Preliminary results of an ongoing study of the Nicobar megapode *Megapodius nicobariensis* Blyth

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Data collected during an ongoing study on incubation mounds and the social organization of the Nicobar megapode *Megapodius nicobariensis* Blyth, 1846, are reviewed. Microbial decomposition of organic matter in mounds is likely to be the major source of heat production within incubation mounds of the Nicobar megapode, though a direct relation between the rate of organic activity and the temperature could not be shown. The size of a mound was found to be the most important factor in the stabilization of incubation temperatures at optimal levels. Data on the social organization of the Nicobar megapode are presented. The use of mounds by multiple pairs, territorial behaviour, extra-pair copulations and the break-up of pairs are highlighted. The mating system in the Nicobar megapode is briefly discussed.

Introduction

The Nicobar megapode *Megapodius nicobariensis* Blyth, 1846, is a monomorphic mound building megapode, endemic to the Nicobar Islands in the Bay of Bengal. It is separated from its nearest congeneric for about 1600 km (Olson, 1980). Two subspecies are recognized: *M. n. nicobariensis* Blyth, 1846, which is found in the Nancowry group north of the Sombrero Channel and *M. n. abbotti* Oberholser, 1919, from the Great Nicobar group lying south of it (Hume & Marshall, 1878; Abdulali, 1964; Ali & Ripley, 1983; Jones et al., 1995; fig. 1), a separation which conforms to other avifaunal assemblages in the Nicobar islands (Sankaran, 1997). The Nicobar megapode was considered to be seriously endangered (Collar & Andrew, 1988; Jones, 1989; Jones & Birks, 1992). However, a survey of Great Nicobar indicated that *M. n. abbotti* was not threatened (Dekker, 1992; Dekker & McGowan, 1995), and based on population estimates of the Nicobar megapode on all the Nicobar islands between 1992 and 1994, Sankaran (1995a, b, 1998) concluded that *M. n. nicobariensis* is vulnerable and *M. n. abbotti* near threatened, and designated the species as vulnerable.

Studies by Dekker (1992) and Sankaran (1995a, b) have described the incubation mounds of the Nicobar megapode. Sivakumar & Sankaran (in press) have quantified site and habitat selection of mounds as well as mound use patterns in this species. This paper presents the preliminary results of an ongoing ecological study of the Nicobar megapode which was initiated in 1995, and focuses on two aspects: incubation conditions within mounds and social organization. Specific questions include:

— do heat sources (microbial decomposition or solar radiation) that create suitable incubation conditions in a mound vary with mound dimensions? Which source provides the most stable incubation conditions?

— do heat sources and mound dimensions have a bearing on the number of pairs that use a mound, the number of eggs laid, and hatching success?

— what relation do home range and/or territory of a pair have to the location of the mound it uses?

— do home range and territory vary between breeding and non-breeding phases?

— how are pair bonds formed, and how permanent are they ?

In this paper, we present our preliminary findings based on data collected over two breeding seasons. A more detailed treatment will follow later, when data have been collected over more breeding seasons.

Study Area

The Andaman and Nicobar Islands (6°45′ to 13°41′ latitude, 92°12′ to 93°57′ longitude) in the Bay of Bengal arch from Arakan Yoma in Mayanmar in the north to Sumatra, Indonesia, in the south (Saldanha, 1989; fig. 1). The islands cover an area of 8,249 km^2, with a total coastline of 1962 km. The Andaman group with more than 325 islands (21 inhabited) cover an area of 6,408 km^2, the Nicobar group with over 24 islands (13 inhabited) cover an area of 1,841 km^2 (Singh, 1981; Saldanha, 1989).

We have been studying the ecology of the Nicobar megapode since January 1996 at the southern tip of Great Nicobar (fig. 2). Our study area lies on the coast, is about 4 km long, and is bisected by a disused metal road which ends at the light house at Indira Point. The intensive study area is a narrow strip of forest between 40 and 300 m wide, that is bounded by the beach to the east and by either wetlands or forests that are inundated during the monsoons to the west. The soil within this strip of forest is sandy and loamy, and the dominant trees are *Barringtonia asiatica*

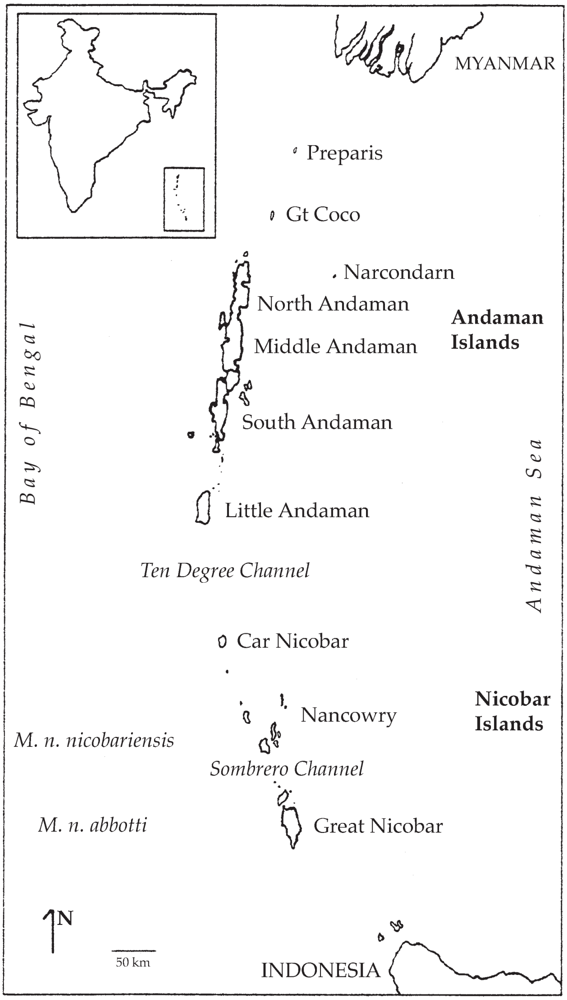

Fig. 1. The Andaman & Nicobar Islands showing the distribution of the two subspecies of the Nicobar megapode *Megapodius nicobariensis*.

