A STUDY ON THE BREEDING BIOLOGY OF THE NICOBAR MEGAPODE *MEGAPODIUS NICOBARIENSIS*

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in
ZOOLOGY

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June 2000

CERTIFICATE

This is to certify that the thesis, entitled " **A study on the breeding biology of the Nicobar Megapode** ***Megapodius nicobariensis*** " is a record of original work done by **Mr. K. Sivakumar** in the Division of Avian Ecology, Sálim Ali Centre for Ornithology and Natural History, as a full time Research Scholar during the period of study 1996 - 2000 under my guidance and supervision for the award of the Degree of Doctor of Philosophy in ZOOLOGY. I further certify that this research work has not previously formed the basis for the award of any other Degree or Diploma or Associateship or Fellowship or other similar title to any candidate of this or any other University.

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DECLARATION

I do hereby declare that the thesis entitled **"A study on the breeding biology of the Nicobar Megapode *Megapodius nicobariensis*"** submitted to the Bharathiar University, Coimbatore, for the award of the Degree of Doctor of Philosophy in ZOOLOGY, is a record of original and independent research work done by me during 1996 -2000 under the supervision and guidance of **Dr. Ravi Sankaran**, Scientist, Sálim Ali Centre for Ornithology and Natural History, Coimbatore and it has not previously formed the basis for the award of any Degree, Diploma, Associateship, Fellowship or other similar title to any candidate of this or any other University.

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Nicobar Megapode on the mound

Nicobar Megapode *Megapodius nicobariensis*

Incubation mound of the Nicobar Megapode

SUMMARY

The family Megapodiidae consists of 22 species in seven genera, most of which are island forms occurring in Australia, New Guinea and surrounding islands, eastern Indonesia, the Philippines, Niuafo'ou island, the Palau and Mariana islands and the Nicobar islands. Thirteen of these 22 species are currently threatened by habitat destruction, introduction of predators and over-exploitation of eggs.

The megapodes are an unique group of birds as they utilise external sources of heat to incubate their eggs. Megapodes exploit external heat sources in two ways. Some species lay eggs in burrows in geothermally heated soil, or on exposed beach, and are called burrow nesters (*e.g. Macrocephalon maleo*). Other species construct mounds of sand, soil and decomposing vegetation within which they lay eggs and are called mound nesters (*e.g. Megapodius freycinet*). The chicks are supra-precocial; they are able to fly soon after emerging from the mound or burrow, and receive no parental care.

The Nicobar Megapode *Megapodius nicobariensis* is a mound building megapode, endemic to the Nicobar group of Islands in the Bay of Bengal. The polytypic Nicobar Megapode has two subspecies *M. n. nicobariensis* Blyth, in the Nancowry group of islands north of the Sombrero channel, and *M. n. abbotti* Oberholser, which is found in the Great Nicobar group of islands lying south of the Sombrero channel.

Megapode mounds are amongst the largest structures made by any non-colonial animal, and represent the harnessing of the energy produced by microbial respiration, and/or solar radiation by concentrating suitable material to provide optimal incubation conditions at about 33-34° C. Three major aspects of this unique breeding strategy were examined by this study.

First, incubation mounds vary considerably in size, location and composition, the majority of which are constructed in a narrow strip of flat coastal forest. Moreover, the distribution and density of the Nicobar Megapode and its mound varies within this coastal habitat. Thus, the microhabitat requirement of the Nicobar megapode was studied, particularly as its habitat is vulnerable to change due to human activity.

Second, variability in size, composition and location of incubation mounds indicates that the mounds differ in their source of heat. The sources of heat, its regulation and stability were studied to understand the effect of mound types and dimensions on the number of pairs that use a mound, the number of eggs laid and the hatching success.

Third, the social organisation of the megapodes is poorly understood. The social organisation of the Nicobar Megapode was studied to understand the behavioural consequences of an incubation mound nesting system.

The field studies were carried out in a 4.5-km strip of coastal forest at the southern tip of Great Nicobar Island. Field studies were conducted between December 1995 and July 1996,

December 1996 and June 1997, September and October 1997, and February and May 1998, covering three dry seasons (peak period of egg-laying) and a part of one wet season. In 1996, the study area was systematically surveyed and mapped, on which all active mounds present were plotted. The substrate of the study area was classified into three major types, sandy, sandy-loam and loamy (moist). Vegetation of the study area was classified into fourteen subtypes that were dominated by one or more species. These patches were measured and plotted on the map. To understand the abundance and dominance of trees, ten 20m x 50m quadrats were laid in the study area. All the trees with a girth at breast height (GBH) of 25 cm and above were sampled. Habitat use by megapodes was assessed by plotting sightings and calls heard according to the microhabitat patch that they occurred in. Habitat preference was arrived at by comparing the available area of the microhabitat with the number of mounds present, and of sightings and calls of the bird. This data was used to identify a) the microhabitat preference for the construction of incubation mound, b) the microhabitat preference of the Nicobar Megapode during dry and wet seasons.

Sandy substrate and the habitat that was dominated by Pandanus spp. was the preferred area for the construction of the incubation mound of the Nicobar Megapode. Habitat with a sandy substrate was utilised more by the birds during the dry season while in the wet season sandy-loam substrate was utilised more. Of the 14 habitats, habitats dominated by *Sterculia* sp., *Pandanus* spp, dense *Pandanus* with *Macaranga peltata*, or *Dracaena* sp., were the most preferred habitats. Microhabitats dominated by *Macaranga peltata* were used more during the wet season than the dry season, while there was no difference between the seasons, in selection and utilisation of other microhabitats.

All the incubation mounds in the study area were visited at least twice every day, during which, the presence of the birds on the mound, or the signs of birds on the mound subsequent to the previous visit were noted. The megapodes were intensively observed from observation hides constructed at four different mounds. The activities of the birds were classified into visit, pit-digging, egg-laying, and raking, covering, pits-filled, and miscellaneous activities. The intensity of digging activity was measured by counting the kick rates. The data collected was used to examine a) the process of mound construction and maintenance, and b) the contribution of sexes to mound construction and maintenance.

Both partners of the pair equally participated in the mound construction and maintenance, which starts from pit-digging and concludes with raking and covering the incubation mound such that all pits present were filled till the surface of the mound was smooth. Pit digging was the major mound activity followed by the raking during the dry season (peak period for egg laying). In the wet season raking was the major mound activity followed by digging. Egg laying was not observed during the wet season.

In 1996, four temperature probes were implanted at depths between 20 and 75 cm, in seven mounds that had been selected for intensive studies. However, after about two months these probes malfunctioned, probably due to high humidity and rainfall. In 1997, a temperature probe placing at the tip of a one metre long steel tube was inserted to depths of 30, 60 and 90 cm in the mound. By this method, the temperature of all the mounds in the study area was measured once a month and for the target mounds once every 10 or 15 days. Microbial

activity was measured using a soil respirometer (PP Systems EGM-1 Environmental Gas Monitor with a SRC-1 Soil Respiration System), once every 10 or 15 days. The intensity of light falling upon the mound was measured using a lux metre and the amount of Photosynthetically Active Radiation (PAR) falling upon the mound and PAR absorbed by the mound were measured by using a Sunfleck Ceptometer. The data were used to examine a) temperature sources of incubation mound, b) the effect of incubation mound size on the incubation temperature, c) the effect of soil respiration and light intensity on the incubation temperature, d) the effects of incubation mound size on egg-laying and hatching success and e) the effect of incubation mound activity on the mound size and egg-laying.

Microbial activity as assessed from the soil respiration, appears to be the primary source of heat in the incubation mound of the Nicobar Megapode. Solar energy warms the surface of the mound, whereby dissipation of heat could reduce. Large sized mounds attract more birds and therefore more eggs were laid in them, but there was no relationship between the hatching success and the mound size.

During the study period, 28 megapodes were colour marked. Of these, both sexes were colour marked in five pairs, one bird each of 16 pairs and two unpaired birds. The sightings of all colour marked birds were plotted on detailed maps of the study area. The megapodes were intensively observed from the observation hides constructed at four mounds and opportunistically away from the hides. Size of the home range was estimated by using a minimum area polygon. The data was used to examine a) the pair bond, b) pair formation, c)

copulation & displays, d) establishment of territory, e) territory size and fidelity, and f) agonistic interactions between megapodes.

Although the Nicobar Megapode is largely monogamous, temporary bonds, change of partners, and extra pair copulation were present. There was no pre- and post-copulation display. However, they exhibited synchronous behaviour such as duetting. A mound was used by more than one pair, and pairs used more than one mound. During egg laying, a pair established a territory at a mound, which was strongly defended from others who used the same mound in the same period.. The territories varied in size and changed in location according to the hierarchical status of the pair at the mound, and whether it was laying eggs. The average size of the territory was 0.81 ha (SE 0.12), the minimum territory size was 0.19 and 2.28 ha was maximum.

The hatching and emergence of chicks from the mound was observed in five cases. The climb of the hatchling from the egg chamber to the surface is a long process that can take up to 83.8 hours (SE=12.7, max=118, min=48 hrs), and the mean rate of movement was about 1.25cm per hour (SE=0.07, n=5). As soon as the chick emerged out from the mound they performed both body and leg preening. Some of the chicks were born with eye disorder. Considering how alert the chicks are, it is likely that those preyed upon by the predators were also born with the eye disorder.

Food of the Nicobar Megapode, as evidenced from the stomach contents of three dead birds and from the stomachs of five birds flushed was identified and estimated its quantity. The percentage of time spent for foraging, and the difference between years is discussed.

The Nicobar Megapode nesting grounds attracted a wide range of predators as the main potential prey *M. n. abbotti* occurs in three types eggs, chicks and adults. Monitor lizard *Varanus salvator,* raptors, man, python sp., cat, dog and some invertebrates preyed on the eggs or chicks or adult megapodes. Monitor lizard not only fed on the eggs of the megapode and also laid its own within the incubation mound.

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Chapter I

INTRODUCTION

The megapodes are a unique group of birds as they utilise external sources of heat to incubate their eggs (Jones *et al.* 1995). The Megapodiidae, literally meaning big feet after the birds disproportionately large feet, were first described to science during Magellan's 1519-1522 expedition to the Far East (Frith 1959). The family Megapodiidae consists of 22 species in seven genera, most of which are island forms occurring in Australia, New Guinea and surrounding islands, eastern Indonesia, the Philippines, Niuafo'ou Island, the Palau and Mariana Islands and the Nicobar Islands (Dekker 1990). Thirteen of these 22 species are currently threatened by habitat destruction, introduction of predators and over-exploitation of eggs (Jones *et al.* 1995).

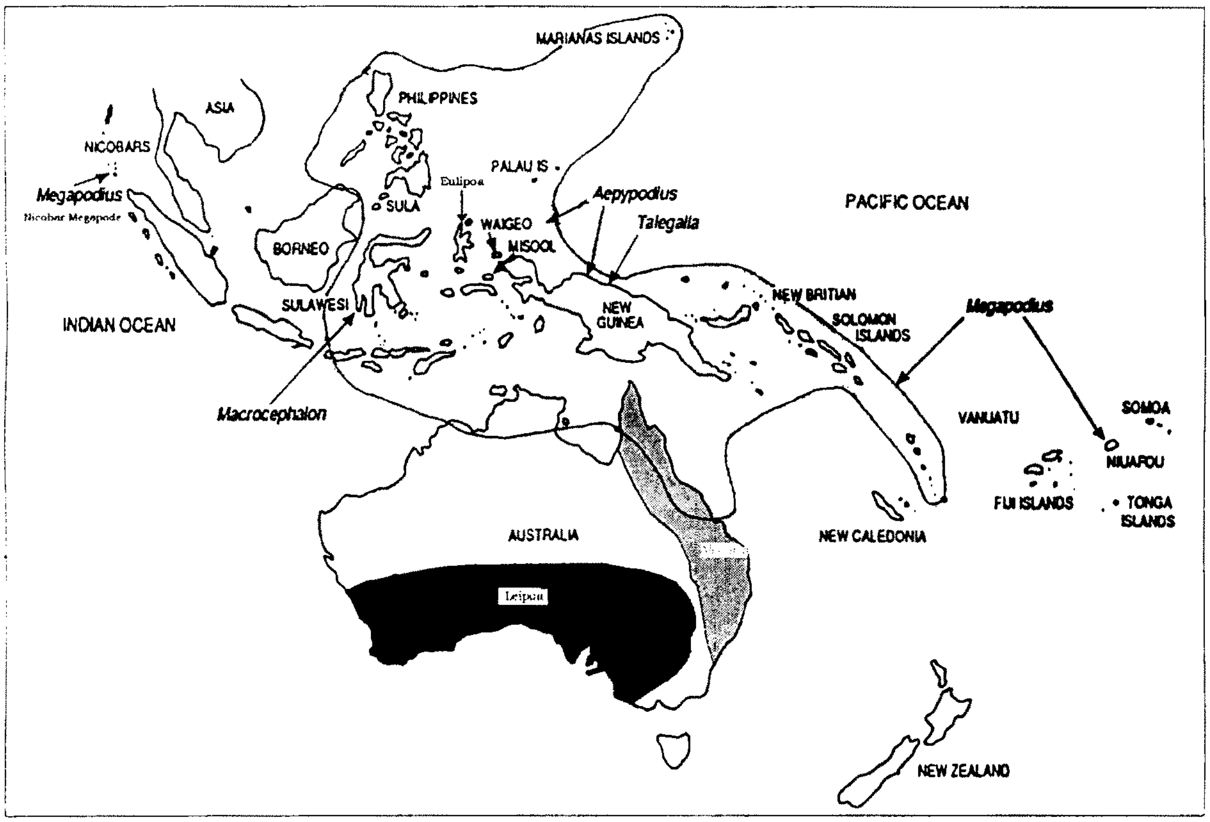
The taxonomic classification of the Megapodiidae is still subject to debate (Jones *et al.* 1995). The megapodes were believed to have more affinities with Charadriiformes, Columbiformes, Passeriformes and even Falconiformes. Later megapodes were included in the order Galliformes and were believed to be closely related to Guans and Curassows. In 1899, Sharpe divided the Galliformes into several suborders; the "megapodii" was first among them. After studying the osteological, karyological and biochemical properties of egg white proteins of megapodes and other galliformes, the monophyletic origin of Megapodiidae was considered as the sister group of all remaining Galliformes (cf. Jones *et al.* 1995).

Megapodes are heavy-bodied birds of the forest floor and resemble other Galliformes in body shape and plumage. Most megapodes are brown, blackish, or grey in colour. Many have virtually bare areas on their face or neck and this exposed skin may be coloured yellow, blue, or dull red. Megapodes are opportunistic ground foragers, eating a wide variety of foods such as insects, seeds, and fallen fruits. Although all are able to fly, and some make considerable flights on a daily basis, most species move primarily by walking (Jones *et al.* 1995).

The family Megapodiidae contains seven genera (Appendix I): Megapodius, Macrocephalon, Talegalla, Aepypodius, Alectura, Leipoa and Eulipoa. The genera Megapodius and Eulipoa have the smallest megapodes and their geographical variation is considerable but most are domestic-chicken-sized birds with short tails and a short pointed nuchal crest (Beehler *et al.* 1986). The monotypic genus Macrocephalon is closely related to the genus Megapodius. The Talegalla species do not have wattles and are large sized black coloured megapodes. Alectura is considered to be closely related to Talegalla and Aepypodius, a group known as the Brush-turkeys, each having a bare neck and face that may be brightly coloured (Jones *et al.* 1995). Alectura and the two Aepypodius species also possess inflatable necksacs or wattles and combs, and have brilliantly coloured heads and necks (Jones *et al.* 1995). The Brush-turkeys are the only group in which sexual dimorphism is evident, with the males being slightly larger and more colourfully ornamented than the females. The Leipoa species is characterised by their contrasting body colour, dense feathering on head and neck, short and thin bill and short legs.

The Megapodiidae are mainly found in the Indo-Australian region east of Wallace's line (Jones *et al.* 1995) (Fig 1.1). There are three exceptions to this: *Megapodius nicobariensis* from the Nicobar Islands, *Megapodius pritchardii* from Niuafo'ou Island and *Megapodius laperouse* from the Pulau and Marianna Islands. Based on these exceptions, Lister (1911) said that these species were introduced into the respective islands by domestication and then transported from one island to another. This theory was later rejected and two new theories were presented to explain the distribution of the megapodes. Olson (1980) considered Phasianids and Megapodes as ecological counterparts that could not co-exist, and suggested that the megapodes were restricted largely to islands, due to the presence of pheasants on neighbouring mainlands. However, the occurrence of the Green Jungle Fowl *Gallus varius* and Orange-footed Megapode *Megapodius reinwardt* in the Lesser Sunda Islands, and similar types of sympatric distribution of both Phasianids and megapodes in Palawan and Borneo, resulted in an alternative theory proposed by Dekker (1989). Based on mammalian predation, especially by cats and civets, Dekker (1989) proposed that mammalian carnivores prevented the expansion of the megapodes westward. The high predation pressure associated with the wide variety of large predators on the Greater Sunda Islands and on the mainland of Southeast Asia rendered these regions unsuitable for mound-building megapodes. The fact that the Nicobar Islands have never had a land connection (Dekker 1989) and are thus devoid of carnivores could explain the occurrence of the Nicobar Megapode. The predation theory, however, is also debatable because of the coexistence of carnivores (Little Civet *Vivericula indica* and Leopard cat *Prionailurus bengalensis*) and the Orange-footed Megapode on the Lesser Sunda Islands (Jones *et al.* 1995)

Figure 1.1. Distribution of the megapodes (source Jones 1989b)



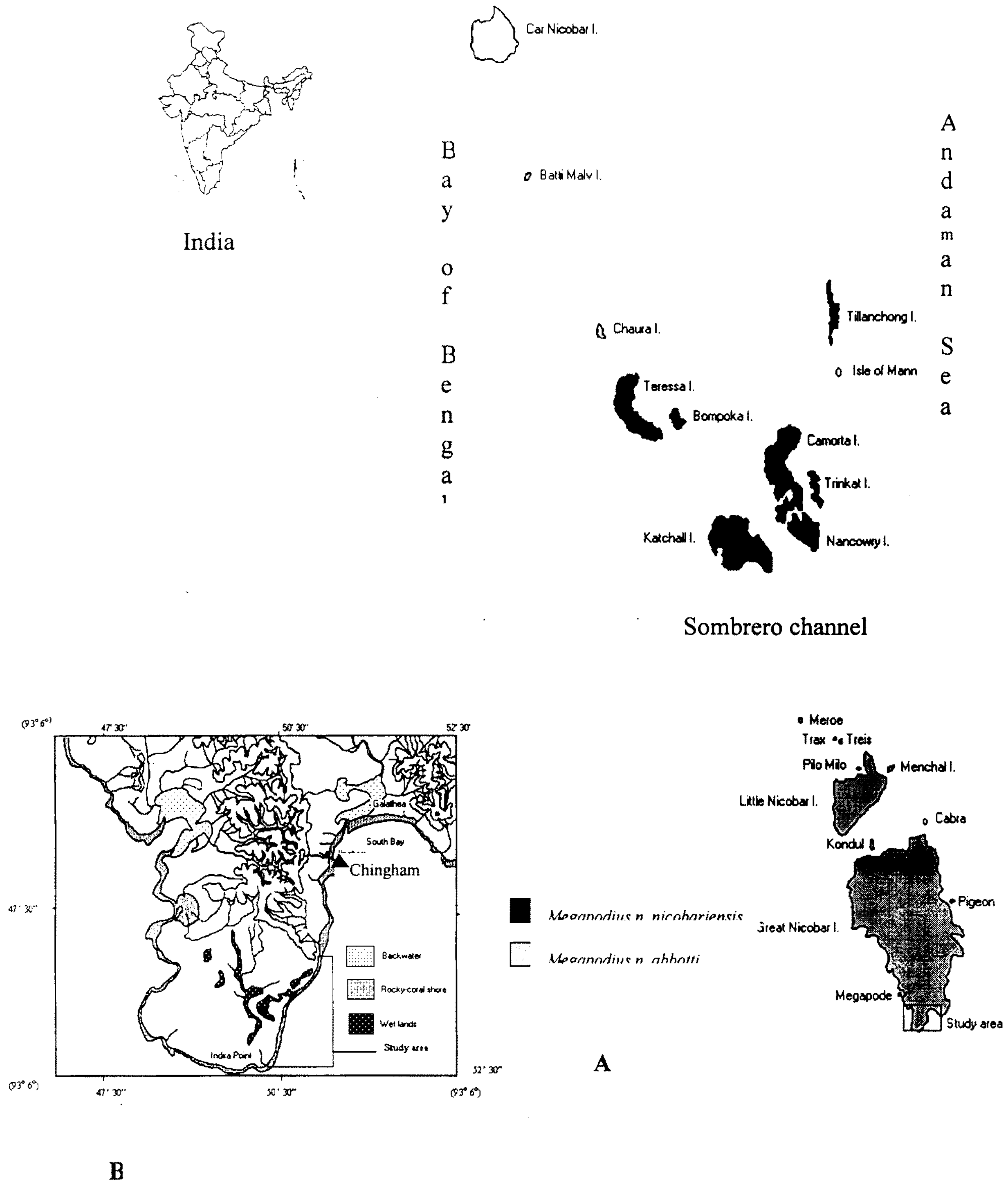
Megapode eggs are large and heavy compared with the eggs of birds of equivalent size, and 48 to 69 per cent of weight of the egg contents is yolk (Dekker and Brom 1990). These large-sized eggs are incubated by the megapodes in mounds or burrows. Based on this, megapodes are divided into two groups: species that lay eggs in burrows in geothermally heated soils are called burrow nesters (e.g. *Macrocephalon maleo*) and the mound builders, which construct mounds of decomposing vegetative matter (e.g. *Megapodius nicobariensis*).

1.1 THE NICOBAR MEGAPODE

The Nicobar Megapode *Megapodius nicobariensis*, a mound nesting megapode, is endemic to the Nicobar Islands in the Bay of Bengal, over 1500-km from its nearest congeneric (Olson 1980). The polytypic Nicobar Megapode has two subspecies. *M. n. nicobariensis* Blyth, is present in the Nancowry group of islands north of the Sombrero channel, and *M. n. abbotti* Oberholser, is found on the Great Nicobar group of islands lying south of the Sombrero channel (Hume and Marshall 1878, Abdulali 1964, Ali and Ripley 1983, Fig 1.2).

The Nicobar Megapode is a terrestrial brown or reddish-brown bird with a pinkish-red bare patch around the eye and a greyish crown; the dorsal side of the leg is blackish-brown and the ventral side

Figure 1.2. Study area. *Megapodius nicobariensis* occurs as two subspecies. *M. n. nicobariensis* found in the Nancowry group of islands north of Sombrero channel and *M. n. abbotti* found in the Great Nicobar group of islands (A). The intensive study area was at the southern tip of Great Nicobar (B).



yellowish. Usually seen in pairs in forests close to the beach, the sexes are alike. The total body length is 37-40 cm (Jones *et al.* 1995, Appendix II). Newly hatched chicks have the crown, upper parts, and upper wing rufous brown, and the under parts a dull cinnamon-brown, sometimes with slight grey tinge, with the lower back inconspicuously rufous and black (Ali and Ripley 1983).

The Nicobar Megapode occurred on most Nicobar Islands (Hume 1874; Kloss 1903; Dekker 1992; Sankaran 1995) but was not found on Car Nicobar (Butler 1899) and Chaura (Abdulali 1967). There were a few records from the Andaman group of islands (Hume 1874; Butler 1899; Sewell 1922) and from the Coco Islands further north (Kloss 1903; Abdulali 1964). None of the records from the Andaman group are of recent origin and the species is believed to be absent there (Sankaran 1995a & b). It may have existed on Car Nicobar (78 km north of Teressa the nearest megapode population) a century ago (Kloss 1903) but no traces of mounds were found there (Sankaran 1995a&b). The island of Chaura is only 11.5 km from Teressa and, considering the megapode's occurrence on the more remote Tillanchong, there is no reason why it should not have existed there (Sankaran 1995). The presence of what was most probably an ancient mound indicates that the megapode did occur on Chaura historically (Sankaran pers. commn.). However, both Car Nicobar and Chaura are much too densely populated for the species to exist there now.

1.1.i. *Megapodius nicobariensis abbotti* Oberholser, 1919.

M. n. abbotti was common in all coastal forests, particularly uninhabited or sparsely inhabited areas, on Great and Little Nicobar. *M. n. abbotti* was believed to have disappeared from all areas colonised by mainlanders (Dekker 1992), but they continued to survive in small remnant pockets (Sankaran 1995a, b). Seven of the nine islets in the Great Nicobar group had habitat suitable for megapodes and two (Cabra and Pigeon) were too small. Small populations of megapodes are present on six of these seven islets. The seventh islet, Pilo Milo, is inhabited, and the islet is mostly under coconut palms. Megapodes are apparently extinct on this islet, though reports of calls heard indicate that it may still survive there. Over 50% of the forests of uninhabited Meroe, Treis, Trak, Menchal and Megapode Island have been converted to coconut plantation, and populations of megapodes on these islands may be threatened.

1.1.ii. *Megapodius nicobariensis nicobariensis* Blyth, 1846.

M. n. nicobariensis occurs on seven islands of the Nancowry group (Sankaran 1995a, b). On Camorta, Katchall and Trinkat, *M. n. nicobariensis* was patchily distributed, with very few locations having active mounds and even fewer where mounds were abundant. Good populations of megapodes existed only on Teressa and Bompoka and the density of active mounds was similar to that of Great and Little Nicobar. Tillanchong is mainly hilly with very little level coastal forest, thus megapodes were naturally scarce except in the level forests.

1.2. THE MOUND OF THE NICOBAR MEGAPODE

The Nicobar Megapode builds mounds of sand, loam, pieces of coral and rotting vegetation within which the eggs are laid. Mounds varied in height from 10 cm to 2.1 m and in basal circumference from 7 m to 45 m (Sankaran 1995a, b). Basically three types of mounds were built by the Nicobar Megapode and have been described by Dekker (1992) as: Type `A' mounds or true mounds, regular in shape and built on an open spot away from trees; Type `B' mounds, irregular in shape, built against the buttress or stem of a large living tree; Type `C' mounds, also irregular in shape but built against, around, under or over a dead rotting tree stump or log.

1.3. STATUS

The Nicobar Megapode was considered to be seriously endangered (Jones 1989b; Jones and Birks 1992), and has featured in several lists of endangered species (e.g. Collar and Andrews 1988). In 1988, the extinction of the megapode from Kondul was reported, a population of less than 400 birds was estimated on Great Nicobar and the extinction of this species was predicted in the next 10 years (Anon. 1988). However, Dekker (1992) estimated the population of *M. n. abbotti* at about 780 breeding pairs (if not more) in the coastal area of Great Nicobar and concluded that it was not threatened there. The population of *M. n. abbotti* was estimated to be between 3400 and 6000 birds and the number of active mounds at 849 (Sankaran 1995a). The population of adult breeding birds of *M. n. nicobariensis* was estimated to be between 1200 and 2100 birds and the number of active mounds to be a little over 300 (Sankaran 1995a). Currently, *Megapodius nicobariensis* is considered as vulnerable (Sankaran 1995a&b).

The Nicobar Megapode is protected under Schedule I of the Indian Wildlife Protection Act (1972) whereby hunting and trade is prohibited. The ethnic tribes of the Nicobar Islands (Nicobarese and Shompen) are exempt from the Act.

Studies on the Nicobar Megapode so far focused on assessing the status of the species (Dekker 1992, Sankaran 1995a, b). There was no other detailed ecological study about this bird in the literature.

1.4. OBJECTIVES

1. To assess the microhabitat preferences of the Nicobar Megapode.
2. To understand the incubation conditions of the mound,
3. To understand the social organisation of the Nicobar Megapode.

1.5. STUDY AREA

1.5.1. The Andaman and Nicobar Islands

The Andaman and Nicobar Islands (latitudes 6° 45' and 13° 41' and longitudes 92° 12' and 93° 57') in the Bay of Bengal arch from Arakan Yoma in Mayanmar in the north to Sumatra in Indonesia in the south (Saldanha 1989; Dagar *et al.* 1991). The islands cover an area of 8,249 km^2, with a total coastline of 1962 km; the Andaman group has more than 325 islands (21 inhabited) covering 6,408 sq km, and the Nicobar group has over 23 islands (12 inhabited) with an area of 1,841 sq. km (Singh 1981; Saldanha 1989).

1.5.2. The Nicobar Islands

The Nicobar Islands can be subdivided into three distinct subgroups based on ornithological affinities (Sankaran 1997). To the south lies the Great Nicobar group consisting of two islands over 100 km^2 in area, nine islets less than five km^2 in area, and a few rocks. Great Nicobar, Little Nicobar, Kondul and Pilo Milo are inhabited. Meroe, Treis, Trax, Menchal, Megapod, Cabra and Pigeon are uninhabited islets. Fifty-eight km north of the Great Nicobar group is the Nancowry group (middle Nicobar Islands), which consists of three islands larger than 100 km^2, two of 36 and 67 km^2, three less than 17 km^2, 2 small islets and a few rocks. Except islets, all other islands of Nancowry group are inhabited. The northernmost subgroup comprises Batti Malv and Car Nicobar, which is 88 km north of the Nancowry group. Batti Malv is uninhabited and Car Nicobar has a population of over 19000 people.

The shore line of Nicobar Islands are endowed with varied landscapes such as rocky shore, sandy beaches, backwaters, bays, lagoons, mangrove forests and coral reefs. To the interior most of the islands have undulating terrain with the main ridges running north-south, falling steeply and irregularly on both sides to the floor of the Bay of Bengal and the Andaman sea. The Great Nicobar groups is significantly more hilly than the Nancowry group, with the high peak, Mt. Thullier at 670 m above MSL.

The soil shows considerable variability from heavy clay, loam, gravely loam, sandy loam and sand. The depth of soil depends on the slope, with deep alluvial deposits often found along the lower reaches of the creeks. The soil lacks humus due to continuous leaching by heavy rainfall.

Four islands in the Nicobar group have areas protected as wildlife preserves, and all islands are tribal reserves. Tillanchong, Batti Malv and Megapode Island, all uninhabited, are Wildlife Sanctuaries. However, a police out post has been established in Tillanchong during the early months of 2000. Great Nicobar has two National Parks (536 km^2) and is also a Biosphere Reserve (885 km^2), whose core areas are the National Parks (Sankaran 1997).

1.5.2.i. *Flora*

The vegetation and the floristic composition of the Car Nicobar group, Nancowry and Great Nicobar groups of islands differ from one another (Thothathri 1962). In general the vegetation of the Nicobar Islands can be classified into six groups: Marine vegetation, beach vegetation, tidal mangrove forest, inland evergreen forests, patches of deciduous forest and grassland and open vegetation (Thothathri 1962).

The beach forests or the dune forests are restricted to the beaches of fine calcareous sand which stretch along the shores. Creepers that mark the beginning of beach vegetation are *Ipomoea per-caprae, Vigna retusa, Ischaemum muticum, Phyla nodiflora* and herbs such as *Acalypha indica* etc. *Scaevola frutescens* is the immediate successor to these plants. *Tournefortia argentina* is a large shrub with silvery pubescent leaves and is very common in Katchall, Camorta and Great Nicobar Islands (Thothathri 1962). *Pandanus leram, Pandanus* *tectorius* and *Pandanus furcatus* grow luxuriantly in this forest. The shrubby layer is followed by trees such as *Barringtonia asiatica*, *Terminalia catappa*, *Calophyllum inophyllum*, *Hernandia peltata*, *Pongamia pinnata*, *Heritiera littoralis*, *Ficus rumphii*, *Odina wodier* and *Syzygium samarangense*. *Cycas rumphii*, *Cerebra manghas* and *Cerbera odollam* grow well under the shade of these trees. *Casuarina equisetifolia* is present on some islands. The ground cover consists of grasses such as *Centotheca lappacea*, *Oplismenus compositus*, *Chrysopogon aciculatus*.

