Temporal and spatial patterns of laying in the Moluccan megapode *Eulipoa wallacei* (G.R. Gray)

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The Moluccan megapode *Eulipoa wallacei* (G.R. Gray, 1860) lays its eggs at night in the sand at communal nesting beaches. The majority of the world's Moluccan megapode population rely on only two nesting grounds on the islands of Halmahera and Haruku, Indonesia. An understanding of the ecological characteristics of these breeding sites is thus important in terms of conservation. Studies of the largest of the two nesting grounds in Halmahera have shown specific temporal and spatial patterns of egg laying. In this paper I discuss the adaptive significance and conservation implications of these laying patterns.

Introduction

The Moluccan megapode *Eulipoa wallacei* (G.R. Gray, 1860) is one of the most poorly known megapodes. It is a restricted range species endemic to the northern and central Moluccas, Indonesia (Dekker & McGowan, 1995). It has been recorded in several Endemic Bird Areas (EBA's), including Seram, Buru and Halmahera. The Moluccan megapode is considered to be the most endangered species of megapode. It is listed by the International Union for the Conservation of Nature (Dekker & McGowan, 1995) as a top priority for research during 1995 - 1999. The Moluccan megapode is a so-called burrow-nester that buries its eggs at night in the sand at sun-exposed beaches. This decade two large nesting beaches have been rediscovered. These two sites are thought to support over half of the world's Moluccan megapode population. At both sites eggs are collected by the local people for consumption. The nesting ground on Haruku has received attention from several researchers (e.g. Dekker, 1991; Dekker et al. 1995; Argeloo & Dekker, 1996; Heij et al. 1997). However, the site on Halmahera has not previously been studied.

In terms of conservation, research into the ecology of Moluccan megapode nesting sites will provide vital clues as to the future management and preservation of this endangered species. On Haruku and Halmahera, Moluccan megapode egg harvesting is strictly controlled by traditional laws. This at present appears to be sustainable (Dekker, 1991). However, changes in tradition have led to uncontrolled harvesting of megapode eggs elsewhere in Indonesia (Dekker, 1991; Argeloo & Dekker, 1996). Therefore, the possibility of a breakdown in traditional management constitutes a serious threat to the survival of these populations. This study of the Moluccan megapode population at the Halmahera nesting ground thus provides new insights into the ecology of this critically endangered species.

Study site

The study site was the nesting ground of the Moluccan megapode near Galela, Halmahera. The nesting site is a 9.8 ha area of black volcanic sand on the beach of Tiabo in the village of Simau, Kecamatan Galela. The nesting beach is essentially an island sand bank flanked by two rivers. The nesting site is 2 km long and stretches from the high tide line of the beach to 100 m inland. The vegetation directly behind the nesting ground is a mixture of grassland, scrub and coconut plantation. Behind the coconut plantation is 150 ha of mangrove forest. The majority of the beach, coconut plantation and mangrove is owned by a local family.

Methods

Vegetation surveys

Thirteen 100 × 100 m quadrats were marked out across the nesting ground along the high tide line. Each quadrat was split into nine equal patches. The predominant vegetation type found in each 5 m^2 was noted in each patch and the percentage vegetation for each patch was established. The percentage of each vegetation type was calculated for each of the 13 quadrats.

Egg collection data

Each day at 6 a.m. the egg collectors working on Pantai Tiabo were followed and the position and depth of each egg found was noted. Each egg was numbered and subsequently weighed using a 200 g spring balance and measured length and breadth ways with callipers. The total number of eggs found each day was noted. The number of eggs found in each patch was calculated and tabulated against the percentage vegetation found in each patch.