Kurz., *Terminalia bialata* Steud., *Terminalia catappa* L., *Syzygium samarangense* (Blume) Merrill & Perry, *Thespesia populnea* Soland. ex. Correa, and *Macaranga* spp. The study area has dense stands of *Pandanus tectorius* Parkinson ex J.P. du Roi and *P. odoratissimus* L. in patches, and the road is fringed by stands of *Leea angulata* Korth. ex Miq., *L. grandifolia* Kurz., and *Draceana* spp. There are a few patches where the ground is open and with little vegetation. The soil of the forest type to the west of this coastal forest, is wet and clayey and covered with *Areca* spp. as well as trees like *Ixora barbata* Roxb., *Pongamia pinnata* Pierre, *Alstonia kurzii* Hook.f., *Aisandra butyracea* (Roxb.) Baehni, *Myristica irya* Warb., *M. andamanica* Hook.f., and *Celtis timorensis* Span.

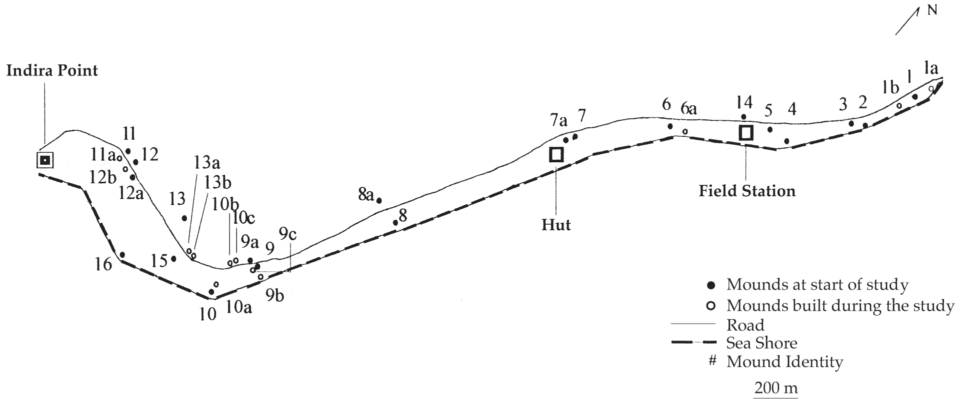

Fig. 2. The southern tip of Great Nicobar island where the ecology of the Nicobar megapode is being studied. The figure shows the location of incubation mounds that were present at the start of the study in January 1996, and the mounds that were subsequently newly built.

Methods

Incubation conditions within mounds

The basal circumference, height and diameter of mounds were measured once a month. The mound size, expressed in m^3, is derived from the equation for the volume of a cone: $1/3\pi r^2 h$, where r is the radius and h the height.

In 1996 we implanted four temperature probes, at depths between 20 and 75 cm, in seven mounds that were selected for intensive studies. However, after about two months these probes malfunctioned, probably due to high humidity and rainfall. In 1997, we used a temperature probe placed at the tip of a 1 m long steel tube which was inserted to depths of 30, 60 and 90 cm. The temperature of all mounds in our study area was measured once a month and for the target mounds once every ten or 15 days.

Microbial activity was measured indirectly using a soil respirometer (PP Systems EGM-1 Environmental Gas Monitor with a SRC-1 Soil Respiration System), assuming that in those mounds where organic activity was high, greater amounts of CO_2 would be emitted. The soil respirometer measures CO_2 changes in a fixed volume over a known period of time and fits a quadratic equation to the data to arrive at a SR value which is the soil respiration rate in g CO_2/m^2/hour.

The intensity of light falling upon a mound at different times of the day was measured using a Lux meter. Both soil respiration and light intensity were measured at least once in a fortnight for seven mounds which were under intensive study. The temperature, soil respiration, and light intensity data presented here are means of all data points. Temporal variations are not dealt with in this paper.

All mounds in the study area were visited twice a day, when we recorded any activity, allowing us to identify whether and when eggs were laid in a particular mound. Whenever possible, a newly laid egg was located by digging into the mound, and the egg was marked. The egg was monitored by relocating it once every 15 days. Incubation temperatures near the egg were measured once every 15 days.

Territory & social organization

We observed megapodes mostly on the mound and opportunistically away from the mound using the focal animal sampling method (Altmann, 1974). We colour-marked 23 birds, which represented 16 paired and two unpaired birds. Their positions were plotted on detailed maps of the study area. All sightings, calls and fights were plotted on this map.

Results

Incubation conditions within mounds

The size of mounds

The size of a mound varies during the season. Between January and June 1996, eight mounds increased in size, four decreased, and nine showed no change (n = 21;

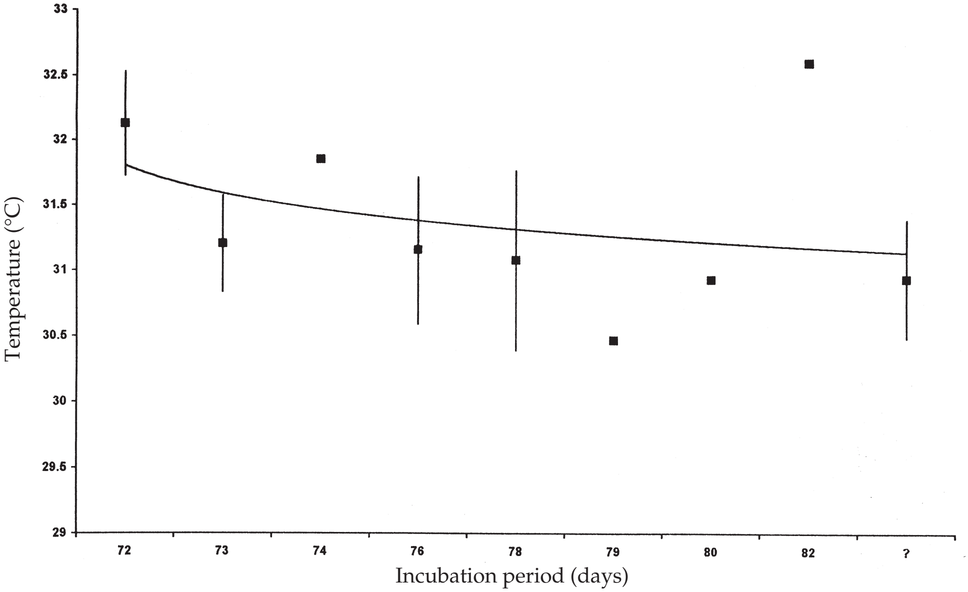

Fig. 3. Relation between core mound temperature (°C) and incubation period (days) of eggs of the Nicobar megapode.

