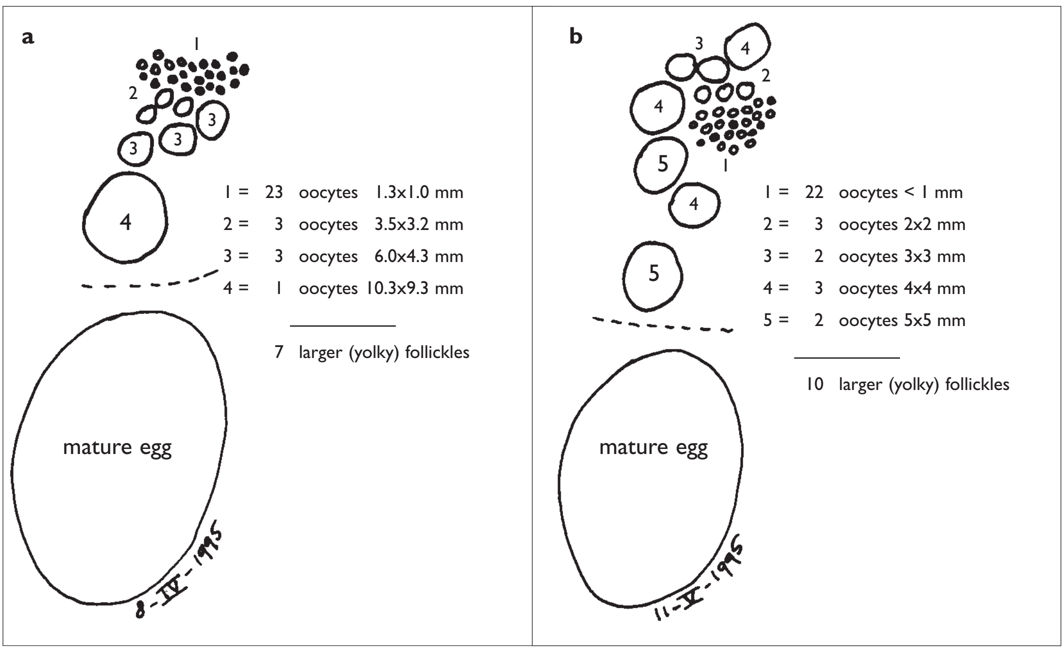


Figure 38 The contents of two ovaries of *Eulipoa wallacei* found dead at Tanjung Maleo: **a** from specimen NMR 999700283 (finding date 8 April 1995); **b** from specimen NMR 999700265 (finding date 11 May 1995). [illustration: C.J. Heij; not to scale]

meter and an average of 9 larger oocytes (yolky follicles) having diameters ranging between 2 and 10 mm (Fig. 38). Assuming that the mature egg was the last of a 'clutch' laid in the course of the preceding months (the rainy season starts in April/May), we expect the larger oocytes to develop further during the next dry season.

Based on these observations and the data on clutch sizes of other megapodes as listed above, we expect the clutch size of *Eulipoa wallacei* to be at least 10 eggs per laying season. The maximum probably does not exceed 12 eggs. With a total production of 42039 eggs (Table 33) the total number of egg-laying females at Tanjung Maleo is about 4200. With the average egg-laying interval of 12.75 days and assuming that eggs are laid at more or less constant intervals during a certain period (mostly coinciding with the dry season), we expect a complete 'clutch' to be laid during an average period of 127.5 days or about four months and one week (range 100-160 days). This assumption is, however, rather speculative as the individual egg-production ('clutch size') of *Eulipoa* is not exactly known.

Recruitment and survival

Based on the data of the 1994/1995 harvest year (Table 33), each egg-laying bird, on average, produces only about one fledgling per year. As we expect the percentage of fledglings reaching sexual maturity to be very low, recruitment, in the end, will be minimal. The fact that, despite the continuous high human pressure on hatching-success, still large numbers of *Eulipoa* visit Tanjung Maleo, is miraculous. We believe that the few individuals that manage to become adult, must have a high life expectancy. Otherwise the breeding population of the Tanjung Maleo nesting grounds should have become extinct long time ago. The question is now, how long the species can sustain the ongoing and intensified exploitation of its eggs.