Temperature measurements

Nine 1.5 m × 10 cm bamboo tubes were planted at 30 m intervals in a square into the centre of the nesting ground. The bottom of each tube was 1 metre below ground, with 50 cm of tube above the ground. A volcanic stone was placed on the open top of each tube to prevent air flow. At four hourly intervals between 8am and 4am a soil thermometer was lowered to the bottom of each tube, so that it sat in the soil 1 metre below ground. Another thermometer was tied to the top of each tube, out of direct sunlight. Both thermometers were left for three minutes to equilibrate, and temperature above and below ground noted. Temperatures were taken at each of the nine replicate tubes at each time point. Each set of data thus took 45 minutes to collect (e.g. tube 1= 8 a.m.; tube 9 = 8.40 a.m.). Four further tubes were planted in quadrat 7, one at each of the following depths: 30 cm, 50 cm, 70 cm and 90 cm. Temperatures were taken as described above. To ensure that the temperature at the bottom of the bamboo tubes were representative of actual soil temperature a pilot study was carried out. One metre deep holes were excavated quickly using a spade and temperatures taken 5 cm into the soil. These measurements were compared with those at the bottom of tubes, and were found to be the same.

Soil composition

It was asserted by one of the egg collectors that the Moluccan megapode prefers to lay its eggs in new sand near to the sea. To test whether the sand in different sites was intrinsically different we compared the weight of stones and vegetation in 10 × 10 litre samples of sand from current nesting sites near to the sea to 10 × 10 litre samples of sand from old or unused nesting sites further inland.

Data analysis

A peak in the number of eggs collected around full moon was noticed. To test whether the egg distribution exhibited lunar periodicity the total numbers of eggs collected in seven day periods around each of the four lunar phases were compared using a G-test (Fowler & Cohen, 1990). Daily egg counts made by the local people at the nesting ground of Kailolo on the island of Haruku were also analysed from data collected by Heij et al. (1997). To examine whether this temporal laying pattern was unique to the Moluccan megapode, data on daily egg numbers laid by the maleo *Macrocephalon maleo* S. Müller, 1846, were also examined.

To examine whether the spatial pattern of eggs also exhibited lunar periodicity, a chi-square value was calculated for each day of the lunar cycle. The number of eggs collected from each quadrat each day were compared with expected values, based on total egg numbers and the area of suitable nesting substrate in each quadrat. Spearman Rank Correlation coefficients (Fowler & Cohen, 1990) and compositional analysis (Aebischer et al., 1993) were used to investigate the relative use of the nesting ground with reference to vegetation type.

The depth at which eggs were buried also appeared to exhibit lunar periodicity. To test this the mean depth of eggs buried in each of the four lunar phases were compared by analysis of variance (Fowler & Cohen, 1990).

Results

Figure 1 shows the temporal distribution of Moluccan megapode eggs harvested at the Halmahera nesting ground. The data is expressed as the percentage of eggs above or below the mean average. There was a peak in the number of eggs harvested in the week after the full moon and a dip in egg number around new moon. The number of eggs collected in each of the four lunar phases were significantly different (G-Test, $P < 0.01$). The data of daily egg numbers collected from Haruku also exhibit lunar periodicity (Baker & Dekker, in press). Figure 2 shows the temporal distribution of eggs laid by the maleo. There was no lunar periodicity in maleo egg distribution.

The spatial distribution and depth of egg burrows also exhibited lunar synchrony. Moluccan megapodes spent longer at the nesting ground around full moon, digging deeper burrows than around new moon (ANOVA, $P < 0.01$). On bright nights egg burrows showed a more clumped distribution than around new moon (Baker & Dekker, in press).

There was a strong negative correlation between egg number and the vegetation cover of quadrats. (Baker et al., 1998). Compositional analysis showed that, as the area of open ground and ruderal grasses increased relative to other vegetation types, there was an increase in egg number.

The incubation temperature at 1 metre below ground remained at 32 °C +/- 1 °C over a 24-hour period. There was no significant difference in temperature between burrows in different positions of the nesting ground. There was little difference in the temperature of burrows varying from 30–90 cm in depth for the majority of the day. However at 4 a.m., when air temperatures had fallen to 24 degrees C, there was a drop in the temperature of the 30 cm burrows. The quantity of stones and vegetation within the nesting substrate varied considerably between samples but there was no significant difference between nesting and non-nesting sites.