Table 1. The history of 27 incubation mounds of the Nicobar megapode.

Mound	Months during which the mound was active												Size of the mound (m^3)			
ID	1996						1997						1996		1997	
	J	F	M	A	M	J	J	F	M	A	M	J	Jan	June	Jan	June
1	—	—	—	—	—	—	—	—	—	—	—	—	0.4	0.4	0.6	0.3
1a										—	—	—				0.8
1b										—	—	—				1.3
2	—	—	—	—	—	—	—	—					0.4	0.4	0.4	0.4
3	—	—	—	—	—	—	—	—	—	—	—	—	4.1	2.8	1.4	3.2
4	—	—	—	—	—	—	—	—	—	—	—	—	6.5	6.9	7.9	14.7
6	—	—	—	—	—	—	—	—	—	—	—	—	0.8	0.7	0.8	1.8
6a						—	—	—	—	—	—	—	0.1	0.2	0.3	0.2
7	—	—	—	—	—	—	—	—	—	—	—	—	0.1	0.1	0.1	0.5
7a	—	—	—	—	—	—	—	—	—	—	—	—	0.1	0.8	0.8	0.8
8	—	—	—	—	—	—	—	—	—	—	—	—	4.5	4.0	3.7	6.2
8a		—	—										0.1	0.1	0.1	0.1
9	—	—	—	—	—	—	—	—	—	—	—	—	5.2	5.6	2.1	7.3
9a	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	2.2
9b				—	—	—	—	—	—	—	—	—	0.1	0.1	0.1	0.1
9c									—	—	—	—	0.1	0.1	2.2	
10	—	—	—	—	—	—	—	—	—	—	—	—	25.6	28.1	25.6	24.1
10a											—	—		0.2	0.2	4.4
11	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.2	0.3
11a		—	—	—	—	—	—	—	—	—	—	—	0.1	0.1	0.1	0.1
12	—	—	—	—	—	—	—	—	—	—	—	—	0.8	0.8	0.9	4.3
12a	—	—	—	—	—	—	—	—	—	—	—	—	0.9	1.5	1.6	5.7
12b									—	—	—	—			2.3	7.1
13	—	—	—	—	—	—	—	—	—	—	—	—	11.1	12.8	13.3	13.1
13a										—	—	—			1.8	1.8
13b										—	—	—			0.4	0.5
14	—	—	—	—	—	—	—	—	—	—	—	—	6.5	5.9	8.8	4.2

table 1). Between January and June 1997, 13 mounds increased in size, four decreased, and seven showed no change (n = 24; table 1). Of the 15 mounds which were active over the entire study period from January 1996 to June 1997, 11 mounds increased in size, and four decreased (table 1). Overall, of the 22 mounds for which size has been monitored for 1996 and 1997, 15 mounds have become larger in volume by 1.5 to nearly 25 times between January or June 1996 and June 1997, three have become smaller, and four mounds showed no size change (two of which had been abandoned during the course of the study).

Incubation temperature

We monitored the temperature near 26 eggs in 12 mounds, and recorded the incubation period for 23 eggs. Three eggs did not hatch. The shortest incubation period was 72 days (fig. 3). The mean temperature near eggs hatching on the 72nd day was 32.1°C.

The effect of mound size on incubation temperature

We studied the effect of mound size on the temperature in 27 mounds (fig. 4). Mound size varied from 0.006 m^3 to 24.27 m^3 ($x = 3.48$ m^3). We found that small mounds ($< x$) are more likely to have a variable, more fluctuating temperature, ranging from 29.2-34.4°C ($x = 31.4 \pm 0.35$°C, $n = 19$), than larger mounds ($> x$) where the temperatures range from 31.9-35.0°C ($x = 33.4 \pm 0.34$°C, $n = 8$).

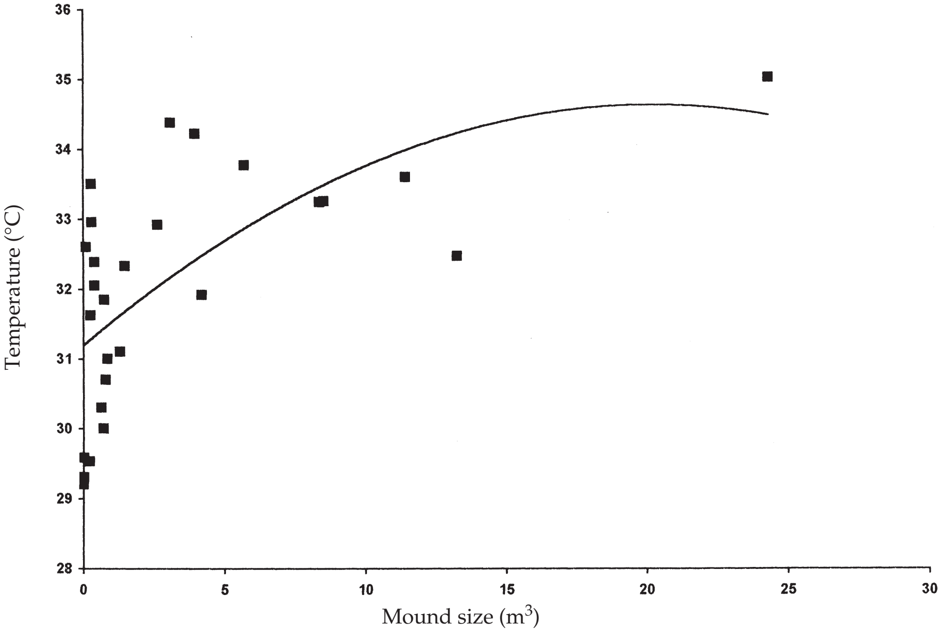

Fig. 4. Relation between mound size (m^3) and temperature (°C) in mounds of the Nicobar megapode.