Mangrove forests are found in patches of varying sizes in most islands. The dominant species present in the mangrove forests are *Rhizophora mucronata*, *Bruguiera gymnorrhiza*, *Excoecaria agallocha*, *Carallia brachiata*, *Sonneratia acida*, *Timonius jambosella* and *Nipa fruticans*.

True tropical evergreen forests are present in the Nicobar Islands (Thothathri 1962). In Great Nicobar the forests are extensive and completely cover the hill ranges and even flat areas. The most common and dominant tree species in tropical evergreen forests of Great Nicobar are *Calophyllum soulattri*, *Sideromylon longipetiolatum*, *Endospermum malaccense*, *Garcinia xanthochymus*, *Adenanthera pavonia*, *Albizzia lebbeck*, *Pisonia excelsa* and *Mangifera sylvatica* (Sahni 1953). Patches of deciduous forest with *Terminalia procera* and *Terminalia bialata* have been reported at low elevations in Great Nicobar (Sahni 1953). The forest floor is covered with herbaceous plants such as *Blumea myriocephala*, *Lasianthus laevicaulis*, *Homalonema aromatica*, *Adenostemma viscosum* and *Maranta dichotoma*. In areas where rainwater accumulates *Helminthostachys zeylanica* is common, growing together with *Polygonum flaccidum* (Thothathri 1962).

Grasslands are peculiar to Camorta, Nancowry, Trinkat, Teressa and Bompoka Islands (Thothathri 1962; Sankaran 1995b) and in some patches on Chaura and Car Nicobar. *Imperata cylindrica* and *Saccharum spontaneum* are the most dominant grass species present in these islands (Thothathri 1962).

1.5.2.ii. *Fauna*

The Nicobar Islands are the summits of a submarine mountain range having a continuation with the Arakan Yoma of Burma (through the Andaman Islands) in the north and the island festoons of Sumatra in the south. The Nicobar Islands contain an impoverished Sumatran fauna (Smith 1930), but Stoliczka (1870) remarked that several species of lizard and snake are common to both Andaman and Nicobar Islands, and the whole fauna generally resembles the Malayan, gradually passing into Burmese fauna. Affinities of mammalian and avian species of these islands seem to be closer to India than Burman and Malay (Abdulali 1964). The islands are characterised by the absence of large mammals and the presence of a considerable number of endemics among the island's vertebrates (Appendix III).

Within the Nicobar group of islands there are significant differences in the faunal profiles (Sankaran 1997). For example, the Blyth's Nicobar Parakeet *Psittacula caniceps* occurs on Great Nicobar, Little Nicobar, Kondul and Menchal but is absent in the Nancowry group.

The Nicobar Bulbul *Hypsipetes nicobariensis* is present in the Nancowry group but is absent in the Great Nicobar group. The Nicobar Racket-tailed Drongo *Dicrurus paradiseus nicobariensis* occur on Great Nicobar, Little Nicobar, Katchall, and Car Nicobar but is absent on other islands of the Nancowry group (Sankaran 1997). The differences are also evident in the herpetofauna; Pit vipers are common on the Nancowry group but are absent in the Great Nicobar group. The Nicobar Crab Eating Macaque *Macaca fascicularis umbrosa* is present only on Great Nicobar, Little Nicobar and Katchall. The Nicobar Tree Shrew *Tupaia nicobarica* is present on Great Nicobar and Little Nicobar Islands but is absent on other Nicobar Islands (Tikadar and Das 1985).

1.6. GREAT NICOBAR

The intensive study area was on Great Nicobar Island, which is located between 6°45' N - 7°15' N, and 93°38' E - 93°55' E. The total area of the island is 1045 km^2 with five perennial rivers and five hill ranges. The highest point is Mt Thullier (670 MSL). Indira Point, where the intensive study area is located, is situated at the southern tip of this island (Fig. 1.2).

1.6.i. Climate and weather

The island is exposed to both Southwest and Northeast monsoons, with an average rainfall of 200 cm (recorded at Campbell Bay between 1996 and 1998; Fig 1.3). The bulk of the rainfall comes during the Southwest monsoon, and the wettest months are August to November, while the driest months are February and March when less than 5 cm of rainfall is received. The climate is humid, tropical-coastal due to its proximity to the equator. The average temperature varies from 25.5°C to 34.4°C. The average relative humidity is 80.8% and seldom goes below 70%. The islands get Northeast wind from November to January and Southwest from May to October. Cyclones sometimes bring huge devastation, endangering life. These islands are prone to earthquakes, which were experienced several times during the study period. Detailed weather data collected between 1996 and 1998 at both Campbell Bay and the study area is presented in figures 1.3 to 1.6.

1.6.ii. People

The survival, amelioration or degradation of ecosystem depends largely on man. Within the confines of an island ecosystem, the arrival of humans, especially in large numbers, can bring about great changes. Great Nicobar shows the impact of such an intervention. The human population on Great Nicobar (6831 people) has both tribal (8%) and mainland Indians including settlers. The tribals are thinly distributed along the southern, western and northern coasts and interior forest. Nearly 55% of the mainlanders are in the township of Campbell Bay midway up the East Coast, and the remainder pursues agrarian livelihoods along the southeastern coast.

Two groups of tribals inhabit Great Nicobar. The Shompen, who now number less than 150, are a semi-nomadic tribe who inhabit the forests of the central uplands. It is probable that they were pushed into inaccessible areas by the Nicobarese who have several settlements along the coast. The Nicobarese constitute the largest tribal group in the islands. Belonging to the Mongoloid race probably the Indomalayans, now number around 400 on Great Nicobar.

1.7. INDIRA POINT (Intensive study area)

The Study area lies at the southern tip of Great Nicobar Island and on the coast, is about 4 km long, and is bisected by a disused metalled road, which ends at the light house at Indira Point (Fig 1.2). The intensive study area, where the mounds are present is a narrow strip of forest between 40 m and 300 m wide, that is bounded by the beach to the east and to the west by either wetlands, or forests that are inundated. The soil within this strip of forest is sandy, loamy and muddy, and the dominant trees are *Barringtonia asiatica*, *B. recemosa*, *Terminalia bilata*, *Terminalia catappa*, *Syzygium samarangense*, *Thespesia populnea*, *and Macaranga* spp. The study area has dense stands of *Pandanus tectorius* and *P. odoratissimus* in patches, and the road is fringed by stands of *Lea angulata*, *L. grandifolia*, 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*, *Bongama pinnata*, *Alstonia kurzii*, *Adentania paranina*, *Aisandra butyracea*, *Horsfieldia irya*, *Myristica andamanica*, and *Celtis timorensis*.

1.8. STUDY PERIOD

The ecology of the Nicobar Megapode was studied between December 1995 and July 1996, December 1996 and June 1997, September and October 1997, and February and May

1998. The study period includes three dry season (peak period of egg laying) and part of one wet season.

Figure 1.3. The average monthly total rainfall and percentage of the humidity recorded at Campbell Bay during the study period.

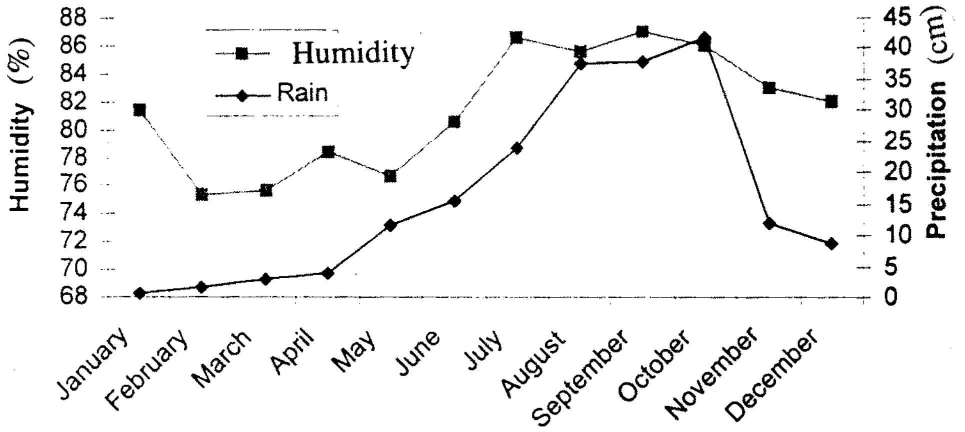


Figure 1.4. The average percentage of the humidity and monthly total of rainfall recorded at the study area in the respective month.

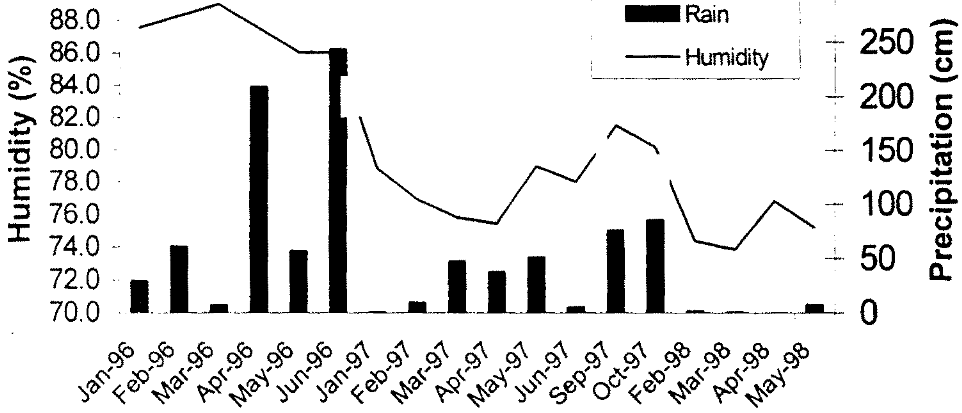


Figure 1.5. Maximum and minimum temperature recorded in the study area. (Average of year)

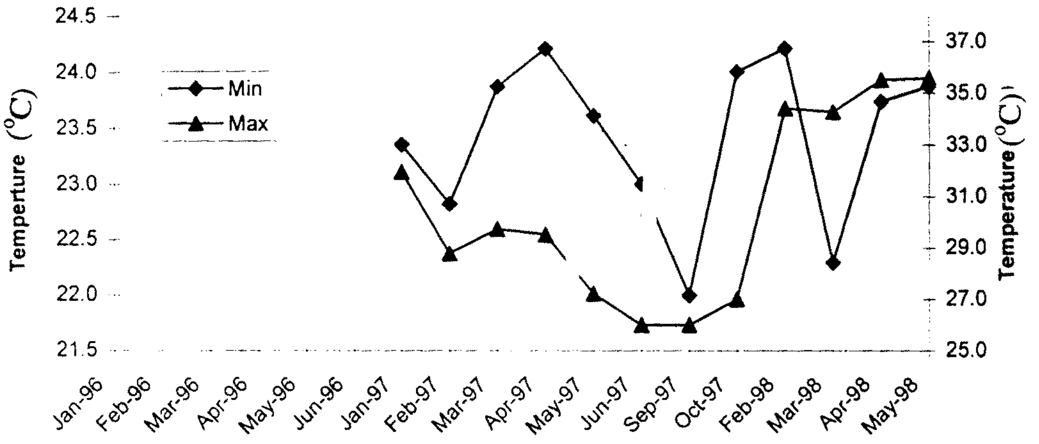
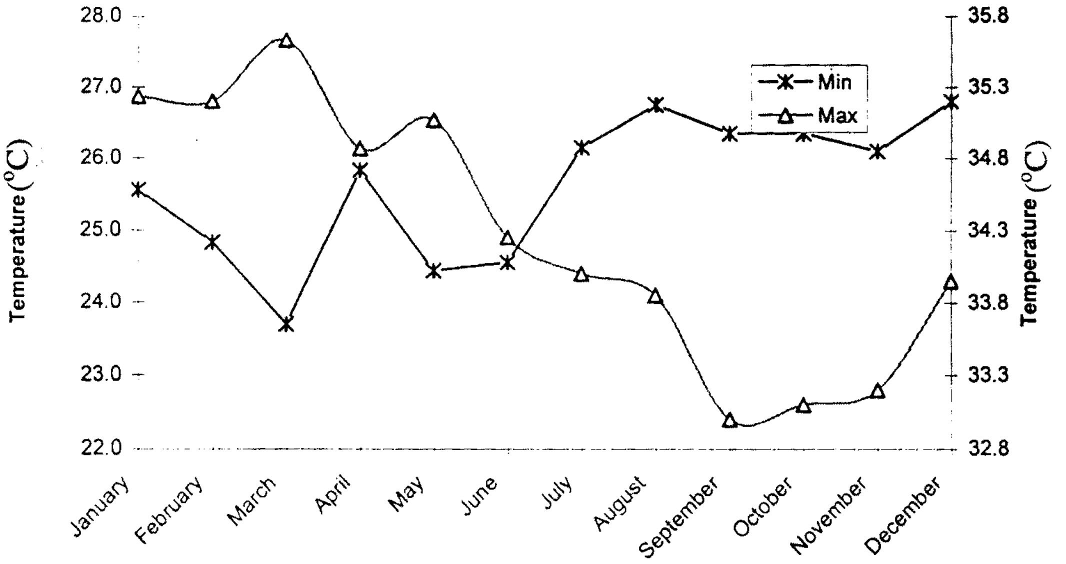


Figure 1.6. The average temperature at Campbell Bay during the study period.(Average of year)



1.9. GENERAL METHODOLOGY

1.9.1. Mapping the study area

In 1996, the study area was systematically surveyed and mapped with the aid of a compass and measuring tapes. The positions of incubation mounds, and other landmarks such as the road, huts and wells, were plotted on this map.

1.9.2. Habitat Utilisation

The vegetation of the study area was classified into fourteen microhabitats that were dominated by one or more species. These patches were measured and plotted to scale on the map. To understand the abundance and dominance of flora, ten 20m x 50m quadrats were laid in the study area. All the trees with a girth at breast height (GBH) of 25 cm or above were recorded. Within each quadrat, five subquadrats sized 1m x 1m were laid within which the percentage of herb, shrub and weed cover, were estimated visually. Relative frequency, relative dominance, relative abundance, important value index (IVI) were calculated by using the formula listed in table 1.

Micro-habitat utilisation (level of utilisation) of the Nicobar Megapode was calculated by using Neu's (1974) method (Alldredge and Ratti, 1992), whereby the sightings and calls heard were identified according to the micro habitat patch that they occurred in. Habitat preference was arrived at by comparing the available area of the microhabitat with the number of sightings and calls of the bird. Ratio of the sightings and calls per unit area of the respective microhabitat was estimated by using the following formula.

Table 1. Formulae used for vegetation analysis.

Frequency	Number of quadrats of occurrence
Relative frequency	Frequency ------------------ x 100 sum of frequencies
Abundance	# of individuals ---------------------------------- # of quadrats of occurrence (FREQ)
Relative abundance	Abundance --------------------- x 100 Sum of all abundances
Density (per quadrat)	# of individuals ------------------ Total # of quadrats
Relative density	Density --------------------- x 100 Sum of all densities
Basal area (or Dominance)	$\text{Sum}(Gbh_i^2/4\pi)$; where $i=1$ to nt; nt=# of individuals of species
Species cover	$\text{Sum}(cover_i/100)$; where $i=1$ to n; n=# of individuals of species
Relative dominance	TREE: Basal area --------------------- x 100 Sum of all basal area
Importance value index	RELA_FREQ+RELA_DENS+RELA_DOMI

1. Ratio of the sightings and calls per unit area of the habitat

$$= \frac{\text{Proportion of the sightings and calls 'in' the habitat}}{\text{Proportion of the area available for the habitat}}$$

2. Proportion of the area available for the habitat

$$= \frac{\text{Total available area of the habitat}}{\text{Total study area}}$$

3. Proportion of the sightings and calls on the habitat

$$= \frac{\text{Total number of sightings and calls on the habitat}}{\text{Total number of sightings and calls on the study area}}$$

Both dead and living tree species present in or on the mound were identified and recorded for studying the tree preference of the Nicobar Megapode for mound building.

The ratio of the mounds distributed per unit area (M) of the various soil substrates or micro-habitats was estimated by using the formula

$$\mathbf{M=P_m/P_a}$$

Where, P_m is proportion of mounds distributed in particular substrates or habitat, and P_a is proportion of area available for that substrates or habitat.

1.9.3. Incubation conditions within mounds

At the start of the study, or as and when a new mound was constructed, detailed drawings to scale were made of the mounds using measuring tapes and compass, and on to these, salient characteristics such as living trees and dead logs or tree stumps were plotted.

1.9.3.i. *Size of mounds*

The basal circumference, height and diameter of mounds were measured once a month. Mounds are uneven in shape with a cone like appearance. The mound size, expressed as a volume, 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, giving an approximate volume of the mound.

1.9.3.ii. *Mound use*

All the incubation mounds in the study area were visited at least twice every day in the morning and in the evening and occasionally during midday, to identify whether megapodes had worked on the mounds, and what type of activity they had engaged in. During the visits to the mound the following data was collected:

a) Presence or absence of megapodes on the mound.

b) Signs of megapode on the mound subsequent to the previous visit.

The activities at the mound were further separated into:

(i) *Scratching*: When the birds scratched on or around the mound.

(ii) *Digging of pits:* The digging of pits was a major activity on the mound. Three types of pits were distinguished as *shallow pits, deep pits* and *egg pits* according to their depth and purpose. As Megapodes usually lay eggs in pits that are over 60 cm in depth, pits that were less than 30 cm were considered to be shallow pits and those deeper than 30 cm were considered to be deep pits. Egg pits were considered to be pits in which eggs were laid. The pits were plotted on a map, and their depth measured and monitored.

(iii) *Raking:* The activity in which materials were collected from the surrounding area of the mound and spread onto the mound was called raking. The materials raked were mainly composed of the surrounding vegetation litter and soil.

(iv) *Egg laying:* After digging a deep pit, the female entered into the pit and laid an egg. Mostly egg laying was confirmed after checking the pit by digging in and marking the egg.

(v) *Pits-filled*: Both pits-filled and mound covering (below) were similar activities that the mound was covered with soil etc. However, the end result was different. In pits-filled only the egg pit or some shallow or deep pits was filled while the other pits on the mound remained unfilled.

(vi) *Mound covering*: Mound covering differs from pits-filled as all the pits were covered till the surface of the mound was smooth.

(vii) *Visit:* A brief arrival and departure of the megapode on the mound without working on it was recorded as a visit. This was also evidenced from tracks on the mound without digging signs.

(viii) *Random activity*: Shallow pit digging, scratching here and there on the mound, raking, covering, all done simultaneously, was recorded as random activity.

At the mound, the megapodes were intensively observed following the focal animal sampling method (Altmann 1974), from observation hides constructed at four different mounds, which were under intensive study. All the hides were positioned between two and 10 meters distance from the mound. Observations from the hide usually started from before the arrival of birds at the mound (at 0500 to 0530 hours) and ended after the birds left the mound. Observation recommenced at about 1400 hours and was carried on till dusk. The activities of the birds were classified into visit, pit digging, egg laying, raking, covering, pits-filled, and random activity. Apart from that the speed of the activity was also measured by counting the kicking rate.

1.9.3.iii. *Mound temperatures*

In 1996, four temperature probes were implanted at depths between 20 and 75 cm, in seven mounds that had been selected for intensive studies. However, after about two months these probes malfunctioned, probably due to high humidity and rainfall. In 1997, a temperature probe placed at the tip of a one metre long steel tube was inserted to depths of 30, 60 and 90 cm to measure the temperature. By this method the temperature of all the mounds in the study area was measured once a month and for the target mounds once every 10 or 15 days. Temperature data from each mound was collected twice a day, in the morning and evening. Occasionally the temperature of the mound was measured during midday.

1.9.3.iv. *Microbial activity*

Microbial activity was measured using a soil respirometre (PP Systems EGM-1 Environmental Gas Monitor with a SRC-1 Soil Respiration System), assuming that in those mounds where microbial activity was high greater amounts of CO_2 would be emitted. The soil respirometre measures the CO_2 change in a fixed volume over a known time and fits a quadratic equation to the data to arrive at a value `SR' which is the soil respiration rate in g CO_2/m^2/hour. Soil respiration was measured for the seven mounds that were under intensive study once every 10 or 15 days. Like temperature, data on the soil respiration of mounds were collected twice a day.

1.9.3.v. *Solar Radiation*

The intensity of light falling upon the mound at different times of the day was measured using a Lux meter. The amount of Photosynthetic Active Radiation (PAR) falling upon the mound and PAR absorbed by the mound were measured by using Sunfleck Ceptometer (Decagon, Pullman, WA). This was also measured outside the mounds. The gap in the canopy cover was measured above the mound by using a concave mirror that was uniformly graduated.

1.9.3.vi. *Humidity*

Soil samples were collected from the surface of the mound and then sun dried for an hour. Percentage of the humidity was measured by using the following formula:

Humidity ={(Wet soil weight-sun dried soil weight)/Wet soil weight} X 100

1.9.4. Fecundity and hatching success

During the breeding seasons of 1996, 1997 and 1998, 37 mounds were monitored. When an egg was laid, it was dug out and weighed to the nearest gram by using a spring balance (Pesola 300 g). Eggs were also measured with Vernier calliper and marked with a number and date by a HP graphite pencil or ballpoint pen. After weighing and marking, the egg was reburied in the same egg chamber and the mound re-built. To observe hatchling behaviour inside the mound, glass plates were placed adjacent to the egg chambers of five eggs.

During 1997 and 1998 thirty-three eggs were marked and monitored directly. The marked eggs were monitored by relocating it once every 15 days. Temperature at the egg chamber was measured once every 15 days to determine the incubation temperatures. At the beginning of 1998, all the mounds were thoroughly checked with the help of 1997 mound maps where the locations of eggs were clearly plotted.

Successful hatching of eggs was evident from eggshell fragments and pieces of shell membrane where the eggs had been. Emergence from the egg by the chicks during the course of incubation and hatching were easily observed through the glass plates. Eggs which remained in the mounds for the entire breeding season, or an egg which covered more than 100 incubation days were opened and examined.

1.9.5. Social Organisation

Adult birds were trapped near their incubation mounds or foraging ground. In 1996, mist nets were placed on the route that megapodes used to or from the mound. When the birds were seen working on the mound, the nets were spread. When the birds had completed work on the mound, they were chased and flushed into the nets. The trapped birds were then ringed with aluminium numbered tags and with a combination of plastic wrap around colour rings whereby individual identity was established. However, this method proved to be both time-consuming and had a very low success rate of six successful captures in 72 attempts. In 1997 and 1998 foot nooses were used which gave a significantly higher success rate of one in six attempts. The disturbances caused by nooses were also less, as evidenced by the time taken between trapping and first mound visit by the colour marked bird. Birds trapped by the mist net returned to the mound after 5 to 10 days but birds trapped by nooses returned the same or the next day. The outer end of the wrap around colour band was glued to the layer below, as the megapodes were easily able to pull off these rings; at least three colour marked birds lost their colour ring during the study period

During the study period, 28 birds were colour-marked, which included 21 pairs and two unpaired individuals. Of these both sexes were colour marked in five pairs.

In 1996, six birds from two mounds were colour-marked which included an unpaired bird, both sexes in two pairs, and one individual of a third pair. In 1997, 17 birds from 9 mounds were colour-marked, including one unpaired bird, both sexes in three pairs, and one bird each of 11 pairs. In 1998, five birds of four pairs were trapped from four mounds.

The sighting of all colour-marked birds were plotted on detailed maps of the study area. Size of the home range was estimated by using minimum area polygon (Odum and Kuenzler 1955), by connecting the outer locations of sightings of the animal.

1.9.6. Food of Nicobar Megapode

The food of the Nicobar Megapode was ascertained from gut samples of two specimens acquired from tribals, which were shot by them, and a dead individual found in the study area. The gut contents were identified, sorted out and then grouped. The stomach contents of two deceased chicks were examined but no volumetric analysis was attempted.

In 1998, a plastic tube of 4-mm diameter attached to a 500-ml plastic bottle filled with saline was moistened with the saline solution for lubrication and inserted into the stomach stopping just above the entrance to the gizzard. The bird was then inverted over a plastic cup so that, as fluid was forced into its stomach, the excess fluid plus the stomach contents flowed into the cup. Hess (1997) used the same methodology in the Red-cockaded Woodpecker *Picoides borealis*. By this method five megapode stomachs were flushed.

The preference rank of each food item consumed by the Nicobar Megapode was arrived at both by volumetric method and occurrence method.

The volume of the food items was estimated by the volumetric method or the water displacement method. This was then expressed as a percentage of the volume of individual food items from the total. Apart from the volumetric estimation, occurrence of food items was recorded from the collected specimen. For example, if ants were present in the stomach of two bird out of the seven then ants were scored two points. This was then expressed as the percentage of each food item from the total points scored.

1.9.7. DATA ENTRY & ANALYSIS

Data analyses were done in Lotus, Microsoft-Excel and SPSS software.

Chapter II

HABITAT PREFERENCE AND ITS UTILISATION

2.1. INTRODUCTION

The native environment of a species or the kind of place that is natural for the life and growth of the species is called its habitat (Levins 1968; Rands 1988). All natural environments are complex mosaics of patches that differ in their intrinsic quality to organisms. The fitness of an individual will be maximised if it successfully establishes itself in an optimal habitat (Levins 1968). Habitat preferences of a bird could either be (a) completely innate, (b) based entirely upon an imprinting to the habitat type within which the individual was raised, or (c) combinations of the two (Orians 1971). Identification of habitat features that directly affect reproduction and survival is the most effective means of indexing habitat suitability because maintenance of viable populations depends on sustaining these fitness components (Conway and Martin 1993).

Most species of megapodes inhabit forests with the sole exception of the Malleefowl, which is present in arid and semi-arid habitats (Jones *et al.* 1995). As a result of their unique breeding behaviour, megapodes have specific habitat requirements. Burrow nesters require sites where sun or volcanic activity provides heat for incubation, while mound builders require habitats where mounds have adequate organic decomposition to provide necessary heat for incubation (Dekker 1990). Despite the obvious importance of habitat to these specialised birds, there have been no detailed studies on habitat preferences and utilisation in this group.

Mounds of the Nicobar Megapodes are usually made close to the shore but are also present some distance inland (Hume and Marshall 1878; Sankaran 1995a, b). In the Nicobar islands, 97% of mounds of Nicobar Megapode were found within 100m of the beach (Sankaran 1995) where the habitat present is generally classified as the "coastal forest" which is comprised of both rain forest as well as deciduous species (Thothathri 1962). Nesting near the beach is also common in some other megapodes (Stuebing and Zazuli 1986). As coastal forests are subject to increasing anthropogenic pressures, understanding habitat requirements of the Nicobar Megapode *Megapodius nicobariensis* is necessary for the better management of habitats in which the species occurs.

2.2. OBJECTIVES

1. To identify the distribution of incubation mounds
2. To identify the microhabitats preferred for mound construction.
3. To identify habitats used by the species for activities other than mound construction.

2.3. RESULTS

2.3.1. Distribution

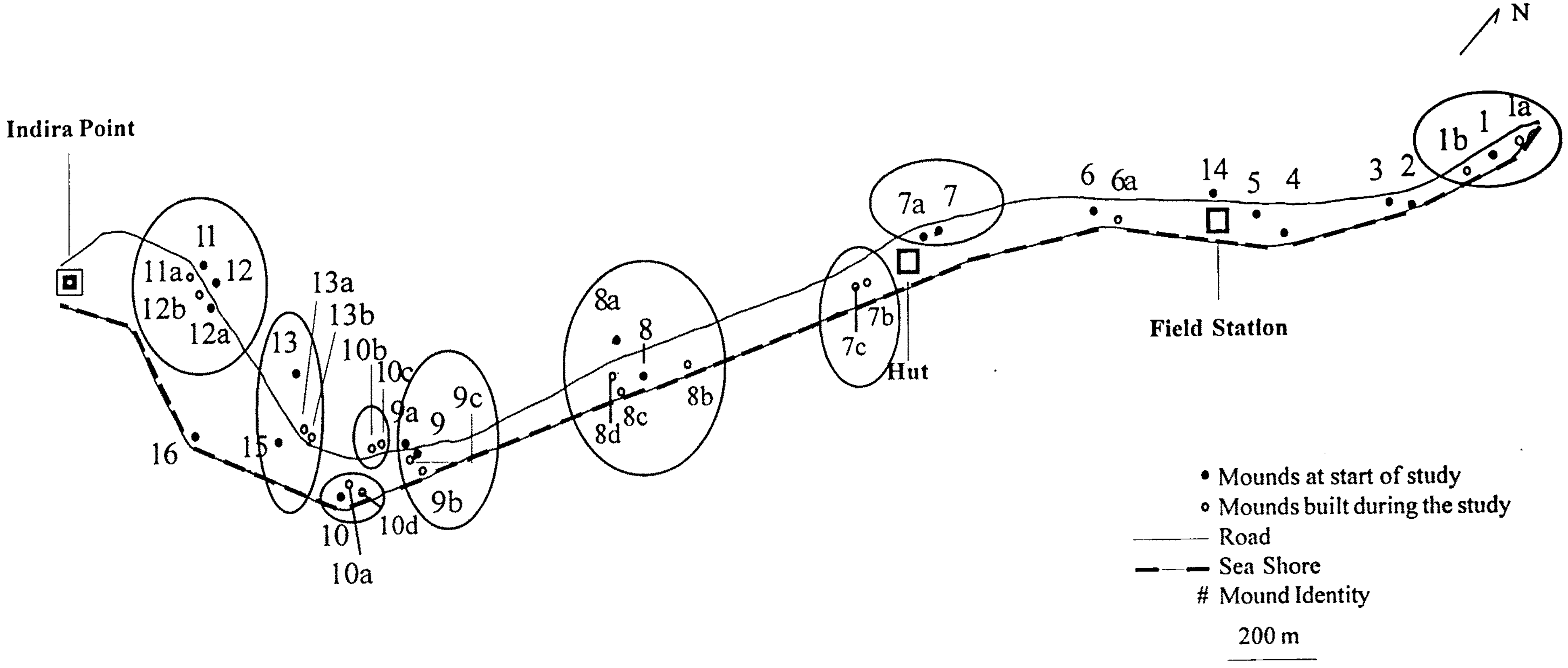
Incubation mounds were present throughout the study area (Fig 2.1). At the start of the study in January 1996, 16 active mounds were located. Between January and June 1996, four more mounds were found, which had been missed in the initial survey, and two new mounds were constructed.

Between December 1996 and June 1997, additionally seven mounds were constructed and two more mounds, which had been missed so far, were located. Two mounds had been abandoned between June 1996 and December 1997. In September - October 1997 two new mounds were constructed, and by November 1997, the study area had 31 active mounds (Fig. 2.1).

Between February 1998 and June 1998, five more mounds were built and six mounds, which were active in previous years, were not being used. At the end of the study, the study area had 30 active mounds, two mounds, which were active at the commencement of this study, had been abandoned, and six mounds were not being used (Fig 2.1); in all 38 mounds.

While mounds were present throughout the study area, some degree of clustering was discernible (Fig 2.1). Of the 38 mounds studied, nine distinct clusters were present, two of five (8,8a, 8b, 8c, 8d and 11,11a, 12,12a, 12b), one of four (9,9a, 9b, 9c), two of three (1a, 1,1b and 10,10a, 10d), and four of two mounds (7,7a, 7b, 7c, 10b, 10c, 13a, 13b). The remaining 10 mounds also showed some sort of clustering but were distributed with space in between (Fig 2.1). In 1996, two new mounds were constructed along with an existing cluster. In 1997, nine mounds were newly constructed, all of which were built so as to add on to an existing cluster, as were the five new mounds built in 1998. Two mounds were

Figure 2.1. Clusters of mounds present in the study area. Totally nine clusters were formed.



built adjacent to the largest mound (M 10), four mounds each were built around medium sized mounds (M 8 and 12), and two mounds were built around a small mound (M1). This indicates that while there did not appear to be a relationship between the size of the mound, and the propensity for additional mounds to be built so as to form a cluster, the greater number of mounds built around medium sized mounds may indicate that these are centres of greater mound construction activity.