Discussion

In this paper I have presented evidence that the Moluccan megapode exhibits lunar periodicity in egg laying and in its behaviour at nesting grounds. Lunar syn-

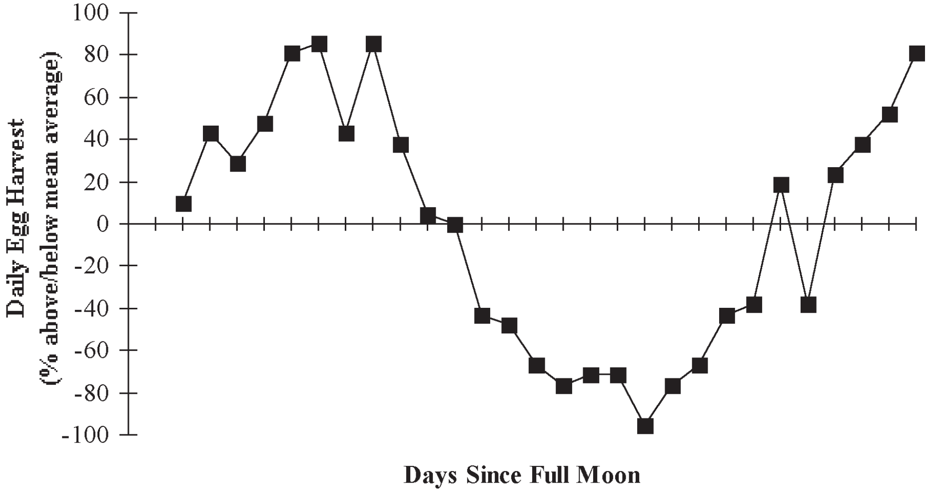

Fig. 1. Daily egg harvest of Moluccan megapode *Eulipoa wallacei* eggs from the Galela nesting ground, Halmahera.

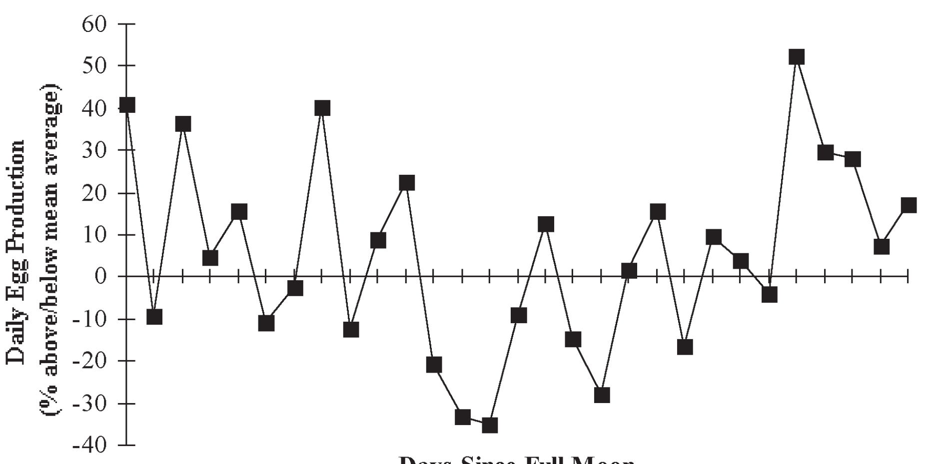

Fig. 2. Daily egg production of maleo *Macrocephalon maleo* eggs at the Tambun nesting ground, North Sulawesi.

chrony of reproduction has rarely been described in birds and is not known to occur in other megapode species. Both the Haruku and Halmahera populations of the Moluccan megapode exhibit a decreased use of nesting grounds in the week around new moon. The diurnally laying maleo on the other hand shows no lunar periodicity in egg laying. The lunar synchrony exhibited by the Moluccan megapode is thus probably an adaptation to nocturnal laying.

There are several hypotheses that might explain why it is advantageous for Moluccan megapodes to visit nesting grounds around full moon. These hypotheses are discussed below.