The role of light intensity and soil respiration on the incubation temperature

Solar radiation does not seem to play a role of significance in establishing suitable incubation temperatures within the mound of the Nicobar megapode as was evidenced by mound surface temperatures usually being 2-4°C less than the temperature within the core of the mound.

The increase in microbial activity inside a mound and the consequent increase in temperature in the same mound in two different years seems to indicate that microbial activity is the primary source of heat in mounds (table 2). The lack of a clear relation between microbial activity and mound temperature may indicate that while microbial activity is the main source of heat production, it may not play a role in either the optimalization or the stabilization of core mound temperatures. Our data indicate that optimalization and stabilization of mound temperatures are probably governed by mound size (fig. 4).

Egg laying and hatching success

Of the 32 mounds that have been active in the study area in 1996 or 1997, eggs have been laid in at least 30. In 1996, 22 mounds were active and contained eggs. Five

Table 2. Factors influencing mound temperature in the Nicobar megapode. The values are means of all data collected between January and June in each year.

Mound ID	Size (m^3)		Temperature (°C)		Soil respiration ($gCO_2/m^2/h$)		Light intensity (lux)	
	1996	1997	1996	1997	1996	1997	1996	1997
3	3.1	3.1	31.5	34.4	4.1	5.7	1066	3460
8	4.1	8.5	31.5	33.3	5.2	6.5	1748	2640
9	5.4	3.9	35.8	34.2	5.1	6.3	6393	1119
10	27.4	24.3	32.3	35.0	3.7	6.1	7006	5230
13	11.2	13.2	31.4	32.4	6.8	7.4	2893	1170
14	6.2	8.4	31.6	33.2	5.5	6.5	6768	6430

of these mounds were not used for egg laying in 1997: two were abandoned, while in the remaining three megapodes did some digging, albeit rarely.

There is a relation between mound size and the number of eggs in a mound (fig. 5, table 3). Overall, the smallest mounds (<1 m^3) contain the least number of eggs (x = 1.6 ± 0.56 eggs, n = 16), though there are exceptions and two mounds in this sample contained six and eight eggs respectively. Medium sized mounds (1-5 m^3) have a larger number of eggs laid in them (x = 6.7 ± 1.48 eggs, n = 6), while, in general, the largest mounds contained the largest number of eggs (x = 8.2 ± 1.91 eggs, n = 6) (fig. 5).

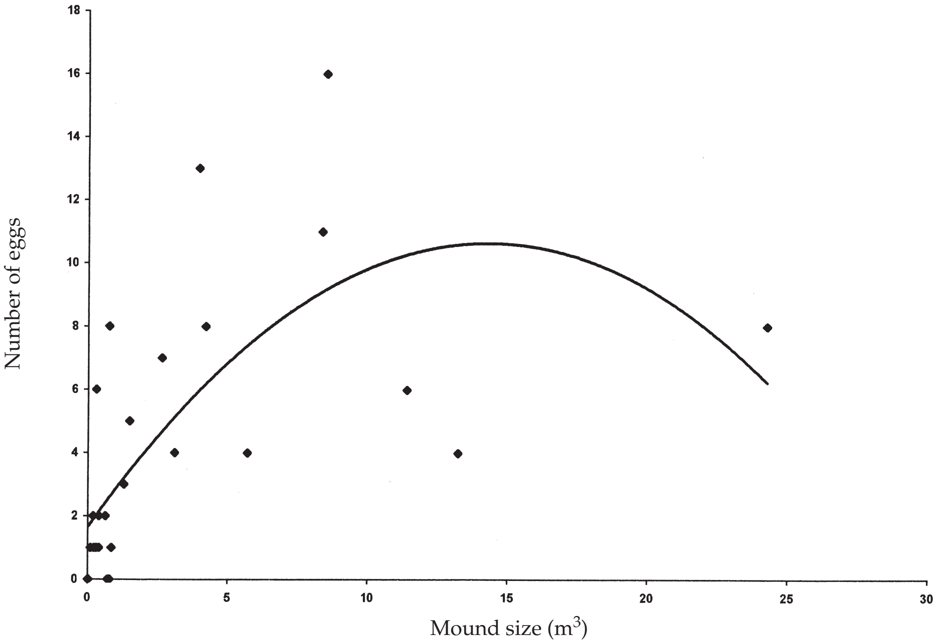

Fig. 5. Relation between mound size (m^3) and the number of eggs in the Nicobar megapode.

Table 3. The number of pairs of Nicobar megapode, the number of eggs laid, and the hatching success in mounds of different sizes. Data only for mounds in which eggs were marked and monitored.

Mound size in m^3 (No. of mounds in size class)	No. of marked (+ unmarked) pairs using the mound [# of mounds]	No. of eggs (mean eggs/) mound	No. of eggs marked and monitored	No. of marked eggs that hatched (%)
<1 (7)	1 (+1), [1]	26 (3.7)	11	10 (90)
1-3 (4)	-	17 (4.3)	11	8 (73)
3-5 (5)	2 (+ ?), [1]	28 (5.6)	17	16 (94)
5-10 (3)	5(+ ?), [3]	34 (11.3)	22	15 (68)
>10 (3)	1(+ 1), [1]	18 (6)	5	2 (40)

Hatching success was recorded in 22 mounds. Our clumped data indicate that the highest hatching success was recorded in small and medium sized mounds (table 3).