Of the 38 mounds that were present in the study area, 36 mounds (94.74%) were found within 200 m of the beach and 23 mounds (60.53%) were found within 100 m of the beach (Fig. 2.2). Only two mounds were present beyond 200 m of the beach, and no mounds were located beyond 250 m of the beach.

2.3.2. Habitat of the study area

2.3.2.i. *Substrate*

The soil of the study area was differentiated into three categories: sand, sandy loam and moist-loam substrates. Sand substrate was present mainly along the sea shore, while the area to the interior, which comprised the majority of the study area was composed of sandy loam, and the area beyond this comprised either sandy loam or moist loam substrates. The soil to the west of this was clayey.

2.3.2.ii. *Vegetation*

The majority of the trees in the study area were small in girth. Large trees, with a girth greater than 200 cm accounted for less than 5 % of the trees present (Fig. 2.3). A total of 27 tree species were recorded, the most dominant were *Barringtonia asiatica*, *B. recemosa*, *Terminalia bialata*, *T. catappa*, *Syzygium samarangense*, *Thespesia populnea*, *Macaranga peltata*, Cherai Kaduva (local name), *Cocos nucifera*, *Hernandia peltata*, and *Mimusops littoralis*. The study area has dense, however, the ground was open and with little vegetation. The wet clayey soil of the forest type to the west of this coastal forest was covered with stands of *Areca* spp. and trees such as *Ixora barbata*, *Pongamia pinnata*, *Alstonia kurzii*, *Adenanthera pavanina*, *Horsfieldia irya*, *Myristica andamanica*, and *Celtis timorensis*.

The tree species composition, relative density and abundance in the study area were determined from 10 quadrats of 20 X 50 m (Table 2.1). The most abundant tree species in the study area was *Pandanus* spp. (223 trees/ha), followed by *Macaranga peltata* (134/ha) and *Syzygium samarangense* (99/ha). However, *Syzygium samarangense* was the most dominant tree species (Importance Value Index = 50.9), followed by *Pandanus* spp. (IVI = 41), *Macaranga peltata* (IVI = 27) and *Terminalia bialata* (IVI = 15.6). The tree species were not uniformly distributed in the study area, and only three species (*Pandanus* spp., *S. samarangense* and *Hernandia peltata*) of over 27 species present almost everywhere.

Figure 2.2. Distribution of Nicobar Megapode incubation mounds in the study area with respect to distance from the beach.

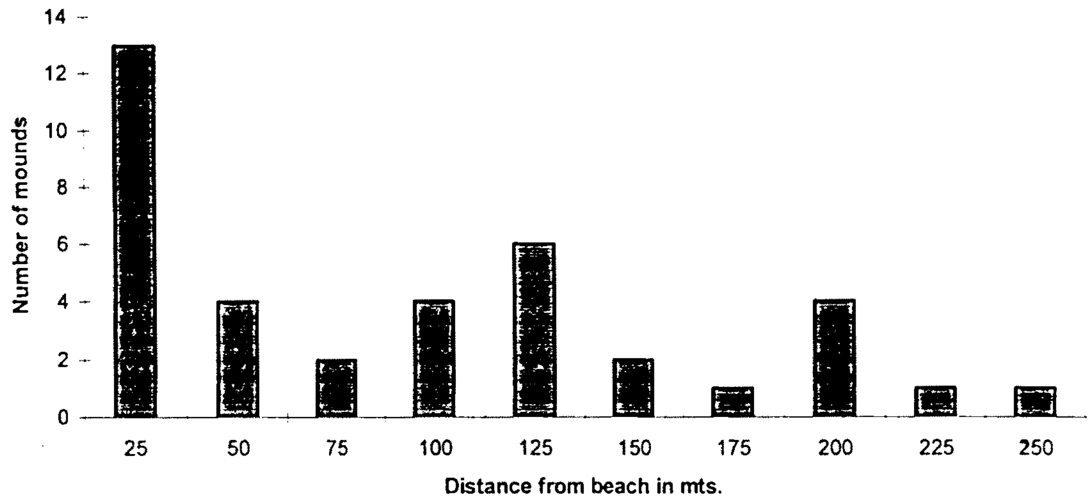


Figure 2.3. Distribution of trees with Girth at Breast Height (GBH>25 cm).

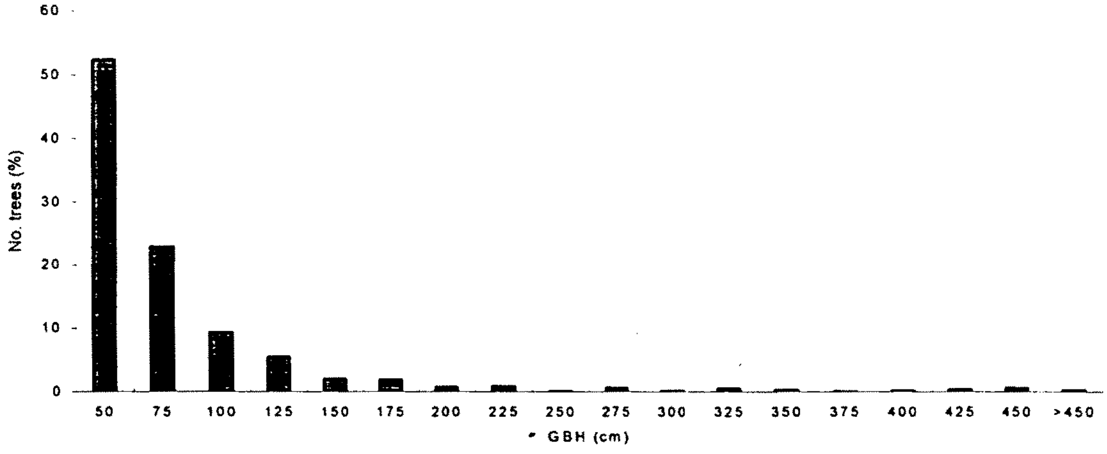


Table 2.1. Relative frequency, abundance, density, total basal area, relative dominance and importance value index of major tree species present in the study area.

SPECIES	Relative frequency	Abundance	Density/ha	Total basal area	Relative Dominance	IVI
Syzygium samarangense	10	8.41	99.00	23344.82	33.10	50.93
Pandanus spp.	10	18.95	223.00	6222.83	8.82	41.00
Macaranga peltata	8	14.23	134.00	4650.48	6.59	27.20
Hernandia peltata	10	4.93	58.00	6039.08	8.56	21.64
Terminalia bialata	4	0.85	4.00	8891.73	12.61	15.62
Mimusops littoralis	8	8.40	79.00	819.27	1.16	15.40
Barringtonia asiatica	8	2.97	28.00	4456.89	6.32	14.66
Cocos nucifera	6	3.40	24.00	3447.04	4.89	11.49
Cerebra spp.	7	3.88	32.00	1819.77	2.58	10.74
Terminalia catappa	5	1.19	7.00	4463.61	6.33	10.32
Stephegyne diversifolia	9	1.51	16.00	249.13	0.35	7.93
Cerai Kaduva (local name)	7	2.67	22.00	342.46	0.49	7.50
Pongamia pinnata	4	6.16	29.00	1057.32	1.50	7.41
Leea grandifolia	7	2.80	23.00	137.18	0.19	7.31
Macaranga indica	7	1.22	10.00	573.54	0.81	6.43
Ficus recemosa	7	0.85	7.00	443.52	0.63	5.90
Spondias mangifera	7	1.10	9.00	191.43	0.27	5.77
Trema macrantha	5	2.89	17.00	405.90	0.58	5.73
Ficus hispida	6	1.70	12.00	128.37	0.18	5.39
Alstonia kurzii	3	0.85	3.00	562.49	0.80	3.06
Odiyam (local name)	2	0.85	2.00	1020.90	1.45	2.95
Adenanthera pavonina	3	0.85	3.00	248.71	0.35	2.62
Knema andamanensis	2	0.85	2.00	515.45	0.73	2.23
Thespesia populnea	2	1.70	4.00	258.52	0.37	2.10
Anura sp.	2	0.85	2.00	20.52	0.03	1.53
Celtis sp.	2	0.85	2.00	9.94	0.01	1.51
Cycas rumphii	1	1.70	2.00	100.07	0.14	1.01

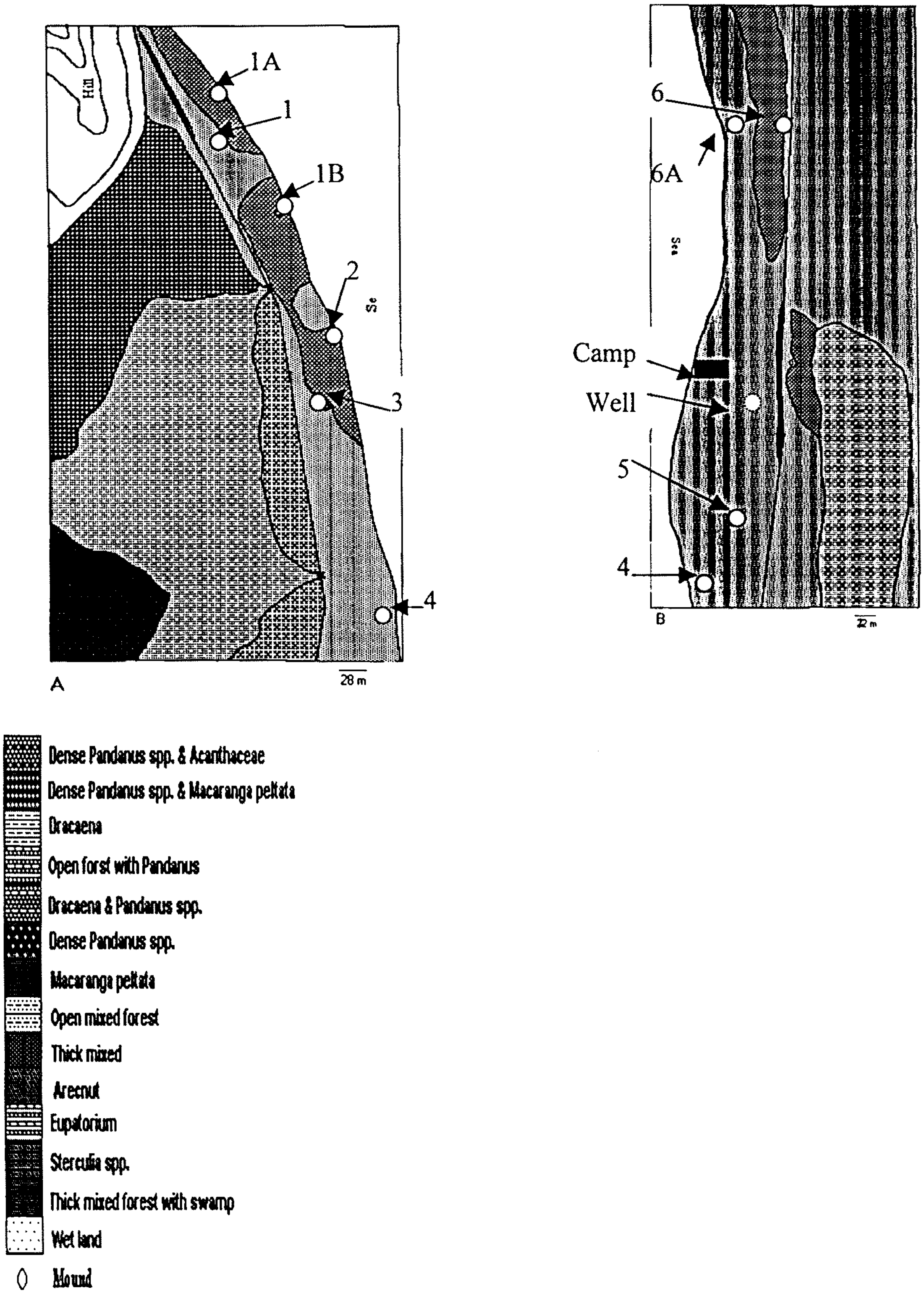
The vegetation in the study area was not homogenous and the associations seen could be classified into 14 categories. There was some relationship between the distribution of plants and soil substrates (Table 2.2). Usually, *Pandanus* spp. and *Dracaena* sp. were seen in sand and sandy-loam, while *Macaranga peltata* was restricted to sandy-loam and moist loam substrates. Moist loam substrates were usually seen in the interior of the forest, where the *Areca triandrus*, wetlands and thick mixed forests were present.

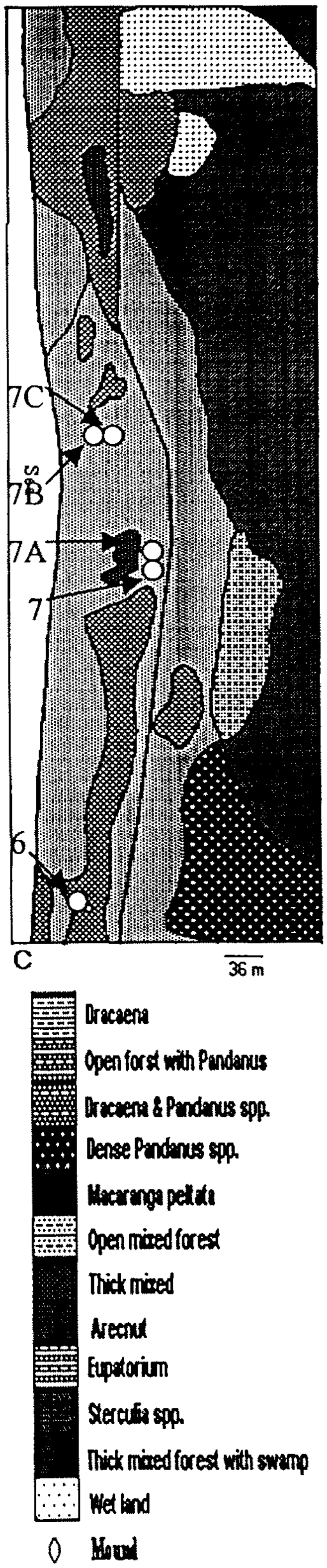
Table 2.2. Association of vegetation patches with different soil substrates.

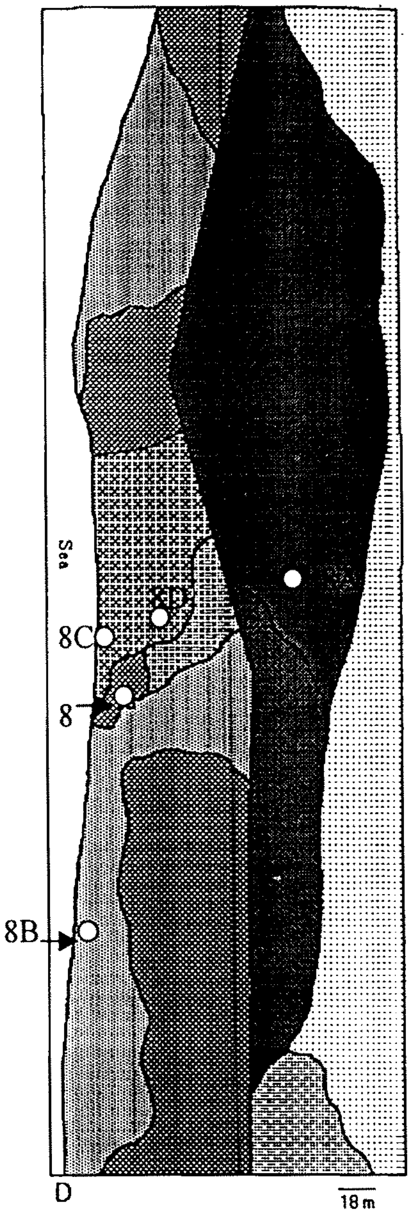
Vegetation patches	**Soil substrates**
Areca triandrus	Moist-loam
Dense *Pandanus* spp.	Sand
Dense *Pandanus* spp. with Acanthaceae	Sand and Sandy-loam
Dense *Pandanus* spp. with *Macaranga peltata*	Sandy-loam
Dracaena spp.	Sand
Dracaena sp. with *Pandanus* spp.	Sand
Eupatorium spp.	Sand and Sandy-loam
Macaranga peltata	Moist-loam
Open forest with *Pandanus* spp.	Sand and Sandy-loam
Open mixed forest	Sandy-loam
Sterculia sp.	Sandy-loam
Thick mixed forest	Sandy-loam and Moist -loam
Thick mixed forest with swamp	Moist-loam
Wetland with grass	Moist-loam

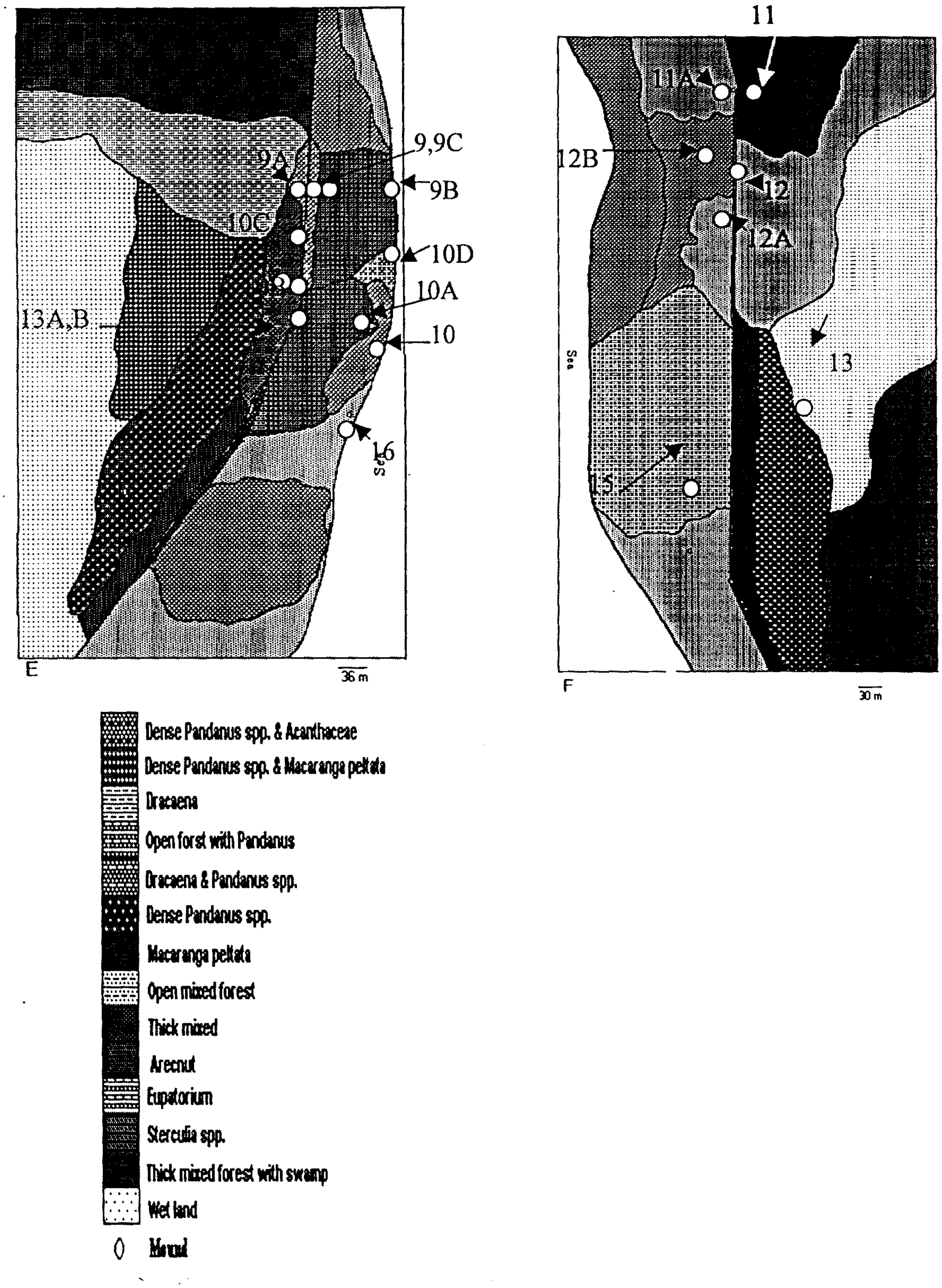
(Table 2.2). For convenience, the study area was divided into six sectors of unequal size and the distribution of the vegetative associations or patches of each sector are given in figure (2.4). Habitats of thick mixed forest with swamp, open mixed forest and thick mixed forest were the dominant habitats towards the interior forest area. Habitats, which had

Figure 2.4. The distribution of the vegetative association or patches around mounds 1, 1a, 1b, 2, 3 and 4 (A), mounds 5, 14, 6, 6a and field station (B), mounds 7, 7a, 7b and 7c (C), mounds 8, 8a, 8b, 8c and 8d (D), mounds 9, 9a, 9b, 9c, 10, 10a, 10b, 10c, 10d, 13, 13a, 13b, and 16 (E), and mounds 15, 12, 12a, 12b, 11 and 11a (F).




Sea
7C
7B
7A
7
6
C
36 m
Dracaena
Open forst with Pandanus
Dracaena & Pandanus spp.
Dense Pandanus spp.
Macaranga peltata
Open mixed forest
Thick mixed
Arecnut
Eupatorium
Sterculia spp.
Thick mixed forest with swamp
Wet land
Mound


Sea
8D
8C
8
8B
D
18 m


11
9,9C
9A
9B
10C
10D
10A
13A,B
10
16
Sea
E
36 m
11A
12B
12
12A
13
15
Sea
F
30 m
Dense Pandanus spp. & Acanthaceae
Dense Pandanus spp. & Macaranga peltata
Dracaena
Open forst with Pandanus
Dracaena & Pandanus spp.
Dense Pandanus spp.
Macaranga peltata
Open mixed forest
Thick mixed
Arecnut
Eupatorium
Sterculia spp.
Thick mixed forest with swamp
Wet land
Mound

Pandanus spp., and open mixed forest were distributed towards the coastal area where large number of mounds were present. Microhabitats of *Sterculia* sp., dense *Pandanus* spp. with Acanthaceae and *Eupatorium* spp. occupied less area. Microhabitats of *Eupatorium* spp. were present on either side of the road.

2.3.3. Habitat of incubation mounds

2.3.3.i. *Substrate*

Of the 38 mounds in the study area, 15 (39.5%) had been constructed on sandy substrate, 19 (50%) in sandy-loam substrate and the remaining four (10.5%) in loamy area. None of the mounds had been constructed in soils that were inundated during the wet season. However, when the proportion of the mound distribution according to available soil substrates was considered, the most suitable substrate for mound construction was sand (2.32 mounds/unit area) followed by sandy loam (1.04 mounds/unit area, Table 2.3). Sand substrates were utilised significantly more than expected but the moist loam substrate was used less than expected (Table 2.4).

Table 2.3. Distribution of the mounds in the various substrates available for the Nicobar Megapode.

Type of substrate	Proportion of the area available	Number of Mounds present	Proportion of mounds present	Ratio of proportion of mounds to proportion of area
Sand	0.17	15	0.395	2.32
Sandy-loam	0.48	19	0.50	1.04
Loam (moist)	0.35	4	0.105	0.30

Table 2.4. Utilisation of various substrates for mound construction by the Nicobar Megapode. The analysis follows Neu *et al.* (1974).

Substrate types	Available Area	Utilisation levels	
		Upper	Lower
Sand	0.17	0.60	0.19
Sandy-loam	0.48	0.71	0.29
Loam (moist)	0.35	0.23	-0.02

2.3.3.ii. *Habitat*

Of the fourteen types of vegetation patches identified (Table 2.2), mounds were present in all habitat types excepting areas under Arecanut, thick mixed forest with swamp, wetland with grass, *Sterculia* spp. and *Eupatorium* spp. The highest number of mounds were present in open forest with *Pandanus* spp. (8), dense *Pandanus* spp. (7), open mixed forest (7), followed by thick mixed forest (4) with one to three mounds occurring in the other habitat types (Table 2.5). However, when the proportion of available habitats was accounted for, dense *Pandanus* spp. with Acanthaceae, dense *Pandanus* spp. with *Macaranga peltata*, *Dracaena* spp., open forest with *Pandanus* spp. and *Dracaena* spp. with *Pandanus* spp. were preferred vegetation for the construction of mounds (Table 2.5). When habitat preference was analysed using Neu *et al.* (1974) method, open forest with *Pandanus* spp., open mixed forest and dense *Pandanus* spp. microhabitats were preferred for mound construction (Table 2.6).

The mean canopy cover above the mound was 58% and it was less than the mean percentage (81%) of canopy cover of the non-mound area ($t = -15.94$, $p<0.01$, $df = 81$).

Table 2.5. Distribution of the mounds in vegetation patches available to the Nicobar Megapode.

Type of vegetation	Proportion of area available	No. of mounds	Proportion of the mound present	Ratio of proportion of mounds to proportion of area
Areca triandrus	0.057	0	0.000	0.0
Dense *Pandanus* spp.	0.097	7	0.184	1.9
Dense *Pandanus* spp. and Acanthaceae	0.011	3	0.079	7.2
Dense *Pandanus* spp. and *Macaranga peltata*	0.015	2	0.053	3.5
Dracaena	0.024	3	0.079	3.2
Dracaena and *Pandanus* spp.	0.020	2	0.053	2.7
Eupatorium	0.009	0	0.000	0.0
Macaranga peltata	0.047	2	0.053	1.1
Open forest with *Pandanus* spp.	0.062	8	0.211	3.4
Open mixed forest	0.179	7	0.184	1.0
Sterculia sp.	0.002	0	0.000	0.0
Dense nixed forest	0.183	4	0.105	0.6
Dense mixed forest with swamp	0.196	0	0.000	0.0
Wet land	0.097	0	0.000	0.0

2.3.4. Selection of trees for mound construction

Of the 38 mounds, 29 mounds were type 'C' and 'BC'. All the type C and type BC mounds were seen along with one or more dead trees. Totally eight species of dead trees were identified at the mound. Of these *Syzygium samarangense* was the most frequently seen followed by *Barringtonia asiatica* and *Hernandia peltata* (Fig 2.5). Totally, 11 species of green trees were present in or around the mounds of the Nicobar Megapode. Of these, *Pandanus* spp. was present in 21 mounds and *Syzygium samaragense* present in seven mounds (Fig 2.5).

Table 2.6. Microhabitat utilisation for the construction of mounds by the Nicobar Megapode.

Type of vegetation patches	Proportion of area available	Utilization levels	
		Upper	Lower
Areca triandrus	0.057	0.00	0.00
Dense *Pandanus* spp.	0.097	0.35	0.02
Dense *Pandanus* spp. and Acanthaceae	0.011	0.19	-0.03
Dense *Pandanus* spp. and *Macaranga peltata*	0.015	0.15	-0.04
Dracaena	0.024	0.19	-0.03
Dracaena and *Pandanus* spp.	0.020	0.15	-0.04
Eupatorium	0.009	0.00	0.00
Macaranga peltata	0.047	0.15	-0.04
Open forest with *Pandanus* spp.	0.062	0.38	0.04
Open mixed forest	0.179	0.35	0.02
Sterculia sp.	0.002	0.00	0.00
Thick mixed forest	0.183	0.23	-0.02
Thick mixed forest with swamp	0.196	0.00	0.00
Wet land	0.097	0.00	0.00

2.3.5. Habitat Utilisation

2.3.5.1. *Sightings and calls*

2.3.5.1.i. *Substrate*

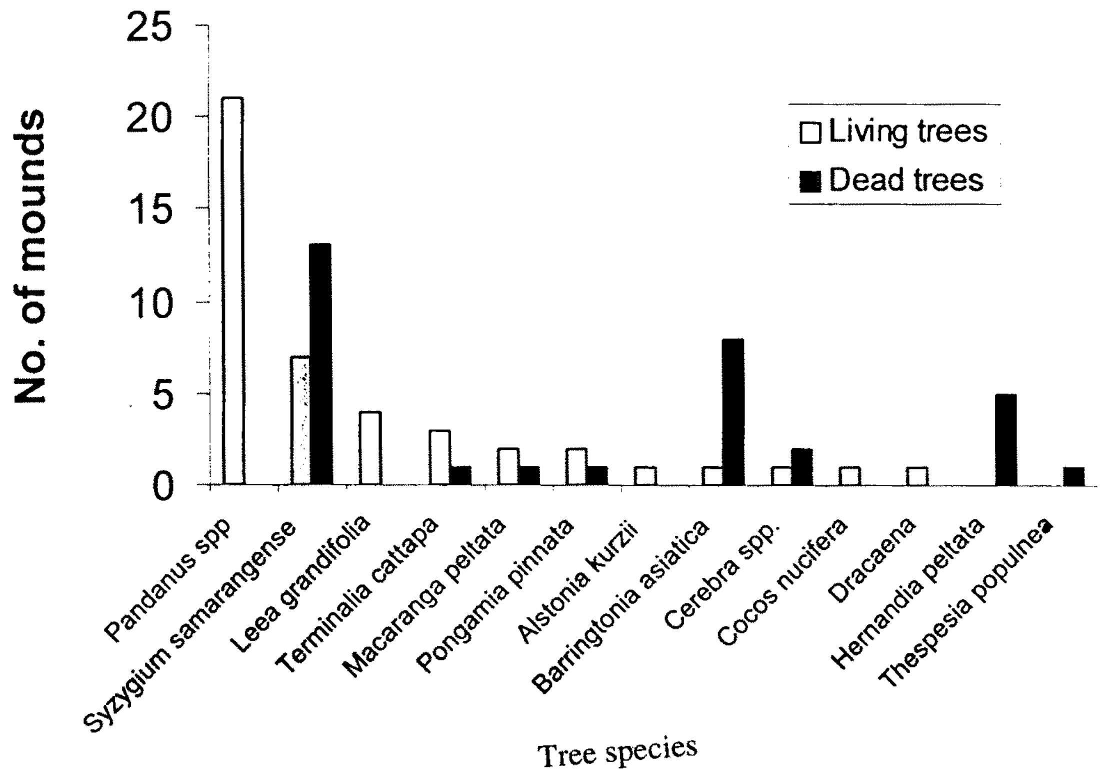
Of the major soil substrates available to the Nicobar Megapode, the majority of sightings and calls between January and June were on sandy-loam followed by sandy substrates, while in September and October, the majority of sightings and calls were in the sandy loam substrate. However, when the proportion of available area of the three major substrates was considered, sand substrate was used more during the dry season followed by sandy-loam substrate. In the wet season (September and October) sandy loam substrate was preferred over the sand substrate. In both seasons loamy substrate was utilised the least (Fig 2.6).

Sandy-loam substrates were utilised significantly more than expected in both seasons (Table 2.7).

Table 2.7. Substrate utilisation by the Nicobar Megapode follows Neu *et al.* 1974.

Substrate types	Proportion of area available	Utilization levels in the dry season		Utilization levels in the wet season	
		Upper	Lower	Upper	Lower
Sand	0.17	0.38	0.02	0.01	0.00
Sandy-loam	0.48	0.60	0.56	0.85	0.75
Loam (moist)	0.35	0.07	0.05	0.02	0.00

Figure 2.5. Living and dead trees preferred by the Nicobar Megapode for mound construction.