Hatching synchrony

Full moon may act as a cue to synchronise egg laying. In many species of communally nesting birds females lay their eggs in synchrony, which leads to a synchrony of fledging. Hatching synchrony has been shown in some species of bird, such as auks, to act as an effective anti-predation strategy for the chicks. If hatching of Moluccan megapodes was timed to coincide with the new moon the chicks would be able to emerge in the dark, when they would be safer from nocturnal raptors. The large numbers of chicks emerging together would also reduce the risk of predation for individual chicks. This is an unlikely scenario in the Moluccan megapode as incubation time varies considerably between individual eggs as it is highly related to the temperature of the surrounding substrate. Incubation period can vary from 49 - 99 days (Heij et al., 1997), so synchrony of laying may not lead to synchrony of hatching. In fact, the temporal distribution of hatchling emergence published by Heij et al. (1997) shows no periodicity.

Navigation

Moluccan megapodes may have less difficulty locating their nesting grounds on bright nights. The adults have to travel distances up to tens of kilometres, often over areas of open sea, from their inland habitat to the nesting grounds. This journey probably requires some light for navigation.

Anti-predation

Adult Moluccan megapodes may be at less risk from predation on moonlit nights. The increase in burrow depth around full moon suggests that it is safer to invest in burrow excavation at this time of the month. The data collected on the spatial distribution of burrows shows aggregation behaviour around full moon and random distribution of burrows around new moon. This may also be interpreted as an anti-predation strategy. The major predators of adult Moluccan megapodes are snakes, which do not rely on vision for hunting. Snakes are thus at an advantage on dark nights when they can not be seen by the birds. During the dark phase of the moon, Moluccan megapodes are thus at risk from snake predation. The random distribution of burrows seen on dark nights may act to reduce detection by these predators. On bright nights, however, it is more advantageous to excavate burrows in communal groups in open areas for extra vigilance. More eggs are laid in quadrats with low vegetation cover. Around full moon burrows are aggregated in quadrats with the lowest vegetation cover. Digging burrows close to vegetation may increase the risk of predation. There is no difference in the soil type or incubation temperature of different areas of the beach. Avoidance of nesting sites near vegetation is thus more likely an anti-predation strategy rather than a reflection of nest site quality per se.

The incubation temperature of burrows between 50 – 100 cm deep does not vary. Excavation of deep burrows is thus likely to be a strategy to reduce egg predation. In our studies of egg harvesting, eggs buried more than 1 metre below ground were often deemed too deep to collect by local people. If deeply buried eggs cannot be excavated by experienced egg collectors they are probably safe from other predators. The depth at which eggs are buried is probably a trade off between adult survival and chick survival. Preferential use of nesting grounds around full moon thus allows Moluccan megapodes to invest time in digging deep egg burrows, whilst being able to look out for potential predators.

I have given some explanations why lunar synchrony of reproduction might occur in Moluccan megapodes. A more difficult question to answer is how do Moluccan megapodes control egg laying on a physiological level. If the average egg interval for Moluccan megapodes is thought to be thirteen days, as Heij et al. (1997) predicts, we would not see the lunar pattern shown in Fig. 1. Moluccan megapodes must therefore be able to increase or decrease their egg laying interval to avoid the darkest period of the moon. Changes in egg laying interval may be caused by changes in feeding habit during the lunar cycle, or by hormonal changes induced by changes in light or the gravitational forces of the moon.

The physiological and adaptive aspects of lunar synchrony discussed are an interesting new area of megapode ecology. The lunar periodicity of Moluccan megapode reproduction and behaviour also has some important conservation implications. Around full moon Moluccan megapodes are investing a great deal in egg production and burrow excavation. Harvesting of eggs at this time of the month will thus have the highest impact on the population. If egg harvesting was banned or controlled around full moon it may be an effective long term management strategy. Our studies have shown that the Moluccan megapode avoids vegetated parts of the nesting area. It is thus important to ensure that all nesting grounds and potential nesting grounds are regularly cleared of vegetation that may harbour predators. Attempts to attract Moluccan megapodes back to disused nesting sites have been made in the village of Haruku. Under the direction of a Japanese charity and other advisors the local people have fenced a cleared area of sand and planted trees. On our visit to this site we noticed that the only areas used by the megapodes were the points most distant from the trees and the fence, as these structures probably constitute a predation risk. Our study has provided some interesting new insights into Moluccan megapode behaviour and the ecological characteristics of their preferred nesting grounds. It is important that this information is taken into account when designing future Moluccan megapode management plans and re-introductions.

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