Social organization

Our study area has a population of more than 50-60 pairs of megapodes as well as several unpaired birds of both sexes. In 1996 and 1997, 23 megapodes were colour marked, which at the time of capture represented 15 pairs and four unpaired individuals, two of which later paired with each other. Of these 16 pairs, both male and female were colour-marked in five pairs.

Distribution of mounds

At the start of the study in January 1996, there were 18 active mounds in our study area (fig. 2). Between January and June 1996, four new mounds were constructed. Between December 1996 and June 1997, an additional eight mounds were built. Two mounds had been abandoned between June 1996 and December 1996. In September - October 1997 two more mounds were constructed, and by November 1997, 30 mounds were actively used within our study area. Two mounds which were active at the commencement of this study had been abandoned.

While mounds are present throughout the study area, some degree of clustering is discernible (fig. 2). Of the 32 mounds studied, eight clusters can be recognized: one cluster of four mounds, one of three and six of two mounds each. Of the 14 new mounds built, eight were built so as to add on to an existing cluster (n = 2), or form a new cluster (n = 6). There did not appear to be a relationship between the size of a mound, and the propensity for additional mounds to be built so as to form a cluster.

Mound use

At least 65% of the mounds were used by more than one pair. The mean number of pairs per mound is 2.3 ± 0.3 (n = 29). Ten of the smaller mounds were used for egg laying by only one pair each. However, data obtained from colour marked birds indicated that even more pairs used a mound than we had calculated from observations of an unmarked population. Between January and June 1997, six mounds were used by one to five colour marked pairs (x = 3.0 ± 0.67 pairs per mound). This is a minimum value as also unmarked pairs used these mound simultaneously. Of the 16 colour marked pairs, 12 pairs (75%) laid eggs in a single mound only, three pairs (18%) used more than one mound for egg laying, and one pair changed mounds.

Territory

The Nicobar megapode is a strongly territorial species. Typically, a territory has a fairly large exclusive area with a mound at one corner. Here, the territory overlaps with that of other pairs that use the same mound (fig. 6). In case of one particular mound, which was not part of a cluster, one of four colour marked pairs had a particularly large territory which included two mounds (G14/O14 in fig. 6). This pair used both mounds for egg laying. In another case where four mounds occurred in a tight cluster, more than one territory overlapped at the cluster (fig. 7): one of three colour marked pairs used two adjacent mounds (9 and 9c in fig. 7), one pair used three mounds (9, 9a and 9c) and one pair initially used three mounds (9, 9c and 9b) but subsequently shifted to a distant mound (10b in fig. 7). The position of the territory varies between egg laying and non egg laying periods. It appears that territories either shrink to exclude the mound outside the egg laying season or the birds establish a new territory away from the mound.

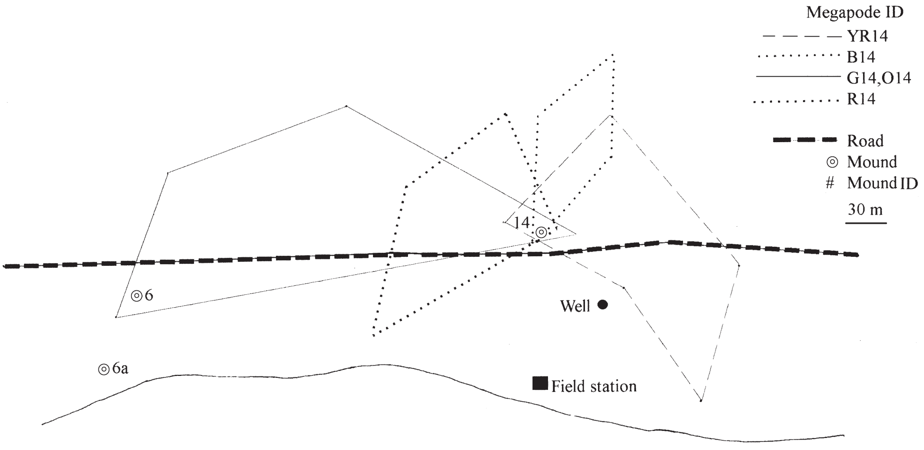

Fig. 6. Most Nicobar megapode incubation mounds are used by more than one pair of birds, whose territories overlap at the mound. Some pairs, like G14, 014, may have large territories that have within them two or more incubation mounds in which the pair may lay eggs.

Defence of a territory is through frequent duetting, physical fights and chases. The duet (contra Jones et al., 1995) is usually initiated by the female. Up to eight birds may aggregate in a very small area calling aggressively. Physical fights take place between pairs, or between solitary birds and pairs, and is largely sex based. The majority of the territorial disputes which result in physical encounters take place in the areas immediately around the mound and the area of overlap between two or more territories (fig. 7).

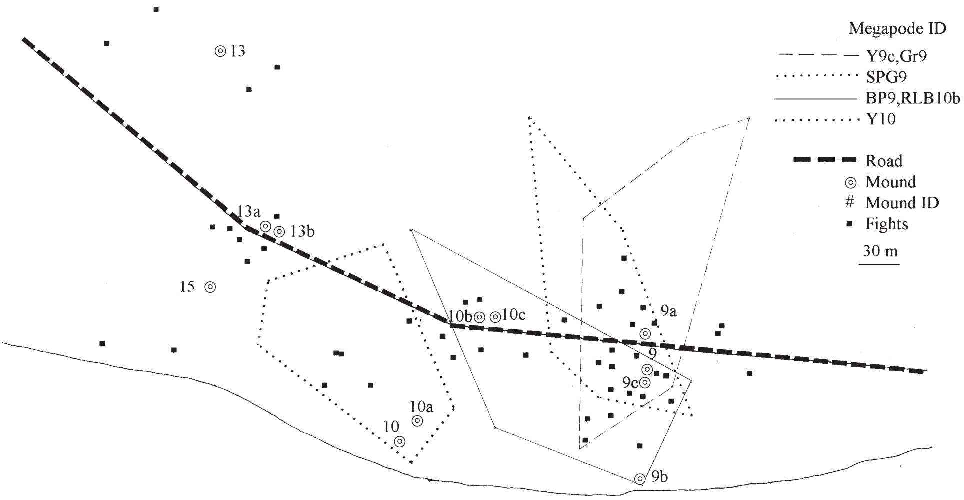

Fig. 7. The territories of four colour marked pairs of the Nicobar megapode. Territories overlap at the incubation mound which may be used by more than one pair, or a pair may use more than one mound present within its territory. The majority of territorial fights take place at or near the mound, and in the area of overlap between two adjacent territories.