2.3.5.1.ii. *Vegetation*

During the dry season, the majority of sightings and calls heard, proportionate to the availability of the 14 vegetation patches identified (Table 2.8) were *Sterculia* sp. followed by dense *Pandanus* spp. with Acanthaceae, dense *Pandanus* spp. with *Macaranga peltata* and Dracaena. Vegetation patches of wet land, *Macaranga peltata*, thick mixed forest and dense *Pandanus* spp. were used the least (Table 2.8).

In the wet season, vegetation patches of *Sterculia* sp. followed by dense *Pandanus* spp. with *Macaranga peltata*, dense *Pandanus* spp. with Acanthaceae and *Eupatorium* sp. were preferred by the Nicobar Megapode. Patches of wet land, open forest with *Pandanus* spp., thick mixed forest with swamp and *Areca triandrus* were least utilised by the Nicobar Megapode (Fig 2.7).

Table 2.8. Habitat utilisation by the Nicobar Megapode follows Neu *et al.* 1974.

Microhabitats	Proportion of area available	Utilization levels (Dry season)		Utilization levels (Wet season)	
		Upper	Lower	Upper	Lower
Areca triandrus	0.06	0.04	0.03	0.02	-0.01
Dense *Pandanus* spp.	0.10	0.13	0.10	0.16	0.06
Dense *Pandanus* spp. and Acanthaceae	0.01	0.09	0.07	0.10	0.02
Dense *Pandanus* spp. and *Macranga peltata*	0.02	0.11	0.08	0.14	0.05
Dracena spp.	0.02	0.03	0.01	0.04	0.00
Dracena spp. and *Pandanus* spp.	0.02	0.01	0.00	0.09	0.02
Euputorium sp.	0.01	0.02	0.01	0.09	0.02
Macranga peltata	0.05	0.20	0.16	0.22	0.10
Open forest with *Pandanus* spp.	0.06	0.12	0.09	0.00	0.00
Open mixed forest	0.18	0.16	0.13	0.34	0.19
Sterculia sp.	0.00	0.07	0.05	0.05	0.00
Thick mixed forest	0.18	0.13	0.11	0.21	0.09
Thick mixed forest with swamp	0.20	0.02	0.01	0.00	0.00
Wet land	0.10	0.02	0.01	0.00	0.00

Figure 2.6. Substrates utilisation of the Nicobar megapode.

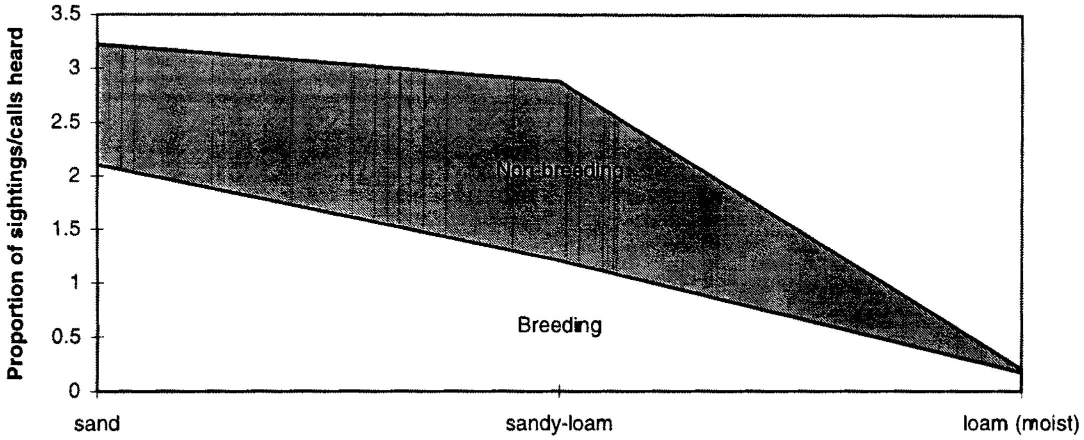
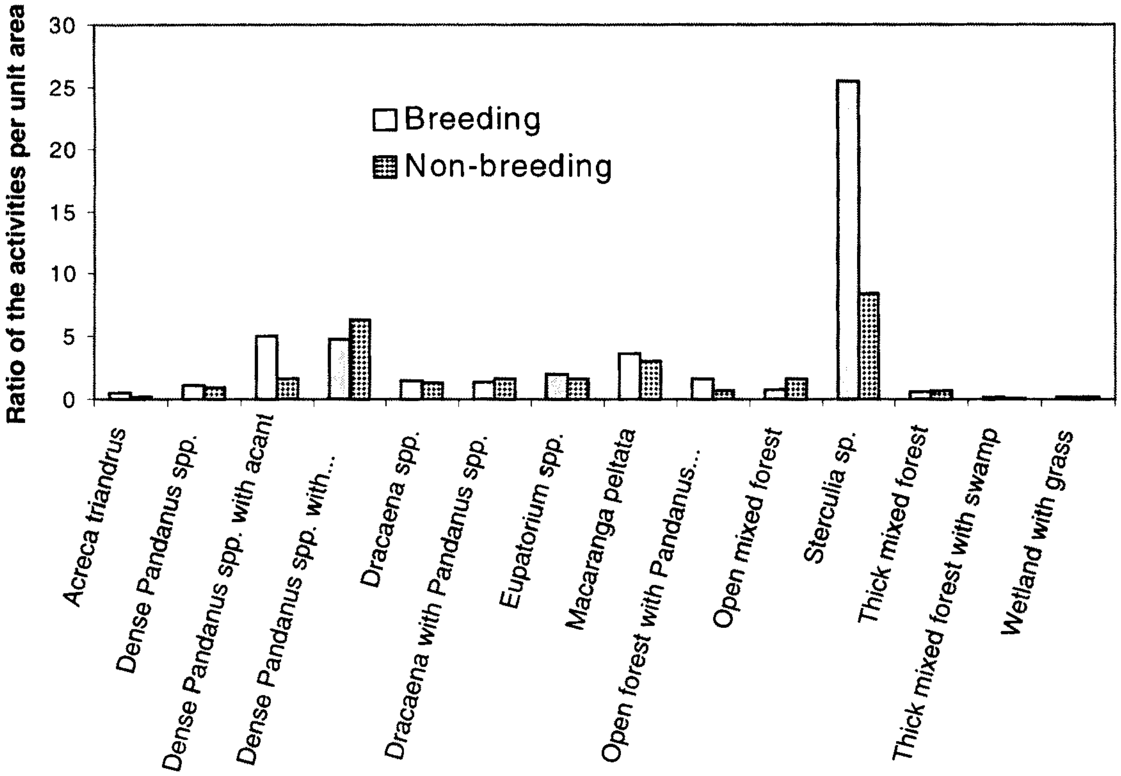


Figure 2.7. Proportion of the microhabitat utilisation of the Nicobar Megapode in different seasons.



Microhabitats of *Macaranga peltata*, dense *Pandanus* spp., dense *Pandanus* spp. with *Macaranga peltata*, dense *Pandanus* spp. with Acanthaceae, Dracaena, and Eupatorium habitats were used by the birds in both summer and rain season, while habitats of *Areca triandrus*, wetland with grass and thick mixed forest with swamp areas were not or barely used in both seasons. Open mixed forest and thick mixed forest habitats had more sightings and calls of megapodes in the wet season than in the dry season.

Microhabitats, which were dominated by or having *Pandanus, Macaranga peltata* and *Draceana* were utilised by the megapode more than expected in both seasons. However, open forest with Pandanus spp. microhabitat was utilised more in the dry season than in the wet season.

2.3.5.2. *Activities*

2.3.5.2.i. *Dry season*

Five major activities: calls, foraging, fighting, resting and flying were recorded during this period. Other activities such as preening and mating were recorded infrequently and hence not included in this analysis. The majority of calls and foraging were recorded in *Sterculia* sp. patches followed by dense *Pandanus* spp. with *Macaranga peltata* and dense *Pandanus* spp. with Acanthaceae (Table 2.9). *Sterculia* sp. patches were used the most by the megapode for fighting and resting. Apart from the use of *Sterculia* sp., the use of dense *Pandanus* spp. with *Macaranga peltata* and *Macaranga peltata* patches for fighting, was relatively high. Dense *Pandanus* spp. with acanthaceae and dense *Pandanus* spp. with

Macaranga peltata patches were also highly utilised by the megapodes for resting (Table 2.9).

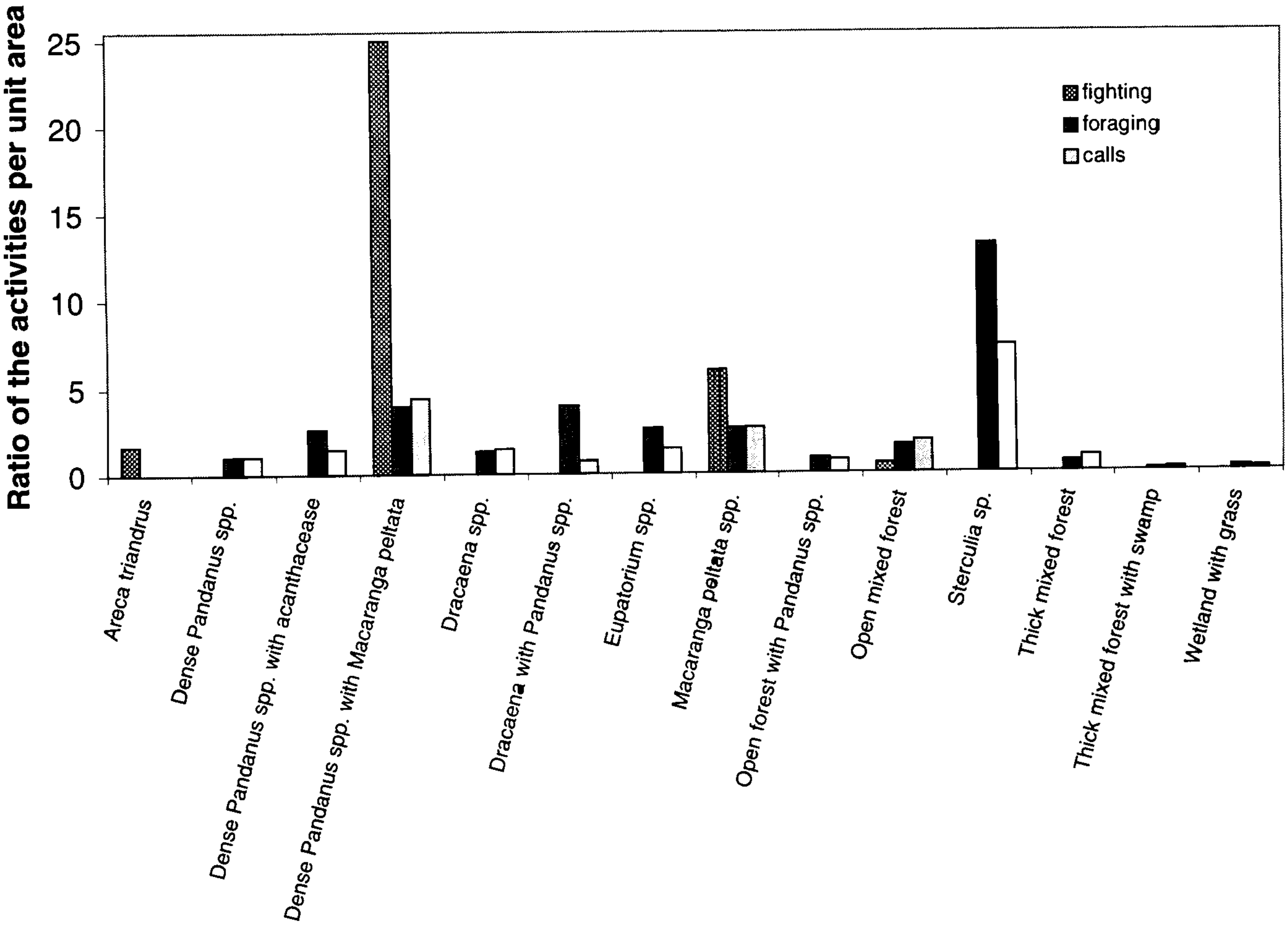
Table 2.9. Habitat choice for different activities in the Nicobar Megapode in the dry season.

Vegetation patches	Area	Ratio of the activities per unit area				
		calls	Foraging	fighting	rest	Flying
Areca triandrus	0.060	0.56	0.52	0.10	0.00	0.00
Dense *Pandanus* spp.	0.100	1.14	1.24	0.48	1.82	0.00
Dense *Pandanus* spp. with Acanthaceae	0.010	5.26	4.79	3.01	13.64	0.00
Dense *Pandanus* spp. with *Macaranga peltata*	0.020	4.58	4.38	9.64	6.82	8.70
Dracaena spp.	0.020	1.35	1.24	4.22	6.82	0.00
Dracaena with *Pandanus* spp.	0.020	1.09	1.32	3.31	2.27	2.17
Eupatorium spp.	0.010	2.03	1.90	2.41	4.55	0.00
Macaranga peltata	0.050	3.77	3.39	3.98	2.73	5.22
Open forest with *Pandanus* spp.	0.060	1.70	1.78	0.20	0.00	0.00
Open mixed forest	0.180	0.75	0.75	1.27	0.00	1.69
Sterculia sp.	0.002	23.27	28.49	24.10	22.73	0.00
Thick mixed forest	0.180	0.67	0.65	0.23	0.76	1.21
Thick mixed forest with swamp	0.200	0.17	0.19	0.09	0.00	0.00
Wetland with grass	0.100	0.13	0.16	0.00	0.00	0.00

2.3.5.2.ii. *Wet season*

During the wet season (September and October), only three major activities calling, foraging and fighting were recorded. Of these, megapodes preferred *Sterculia* sp. and dense *Pandanus* spp. with *Macaranga peltata* for calling (Fig 2.8). Foraging mostly took place in *Sterculia* sp., dense *Pandanus* spp. with *Macaranga peltata* and *Eupatorium* patches. Fights mostly took place in patches of dense *Pandanus* spp. with *Macaranga peltata* followed by *Macaranga peltata* and *Areca triandrus* (Fig 2.8).

Figure 2.8. Microhabitats utilisation of the Nicobar Megapode were varied while performing fighting, foraging and calling during the wet season.



2.4. DISCUSSION

2.4.1. The distribution of mounds according to substrate and habitat

Of the three major types of soil substrates present in the study area, the Nicobar megapode preferred to construct mounds in sandy substrates, followed by sandy-loam and the least in moist-loamy substrates. This preference is largely because digging by the bird is easier in soil with high sand content. This preference for constructing mounds on sandy substrates could indicate why mounds are found in high densities in coastal forest when compared to interior forests, and within coastal forests in a narrow belt adjacent to the beach (Sankaran 1995a, b). Coastal habitat of the Nicobar Islands is mainly composed of sand and sandy-loam system of soil (Thothathri 1962; Saldanha 1989) and may be the reason for the clumped distribution of the Nicobar Megapode towards the coastal region (Dekker 1992; Sankaran 1995; Jones *et al.* 1995; this study) than the interior forest.

The vegetation patches preferred by the Nicobar Megapode are those vegetation, which occurred either on sandy or sandy-loam substrates. Thus vegetation patches dominated by species of *Pandanus* spp., Acanthaceae, *Macaranga peltata*, and *Sterculia* sp. which are largely restricted to sandy and sandy-loam substrates where the major proportion of mounds were located.

Of the 14 vegetation patches distinguished, dense *Pandanus* spp. with Acanthaceae, dense *Pandanus* spp. with *Macaranga peltata*, *Dracaena* sp., open forest with *Pandanus* spp., and *Dracaena* sp. with *Pandanus* spp. were highly utilised for mound construction. This could indicate that habitats with *Pandanus* spp. are the most suitable habitat for the incubation mound of the Nicobar Megapode. As *Pandanus* spp. are distributed mostly in the coastal area (Thothathri 1962), this could also indicate why there is a clumped distribution of the Nicobar megapode towards coastal forest.

2.4.2. Seasonal difference in substrate and habitat utilisation

2.4.2.i. *Substrates*

Breeding characters of the birds like mating, egg laying and incubation are generally governed by the various ecological or environmental factors like temperature and rain (Rands 1988), as these factors affect the abundance and quality of food apart from directly influencing behaviour (Hudson and Rands 1988). As the summer is the peak period of the egg laying, megapodes concentrated around the incubation mounds. As sand substrates were preferred for mound construction, and sandy-loam substrates for food as well as mound construction, most sightings of the Nicobar Megapode were on these substrates. Areas with greater leaf litter are believed to be richer in soil invertebrates (Goth and Vogel 1996). As relative abundance of food resources were not studied the influence of this in both substrate and habitat selection could not be determined. Choice of substrate in the dry season would be largely governed by location of mounds, whereas in the wet season food could be the main criterion of habitat selection, and choice of substrates would be governed largely by food. It is probable that sandy-loam substrates are richer in food than sandy substrates, indicating as to why this substrate was preferred in the wet season. During the wet season most of the available moist loam substrates were inundated with rainwater.

2.4.2.ii. *Microhabitats*

Of the 14 microhabitats, *Sterculia* sp. dense *Pandanus* spp. with Acanthaceae, dense *Pandanus* spp. with *Macaranga peltata* and *Macaranga peltata* were used the most. *Sterculia* sp. was present along either side of the road and not away from it with the result that the total available area of this vegetation type was the least (Table 2.9). Most of the mounds in the study area were between the seashore and the road. Thus, megapodes from the interior forest had to cross the road to access mounds. As the majority of sightings and calls heard were from the road, this was the most probable reason for the maximum sighting in *Sterculia* sp. in both dry and wet seasons.

Compared to the dry season, in the wet season the vegetation patches like *Sterculia* sp., dense *Pandanus* spp. with Acanthaceae, open forest with *Pandanus* spp., *Dracaena* sp. was utilised less. On the other hand, dense *Pandanus* spp. with *Macaranga peltata*, Dracaena with *Pandanus* spp., and Eupatorium patches were highly utilised. Use of mounds was the least during the wet season and hence vegetation around mounds or along the road was utilised less.

Open forest with *Pandanus* spp. was preferred more in the dry season than in the wet season, as this microhabitat had a large number of mounds.

2.4.3. Did the Nicobar Megapode exhibit any activity specific to habitat?

In general, there was no habitat specific activity in the Nicobar Megapode. Patches of *Macaranga peltata* had high sightings, as the seed of *Macaranga peltata* was a preferred food for the Nicobar Megapode (see chapter V). Fighting mostly took place in the habitats, which were around the mound, indicating that the mound was the most important factor for fights.

2.5. CONCLUSION

Most of the mounds were distributed within 200 m from the high tide mark. Sandy and sandy-loam substrates were preferred for mound construction. Microhabitats of open forest with *Pandanus* spp. and open mixed forest were highly utilised for mound construction. Microhabitats, which are dominated or having the species of *Pandanus, Macaranga peltata* and *Draceana* were utilised by the megapode for breeding and foraging in both seasons. However, open forest with Pandanus spp. was utilised more in the dry season. In general there was no habitat specific activities seen in the Nicobar Megapode.

Chapter III

THE INCUBATION MOUND OF THE NICOBAR MEGAPODE

3.1 INTRODUCTION

Megapodes are unique among birds because they incubate their eggs in mounds of rotting leaves or in burrows or geothermally heated ground (Frith 1956; Dekker and Wattel 1987; Jones 1988; Dekker 1990). Perhaps the best-studied aspects of the Megapodiidae are the incubation conditions within mounds and communal nesting grounds (Frith 1956, 1959, Crome and Brown 1979; Seymour *et al.* 1986; Booth 1987, Seymour *et al.* 1987; Dekker 1988; Jones 1988).

Within the Megapodiidae, there are variations in the incubation and breeding strategies. Two groups, burrow nesters and mound builders, exist in this family. Burrow nesting Macrocephalon and Eulipoa lay eggs at communal nesting grounds where sun or volcanic activity provides heat for incubation (Dekker 1988, 1990; Heij *et al.* 1997). Talegalla, Aephypodius, Alectura, and Leipoa build incubation mound of forest litter where organic decomposition provides necessary heat (Dekker 1990). Of the 13 species, that comprise the genus Megapodius, 10 are mound builders, two are burrow nesters, and one nest in both burrow and mound (Jones *et al.* 1995).

Megapode mounds are amongst the largest structures made by any non-colonial animal, and represent the harnessing of the energy produced by microbial respiration (Seymour *et al.* 1986; Jones 1989b), and/or solar radiation (Frith 1956, 1959) by concentrating suitable material to provide optimal incubation conditions at about 33-34°c (Dekker 1992). In some species, microbial respiration and solar radiation may be used sequentially to create incubation conditions (Frith 1956, 1959). Birds incubate their eggs in a narrow temperature range, though short-term drops in temperature are tolerated in naturally incubated eggs (Booth 1987), but exposure of eggs to either high or low temperatures is fatal. Incubation temperatures in megapode incubation mounds do show considerable fluctuation, and while such temperature fluctuations are largely offset by having a variable incubation period (Booth 1987), there are strategies to balance both heat loss and gain (Jones 1989a; Jones and Birks 1992). While mound maintenance by megapodes is thought to play a role in maintaining incubation temperature. Seymour (1985) proposed that heat production and heat loss tends to stabilize mound temperatures at an equilibrium state due to the great thermal inertia of mounds once it crosses a certain size, has adequate moisture content with the regular incorporation of fresh organic materials in the mound. This model has gained further support from other studies (Jones 1988; Jones and Birks 1992).

The Nicobar Megapode builds incubation mounds of sand, loam, coral bits and rotting vegetation within which eggs are laid. Basically three types of mound are built by the Nicobar megapode and have been described by Dekker (1992), Sankaran (1995), Sivakumar and Sankaran (in press) as: Type `A' incubation mounds or true incubation mounds, regular in shape and built on an open spot away from trees. Type `B' incubation mounds, irregular in shape, built against the buttress or stem of a large living tree. Type `C' incubation mounds, also irregular in shape but built against, around, under or over a dead rotting tree stump or log. Combinations within these types of incubation mounds are present, with some incubation mounds very like a Type `A' but large enough to extend into the buttress or stem of a nearby tree (type AB), or have a dead log across them (Type AC). Some type `B' incubation mounds have a dead log or branch fallen across it giving it the appearance of a type `C' incubation mound (Type BC). Thus, type `AB' incubation mounds have both characters of type `A' and type `B' type incubation mounds, type `AC' incubation mound have the characters of type `A' and `C', and type `BC' incubation mounds have both characters of type `B' and `C'. Mounds have also been recorded as being built under a copra-making platform, and just inside the entrance of a cave (Sivakumar and Sankaran in press).

Incubation mounds vary in height from 10 to 210 cm and in basal circumference from seven to 45 m (Sankaran 1995a, b). Type A and B incubation mounds were significantly larger than type `B' and both were greater than type `C' incubation mounds (Sivakumar and Sankaran in press). The incubation mound substrate varies and is largely composed of sand, coral rubble and decomposing material. However, at one extreme some incubation mounds are largely composed of decomposing material, while at the other some incubation mounds have little rotting vegetation and are largely composed of either sand and/or coral rubble. Incubation mounds occurred in interior forests, and sunlight fell directly on the mound through either a very thin canopy cover, or a gap in the canopy. Some mounds were so close to the edge of the forest abutting the beach that light fell directly on them either in the morning or evening or were warmed by heat radiation from the beach.

The factors governing incubation conditions within the mound of the Nicobar Megapode has so far been unstudied. In this chapter, the incubation mound of the species is described, and the factors governing incubation conditions within the mound are identified. The activities associated with mounds by the Nicobar Megapode are documented.

3.2. OBJECTIVES

1. To identify activities associated with the incubation mound
2. To find out whether heat sources that create suitable incubation conditions in a mound vary with mound dimension.
3. To find out the temperature sources which provides the most stable incubation condition.
4. To find out whether heat sources and mound dimensions have a bearing on the number of pairs that use a mound, the number of eggs laid, and the hatching success.

3.3. RESULTS

3.3.1. Description of incubation mounds

In the study area, the incubation mounds of the Nicobar Megapode varied in shape and size (Table 3.1). Usually incubation mounds were constructed with either sand or sand with vegetative materials, such as leaves twigs, and bits of decomposing wood, which were available in the surrounding areas. Incubation mounds were present on slightly elevated areas, and most of the incubation mounds were seen close to the seashore (see chapter 2).

Of the 38 incubation mounds present in the study area between 1996 and 1998, three were type ‘A’ incubation mounds, three type `B' incubation mounds, and 25 were type `C' incubation mounds. Of the remainder, four incubation mounds were type `BC' (built against the buttress of a partially living tree, or with a dead log in it), of which two later became type `C' in 1998 because the trees died out completely. One incubation mound was type `AB' as it was built against two living Pandanus palms (Table 3.1). Two incubation mounds were unusual as they were built against the edge of the disused metal road that bisected the study areas.

Of the16 incubation mounds that were newly constructed during the study period, 13 were type `C' incubation mounds, one was a type `B' incubation mound, and two were built against a road (Table 3.1).

3.3.2. Construction of the incubation mound

The construction and maintenance of an incubation mound involves several activities. Usually, the site selected for a new incubation mound was a fallen log, tree stump, or the decomposing roots of a tree. The megapodes begin construction of the new incubation mound by either digging a pit if the site is over decomposing roots or by covering the decomposing log or tree stump by raking soil and litter from surrounding areas as well as digging pits at the base. The process of raking soil and litter onto the site, or the pile up of soil and other material from the pits dug soon results in the formation of a new incubation mound.

Table 3.1. The history of incubation mounds in the study area.

S. No.	Incubation mound	Birds/year	First located on	End date	Status	Type	Distance from the shore	Average Size[1]
1	1A	2.67	16-Apr-97	May-98	NC	C	15	0.35
2	10A	2.00	7-May-97	May-98	NC	C	35	0.50
3	11A	2.33	12-Feb-96	Feb-98	NC	C	180	0.37
4	12A	3.33	3-Feb-96	May-98	NF	C	185	9.14
5	13A	1.33	19-Mar-97	Feb-98	NC	R	120	0.64
6	6A	3.00	21-Mar-96	Apr-98	NF	B	30	0.32
7	7A	2.00	3-Jan-96	May-98	PS	C	105	0.66
8	8A	1.33	19-Mar-96	Mar-98	NF	C	110	1.57
9	9A	4.00	30-Jan-96	Feb-98	PS	AB	95	3.11
10	1B	2.33	23-Apr-97	May-98	NC	C	15	0.76
11	10B	3.00	7-May-97	May-98	NC	C	132	6.98
12	12B	2.00	28-Jan-97	Apr-98	NF	C	190	6.26
13	13B	0.67	19_Mar-97	Feb-98	NC	R	120	0.38
14	7B	1.00	6-Feb-98	May-98	NC	C	20	0.26
15	8B	0.67	27-Mar-98	May-98	NC	C	10	0.39
16	9B	1.00	10_Feb-96	Feb-98	NC	B	10	0.49
17	10C	1.33	5-Sep-97	Feb-98	NC	C	130	-
18	15	2.00	Feb-96	Mar-98	NF	C	160	3.74
19	7C	1.00	26-Sep-97	Mar-98	NC	B	22	1.75
20	8C	1.33	11-Apr-98	May-98	NC	C	42	2.96
21	9C	9.00	13-Feb-97	Apr-98	NC	C	80	2.02
22	10D	0.67	27-Mar-98	May-98	NC	C	8	0.76
23	8D	1.33	11-Apr-98	May-98	NC	C	6	0.99
24	1	5.00	3-Jan-96	May-98	PS	C	52	2.29
25	2	2.00	3-Jan-96	Feb-97	PS	A	15	3.98
26	3	6.50	3-Jan-96	May-98	PS	BC	20	4.03
27	4	7.00	3-Jan-96	May-98	PS	BC	25	15.31
28	5	1.50	3-Jan-96	Jan-96	PS	C	85	6.88
29	6	5.50	3-Jan-96	May-98	PS	C	74	2.74
30	7	4.50	3-Jan-96	May-98	PS	C	105	0.93
31	8	18.00	3-Jan-96	May-98	PS	BC	27	8.02
32	9	15.50	5-Jan-96	May-98	PS	BC	83	6.67
33	10	9.50	5-Jan-96	May-98	PS	A	25	40.24
34	11	2.33	5-Jan-96	May-98	PS	C	195	0.76
35	12	4.33	5-Jan-96	May-98	PS	C	205	8.17
36	13	7.00	5-Jan-96	May-98	PS	C	240	12.88
37	14	11.00	28-Jan-96	May-98	PS	C	105	8.98
38	16	-	17-May-97	May-98	NF	A	5	12.12

NC= New construction; PS= Present at start of study, NF= Newly found

[1] As mounds change in size over time, the mean value for all mound size data collected during the study is given.

3.3.3. Description of the activities related to mound construction

(i) *Pit Digging:* Megapodes dug the pits by backward kicks of the soil. Different types of pits were classified according to their depth and fate. The three types of pits distinguished were *shallow pits, deep pits* and *egg-pits*. As megapodes usually laid eggs in pits that were over 60 cm in depth, pits that were less than 30 cm were considered to be shallow pits and those deeper than 30 cm were considered to be deep pits. Egg-pits were those pits in which eggs were laid.

(ii) *Pit-filling*: Once egg laying was over, the egg-pit was filled with the materials, which were available on the mound. During pit filling, the mound was also covered with soil and vegetative materials (see below).

(iii) *Raking:* For pit-filling and mound covering, materials were raked by the megapodes from the area around the mound. Raked materials were mainly composed of the surrounding vegetation litter and soil. The material was raked to and onto the mound top (see `mound covering' below) by vigorous backward kicking.

(iv) *Scratching*: Often the birds visited the mound, scratched on or around the mound. There was no pattern in the scratching in respect of place, and very shallow pits could be made during the process.

(v) *Egg-laying:* After deep pit-digging, the female entered into the pit and laid an egg. The presence of an egg in a pit was confirmed after checking the pit that was covered by the bird. Sometimes unpaired female birds also laid an egg.

(vi) *Mound covering*: During mound covering and raking, the surface of the mound was smoothened and all signs of pits and digging activity were obliterated. The difference between *pit-filling* and *mound covering* was that in the case of *pit-filling* signs of pits and other activities remained.

(vii) *visit:* Often the megapodes arrived at a mound and left without working on the mound. Such *visits* could take place several times in a morning or evening. *Visits* were common during the dry season but were not recorded during the wet season.

(viii) *Random activities*: Often the megapodes on the mound would dig shallow pits, scratch here and there on the mound, rake, and cover before leaving the mound.

3.3.4. The process of mound construction and maintenance

Prior to egg-laying in the incubation mound, the initial work was preparation of the incubation mound which usually involved scratching over the surface of the mound, covering and enlarging the mound by raking material onto the mound. During this process pits, both shallow and deep, were dug in the mound.

3.3.4.i. *Digging the pits*

The digging and filling of pits was a major activity on the incubation mounds. In newly constructed incubation mounds, usually only one pit was dug at a time, though more than one pit might be present. In one new mound, no pit was dug though mound construction through raking, went on for several weeks. The first deep pit dug into a newly constructed incubation mound was invariably used to lay an egg in (n=15 mounds). On the other hand, old mounds may have several pits, both shallow and deep, at any given time (as many as 10 pits have been recorded once in mound '8' and four in mound '9'), and the pits were not necessarily used to lay eggs in. On average, a pit was dug once in every 3.7 visits to the mound, and an egg was laid in every 2.4 pits dug, or in 1.8 deep pits dug.

Pit digging activity was distributed throughout the year but varied between months (Table 3.2). During the dry season in 1996, 28.5 % of the mound activity was digging, in 1997 it was 24.2%, and 26.7% in 1998. However, during September and October (rain season) of 1997 the proportion of pit digging in the incubation mound activity was only 17.7 %. In general during the dry season pit digging was the major activity (26.4 %) followed by raking (26.1 %). In the wet season, raking was the major activity on incubation mounds (61.4 %) followed by digging (17.7 %) (see Table 3.4).