There seems to be a strong hierarchy between pairs that use a mound at any given time. This hierarchy is evidenced by the dominant pair (the pair in which both male and female are dominant) usually spending most of the time at the mound, its greater involvement in mound defence and the likelihood of it disrupting other pairs while working on the mound. The defence of a territory requires equal participation of both sexes. However, this hierarchy varies temporally and spatially. The dominant pair maintains its position at the mound apparently only as long as it is laying eggs, subsequent to which its hierarchial position is occupied by either a pair which was already present at the mound, or by a new pair. Subdominant pairs may shift territories to occupy a different mound (BP9 in fig. 7), or may lay eggs in two mounds (GOF8 in fig. 8). Dominant pairs may also lay in more than one mound (G14, 014 in fig. 6). Solitary birds of either sex do not defend territories, but usually attach themselves to a mound, working on it when pairs that use that mound are absent. Solitary birds as a rule do not vocalise in response to duets, but have been recorded calling on occasion during aggressive encounters.

Pair bond, pair formation, copulation & displays

Pairs L8 and P8 which were colour marked in 1996 had, by the commencement of the 1997 season, separated from their original partner. The female of L8 was paired with an unmarked male and laid two eggs in the mound in which she laid eggs in 1996, when along with the male L8, she formed the dominant pair (fig. 8). The male of L8 had paired with an unmarked female who was later ringed as GO8. While paired with male L8, GO8 laid two eggs in the same period and in the same mound in which female L8 laid her eggs (fig. 8). Male L8 and GO8 became the dominant pair. In

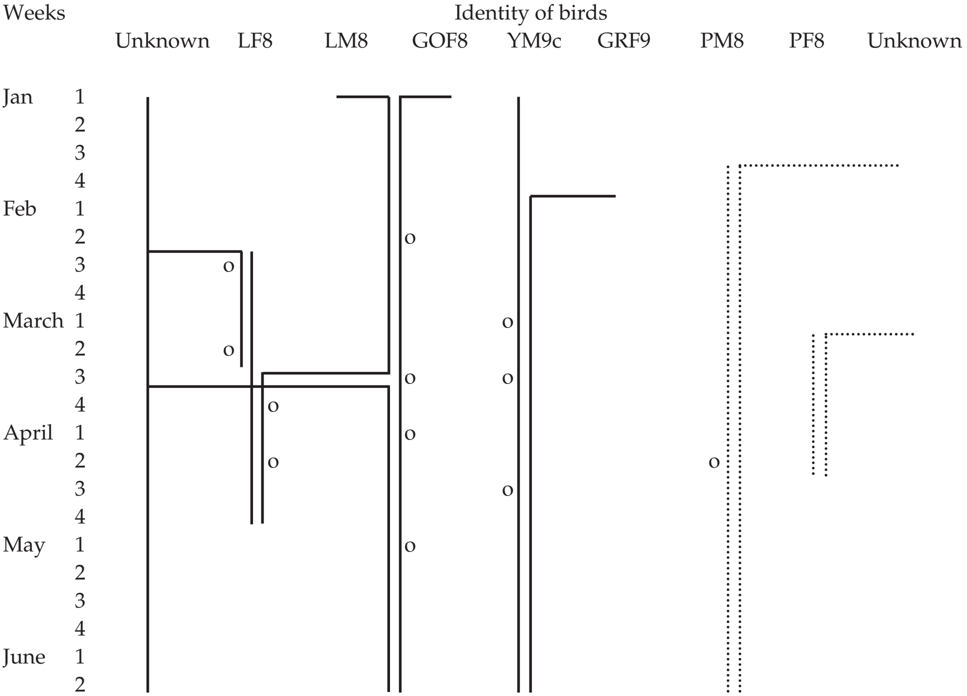

Fig. 8. Pair bonds in the Nicobar megapode in 1997. The tenure of pair bonds is tracked by solid or dashed vertical lines. The solid lines indicate frequent use of a mound and the dashed line indicates infrequent use. The 'o' sign indicates the laying of an egg. F or M in the individual identity indicates sex, and the number indicates the mound used by that individual. Note changes in partners midway through the egg laying period of the female.

March, male L8 and female L8 rejoined and became the dominant pair of the mound again, and together laid two more eggs (fig. 8). GO8 paired with an unmarked male and continued to use the same mound. They became the dominant pair when pair L8 had completed egg laying in April (fig. 8). The male and female P8 who, after their separation, were paired with unmarked birds, did not rejoin.

We only have one instance of a new pair being formed from two colour marked birds that were unpaired when trapped (fig. 8). Male Y9c built a new mound (9c, fig. 7) adjacent to an existing mound where solitary female GR9 had attached herself to (9 in fig. 7). We suspect that, to form a pair, a solitary bird either has to attach itself to a mound or construct a new one. One marked solitary megapode has now remained unpaired for nearly two years, though it had briefly formed a pair for about one week. This solitary male has a home range that included at least three mounds.

Copulation within a pair has been observed three times. On one occasion, a male chased its partner and mated with her repeatedly. On another occasion, a male chased its partner onto a branch and copulated with her on the branch. The third observation was after a fight with another pair, after which the winning male returned to its partner and mated with her.

Extra-pair copulation has also been recorded. On one occasion in 1997, the male of a pair copulated or attempted copulation six times with the female of another pair during a fight which lasted for about 45 minutes, and during which it continually chased the female of the other pair into trees where copulation was attempted. Their respective partners were calling but neither fought or attempted mating. In 1998, extra-pair copulation was seen twice, in both instances it was part of physical fights. The second instance was between nine birds that included three pairs and three unpaired birds, two of which were males. In this instance the fight was initiated between a pair and an unpaired female who was raped by the male. They were then joined by another pair, whose male raped both the paired and unpaired female. These were then joined by two unpaired males, and then by one more pair. Intra-sexual physical fights and inter-pair copulation took place apparently indiscriminately for about an hour. In at least five other instances, rape has been attempted but copulation was not observed by us.

We have not observed any intra-pair displays between a male and female Nicobar megapode. On one occasion a male exposed food two to three times while working on a mound when the female reacted to his signals and ate it. The maintenance and confirmation of the pair bond appears to lie solely in the duetting, the joint defence of territories and mounds, and in the digging of mounds. Pairs may keep in touch by low contact calls, and display anxiety when separated.

Discussion

Incubation conditions within mounds, egg laying and hatching success

Megapode mounds are amongst the largest structures made by any non-colonial bird, and represent the harnessing of the energy produced by microbial respiration (Seymour et al., 1986; Jones, 1989) and/or solar radiation (Frith, 1956). Incubation temperatures in megapode mounds show considerable fluctuation, and while the negative effects of these fluctuations on eggs are largely offset by a variable incubation period (Booth, 1987), there are strategies to balance both heat loss and gain (Jones, 1989; Jones & Birks, 1992). While mound maintenance is thought to play a role in maintaining suitable incubation temperatures, Seymour (1985) proposed, for mounds of the Australian brush-turkey *Alectura lathami* J.E. Gray, 1831, and malleefowl *Leipoa ocellata* Gould, 1840, that heat production and heat loss tend to stabilize mound temperatures at an equilibrium. This is due to the great thermal inertia of mounds once they reach certain dimensions, because they have an adequate moisture content, and because of the regular incorporation of fresh, moist organic material. However, the incubation mound of the Nicobar megapode does not fully fit these assumptions. First, the size of the mound can vary in height from ten cm up to 2.1 m and in basal circumference from seven to 45 m (Sankaran, 1995b). Second, the proportion of organic material in a mound varies (Sivakumar & Sankaran, in press), and third, the gap in the canopy above a mound varies resulting in differences in the amount and duration of sunlight falling on a mound. This might indicate that the heat sources which create suitable incubation conditions within a mound may vary, with some mounds appearing to rely on organic decomposition and others on sunlight.

Solar energy, however, probably does not increase mound core temperatures directly. The canopy above a mound causes direct sunlight to fall on a mound only for very short periods, with the result that both ambient temperature and mound surface temperatures are almost always lower than mound core temperatures. Thus, the role of solar energy is probably restricted to warming the surface of the mound, whereby dissipation of heat is reduced.

Microbial respiration is the primary source of heat harnessed by most mound building megapodes in their mounds (Jones et al., 1995). A clear relation did, however, not exist between mound temperatures and organic activity as evidenced from soil respiration. An overall increase in mound temperatures and soil respiration between years in the same mounds indicated that organic activity is probably the primary source of heat in the mounds of the Nicobar megapode. Microbial respiration, however, does not have a linear relation to the temperature of the mound, and mounds with higher levels of soil respiration did not necessarily have higher temperatures (table 2). Two factors could be responsible for this. First, there might be differences in the amount of heat produced by decomposition due to the kind of leaves and other organic litter added to the mound. Second, the rate of heat loss probably differs between mounds, caused by differences in the proportion of surface area to the volume of mound or to the amount of moisture content within the mound (Jones et al., 1995).

Our observations on the influence of mound size on mound temperatures are consistent with the model of mound homeothermy (Seymour, 1985; Jones et al., 1995). Small mounds show a greater variation in mound temperature than large mounds, with small mounds showing temperatures below, at or above optimal incubation temperatures (32-35°C; Dekker, 1990) while the incubation temperatures of large mounds lay within the optimal incubation temperature range. Thus, while the rate of microbial respiration is independent of size, and small mounds may have higher levels of microbial activity, stabilization at optimal incubation temperatures is consistent only in large mounds. One would therefore expect that eggs in large mounds are more likely to hatch successfully than those in smaller mounds. However, hatching success does not reflect these trends. Small and medium sized mounds had a higher hatching success than the largest mounds. We do not have an adequate explanation for this as yet, though more digging activity in larger mounds, and consequently greater exposure of eggs to the atmosphere is a possible factor.

The optimalization of incubation conditions in large mounds is reflected in an overall trend of a greater number of pairs using these mounds, and consequently, a greater number of eggs laid in them. However, we interpret the exceptions, that is small mounds having a greater number of eggs, or larger mounds having fewer eggs, an indication that size is not the only criterion. The quality of the mound, and the number of pairs using a mound, which appears to be somewhat independent of mound size, are probably other determining factors. The data indicate that medium sized mounds have the largest number of eggs. The smallest mounds probably have physical limitations as to the number of eggs that can be laid in them, and the largest mounds are probably moribund, and hence used by fewer pairs.

Social organization

The social organization of megapodes is poorly understood. Most megapodes, particularly those belonging to the genus *Megapodius*, are believed to be monogamous as most species exhibit features such as monomorphism, highly synchronised behaviours, and duetting (Jones et al., 1995). These characteristics indicate that pair bond in most megapodes is strong therefore excluding the need for and the chance of extra-pair copulations (Jones, 1989). It is also believed that monogamy is inevitable in mound building species since high paternal investment can only be expected if male parental care benefits their own progeny (Jones, 1989). Monogamy in megapodes, however, is an anomaly as female emancipation from parental care, and the presence of resources (the incubation mound) that can be dominated by males, should result in a polygynous mating system (cf. Orians, 1969). Promiscuity has been documented or suspected in some mound building megapodes that exhibit sexual dimorphism (Jones, 1989; Jones et al., 1995), and an instance of polygamy has also been documented for the monomorphic malleefowl which was believed to be strictly monogamous (Weathers et al., 1990; Jones et al., 1995).