Table 3.2. Monthly distribution of the various activities (%) of the Nicobar Megapode.

Year	1996							1997								1998			
Month	J	F	M	A	M	J	D	J	F	M	A	M	J	S	O	F	M	A	M
Activities																			
Random	0.0	0.0	0.0	0.0	0.0	0.0	32.0	12.0	0.0	0.0	0.0	8.0	24.0	0.0	8.0	0.0	8.0	0.0	8.0
Pits-Filled	0.4	1.8	3.2	5.4	12.9	7.9	0.0	0.4	0.7	6.8	20.8	7.9	10.4	0.0	7.5	1.1	7.5	2.9	2.5
Digging	9.9	10.1	3.2	5.4	3.9	0.3	8.1	7.3	6.2	6.3	4.6	6.5	5.8	2.7	1.2	7.4	5.5	2.8	2.7
Egg Lay	5.2	13.3	7.7	11.1	3.7	0.4	0.0	6.3	11.1	15.1	9.6	3.0	0.7	0.0	0.0	6.6	2.2	2.2	1.8
Fighting	0.0	0.0	0.0	5.3	5.3	0.0	0.0	0.0	5.3	31.6	26.3	0.0	0.0	0.0	0.0	21.1	5.3	0.0	0.0
pit-filling	47.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	4.8	9.5	0.0	4.8	4.8	14.3	0.0	9.5
Foraging	0.0	0.0	66.7	11.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	11.1	0.0
Hatching	0.0	0.0	0.0	6.1	9.1	0.0	0.0	0.0	0.0	15.2	27.3	15.2	3.0	0.0	0.0	0.0	0.0	9.1	15.2
Covering	0.0	3.3	9.8	1.6	4.9	0.0	0.0	8.2	1.6	8.2	6.6	21.3	6.6	0.0	1.6	16.4	8.2	1.6	0.0
Raking	0.7	1.9	8.9	4.0	8.8	10.4	0.0	0.1	0.1	6.8	9.9	14.1	9.6	1.6	11.0	0.4	3.0	6.9	1.6
Scratching	5.4	9.7	13.6	5.2	4.8	2.9	0.7	4.5	7.2	6.6	2.3	9.0	8.4	2.0	0.2	2.9	4.5	7.2	2.7
Standing	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Visits	5.7	7.0	5.7	3.2	4.4	4.4	0.0	3.8	5.7	1.9	1.3	1.3	0.0	0.0	0.0	8.2	13.9	24.7	8.9

Table 3.3. Diurnal distribution of the various activities (%) performed by the Nicobar Megapode during the study period.

Period (Hrs)	4-5	5-6	6-7	7-8	8-9	9-1	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18
Activities														
Random	0.0	0.0	4.0	8.0	8.0	12.0	8.0	16.0	0.0	0.0	4.0	20.0	16.0	4.0
Pits-filled	0.0	1.8	7.2	10.0	11.8	18.6	7.9	2.2	0.0	3.6	2.5	8.2	16.1	10.0
Digging	0.0	2.0	6.9	13.0	14.7	12.0	6.3	3.5	0.9	1.2	5.7	11.3	15.2	7.2
Egg Lay	0.0	5.5	8.5	11.4	16.6	8.1	3.0	1.5	0.4	1.1	1.1	17.0	20.3	5.5
Fighting	0.0	10.5	15.8	26.3	10.5	5.3	0.0	0.0	0.0	0.0	0.0	5.3	21.1	5.3
Pit-filling	0.0	0.0	9.5	9.5	33.3	9.5	0.0	0.0	0.0	0.0	4.8	19.0	9.5	4.8
Foraging	11.1	11.1	11.1	22.2	0.0	0.0	11.1	0.0	0.0	0.0	0.0	11.1	11.1	11.1
Hatching	0.0	6.1	6.1	15.2	12.1	3.0	9.1	3.0	0.0	6.1	9.1	18.2	12.1	0.0
Covering	0.0	0.0	4.9	3.3	18.0	23.0	4.9	3.3	0.0	1.6	3.3	9.8	19.7	8.2
Raking	0.2	0.9	5.7	24.3	15.6	7.2	3.5	0.1	0.0	0.9	15.3	15.9	7.1	3.3
Scratching	0.2	3.8	6.1	12.2	8.6	13.8	8.8	1.4	0.5	0.9	2.0	13.8	21.3	6.6
Standing	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Visits	0.6	11.4	15.2	21.5	14.6	12.7	2.5	0.6	0.0	0.0	1.9	7.6	6.3	5.1

Table 3.4. Seasonal distribution of the various activities of the Nicobar Megapode.

	Dry (1996)[1]	%[2]	Dry(1997)[1]	%[2]	Wet(1997)[1]	%[2]	Dry(1998)[1]	%[2]
Random	8	0.75	11	0.98	2	1.20	4	0.78
Pits-Filled	88	8.28	131	11.64	21	12.65	39	7.60
Digging	303	28.50	272	24.18	29	17.47	137	26.71
Egg-Laying	112	10.54	124	11.02	0	0.00	35	6.82
Fighting	2	0.19	12	1.07	0	0.00	5	0.97
Pit-filling	10	0.94	4	0.36	1	0.60	6	1.17
Foraging	7	0.66	0	0.00	0	0.00	2	0.39
Hatching	5	0.47	20	1.78	0	0.00	8	1.56
Covering	12	1.13	32	2.84	1	0.60	16	3.12
Raking	280	26.34	328	29.16	102	61.45	96	18.71
Scratching	187	17.59	168	14.93	10	6.02	77	15.01
Standing	1	0.09	1	0.09	0	0.00	0	0.00
Visit	48	4.52	22	1.96	0	0.00	88	17.15

[1]Number of occurrences, [2] percentage of occurrences

The majority of the pits dug in an incubation mounds were deep pits. Over the course of this study, 179 shallow and 468 deep pits were recorded in 35 mounds (detailed data on 3 mounds was not collected; Table 3.5). Shallow pits accounted for 27.67% (5.1±SE 1.46 shallow pits per mound, n=35 mounds, max=44, min=0). Deep pits accounted for 72.33% (13.37±SE 2.98 deep pits per mound, n=35 mound, max=67, min=0). Of these 468 deep pits, 54.06% were used for egg-laying. Deep pit-digging was significantly greater than the shallow pits digging in the mound of Nicobar Megapode ($t=-4.54$, $p<0.001$, df=34).

Highest numbers of pits dug by the birds in mound 8 were 111 pits, of these 44 pits were shallow and 67 deep. In this mound 18.2% of shallow pits developed into deep pits. Remaining shallow pits were filled up. Of these 18.2% shallow pits, the average time taken by a shallow pit to became a deep pit was 4.9 days (SE 3.5, n=8, max=12 days, min=1 day). Mean duration over which a shallow pit persisted was 8.3 days (SE 1.13, n=30, max=20, min=1). Average duration over which a deep pit persisted was 12.56 days (SE 1.05, n=64, max=30 days, min=1).

Mound 7, which had 20 pits was close to an average number of pits per mound. Of these seven pits were shallow and 13 were deep pits, nine of which became egg pits. In this mound 28.6% of shallow pits developed into deep pits. Remaining shallow pits were filled. Of these 28.6% shallow pits, the average time taken by a shallow pit to became a deep pit was five days (max=8 days, min=2 days). Mean duration over which a shallow pit persisted was 16.3 days (SE 4.8, max = 40 days, min = 1 day).

One pit each was dug in four new mounds. Of the four deep pits, one pit was used for egg laying, other pits including the shallow pits persisted for a long time and later those pits disappeared due to wind and rain (Table 3.5).

3.3.4.ii. *Pit-filling and pits-filled*

Pit-filling along with covering activities on the mound was seen throughout the year (Table 3.2). The filling of pits was a major activity on the incubation mounds, and accounted for 9.7% of activities on the mound. In the case of pits in which eggs had not been laid, the pits were filled, either directly after they had been dug, or indirectly while the birds were raking or while they were digging another pit, or remained unfilled for several days or weeks.

Table 3.5. The number of visits by the Nicobar Megapode to respective mounds is directly influenced the number of eggs laid in it.

Mound	Visits	Type of pits		
		Shallow	Deep	egg
1	32	2	13	8
2	23	0	6	6
3	103	11	30	14
4	70	12	17	7
5	?	2	0	?
6	42	2	19	8
7	45	7	13	9
8	371	44	67	34
9	303	14	57	30
10	252	21	45	28
11	84	6	12	0
12	220	8	34	17
13	241	9	34	24
14	166	17	46	25
A13	16	0	1	1
16	4	0	2	1
A1	39	2	4	1
A10	28	0	2	1
A11	22	?	?	9
A12	130	8	12	11

"?"- unknown

Mound	Visits	Types of pits		
		Shallow	Deep	egg
A6	5	?	?	?
A7	29	3	7	2
A8	3	0	3	3
A9	95	2	12	12
B1	23	2	5	2
B10	?	1	11	?
B12	?	2	7	?
B13	?	0	1	?
B7	?	0	2	2
B8	?	3	0	?
B9	3	0	1	?
C10	4	0	0	0
C12	16	?	?	?
C7	2	0	1	0
C8	11	1	0	0
C9	45	0	4	4
D10	3	0	0	0
D8	4	0	0	0

The egg-pit was filled immediately after the egg was laid. During the process of the filling of the egg-pit, the megapodes would not leave the mound till the filling process was completed, despite danger from man or from monitor lizards.

After the egg-pit was filled, the Megapodes filled the mouth of the egg-pit by raking soil from either the mound itself or from surrounding areas during which the egg-pit and sometimes adjacent pits were covered and built over. During pits-filled activity, some pits may continue to remain as such. Some times, after laying egg the birds raked so much material onto the mound that all traces of pits were completely obliterated. The complete covering of the mound was 2.1 % of the total mound activities.

Pits-filled activity was distributed throughout the year but it varied between months (Table 3.2). In 1996, 8.3 % of the incubation mound activity was pits-filled, while in 1997 it was 11.6 % and 7.6 % in 1998. The mean proportion of pits-filled during the dry months was 9.6%, which was lower than the proportion of pits-filled during September and October (wet season) which was 12.7% of mound activities.

3.3.4.iii. *Raking*

The three-fold increase of incubation mound volume occurred because of an activity called raking. Raking is the collection of the sand and vegetative litter from the areas surrounding the mound. This material is then used to cover and build up the mound. Raking was a very important activity performed by both partners of a pair. Unpaired birds also did raking activity.

Raking activity on the incubation mound was distributed throughout the year. During the breeding season in 1996, raking activity was 26.3% but in 1997 and 1998 it was 29.2% and 18.7% respectively. The mean proportion of raking activities during the dry season was 26.1% of the activity which was significantly less than raking during the wet season which was 61.5%.

3.3.4.iv. *Scratching*

Apart from the activities described above, which are time consuming, megapodes, particularly the dominant pairs of the mound visit the mound frequently. During such visits, which are generally brief, they usually scratched on the surface of the mound before departing. Scratching activity was distributed throughout the year. In general, 15.4 % of incubation mound activity was scratching on the incubation mound. Scratching activity was more in the breeding season (16%) than in the non-breeding (6%) season. The proportion of scratching to all mound activities remained more or less constant between years (17.6, 14.9, and 15% respectively, see Table 3.4).

3.3.4.v. *Egg-laying*

While laying of eggs inside the mound took place several times during observations, the actual process of egg-laying by the Nicobar Megapode was observed thrice. On one occasion, after digging a deep pit, the male descended and checked the bottom, and returned to the top of the incubation mound. The female then descended into the pit and dug a small hole at the bottom. She then sat down, and looking upward with opened bill, extended her wings slightly. Within a minute egg-laying was over, and the female covered the egg with sand, simultaneously the male also started filling the egg-pit. In the other two occasions, the behaviour of the male prior to egg-laying by the female could not be ascertained. The male was also heard making a soft contact call that can be sylabalised as "miyaou, miyaou". Other activities of the male included walking on the mound, scratching on the incubation mound, and occasionally visiting the entrance of the pit and watching the female.

Unpaired females were observed laying eggs twice. This was slightly different from the egg-laying by a pair as she dug the pit and filled it alone. Once the egg-pit was dug, she entered the pit and returned after laying an egg within a few seconds. Egg-laying by an unpaired female appears to be quicker than by a paired female.

The egg-laying interval between two consecutive eggs and the clutch size was estimated with colour marked birds. The mean egg-laying interval was 14.91± SE 1.43 days (n=11 intervals in 17 eggs). The average number of eggs laid in a mound was 4.5 (±SE 0.6, n=58) but it significantly varied between the years (K.W. test, $\chi^2 = 8.203$, df=2, p=0.017) (Table 3.6 & 3.7). Clutch sizes of the Nicobar megapode varied between one to four eggs per season or year (Table 3.8). Data on the clutch size was collected only for seven colour marked birds in 1997 and five in 1998. Of the 12 colour marked pairs, five pairs laid four eggs per year in one or two mounds (Table 3.8). In general, the average clutch size of the Nicobar megapode was 2.75 eggs (± 0.35, n=12).

The peak period of the egg-laying was between February and May (Table 3.2, Fig 3.1) during which 86.6 % and 84.7 % of the eggs were laid in 1996 and 1997 respectively. In 1998, data collected was only between February and May. Egg-laying was not observed during the wet season (September and October of 1997). Total number of eggs laid in 1996, 1997 and 1998 are 112, 124 and 35 respectively.

Table 3.6. Mound size and number of eggs laid in it at different years.

Mound	1996		1997		1998	
	No. Egg laid	size	No. Egg laid	size	No. Egg laid	Size
1	7	4.73	1	0.44	0	0.31
2	6	6.85	0	0.68	0	0.46
3	6	4.75	5	3.33	3	3.79
4	1	21.65	6	11.20	0	9.36
6	2	3.52	5	1.98	1	2.34
7	1	1.58	6	0.46	2	0.39
8	13	7.76	17	7.94	4	8.59
9	13	8.37	16	4.29	1	7.28
10	13	53.35	11	27.78	3	35.99
12	7	13.97	7	3.77	3	4.63
13	14	17.27	6	12.45	4	5.85
14	10	9.40	11	8.87	4	8.49
a1	0		2	0.46	1	0.25
a10	0	0.23	1	0.62	0	0.48
a11	9	0.25	0	0.35	0	0.57
a12	1	11.40	8	8.87	2	6.16
a13			2	1.24	1	0.19
a6	1	0.28	1	0.29	0	0.36
a7	0	0.50	1	0.75	1	0.74
a8	3	1.88	0	0.65	0	
a9	4	6.45	8	1.40	0	0.64
b1	0		2	0.59	0	0.94
b10			0	6.98	1	
b12	0	1.98	2	6.02	1	7.71
b13			2	0.38	0	
b9	1	0.60	1	0.41	0	0.49
c9	0		3	1.39	1	2.97

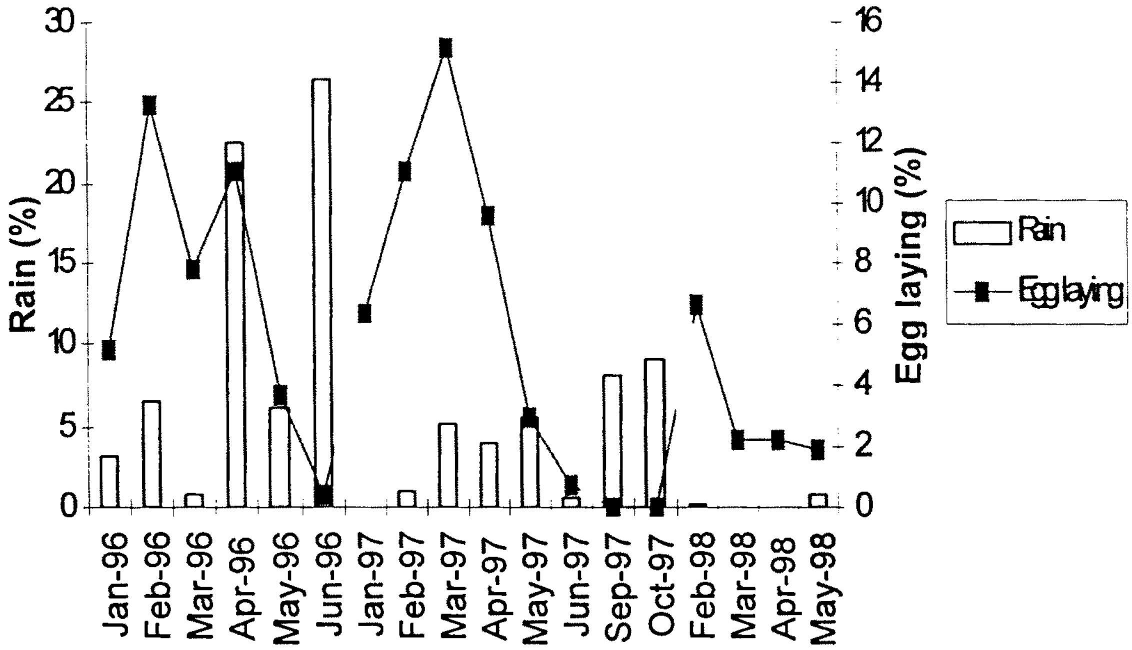
Table.3.7. Average number of eggs laid in a mound in different years.

	1996	1997	1998	Over all
Average	5.7	5.4	2.1	4.5
Standard error	1.1	1.0	0.3	0.6
Number of mounds	18	23	17	30

Table 3.8. Clutch sizes of colour marked megapodes. Some pairs used more than one mound for egg laying.

Bird	1997	1998	No. of mounds
G-O14	4		1
GO8	2		1
PAYU	1		1
GR9-Y9C	4		2
BP9	4		2
SPG9	2		2
YR14	4		1
WOR3		3	3
WO3		2	1
PAYU		4	1
GR9-Y9C		1	1
Y10		2	1

Figure 3.1. Influence of precipitation on the egg-laying of the Nicobar Megapode



3.3.4.vi. *Other activities*

About 0.9% of all activity on the mound was not distinct, as the birds simply walked apparently aimlessly on the incubation mound, making small pits which were immediately filled, then covering or raking etc. This type of activity was usually performed by unpaired birds, but frequently by paired birds as well.

About 5.5 % of mound activity consisted of Megapodes visiting the mound briefly, during which none of the incubation mound activities described above were performed. These visits were not observed during the wet season. Occasionally, an unpaired bird stood/walked on the incubation mound without doing any other activity, which has been recorded for as long as 38 minutes.

Fighting and foraging activities of the Nicobar Megapode were also seen occasionally on the mound (Table 3.2).

3.3.5. Differences between pairs in mound activity

Three levels of digging activities were recorded on mounds: "Vigorous digging" (>60 kicks/min) "Moderate digging" (30-60 kicks/min) and "Slow digging" (<30 kicks/min). Statistically there was no difference between the kick rates by paired and unpaired birds in the incubation mound ($t=0.27$, $df=35$, $p=0.39$). Due to a paucity of data on more marked pairs, the rate of digging activity between pairs could not be ascertained.

3.3.6. Contribution of the sexes to mound construction and maintenance

Both partners participated equally in the construction and maintenance of incubation mounds and there was no significant difference between the partners of a pair in respect to the quantum of work on the incubation mound (t=-0.55, p=0.29, df=27) when kick rates were compared.

3.3.7. Influence of rain on the activities of the Nicobar Megapode

On Great Nicobar, the dry season is characterised by occasional rains (Fig 1.4 & 3.1). However, when compared to 1996 and 1997, fewer showers occurred in 1998 between February and May. The average number of eggs laid per mound was lower in 1998 than in 1996 and 1997. Pit-digging activity was more during the dry season than the wet season (Fig 3.2). However, within the dry season moderate rains increased the pit-digging activity of the Nicobar megapode. Because of drought in 1998, pit digging was drastically reduced in April and May. More or moderate precipitation in dry season also increased the raking activity of the megapode on the mound (Fig 3.2).

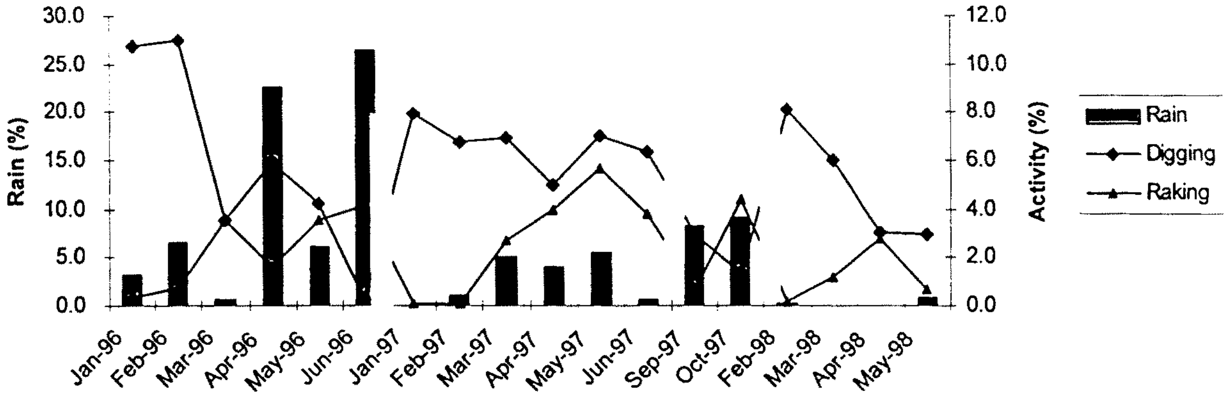
3.3.8. Incubation conditions within incubation mounds

3.3.8.i. *Temperature and Soil Respiration in and out of the incubation mound*

Mean core temperature at the depth of 50-60 cm in incubation mound was 31.94°C (se 0.075, N=634). The mean temperature at the 60 cm depth from the forest ground was 28.72°C (se=1.66, n=105). The mean soil respiration ($gCO_2/m^3/h$) rate (SR) on the active incubation mound was 5.55 (se=0.13, n=920), on abandoned incubation mound SR was 2.88

(se=0.92, n=140) and the soil respiration rate recorded on the normal ground was 3.7 (se=0.86, n=130).

Figure 3.2. Influence of precipitation on the major activities like raking and digging of the Nicobar Megapode.



3.3.8.ii. *Incubation period and optimal incubation temperature*

The temperature of the egg chamber of 34 eggs in 16 incubation mounds was monitored, and the incubation period for 30 eggs was determined. Four eggs did not hatch. The shortest incubation periods were 70 days (n=1 egg) and 72 days (n=6 eggs) and the longest incubation period was 81 days (n=1 egg). The mean temperature of the egg chamber for successful hatching was 32.44 (se=0.21, n=30). The mean incubation period of the monitored eggs was 74.73 (se=0.52, n=30 eggs) days. Though the data (Fig. 3.3) indicates that as temperature decreases the incubation period increases, there was no significant correlation between the length of incubation period and incubation temperature (Pearson correlation: r=-0.31, n=30, p=0.095). Moreover, as eggs incubated at different temperatures could hatch in the same period (fig. 3.3), indicating that fluctuation in the temperature of the egg-chamber within the observed range did not appear to affect incubation period (Fig 3.3).

3.3.8.iii. *The effects of incubation mound size on incubation temperature*

The effect of incubation mound size on temperature in 37 incubation mounds was studied (Table 3.9). The size of the 37 incubation mounds varied from 0.15 m^3 to 40.24m^3 with a mean size of 4.78m^3 (SE 1.19). As mound size increased the temperature of the mound increased (fig 3.4) at the depth of 31 to 49 cm ($r=0.162$, $n=518$, $p<0.001$), 50 to 60cm ($r=0.177$, $n=532$, $p<0.001$) and the depth of 61 to 90cm ($r=0.307$, $n=526$, $p<0.001$). There was some fluctuation in the incubation temperature of the mound, irrespective of sizes (Fig 3.5).

Figure 3. 3. Relation between the mound core temperature (°C) and incubation period (days) of egg of the Nicobar Megapode (trend line is linear).

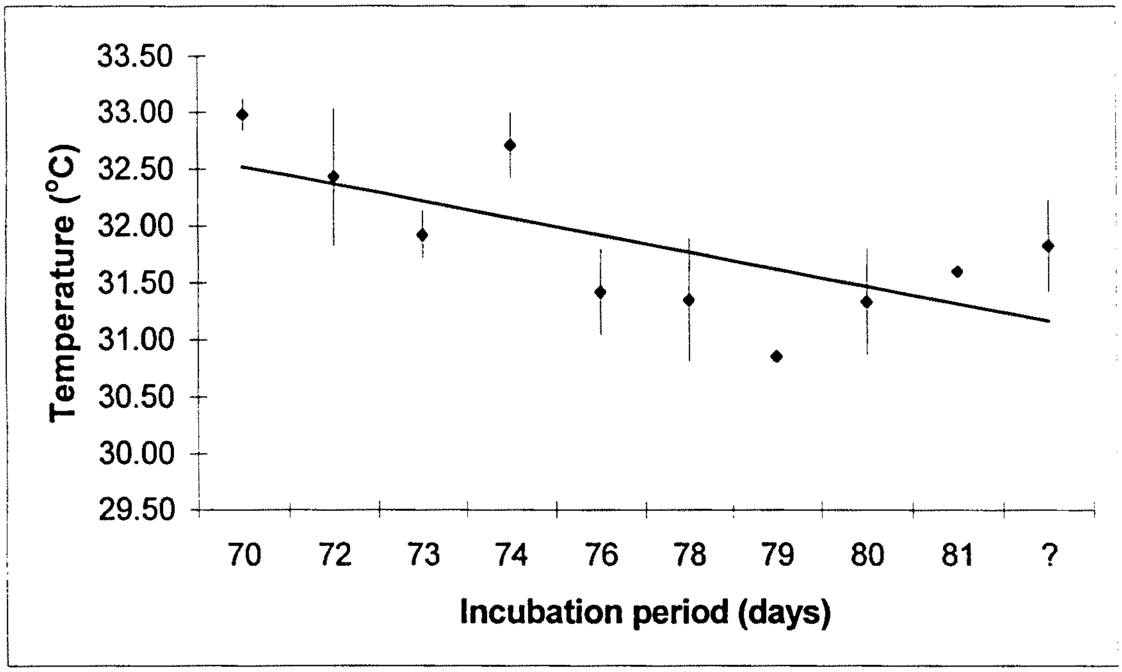


Figure 3. 4. Relation between the mounds size (m^3) and temperature (°C) in mounds of the Nicobar Megapode (trend line is linear).

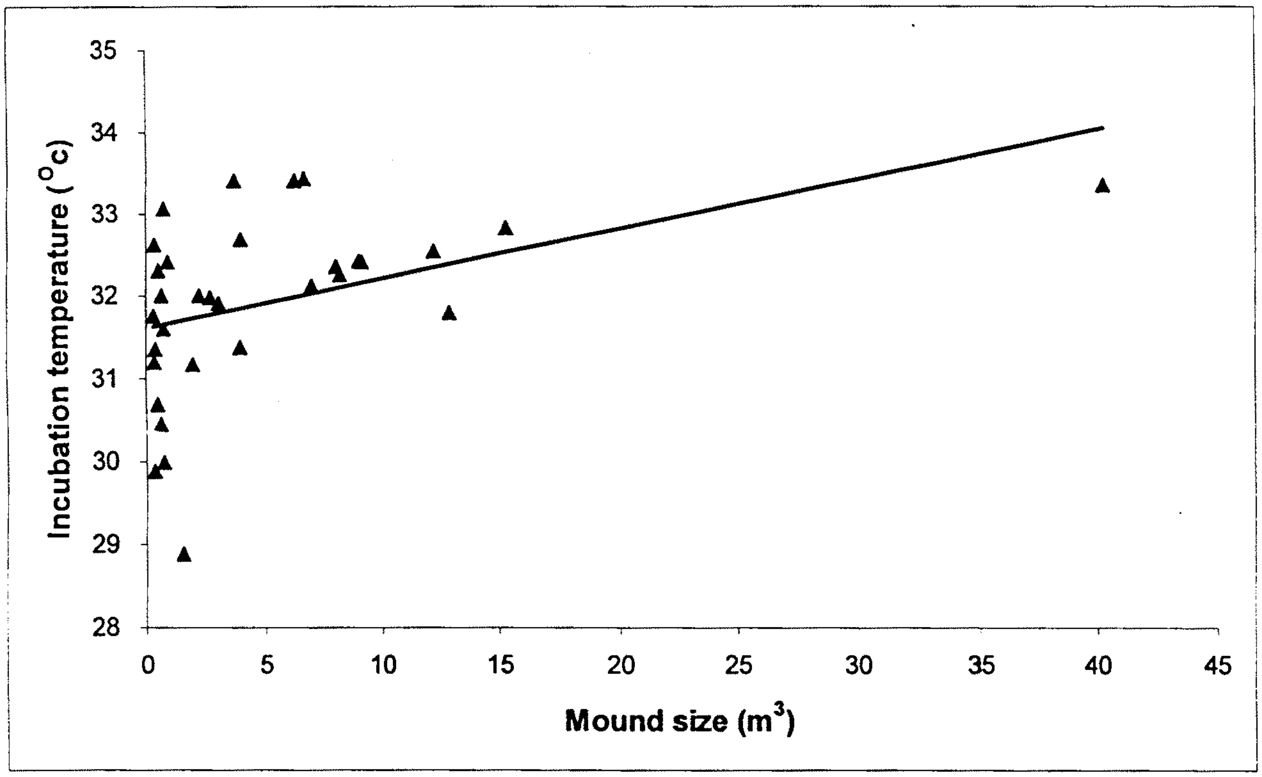


Figure 3. 5. Relation between mound size and incubation temperature. If mound size increased then the core temperature of the mound increased. There was, however, some fluctuation in all the mounds irrespective of sizes.

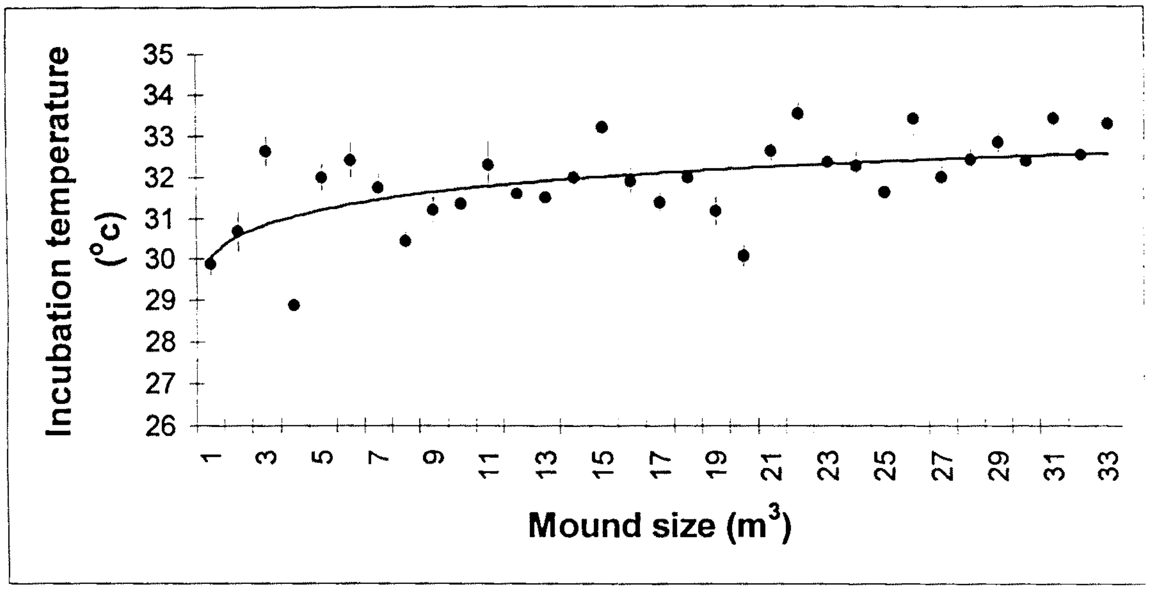


Table 3.9. Monthly averages of size, temperature at different depths and soil respiration of all focal mounds.

Time	Mound size	Ambient	Surface	Depth 20-30cm	D 31-49cm	D 50-60cm	D 61-90cm	Soil respiration
Jan-96	9.23	27.18	26.65	29.47	30.33	31.32	31.56	3.44
Feb-96	7.17	27.75	26.94	30.91	31.6	32.05	32.89	5.31
Apr-96	11.81	27.75	27.28	29.28	29.63	31.45	33.21	7.25
May-96	13.46	28.05	27.13	32.25	33.23	36.64	33.53	8.8
Jun-96	15.09	28.85	28.13	29.83	33.04	33.44	33.64	5.53
Jan-97	3.32	27.46	26.92	29.33	31.95	32.33	31.68	5.68
Feb-97	3.24	29.12	28.73	30.53	33.27	33.28	32.8	4.31
Mar-97	3.85	27.99	27.74	30.42	30.18	31.88	32.52	5.88
Apr-97	4.47	27.03	26.62		29.73	31.88	33.03	7.94
May-97	5.00	28.08	27.96		29.94	31.71	32.77	6.47
Jun-97	7.23	28.09	28.05		31.24	33.03	33.61	
Feb-98	3.52	29.88	29.39		31.06	32.02	32.55	
Mar-98	3.67	29.9	28.64		31.04	32.15	32.85	
Apr-98	4.24	29.77	28.67		31.08	32.1	32.98	

3.3.8.iv. *The role of sunlight on incubation temperatures*

The development and maintenance of incubation conditions within incubation mounds is complex. Intensity of the light falling on the mound (Lux value) was significantly correlated with the ambient ($r=0.24$, $n=168$, $p<0.01$) and surface temperatures of the mound ($r=0.25$, $n=168$, $p<0.01$) but not with the mound core temperatures (e.g. at 61 to 90cm depth $r=0.053$, $n=96$, $p=0.610$). However, there was a significant correlation between the surface and mound core temperatures (at the depth of 61 to 90cm, $r=0.23$, $n=626$, $p<001$). The mean temperature of ambient and surface was always lower than the mound temperatures at different depths (Table 3.10).

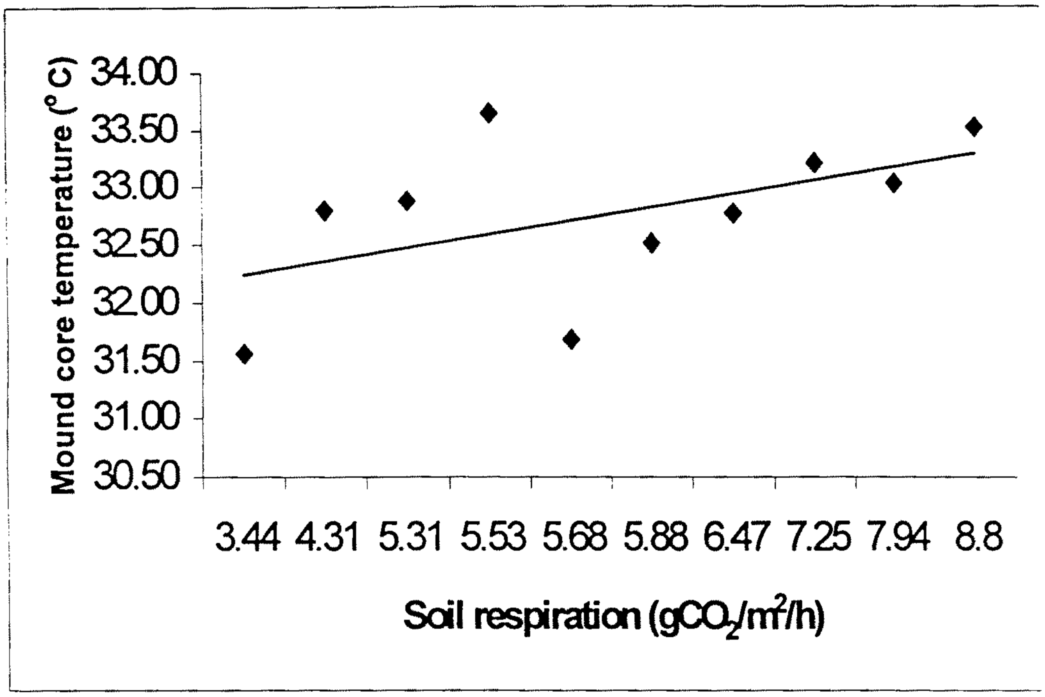
Table 3.10. Average temperature of the mounds at various depths.

	Ambient	Surface	Upper layer	Middle layer	Deep layer	Deepest layer
Mean(X)	28.17	27.57	29.91	30.65	31.94	32.51
N	735	745	196	618	634	628
SE	0.065	0.055	0.177	0.0747	0.075	0.072

3.3.8.v. *The role of microbial activity on mound incubation temperatures*

The relationship between microbial activities as evidenced by soil respiration and incubation temperatures is complex. There was a statistically significant correlation between soil respiration and incubation temperature (at the depth of 50 to 60cm) of the incubation mound ($r=0.15$, $n=204$, $p=0.02$). There was a relationship between the average value of microbial activity and incubation mound temperature (Fig 3.6) of the incubation mounds indicating that the microbial activity was the source of heat.

Figure 3. 6. Effect of microbial activity on the incubation temperature (trend line is linear).



3.3.8.vi. *Humidity and incubation temperature*

There was a significant correlation between the humidity of mound substrates and the temperature of the mound. Humidity of the mound influenced the incubation temperature at 33 to 49 cm depth ($r=0.272$, $n=166$, $p<0.001$), 50 to 59 cm ($r=0.407$, $n=166$, $p<0.001$) and 60 to 90cm ($r=0.534$, $n=166$, $p<0.001$).

3.3.9. Incubation mound size and egg-laying

Of the 38 incubation mounds that have been active in the study area in 1996, 1997, or 1998, eggs have been laid in at least 35. Of these, only 10 incubation mounds were used in all the dry seasons from 1996 to 1998 for egg laying.

The very small sized incubation mounds (<1 m3) had the least number of eggs laid in them (2.30 ± SE 0.77 eggs/mound/year, n=10 incubation mounds). Small sized incubation mounds (1-5 m^3) have an average 4.05 eggs laid in them (± SE 0.60, n=7), medium sized incubation mounds (6-10 m^3) contained on average 5.93 eggs (± SE 1.15, n=7), while large sized incubation mounds (>10m^3) had the most number of eggs in them (Table 3.11). There was a significant positive correlation between the mound size and number of eggs laid in it ($r=0.456$, $n=71$, $p<0.001$). Table 3.11 shows the variation in mound size and number of eggs laid during the study period.

Table 3.11. Effects of the incubation mound size on the egg laying, during the entire study period.

Size of incubation mound	Number of mounds	Eggs laid/year
<1 m^3	10	2.3 ± 0.77
1.1 – 5 m^3	7	4.05 ± 0.60
5.1 – 10 m^3	7	5.93 ± 1.55
> 10 m^3	3	6.83 ± 1.69

3.3.10. Hatching success

Hatching success was determined in 32 incubation mounds in 1997, where one to five eggs were laid in 13 incubation mounds, six to 10 eggs in six incubation mounds, and more than 10 eggs in four incubation mounds. Five incubation mounds were not used for egg-laying in 1997, and the number of eggs laid in four incubation mounds could not be determined. Mean hatching success in the incubation mounds in 1997 was 58.87%. Of the 124 eggs laid in 23 mounds, 10.48% of eggs did not hatch and those eggs were unearthed in the next season. 29.84% eggs disappeared or were preyed on, and the fate of 3.23% of eggs was not clear (if these eggs successfully hatched then the hatching success was 62.1%; table 3.12).

Small incubation mounds had less number of eggs while medium sized incubation mounds were used by the birds for more egg laying (table 3.13). However, there was no significant correlation between the incubation mound size and hatching success (Table 3.13).

Table 3.12. Hatching success in 1997.

Mound	Size	Eggs	Hatched	Unhatched	Disappeared	Doubtful	%success
A1	0.46	2	2	0	0	0	100.00
B1	0.59	2	2	0	0	0	100.00
1	0.44	1	1	0	0	0	100.00
2	0.68	0	0	0	0	0	
3	3.33	5	4	1	0	0	80.00
4	11.20	6	4	0	2	0	66.67
14	8.87	11	7	3	1	0	63.64
6	1.98	5	3	0	2	0	60.00
A6	0.29	1	1	0	0	0	100.00
7	0.46	6	4	0	2	0	66.67
A7	0.75	1	0	0	0	1	0.00
B7	0.26	?	2	0	0	0	
8	7.94	17	10	3	4	0	58.82
9	4.29	16	9	2	5	0	56.25
A9	1.40	8	1	0	7	0	12.50
C9	1.39	3	2	1	0	0	66.67
10	27.78	11	5	2	4	0	45.45
A10	0.62	1	1	0	0	0	100.00
B10	6.98	?	0	0	0	0	

Contd.. Table 3.12

Mound	Size	Eggs	Hatched	Unhatched	Disappeared	Doubtful	%success
C10		0	0	0	0	1	
A13	1.24	2	1	0	1	0	50.00
B13	0.38	2	0	0	1	1	0.00
13	12.45	6	4	1	1	0	66.67
A12	8.87	8	4	0	3	1	50.00
12	3.77	7	3	0	4	0	42.86
B12	6.02	2	2	0	0	0	100.00
11	6.98	0	0	0	0	0	
A11	0.35	0	0	0	0	0	
D10		?	?	?	?	?	
B8	0.39	?	?	?	?	?	
B9	0.41	1	1	0	0	0	100.00
A8	0.65	0	0	0	0	0	
Total		124	73	13	37	4	
Percentage		100	58.87	10.48	29.84	3.23	

Table 3.13. Effects of the mound size on the egg-laying and its hatching success in 1997.

Size of Incubation mound	N	Eggs laid	Hatching success %
< 1 m^3	9	1.9 ± SE 0.5	74.1 ± SE 14.5
1.1 - 5 m^3	7	6.6 ± SE 1.8	52.6 ± SE 8.1
5.1 – 10 m^3	4	9.5 ± SE 3.1	68.1 ± SE 11.0
> 10 m^3	3	7.7 ± SE 1.7	59.6 ± SE 7.1

3.4. DISCUSSION

3.4.1 Mound activities

Mound building in the Australian Brush-turkey has been classified into construction and maintenance phases (Jones 1988). In the Nicobar Megapode, these two phases could not be distinguished as all activities like pit digging, raking and mound covering were performed throughout the dry season. Raking was the major maintenance activity during the wet season, and could be because, more wetting of the mound during the wet season could affect the stabilisation of incubation temperature and also affect the egg hatchability (Seymour *et al.* 1987). However, as most pairs did not visit the mound after egg-laying was over, it could indicate that mound activity of the megapode during wet season was associated with holding the mound from strangers or neighbours, rather than deliberate regulation of the mound at a specific temperature (Jones 1988).

3.4.2. Influence of precipitation on the egg-laying

Rainfall and clutch size might be linked via food availability (Goth and Vogel 1996). While comparing the dry seasons of three years (Table 3.7), the average number of eggs laid per mound was very low in 1998, and can be linked to low precipitation in 1998. Moisture is necessary for microbial activity, and drops in moisture content disturb the mound incubation temperature (Seymour *et al.* 1986). The lower number of eggs laid in a dry year appears to be consistent with other species as mounds constructed during severe drought season contained lesser number of eggs in the case of Brush-turkey and Malleefowl (Seymour *et al.* 1986). Moreover, digging pits becomes difficult as the dry and loose soil easily slides down.

3.4.3. Incubation conditions within incubation mounds

Megapode incubation 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 1989b) and/or solar radiation (Frith 1956). Mound temperatures usually stabilise between 32 – 35°C (Jones *et al.* 1995), which is consistent with that of the Nicobar megapode (32.44°C). Incubation temperatures in mounds shows 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 1989a; Jones and Birks 1992). While incubation mound maintenance is thought to play a role in maintaining suitable incubation temperatures, Seymour (1985) proposed that heat production and heat loss tend to stabilise incubation mound temperatures at equilibrium. This is due to the great thermal inertia of incubation 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 in the assumptions mentioned above by Seymour (1985). First, the size of the incubation mound can vary in height from ten cm up to 2.1 m and in basal circumference from seven to 45 m (Sankaran 1995a, b). Second, the proportion of organic material in an incubation mound varies due to location of the mound. For example a mound present very near to a coral beach was built with more corals, and if it was against a dead log it had more vegetative materials. And third, the gap in the canopy above the incubation mound varied resulting in differences in the amount and duration of sunlight falling on it. This might indicate that the heat sources, which create suitable incubation conditions within an incubation mound may vary, with some incubation mounds appearing to rely on sunlight and others on organic decomposition (Sankaran and Sivakumar 1999).

Solar energy, however, probably only optimises the incubation mound temperatures. Though the canopy above an incubation mound was less than the canopy above non-mound areas, direct sunlight falls on the mounds for very short periods, with the result that both ambient temperature and incubation mound surface temperatures were always lower than incubation mound core temperatures (Table 3.10). Thus, the role of solar energy appears to be restricted to warming the surface of the incubation mound, whereby dissipation of heat was reduced.

Microbial respiration is the primary source of heat harnessed by most mound building megapodes (Jones *et al.* 1995). In the Nicobar Megapode, a clear relation exists between the incubation temperatures and the organic activity as evidenced from soil respiration. Microbial respiration has a linear relation to the temperature of the incubation mound of deeper layer. However, incubation mounds with higher levels of soil respiration did not necessarily have higher temperatures. 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 vegetative materials added to the incubation mound. Second, the rate of heat loss probably differs between incubation mounds, caused by differences in the proportion of surface area to the volume of incubation mound or to the amount of moisture content within the incubation mound (Jones *et al.* 1995) or the amount of sunlight or radiation from the beach falling on the mound.

Observations on the influence of mound size on mound incubation temperatures are consistent with the model of incubation mound homeothermy (Seymour 1985, Jones *et al.* 1995). Small incubation mounds show a greater variation in mound incubation temperature than large incubation mounds, with small incubation mounds showing temperatures below, at or above optimal incubation temperatures (32 - 35°C; Dekker 1990) while the incubation temperatures of large incubation mounds lay within the optimal incubation temperature range. Stabilisation at optimal incubation temperatures was consistent only in large incubation mounds

3.4.4. Mound size, egg-laying and hatching success

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

As optimal temperature were consistently present in large mounds, one would therefore expect that eggs in large incubation mounds are more likely to hatch successfully than in smaller incubation mounds. However, hatching success of the Nicobar Megapode does not reflect these trends. This study reveals that there was no significant relationship between the incubation mound size and hatching success. Very smaller and medium sized incubation mounds showed more hatching success than the smaller (1-5 m^3) sized ones. The probable reason for the lower hatching success in the smaller (1-5 m^3, Table 3.12) sized incubation mounds was because of the large number of birds that used them. Greater digging activity and consequently greater exposure of eggs to the atmosphere was a possible factor for lower hatching success. Secondly, more mound activities may attract more predators, especially monitor lizard. About 30% of megapode eggs were preyed on in 1997, when activities at the mound were also the most. Clutch size of the Nicobar Megapode was lower than other mound building megapodes (Jones *et al.* 1995).

3.5. CONCLUSION

Incubation mounds of the Nicobar Megapode were constructed with either sand or sand with vegetative materials, such as leaves, twigs and bits of decomposing wood, which were available in the surrounding areas. Usually, the site selected for a new incubation mound was a fallen log, tree stump, or the decomposing roots of a tree. Mound construction began by the birds either digging a pit at the site or by covering the decomposing log or tree stump with soil and litter. The mean egg-laying interval was 15 days, the average number of eggs laid in a mound was 4.5 but it significantly varied between the years and the average clutch size of the Nicobar megapode was 2.75 eggs. Moderate rainfall in the dry season enhances the egg production. Sun light and microbial activities appear to be the primary sources of mound temperature. The average incubation temperature was 32.5°C and the average incubation period was 75 days. If the size of the mound increased then the temperature of the mound increased. There was, however, no significant relationship between the mound size and hatching success of the Nicobar Megapode.

Chapter IV

SOCIAL ORGANISATION OF THE NICOBAR MEGAPODE

4.1. INTRODUCTION

4.1.i. Social organisation

Social organisation is as a complex of behavioural characteristics determining the mode of dispersion of a population and the individual encounters within it (Crook 1965). Studies of social organisation have focused mainly on either reproductive situations (Lack 1968, Emlen 1982, Oring 1982) or as factors influencing gregariousness in non-breeding situations (Matthysen 1990). Less attention has been paid to spatial defence and prolonged social bonds (Matthysen 1990).

Most of the avian species breed in monogamous pairs (Oring 1982, Krebs and Davies 1989) because of the necessity of biparental care of the young (Lack 1968). However monogamy is not a monolithic mating system since monogamous individuals may engage in extra-pair fertilisation (Black 1996). Avian mating systems that deviate from monogamy are therefore of particular interest, especially in relation to the extent and form of parental care provided. Extensive parental care by males is expected only where males have a high certainty of paternity (Ridley 1978). Where this certainty is low, males may be expected to reduce or abandon parental care in favour of concentrating on acquiring additional matings (cf. Jones 1990b).

Megapodes leave their eggs in warm and safe environments, rather than incubating it by using body temperature. Megapode eggs are relatively very large; around 20% of the females' body weight (Jones *et al.* 1995). A female typically lays 12 to 30 eggs per season (Jones *et al.* 1995) over a breeding season of many months. This means that hatchlings may emerge from the incubation site at any time and it is impossible for the parents to keep their chicks together. A super precocious chick hatches from the egg after a long incubation period. The adults have no direct control over the time of emergence of chick. Newly emerged hatchlings are able to survive alone from the start (Dekker 1990; Jones *et al.* 1995). Hatchlings remain solitary until they mature and pair.

Most megapodes are monogamous (Jones *et al.* 1995), however, promiscuity has been documented or suspected in some mound-building megapodes that also exhibit sexual dimorphism (Jones 1989b; Jones 1992; Jones *et al.* 1995). An instance of polygamy has also been documented for the monomorphic Malleefowl *Leipoa ocellata* which was believed to be strictly monogamous (Weathers *et al.* 1990; Jones *et al.* 1995).

The social organisation of many species of megapodes is not well known (Jones *et al.* 1995). Most of the detailed studies on the reproductive behaviour of megapodes have been conducted in captivity (Jones *et al.* 1995), but Jones (1990a & b), Coates (1985) and Birks (1991) have studied it in the wild. Megapodes are generally monogamous even though they do not engage in post-parental care. Therefore understanding the necessity of monogamy, why extra-pair copulation occurs and what is its role in the Nicobar Megapode is important.

4.1.ii. Territoriality

Home range is the area over which an animal normally travels in search of food (cf Brown 1964) and its size has been positively correlated with food density in birds (Shoener 1968). According to Brown (1975), territory is a fixed area from which intruders are excluded by some combination of advertisement, threat, and attack. Territories serve varied functions, such as exclusive feeding areas, nesting and /or pairing sites, or both, or a `mobile' territory that an individual exhibits to guard a resource that is not spatially fixed (Tinbergen 1957). Correspondingly, the definition of the term territory has varied from `fixed exclusive area with the presence of defence that keeps out rivals' (Brown and Orians 1970), to a less rigid definition 'whenever individual animals or groups are spaced out more than would be expected from a random occupation of suitable habitats' (Davies 1978). The measurement of the sizes of breeding territories of birds is important for a variety of theoretical and applied considerations. For example, territory size often bears a relationship to body size in a manner that varies as a function of the food habits of the organism (Shoener 1968). Territory size also varies among individuals within a species because of habitat quality, as individuals occupying poorer habitats may have to establish larger territories to obtain sufficient resources (Wiens 1973). Territory size also may be related to mating status, with individuals defending larger territories having an enhanced probability of attracting multiple mates in polygynous species. There are likely to be upper and lower limits of territory size within species, determined by the economic defensibility of the territory (Wiens 1973).

In megapodes, territorial behaviour has been documented in *Leipoa ocellata* (Frith 1959 and Booth 1987), *Megapodius reinwart* (Crome and Brown 1979), *Alectura lathami* (Jones 1990a&b) and *Eulipoa wallacei* (Heij *et al.* 1997). During the breeding season the male Mallee fowl usually stay within 100 m of their breeding mounds and females within 250 m (Booth 1987), remarkably small areas for such large birds (Frith 1959; Booth 1987). There was no significant difference in the home ranges of Mallee fowl between the breeding and non-breeding seasons (Frith 1959) unlike in Australian Brush-turkeys (Jones 1990a). The home range of Malleefowl in low-rainfall Murray Mallee was approximately 4 km^2, but home ranges of birds from different mounds overlapped to a considerable degree, resulting in an overall breeding density of 1.1 pairs per km^2 (Booth 1987). However, Jones (1990a) estimated that the home range size of the Australian Brush-turkeys varied between 0.22 ha to 7.61 ha. The home range of Moluccan Megapode regularly occurs in degraded secondary forests at rather low altitudes (Heij *et al.* 1997).

The distribution of the Nicobar Megapode was clumped and most of the population was distributed towards the coastal habitat of the islands (Sankaran 1995a, b). Considering the low availability of space for breeding, understanding the mechanism of territoriality in the Nicobar Megapode became important. Knowledge of the size of the home range and the degree of overlap is important for wildlife management, because it enables the potential carrying capacity of an area for a particular species to be estimated (Swihart and Slade 1985).

4.2. OBJECTIVES

1. To find out the establishment, structure and function of the territory.
2. To observe the territorial behaviour of the Nicobar Megapode
3. To find out the processes of pair formation, the longevity of pair bonds and the advantages conferred by pair formation.
4. To examine the use of incubation mounds by multiple pairs
5. To identify the type of mating system in the Nicobar Megapode.

4.3. RESULTS

4.3.1. Agonistic Behaviour

The agonistic behaviour of the Nicobar Megapode can be differentiated into warning calls, chases and physical fights. Throughout the year both the male and female of a pair threatened, chased or fought with any other unpaired or paired bird that came in contact with it. An encounter was considered to be agonistic when expressions of a mixture of aggression or threat and fear or avoidance was performed.

4.3.1.1. *Calls*

The Nicobar Megapode advertises its presence by duetting. The male gives a long call and female makes short calls. Although the duet was most often heard up to noon and again in the evening, it could also be heard at other times of both day and night. If one pair called, neighbouring pairs often called moments later in apparent response, suggesting that the call announced the presence of birds to defend territory.

Around mound '9', where four mounds were very close to each other, more than four pairs used this cluster. If one pair started duetting, other pairs responded by duetting. Except during fights, unpaired birds usually did not call.

Totally1264 duets were recorded during the dry months of the year between 1996-98 (Fig 4.1). An average of 75 calls was recorded in a month during the dry season but in the wet season only 42. Warning calls were more in the evening hours than in the morning and midday (Fig 4.2). Duets not only warned the neighbours but were also used as a threat during the physical fights. Duets were usually initiated by the female and continued by her partner.

4.3.1.2. *Chasing*

Prolonged chases were seen mainly during the dry season. On coming across another pair or unpaired bird on or away from the mound, one pair usually began chasing the other with or without performing calls. Such chases ended quickly. The chase consisted merely of an aggressive male running behind another male or aggressive female running behind another female or on occasion chasing them onto the branches of trees. Such chases stopped when the aggressor lost sight of the stranger or apparently lost interest. After stopping, the aggressive birds duelled for some time.

4.3.1.3. *Physical Fights*

Fights were usually brief but have, on occasion, gone on for an hour. Physical fights ended when one of the contestants ran away, or flew for a few metres before running away, with the winner chasing it for a few metres. Immediately after this, the winner starts calling (duet) vigorously at the location of the fight. The loser usually moves away to a nearby location where it also calls, sometimes intensively and sometimes sporadically.

Out of a total of 195 fights, 9.7% of fights happened on the mound. Most fights were seen within 50-m distance of the mound (Fig 4.3).

In 1997, fights were far more on the mound (63.2%) than in 1998 (26.3%) or in 1996 (10.5%). 94.7% of fights were seen during March, April and May of 1996-98 (Fig 4.1). Fights were not noticed on the mound during the rains in September and October of 1997.

Figure 4.1. Distribution of agonistic activities throughout the study period.

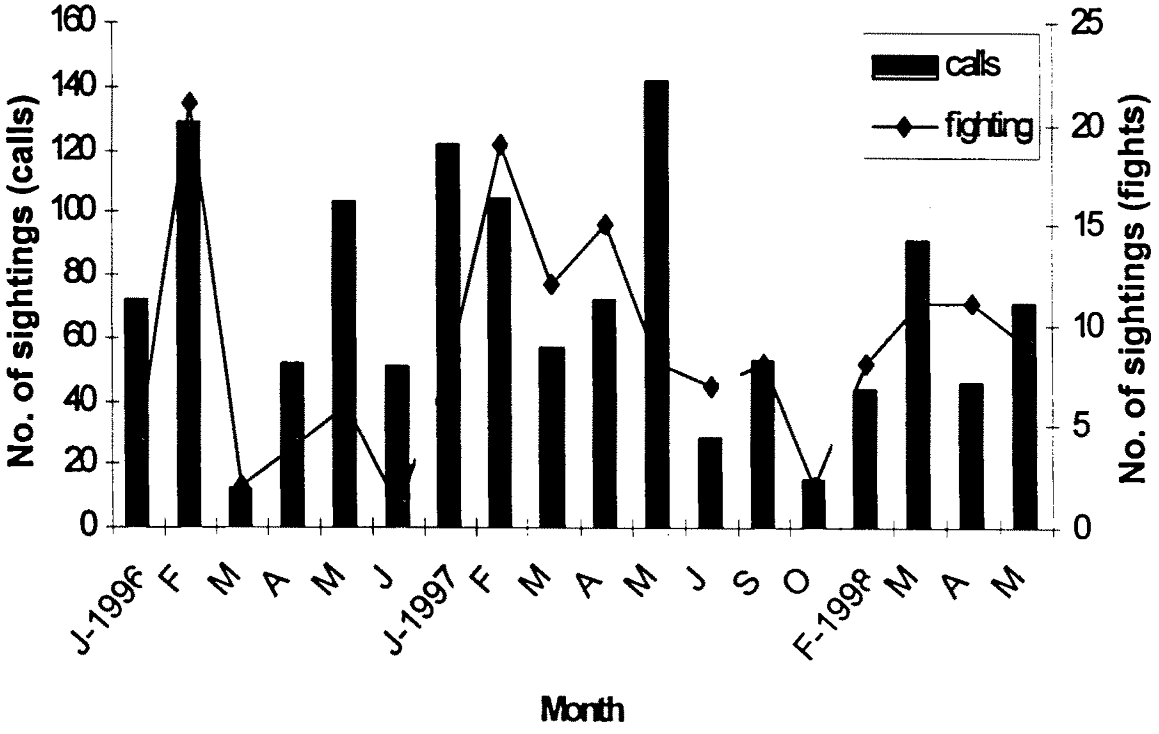


Figure 4.2. Distribution of calls through the day.

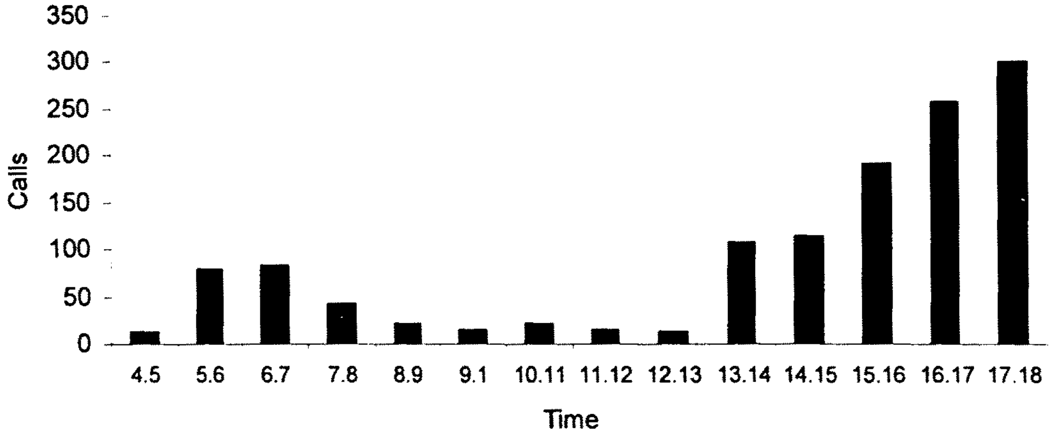
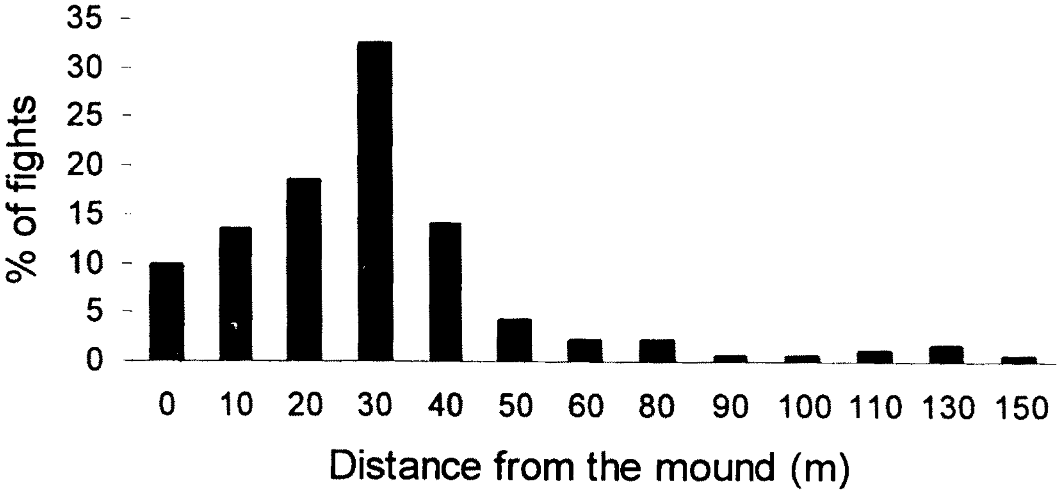


Figure 4.3. Distribution of the fights on and around the mound (n=195 fights).



Away from the mound, fights were distributed throughout the year. Totally 166 fights were recorded during the summer months of 1996-98 and 10 fights were observed within two months of the wet season (September and October, 1997). Fights on the ground were high during the morning 0500-0600 hours and the evening 1600-1800 hours (fig 4.4).

During physical fights the Nicobar Megapode performed different types of action. Two different types of physical fights took place based on where the fight happened. If it was on the ground it was called a ground clash, and in the air it was called an aerial clash. In the initial stage of physical fights one bird kicks the opponent's leg with its leg (fig 4.5). This 'leg and leg clash' then escalated into the 'leg and body clash' where both contestants attacked the body of the opponent with their legs. While performing a 'leg and leg clash' or 'leg and body clash' both the birds sat on the ground (tail and wings on the ground for balance) making calls. After a leg and body clash, the fights usually stopped. If it continued, the next stage was named as 'leg and head clash' when the legs targeted the head. This would then escalate into aerial clashes after which birds stopped their fight and separated. While performing an aerial clash, both birds jumped up to 1 to 1.5 meters high and fought, not unlike domestic chickens (Fig 4.6).

Figure 4.4. Distribution of fights through the day.