Though the Nicobar megapode exhibits characteristics of permanent pair bonds which are consistent with several other species of mound building megapodes (Crome & Brown, 1979; Jones et al., 1995), our finding is that the break up of pairs either between years, or within the breeding season, is prevalent. Moreover, extra pair copulation does occur, and is probably a regular component of the innumerable agonistic interactions. This indicates that the pair bond in this species, and possibly in other mound building megapodes, may be far less permanent than was thought (cf. Jones et al., 1995).

The apparently equal role of both sexes in the defence of a territory and the incubation mound, and the temporal hierarchies that are evident between pairs that use the same mound, indicate that the pair bond in the Nicobar megapode serves the primary function of giving a pair access to an incubation mound, and enabling them to defend this access. Either sex may therefore change partners to improve access to or defence of a mound. That access to a mound appears to be the primary function of the pair bond is also evidenced by the total absence of courtship display that in most other monogamous species serves as precopulatory display and strenghtens or reinforces the pair bond. The lack of courtship display is apparently consistent in most megapodes.

The presence of sexually mature unpaired birds of both sexes for apparently extended periods of time is of particular interest. Megapodes probably remain unpaired due to absence of space within which to establish a territory. This appears to be a key function of pair formation. The frequent fights between solitary birds and pairs, and the intra-sex fights that takes place during such encounters, may indicate that solitary birds attempt to steal mates from existing pairs. Unpaired birds of either sex, however, probably do breed successfully. Unpaired males attempt to forcibly copulate with the females of pairs during agonistic interaction, and unpaired females have been recorded copulating with males of pairs. Also, solitary females have been observed egg laying eggs. It is not known whether unpaired males and females copulate, though a very brief pair bond was formed between two such individuals.

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References

Abdulali, H., 1964. The birds of the Andaman and Nicobar Islands.— J. Bombay nat. Hist. Soc. 61: 483-571.

Ali, S. & S.D. Ripley, 1983. Handbook of the birds of India and Pakistan. Compact edition.— New Delhi.

Altmann, J., 1974. Observational sampling of behaviour: sampling methods.— Behaviour 48: 227-265.

Booth, D.T., 1987. Effect of temperature on development of Mallee Fowl *Leipoa ocellata* eggs.— Physiol Zool. 60: 437-445.

Collar, N.J. & P. Andrew, 1988. Birds to watch. The ICBP world checklist of threatened birds.— ICBP Tech. Publ. 8.

Crome, F.H.J. & H.E. Brown, 1979. Notes on the social organization and breeding of the Orange-footed Scrubfowl *Megapodius reinwardt*.— Emu 79: 111-119.

Dekker, R.W.R.J., 1990. Conservation and biology of megapodes (Megapodiidae, Galliformes, Aves): 1-132.— Thesis, Univ. of Amsterdam, Amsterdam.

Dekker, R.W.R.J., 1992. Status and breeding biology of the Nicobar megapode *Megapodius nicobariensis abbotti* on Great Nicobar, India: 1-20.— Rep. Nat. Museum nat. Hist., Leiden.

Dekker, R.W.R.J. & P.J.K. McGowan, 1995. Megapodes: an action plan for their conservation 1995-1999: 1-41.— Gland.

Frith, H.J., 1956. Temperature regulation in the nesting mounds of the mallee-fowl, *Leipoa ocellata* Gould.— CSIRO Wildl. Res. 1: 79-95.

Hume, A.O. & A.H.T. Marshall, 1878. The game birds of India, Burmah and Ceylon.— Calcutta.

Jones, D.N., 1989. Modern megapode research. A post-Frith review.— Corella 13: 145-154.

Jones, D & S. Birks, 1992. Megapodes: recent ideas on origins, adaptations and reproduction.— Trends Ecol. Evol. 7: 88-91.

Jones, D. N., R.W.R.J. Dekker & C.S. Roselaar, 1995. The Megapodes: 1-262.— Oxford.

Olson, S.L., 1980. The significance of the distribution of the Megapodiidae.— Emu 80: 21-24.

Orians, G.H., 1969. On the evolution of mating systems in birds and mammals.— Amer. Nat. 103: 589-603.

Saldanha, C.J., 1989. Andaman, Nicobar and Lakshadweep. An environmental impact assessment.— Delhi.

Sankaran, R., 1995a. The distribution, status, and conservation of the Nicobar megapode *Megapodius nicobariensis*.— Biol. Conserv. 72: 17-25.

Sankaran, R., 1995b. The Nicobar megapode and other endemic avifauna of the Nicobar islands: status & Conservation: 1-44.— SACON Techn. Rep. 2. Coimbatore.

Sankaran, R., 1997. Developing a protected area network in the Nicobar Islands: the perspective of endemic avifauna.— Biodiv. & Conserv. 6: 797-815.

Sankaran, R., 1998. An annotated list of the endemic avifauna of the Nicobar islands.— Forktail 13: 17-22.

Seymour, R.S., 1985. Physiology of megapode eggs and incubation mounds.— Acta XVIII congr. int. Orn. 2: 854-863.

Seymour, R.S., D. Vleck & C.M. Vleck, 1986. Gas exchange in the incubation mounds of megapode birds.— J. Comp. Physiol. 156 B: 773-782.

Singh, B.K., 1981. Census of India 1981. Series - 24. Andaman & Nicobar islands.— Govt. of India.

Sivakumar, K. & R. Sankaran, in press. Incubation mound and mound use patterns in the Nicobar megapode.— First Pan-Asian orn. Congr., Coimbatore.

Weathers, W.W., D.L. Weathers & R.S. Seymour, 1990. Polygyny and reproductive effort in the Malleefowl *Leipoa ocellata*.— Emu 90: 1-6.

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