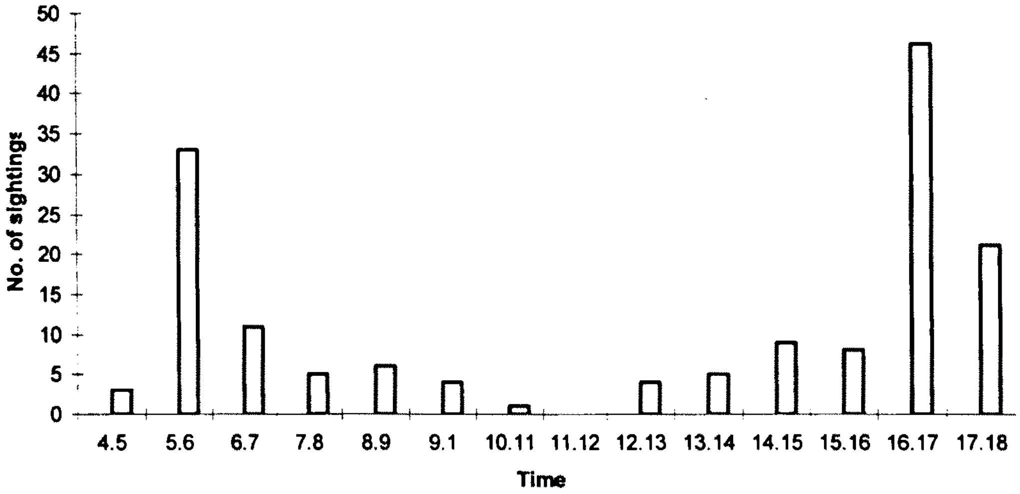


Figure 4.5. Fight between the two megapodes, a) first stage of fight, where target is legs of opponents and b) second stage of the fight, where the target is head and body of the opponents.

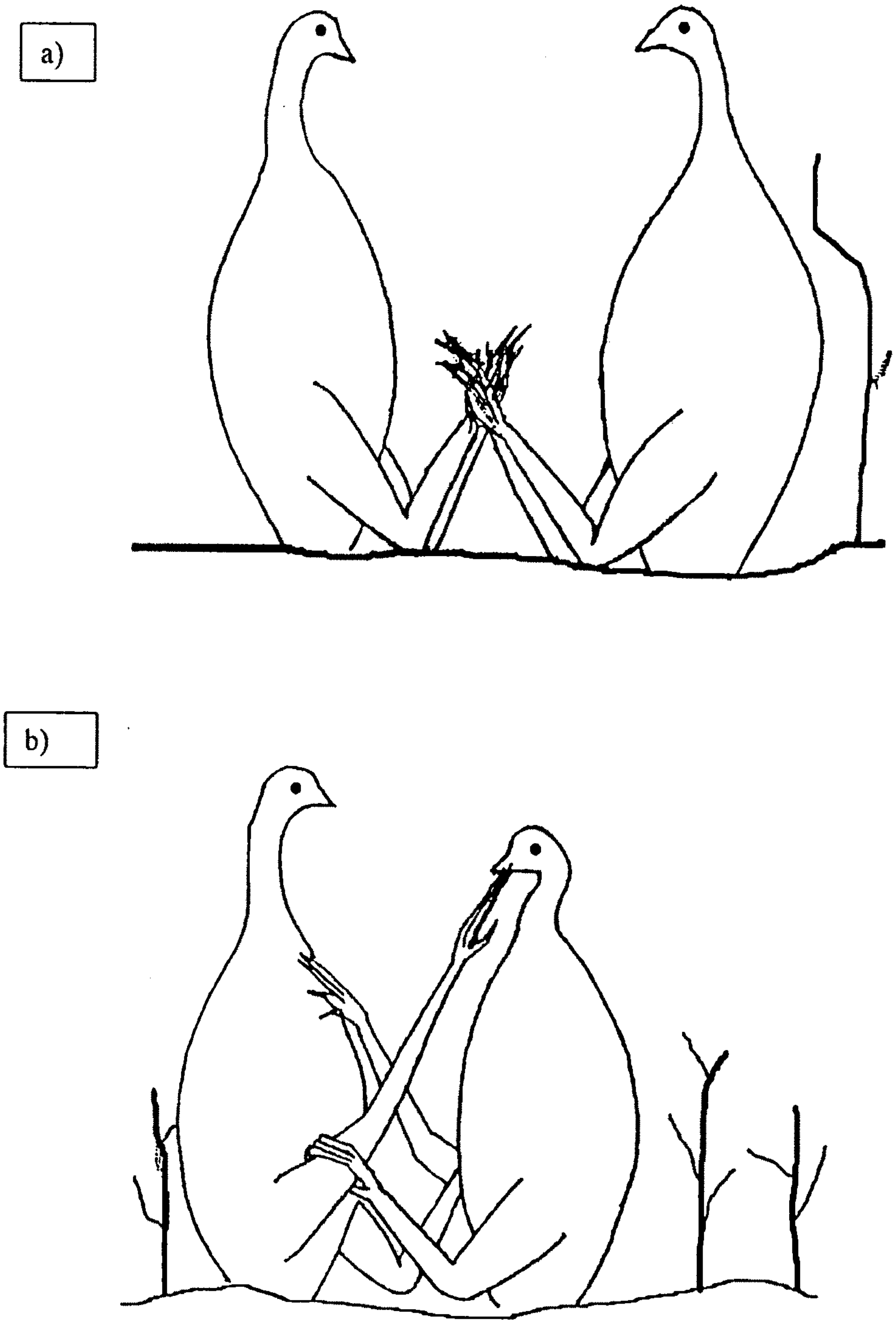
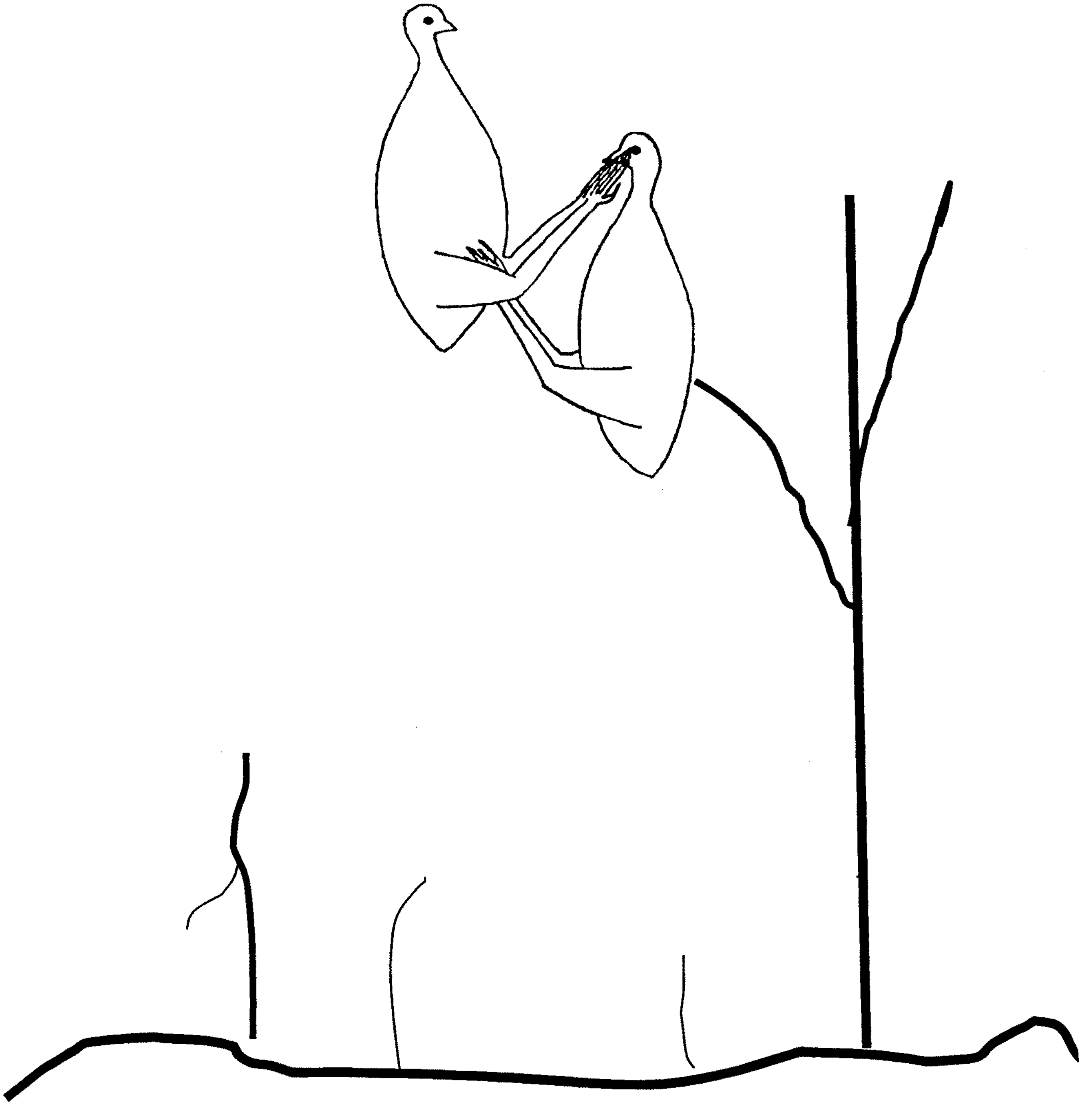


Figure 4.6. Aerial clash is the final stage of fight between the two megapodes, while performing this aggressive action both birds jump up to 1 to 1.5 meters high.



4.3.1.4. *Distribution of agonistic behaviour*

The distribution of agonistic behaviour like aggressive calls and fights over the month of the study time has been plotted in Figure 4.1. There was a relationship between the calls and fights with the months of the year ($r=0.54$, $n=18$, $p<0.001$).

4.3.2. Non-agonistic interactions

Rarely two pairs or a pair and unpaired birds came into contact without it resulting in fights and calls. Of two such occasions, when agonism was not observed, one was when two pairs worked on the mound, one of which laid an egg in the mound, and on the other occasion, three birds foraged and walked within 2 to 4 m of each other.

4.3.3. History of the territory of the different pairs using different mounds

During the study period, 28 megapodes were colour-marked, which included 21 pairs and two unpaired individuals. Of these both sexes were colour marked in five pairs. In 1996, six birds from two mounds were colour-marked which included an unpaired bird, both sexes in two pairs, and one individual of a third pair. In 1997, 17 birds from 9 mounds were colour-marked, including one unpaired bird, both sexes in three pairs, and one bird each of 11 pairs. In 1998, five birds of four pairs were trapped from four mounds (Table 4.1).

Table 4.1. Information about the colour-marked Nicobar Megapode

Mound	Name	Date	Tarsus (mm)	Culmen (mm)	Wing (mm)	Wt (g)	Colour bands		Ring No.	Last sighting	Sex
							Left Leg	Right Leg			
1	O1	16/02/97					Orange	Green		05/10/97	
3	WO3	27/02/97	71.2	27.8	23.8	615	White	Orange		19/04/98	m
3	WOR3	19/02/97	74.1	28.3		913	White	Red, Orange		17/05/98	f
8	MPAYU	13/02/96				750		Blue, Metal	g 352	07/05/98	m
8	FPAYU	13/02/96				820	Blue, Metal		g 353	15/01/97	f
8	FLOONG	13/05/96	74	27	228	755	White, Metal		g 354	20/05/98	f
8	MLOONG	06/05/96	76	28	245	760	metal	White	g 355	20/05/98	m
8	ONG	13/05/96	71	27	216	710	Blue	Metal	g 356	24/04/98	f
8	GO8	09/02/97	71.1	27.8	23.9	833		Green, Orange, Metal	g 362	12/09/97	m
9c	Y9C	09/02/97					Yellow	Yellow, Metal	g 361	23/05/98	m
9	SPG9	21/02/97	74.3	27.9	23.8	785	Pink	Saffron, Pink, Green, Metal	g 363	20/04/98	
9	BP9	22/02/97	74.6	28.1	24.1	688	Blue, Pink, Metal	Rose	g 364	08/05/98	m
9	GR9	14/02/97	73.3	28.1	24.1	765	Green, Red, Metal	Red	g 400	23/05/98	f
10	SHOMBABH	10/02/96	79	27	233	755		Red, Metal	g 351	25/04/97	m
10	Y10	19/01/97					Yellow, Metal	Yellow	g 357	15/05/98	m
10b	RLB10B	05/06/97						Red, Blue, Metal	g 367	08/05/98	f
12	RW12	06/04/97						White, Red, Metal	g 365	17/05/98	m
12a	GW12A	13/03/98	74.8	28.3	24.6	880	White, Green, Metal		g 369	15/05/98	
12c	SB12C	22/03/98	73.6	24.3	27.2	720		Blue, saffron, metal	g 372	02/05/98	m
13	RB13	05/03/98	72.3	27.9	23.7	782	Red, Blue, Metal		g 368	13/05/98	m
14	G14	01/02/97	67.8	28.1	24.8	915	Green, Metal		g 358	02/03/97	m
14	O14	01/02/97	67.1	29.8	24.3	823	White	Organge, Metal	g 359	02/03/97	
14	B14	02/02/97	68.3	26.9	24.7	960	Blue	Blue, Metal	g 360	12/04/97	
14	YR14	06/03/97	71.2	28.6	23.2	725	Metal	Yellow, Red	g 366	06/05/98	
14	GB14	13/03/98	73.2	27.3	23.8	704	Green, Blue, Metal		g 370	20/05/98	m
14	BRG14	14/02/98	73.8	27.1	24.2	735		Green, Brown, Metal	g 371	08/05/98	m
14	R14	05/03/97	73.8	29.1	24.8	806	Red, Metal	Red	g 398	21/03/97	
14	G-O14	16/02/97	74.1	29.2	24.6	785	Green, Metal	Orange	g 399	02/03/97	

While mounds were present throughout the study area, some degree of clustering was discernible (Fig 2.4). Of the 38 mounds studied, nine distinct clusters were present, two of five (8,8a, 8b, 8c, 8d and 11,11a, 12,12a, 12b), one of four (9,9a, 9b, 9c), two of three (1a, 1,1b and 10,10a, 10d), and four of two mounds (7,7a, 7b, 7c, 10b, 10c, 13a, 13b). The remaining 10 mounds also showed some sort of clustering but were distributed with space in between (see chapter II). The different territories of colour-marked birds are described below cluster-wise.

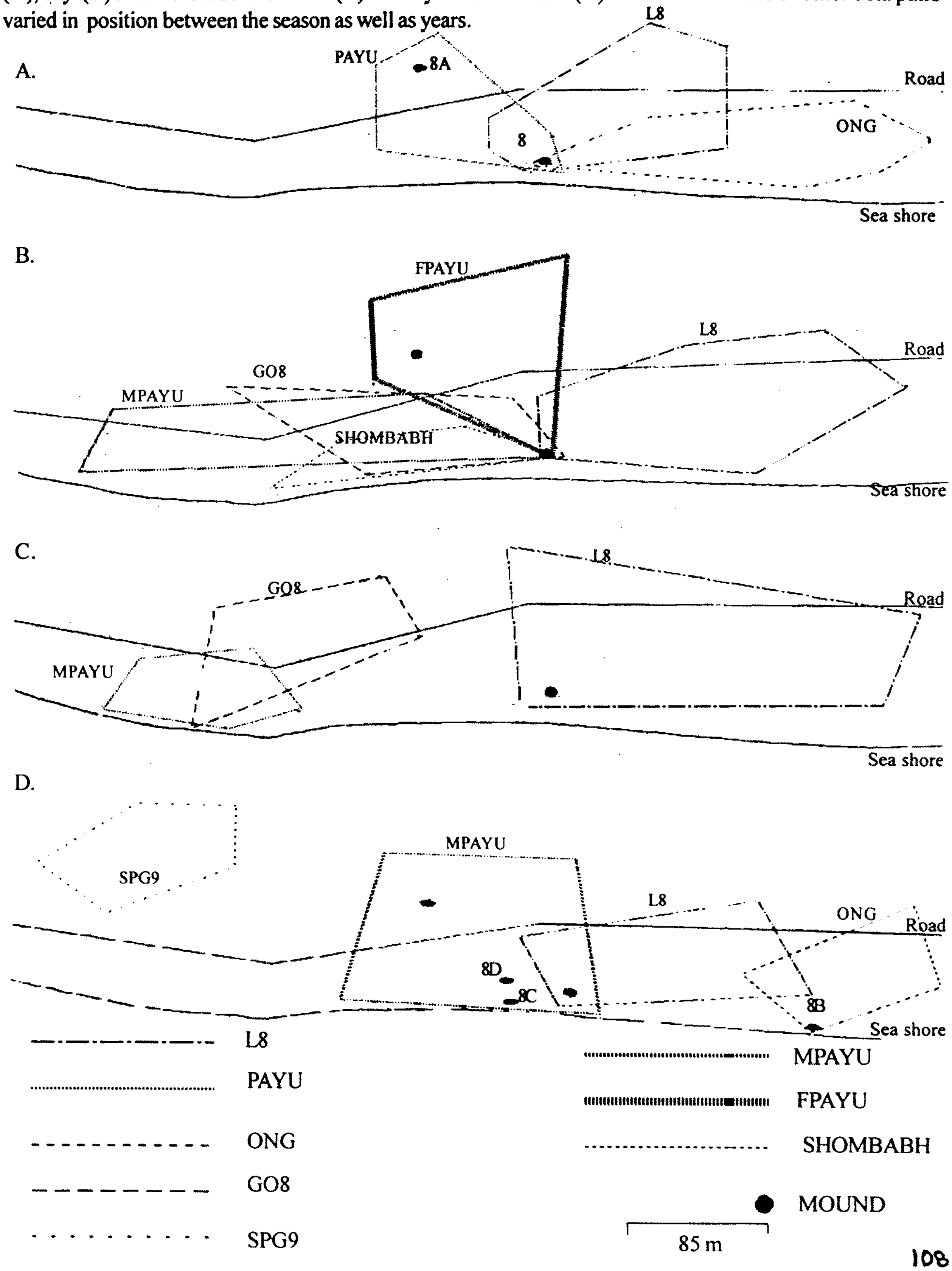
4.3.3.1. *Mound 8 (Cluster).*

This cluster included five mounds: 8, 8a, 8b, 8c, and 8d. Of these, mound No.8 was very active throughout the study period and was the focal mound (the mound that was studied intensively), and 8a was active in 1996 but less in 1997 and 1998. The other three mounds were formed in 1998.

In 1996

Five birds were colour- marked at mound 8, of which both sexes were colour-marked in two pairs and one bird of a pair. All the territories were attached to the mound (Fig 4.7A). During the dry season, the territory position of L8 was between the territories of Payu and Ong.

Figure 4.7. Territorry position of the alpha pair 'L8' at mound 8 was same during the dry season of 1996 (A), dry (B) and wet seasons of 1997 (C) and dry season of 1998 (D). But the territories of other beta pairs varied in position between the season as well as years.



In 1997

At the beginning of the year, two territories were maintained by the male L8-Go8 pair and the female L8-Unmarked male pair around this mound. After a few days both the male and female of L8 rejoined and became a pair. During this time two more pairs (the male Payu pair (MPAYU) and the female Payu (FPAYU) pair) established their territories at this mound. Hierarchically the L8 pair dominated the female Payu pair who dominated both the male Payu and the Go8 pairs. The female Payu pair established their territory between the L8 and the Go8 pairs' territories. This territory was not close to the previous year's territory of the Payu pair. The territories of the male Payu and the Go8 pairs overlapped. In February 1997, Shombabh (colour-marked at Mound No.10 as unpaired) reached this area and established his territory and paired. Shombabh could not hold his territory, and subsequently the pair separated (Fig. 4.7B).

During the wet season (September and October) the female Payu disappeared from the site (Fig 4.7C) and the territories of the Go8 and the male Payu pairs shrunk and moved away from the mound. The 'L8' pair expanded its territory area but continued to be attached to mound 8.

In 1998

During February, the male Payu and the L8 pairs maintained two territories independently. This time the L8 pair's territory shrunk, while the male Payu pair's territory was enlarged (Fig 4.7D). Both territories slightly overlapped at the area where the mound was located and the territory of the 'male Payu' pair covered three mounds (8, 8a and 8c), and this pair possibly used mound No.8d. During this period, the male Payu pair was chased by the L8 pair whenever the male Payu pair worked on mound No.8, and the male Payu pair was chased by the unmarked pair(s) who used mounds No. 8, 8c and 8d as well. During March and April, the territories of the L8 pair and the male Payu shrunk and moved towards mound 8 as a result of invasion of Ong and an unmarked pair on either side of the territories of the L8 pair and the 'male Payu'. Ong established its territory at mound No.8b (Fig 4.8). While establishing territory, both neighbouring pairs marked their territory boundary by vigorous duetting. At the same time the 'SPG9' pair established its territory far away from mound no.8 but near to mound no.9a, but the birds disappeared in April (Fig 4.8).

4.3.3.2. *Mound No.9*

This cluster included five mounds: 9, 9a, 9b, and 9c. Here three pairs ('Y9c-Gr9', 'SPG9', and 'BP9-Rlb10b') were colour-marked.

In 1997

During the dry season, three pairs maintained three territories. The territory of 'Y9c-Gr9' covered mounds 9, 9a and 9c but they primarily used mounds 9 and 9c. The territory of 'SPG9' covered mounds 9, 9a and 9c, but they primarily used mounds 9 and 9a. A male of the pair was trapped close to the mound 9; later these pair was named 'BP9'. After four months but in the same season the 'BP9' was sighted with 'Rlb10b' on the mound 10b. The territory of 'BP9-Rlb10b' covered five mounds (included two clusters): 9, 9b, 9c, 10b and 10c but work was concentrated on mounds 9b and 9 (Fig 4.9).

Fig ure 4.8. The territory position of various pairs using the mound '8' cluster during the dry season of (1998) February (A), March (B), April (C) and May (D). Territory position of the Nicobar Megapodes sometimes varied between the month of the same season.

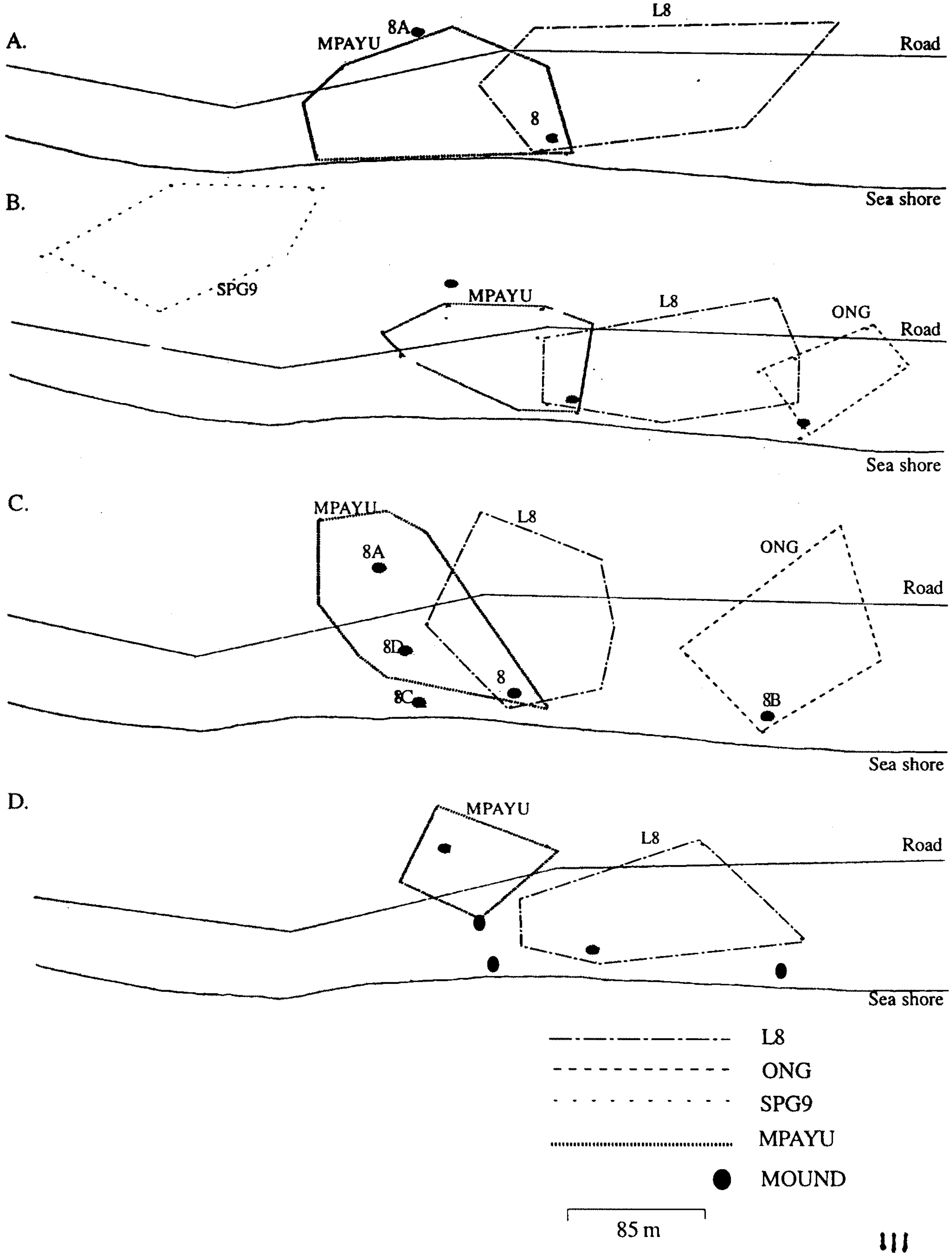
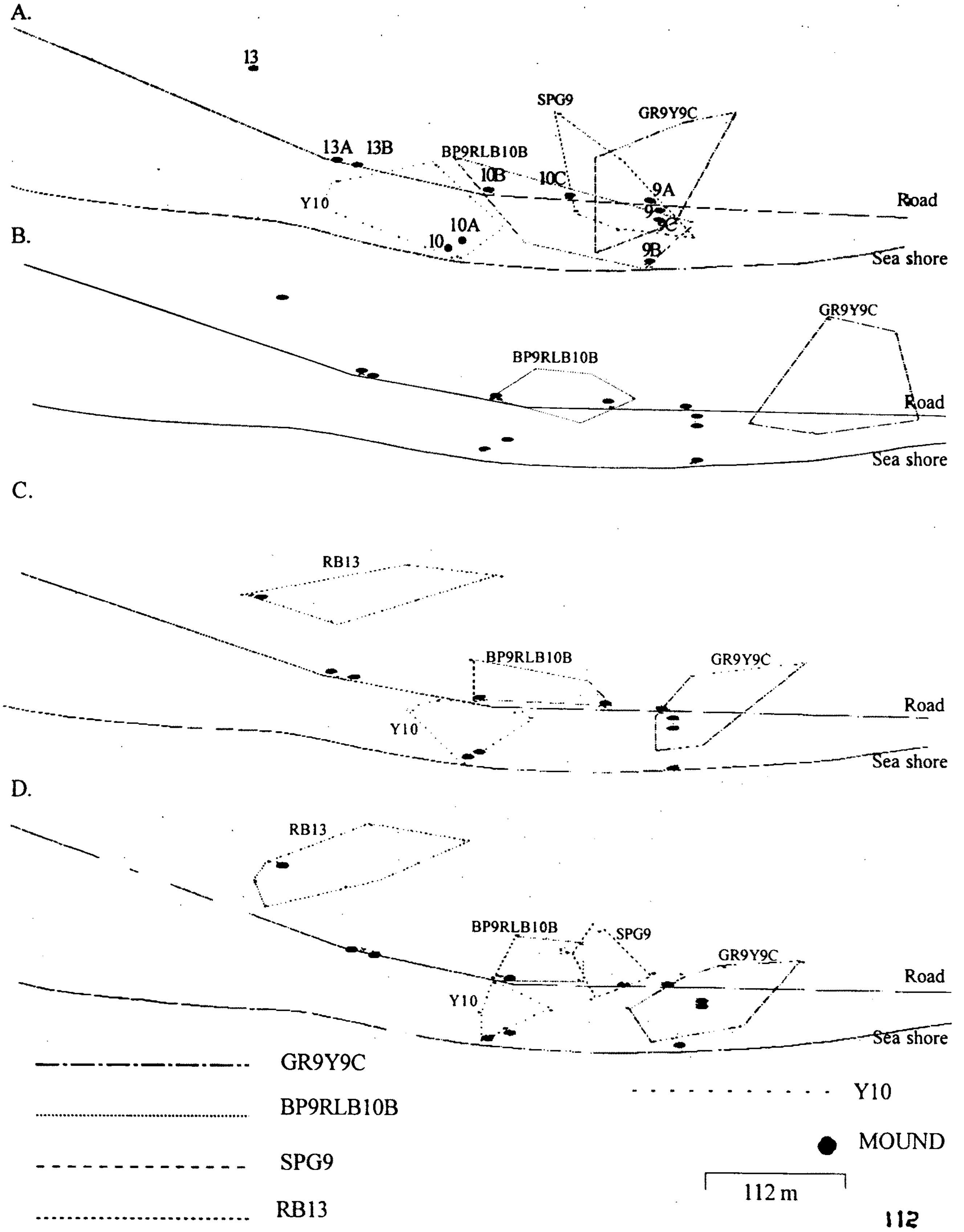


Figure 4. 9. Territory posititon, size and level of overlaping varied between the dry season of 1997 (A) and wet season of 1997 (B). Within a season itself territories position and size varied because of intruders;February and March (C), and April and May (D).



During the wet season, 'SPG9' and 'Y10' pairs disappeared from the mound. The territory of 'Y9c-Gr9' moved away from the mounds. The 'BP9-Rlb10b' pair included mounds 10b and 10c in its shrunken territory (Fig 4.9). During this time a number of unmarked megapodes were sighted but none of them worked on the mounds of this cluster.

In 1998

During February and March, the 'Y9c-Gr9' pair moved into the mound area and established its territory, which covered mounds 9, 9a and 9c, unopposed by the other pairs. There was no significant change in the size and position of the territory of 'BP9-Rlb10b' when compared to the wet season of 1997. On 5th March 1998 the 'RB13' pair was colour-marked and their territory is plotted in figure 4.9. During April, the 'SPG9' pair came and established its territory in between the territories of 'BP9-Rlb10b' and 'Y9c-Gr9' and covered mound 10c. While establishing its territory the 'SPG9' pair fought with both neighbouring pairs, but more often with 'BP9-Rlb10b'. Y9c-Gr9 was dominant over mounds 9, 9a and 9c and did not allow the 'SPG9' and the 'BP9-Rlb10b' to establish their territory on its area. In 1997 these territories overlapped slightly (Fig 4.9).

4.3.3.3. *Mound 10*

This cluster included three mounds: 10, 10a, and 10d (Fig 4.9). Here three birds were colour-marked of which one was pair 'Y10', another pair called 'BP9-Rlb10b', of which male was trapped at mound 9 and female was trapped at mound 10b, and the solitary bird 'Shombabh'.

In 1996

Shombabh was trapped at mound No.10 but it was not relocated during the same year. It was sighted in May 1997 at the area of mound No.8. This year Shombabh could not established a territory.

In 1997 & 1998

The territory of 'Y10' covered mounds 10 and 10a (Fig 4.9). In 1998, 'BP9-built mound 10b and, though their territory included mound 10c, they did not work on that. This pair performed a lot of territorial calls in response to their neighbour 'BP9-Rlb10b'.

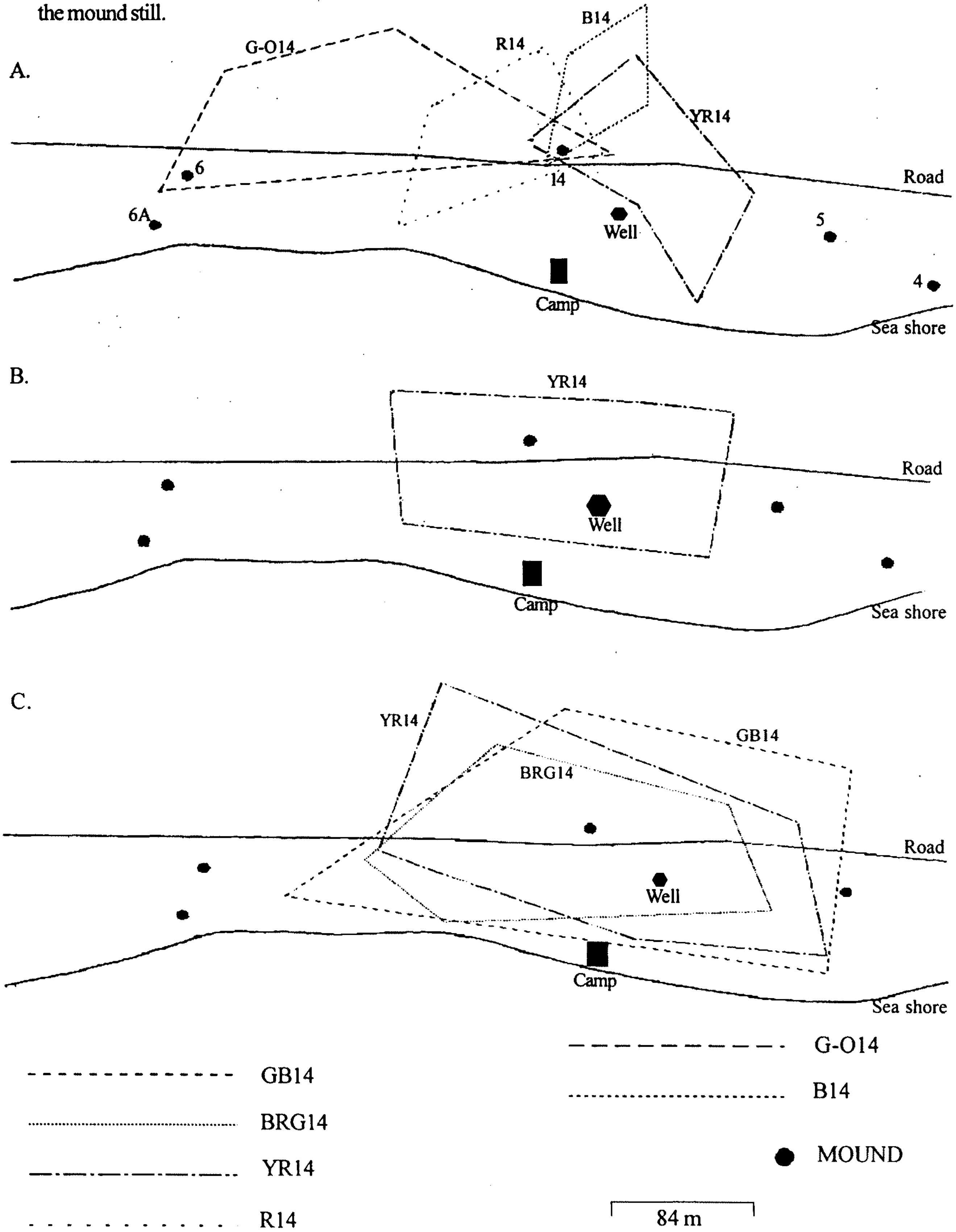
4.3.3.4. *Mound 14*

A total of eight birds were colour-marked at mound 14, which included seven pairs. All the pairs used mound 14 alone except 'G-O14' who used both mounds 6 and 14.

In 1997

During the dry season four pairs used this mound. Of these, the 'G-O14' pair maintained its territory and covered mounds No.6 along with 14 (Fig 4.10). Compared to other territories G-O14's was larger. G-O14 laid eggs in mound 6 and also worked on mound 14. 'YR14' was dominant over the 'B14' and 'R14' pairs but the 'G-O14' appeared to be equal to 'YR14' pair. After egg laying 'G-O14' disappeared from the 14th mound area. During the wet season, the 'YR14' pair alone maintained its territory in the 14th mound area, when its

Figure 4. 10. During the dry seasons of 1997 (A) and 1998 (C) large number of pairs of megapodes occupied the mound '14' for laying eggs, during this period lot of aggression and more territory overlapping was seen. But during the wet season of 1997 (B) most of the pairs left the mound but the alpha pair holding the mound still.

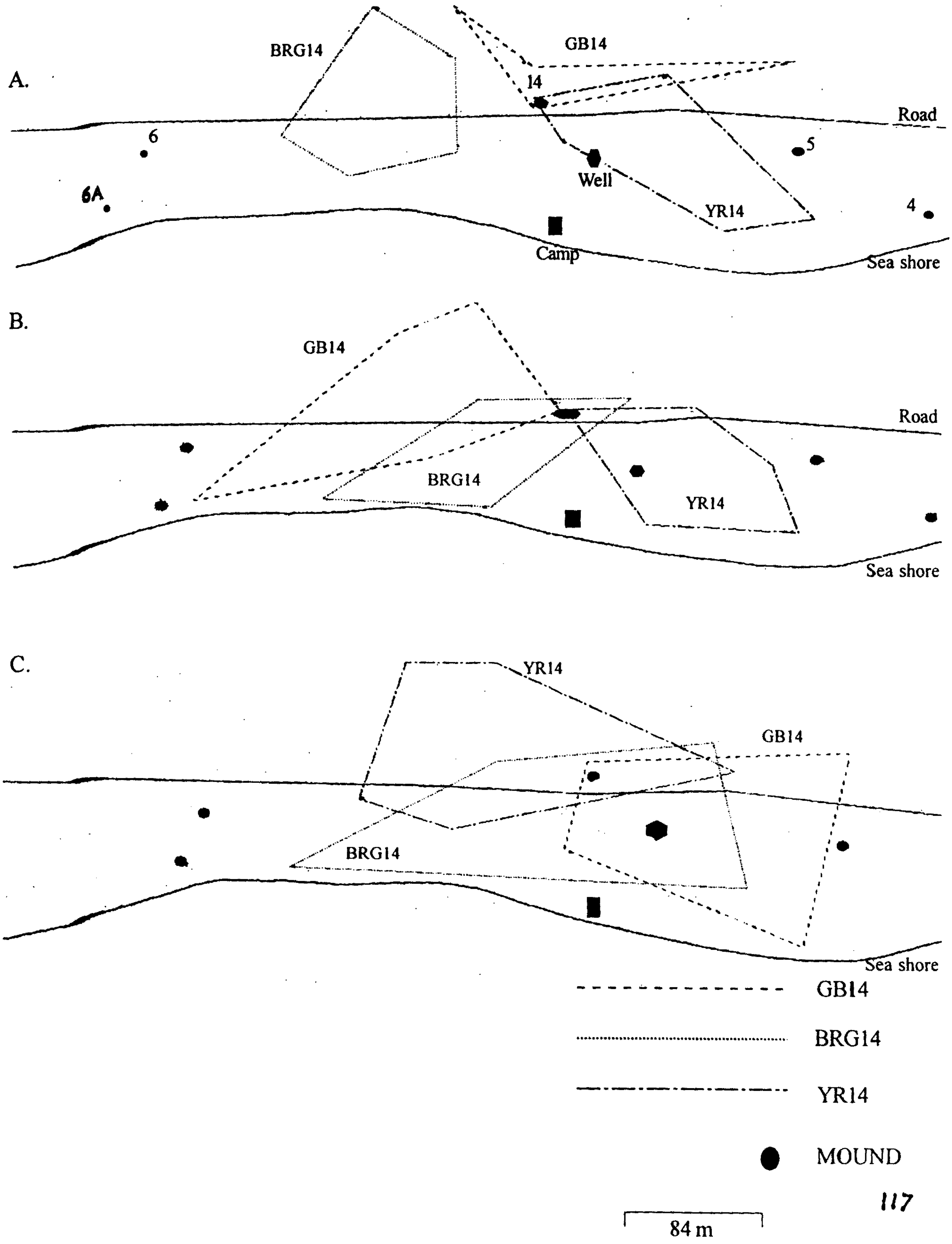


territory was bigger. Pairs like G-O14, B14 and R14 occupied the mound only for a short time after which they disappeared.

In 1998

During February the 'YR14' pair maintained its territory at mound 14 along with two more pairs that were colour-marked later. Those pairs were 'GB14' and 'BRG14' (Fig 4.11). The territory of 'BRG14' was positioned just away from mound 14 but the territory of 'GB14' was small and slightly overlapped with the territory of 'YR14'. During this period 'YR14' was dominant over the others. Great changes took place in size and position of territories of the above mentioned three pairs during the month of March and later (Fig 4.11). In March the 'GB14' pair expanded its territory by moving towards the south of mound 14. The territory of 'BRG14' was positioned between the territories of 'YR14' and 'GB14'. The territories of 'GB14' and 'BRG14' overlapped and the territories of 'BRG14' and 'YR14' overlapped at the mound area. During this period 'BRG14' and 'YR14' were equally strong and both used mound 14 for egg laying and were dominant over GB14. During May, the 'YR14' and 'GB14' pairs shifted their territory. There was no change in the position of the territory of 'BRG14'. During this month, both 'BRG14' and 'GB14' pairs laid egg and both pairs were equally strong while fighting but the 'YR14' pair was chased by GB14 whenever they met. Clashes between 'BRG14' and 'YR14' were not noticed, even though both territories were adjacent and overlapped (Fig 4.11).

Figure 4.11. Territory position, size and level of overlapping of megapodes varied within a season due to the egg laying time or social hierarchy of a particular pair at a particular time. During February 1998, GB14 pair was beta pair (A) and their territory was small but during March (B) and April-May (C) territory was expanded and laid eggs during this period.



4.3.3.5. *Mound 1 (cluster), 2 & 3*

In this area three pairs were colour-marked in 1997. One bird (O1) of a pair was colour-marked at mound 1 and two more pairs (WO3 & WOR3) were colour marked at mound 3.

In 1997

During the dry season, the territory of 'O1' covered three neighbouring mounds 1, 1a, and 1b (Fig 4.12) and the territories of 'WO3 &WOR3' were at mound 3. The WO3 and WOR3 pairs maintained separate territories but they overlapped at the mound area where lot of aggressive encounters took place.

During the wet season, the position of the territories of the 'O1' and WOR3' pairs changed. WOR3 slightly moved its territory towards the territory of 'O1' and their territories overlapped at the Arecanut grove area (Fig 4.12). The territory size of 'WO3' did not change significantly between the summer and the wet seasons. Some changes in the territories of the 'WO3' and 'WOR3' pairs can be attributed to rain water that filled the wet lands.

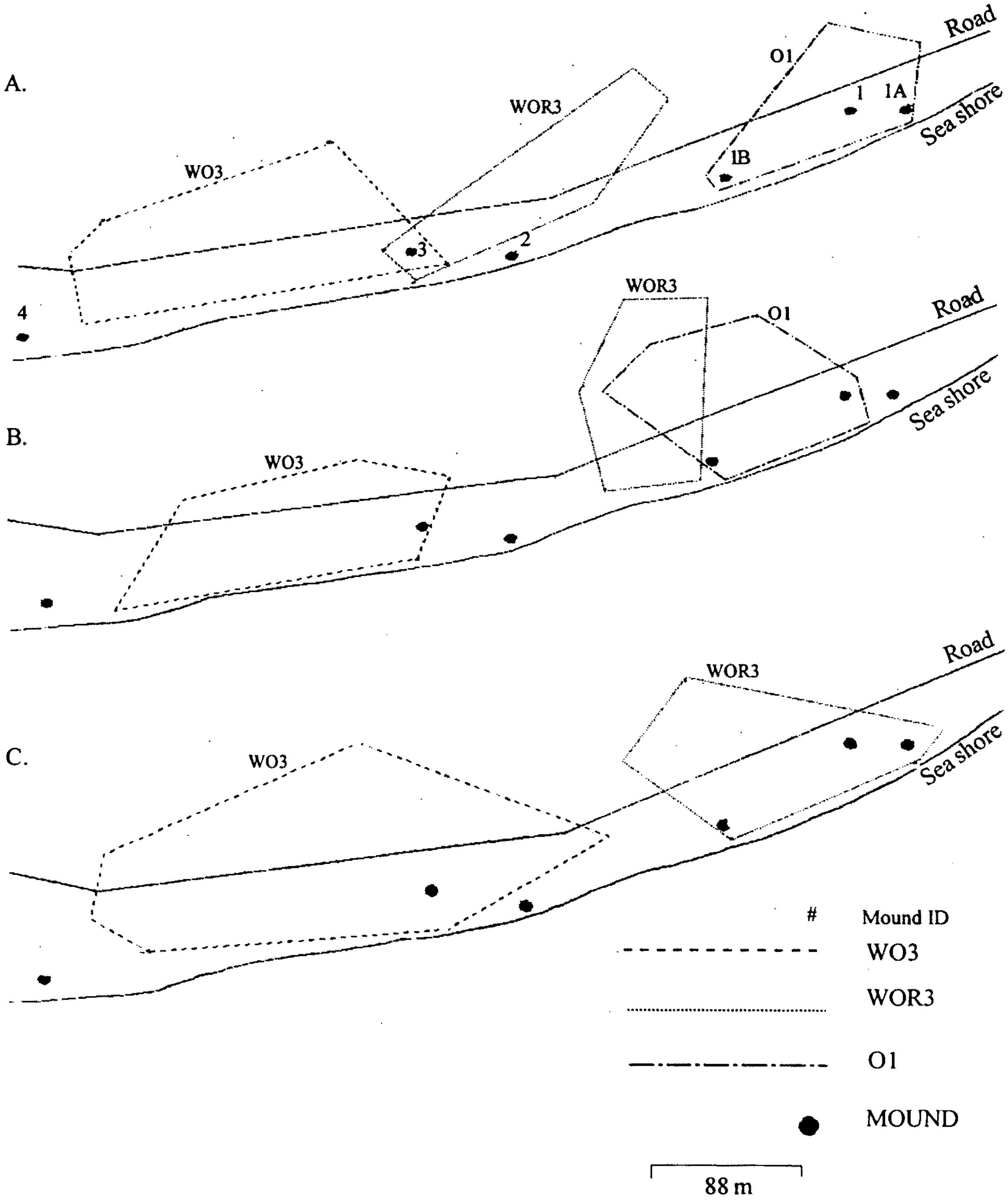
In 1998

During the dry season, the territory of the 'O1' pair disappeared and that space was occupied by the 'WOR3' pair (Fig 4.12). 'WO3' pair expanded its territory. In the territory of 'WO3' one (or more) unmarked pair(s) were frequently sighted.

4.3.4. Establishment and maintenance of territories

The Nicobar Megapode visited the mound daily. Except for the alpha pair, others usually arrived at the mound during the onset of the egg-laying period and established their own

Fig ure 4.12. Single mound '3' was used by the two pairs of megapodes and single pair 'O1' was used many mounds in the dry season of 1997. Territory position of 'Wor3' was drastically changed between dry season (A) and wet season (B) of 1997. Disappearance of a pair 'O1' gave way to other 'Wor3' to occupy the territory position and mounds used by 'O1' during the dry season of 1998(C).



territory, which included the mound. While establishing territories a lot of clashes took place between the new pair and existing pairs (Fig 4.1) with most fights taking place near mounds (Fig 4.3). The territories of birds in the non-egg-laying period were away from the mound and their exact position could not studied. Generally, all the pairs successfully maintained their own territories when they were laying eggs. Compared to unpaired birds, pairs could easily establish and maintain their territories. Colour-marked pairs like the L8 and Y9c-Gr9, territories were always attached to the mound or close to the mounds (Fig 4.7 & 4.8) throughout the year.

4.3.5. Territory size

The birds maintained territories that included one or more mounds during the dry season. The size of the territory varied between the dry and wet seasons or some times between months of the same season (fig 4.13 to fig 4.16). In the wet season mounds might or might not be within the territory area.

When comparing the territory sizes in both seasons of 1997, the mean area in the dry season was 0.98 ha (SE 0.15, n=8) and in the wet season 0.93 ha (SE 0.24, n=8). There was no significant differences in the territory size between the two seasons (t=0.2, p=0.42, df=14). The average size of the territory was 0.81 ha (SE 0.12), with a minimum of 0.19 ha and maximum of 2.28 ha. There was no significant relationship between the body weight and territory size of the Nicobar Megapode ($r_s = 0.05$, $p = 0.82$, $n = 20$); however, there was a negative correlation between the tarsus length and territory size ($r_s = -0.55$, $p = 0.02$, $n = 18$).

Figure 4.13. Trend of the territory size among the users of mounds 1, 1a, 1b, and 3 (name of the pair in the legend box).

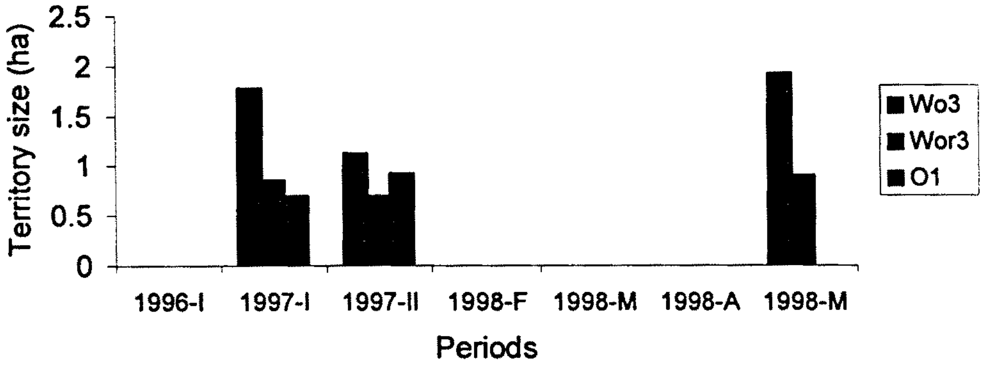


Figure 4.14. Territory size among the users of mounds 14 and 6 (name of the pair in the legend box).

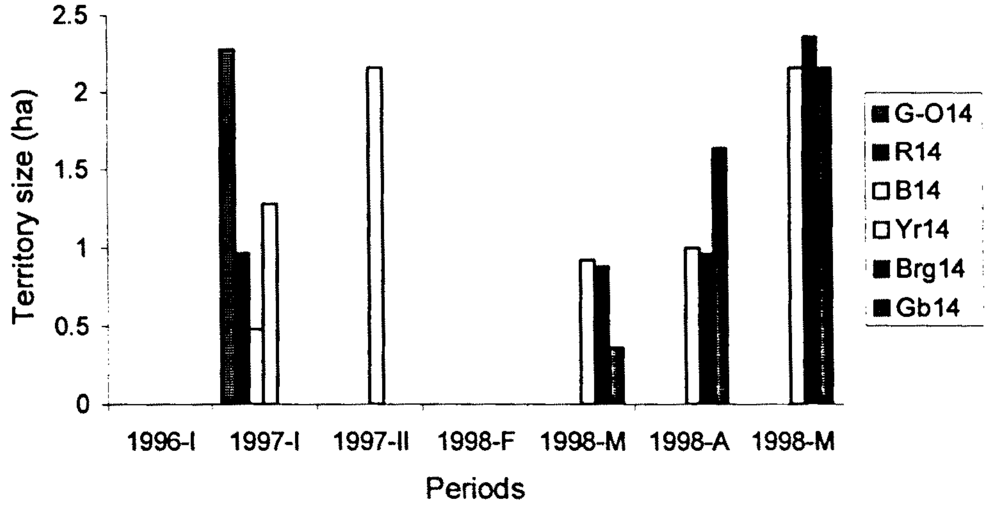


Figure 4.15. Territory size of the megapodes at mound 8 in different periods.

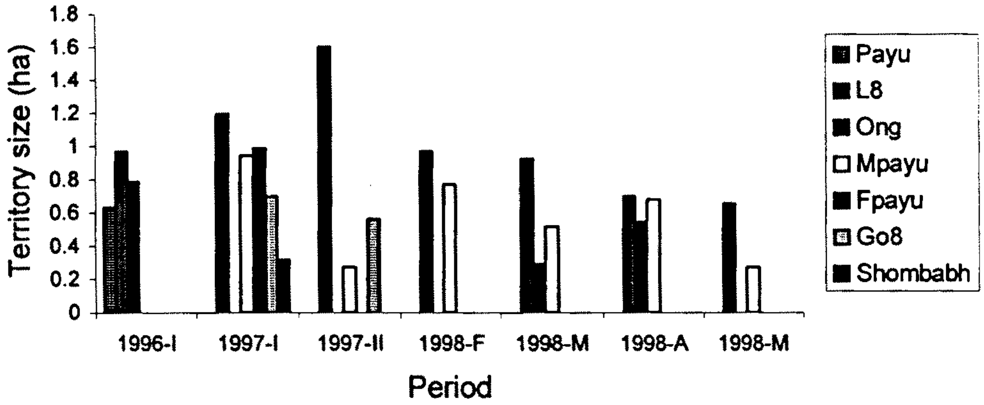
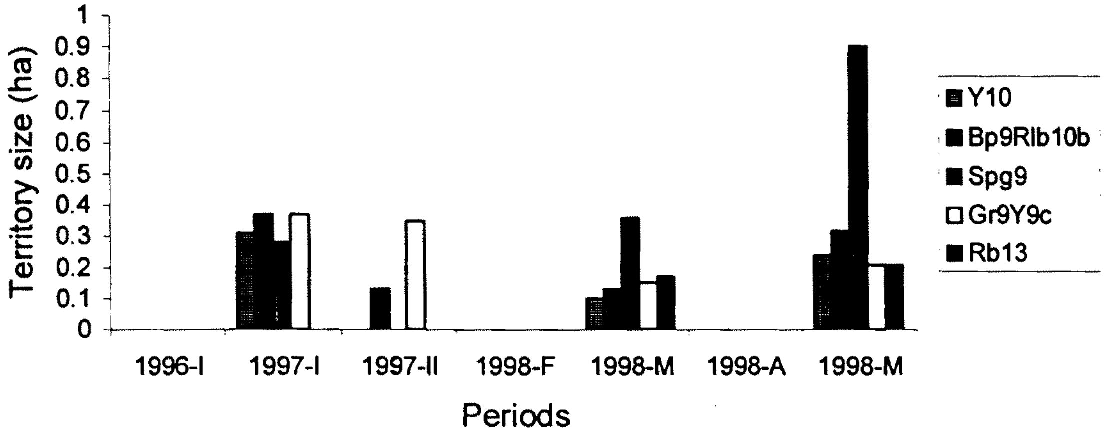


Figure 4.16. Territory sizes among the users of mound '9' cluster, in various periods.



4.3.6. Territory overlapping and fidelity

In 1997, 22 territories were monitored. A wide range of overlap between dry and wet seasons territories was seen in 16 territories of eight pairs (Table 4.2). The average overlap between seasons was 47.11% (SE 12.22, n=8), ranging from 3% to 91%. Only in nine territories was some sort of overlap seen between 1997 and 1998. The average area of overlap between the 1997 and 1998 territories was 41% (SE 7.02, n=9) ranging from 13% to 67%. The overlaps between the years in colour-marked megapodes territories are give in Table (4.3).

Changing of the territory position was common in the Nicobar Megapodes. During the dry season of the 1997, territory of the 'BP9RlB10B' covered mound 9, 9b, 9c, 10b and 10c. During the wet season of 1997 and onwards their territory restricted to mound 10b and 10c (Fig. 4.9). 'Wo3' also shifted their territory from mound 3 to mound 1 in 1998 (Fig. 4.12).

Table 4.2. Territory overlap between season in 1997

Name of the Territory	Territorial area		% overlap
	Dry season (ha)	Wet season (ha)	
Loong (L8)	1.193	1.598	91
Mpayu	0.945	0.270	17
Go8	0.698	0.563	26
Wor3	0.855	0.698	89
Wo3	1.778	1.103	3
O1	0.698	0.923	68
Yr14	1.280	2.160	63
Bp9-Rlb10b	0.370	0.130	22
FPayu	0.990	Disappeared	-
Shombabh	0.315	Disappeared	-
G-O14	2.280	Disappeared	-
R14	0.960	Disappeared	-
B14	0.480	Disappeared	-
Y10	0.310	Disappeared	-

Table 4.3. Territory overlaps between years.

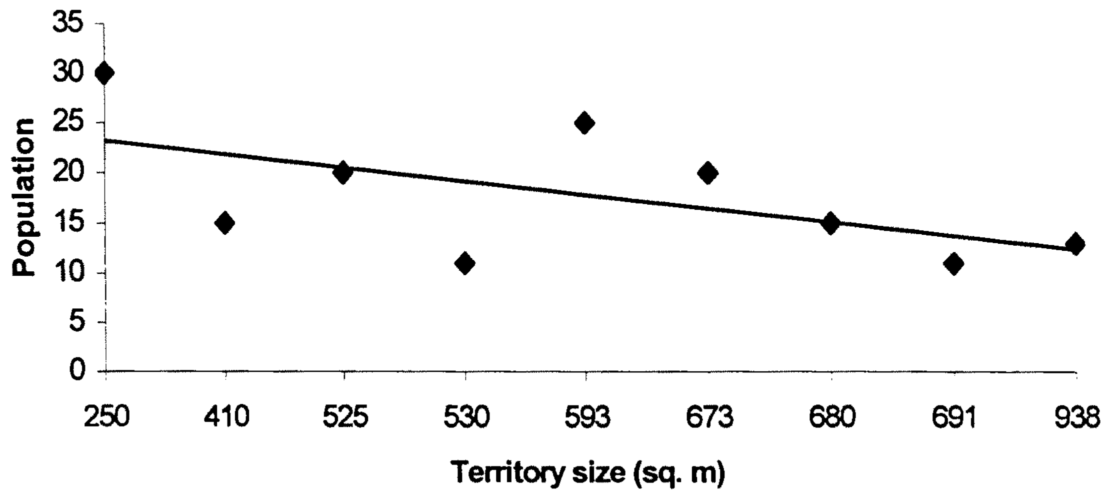
Name of the pair	Territory overlap between 1996-97 (in %)	Territory overlap between 1996-98 (in %)	Territory overlap between 1997-98 (in %)
Y10	?	?	61
BP9-RLB10	?	?	19
SPG9	?	?	21
GR9Y9c	?	?	30
YR14	?	?	42
WO3	?	?	67
WOR3	?	?	13
LOONG	63	81	53
FPAYU	57	?	?
MPAYU	25	86	64
ONG	?	51	?
O1	+	+	+
SHOMBABH	+	+	+
G14	+	+	+
O14	+	+	+
B14	+	+	+
GO8	+	+	+
RW12	+	+	+
RB13	+	+	+
GW12A	+	+	+
GB14	+	+	+
BRG14	+	+	+
SB12C	+	+	+
R14	+	+	+
G-O14	+	+	+

[?] When birds were not either trapped or located, [+]no territory overlapping between years, or birds trapped in 1998 or not located

4.3.7. Population and territory size

Colour marking took place in seven clusters of mounds (1, 3, 8, 9, 12, 13, & 14). The total number of birds was estimated using colour-marked birds. Seven to 30 birds used these clusters during a year. The average territory size of a cluster in the three-year study period was plotted against the average number of megapodes using the same cluster. Results show that if the population of megapodes at a particular mound increased then the territory sizes of those birds decreased (Fig 4.17).

Figure 4. 17. Relationship between the population and territory size of the Nicobar Megapode (Trend line is linear)



4.3.8. Partnerships

Two pairs (L8 and P8) that were colour-marked in 1996, had by the commencement of the 1997 season, separated from their original partners and taken new partners. The female of L8 had paired with an unmarked male, and laid two eggs in the mound that she used in 1996, when along with male L8, she was part of the dominant pair (Fig 4.18). The male of L8 had paired with an unmarked female who was later ringed (GO8), and who laid two eggs while paired with male L8, during the same period and in the same mound that female L8 was using (Fig. 4.18). Male L8 and GO8 became the dominant pair. Subsequently, the male L8 and the female L8 rejoined after a vigorous fight between the 'male L8-GO8' and 'female L8-UN?' pairs, and became the dominant pair of mound 8 again, and subsequently laid two more eggs together. GO8 combined with an unmarked male and continued to use the mound, and became the dominant pair when the L8 pair had completed egg laying. The L8 pair was dominant over the mound during the rainy season of 1997 and the egg laying season (up to end of this study) of 1998. L8 pair did not separate after rejoining in 1997. The male and female P8 who had paired with unmarked birds did not rejoin. One solitary colour-marked male ('Shombabh'), at Mound No.10 in 1996 was re-sighted at Mound No.8 in May 1997 and was still solitary. This male had a partner for a brief period when they were subordinate to the other pairs using mound No.8. This pair bonding was not strong and was lost within four days, and Shombabh once again unpaired and roamed around the mound 8 and 9.

Three pairs were colour marked in the mound cluster 1, where one pair (WOR3, fig 4.20) used two mounds. Longevity of the partnerships could not be studied because one partner of a pair only was colour marked instead of both partners. O1 pair disappeared from the cluster area after May 1997.

In the mound cluster 9, Y9C-GR9 and BP9-RLB10B pairs continued their partnerships throughout the study period (Fig 4.19). Both pairs used more than one mounds for egg laying. SPG9 pair was not sighted on the mound 9 after April 1997.

Both sexes of the pairs from the mound cluster 14 were not colour marked. Colour marked birds used the mounds throughout the study period from the date of colour marking (Fig 4.21).

The confirmation and maintenance 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.

4.3.9. Pair formation

The formation of a new partnership was seen once. A [illegible] pair was formed between two megapodes that were solitary when trapped (Fig. 4.19). The male (Y9c) built a new mound (9c, Fig 2.1) adjacent to an existing one where a solitary female (GR9) had attached herself (9 in Fig. 2.1).

4.3.10. Unpaired birds (solitary)

The total number of observations about mound activities was 3678. Of these 1778 was with birds on the mound. Of the 1778 observations, 7% were of solitary birds and remaining was of pairs. One of the colour-marked solitary birds remained unpaired for nearly two years (Shombabh), though it briefly formed a pair for about a week. This solitary male has a home range that covers at least three main clusters of mounds. As a rule solitary birds do not call, but have been heard to do so on occasion. While solitary birds did visit mounds, and worked or laid eggs in them, they generally left the mound on arrival of pairs. Away from the mound, the solitary birds tended to stay close to the edge of the road, or in between the territories of pairs. Solitary birds were also less shy than pairs and closer approaches by observer were possible than with pairs.

4.3.11. Copulation and display

There were three observations of copulation within the pair. On one occasion, a male chased his partner and mated with her repeatedly. In the second, a male chased his partner onto a branch and copulated with her on it. The third, when after a fight with another pair, the male returned after chasing the loser and mated with his partner.

The male usually attempted copulation with his partner without making any pre-courtship display. While holding her crown or nape feathers the male made treading movements with his feet which were placed over the lower extremities of the female's scapulars. During mating the male flapped on the back of the female to maintain balance. The male made pushing movements with each foot alternately with the tarsi flat against the female's back as his tail and rump make side-to-side movements in an effort to establish cloacal contact. After several such attempts the male dismounted from the female without any post copulatory display.

Figure 4.18. Partnerships between sexes in the Nicobar Megapode are not permanent. Bonds break and the partnership may be reformed (LF8 & LM8) or break permanently (PM8 & PF8). Dotted line represents unmarked birds and solid lines represent colour-marked birds. Continuity of possession as indicated by continue lines was assumed that a pair using a mound was sighted at the same mound after a break. The 'O' sign indicates the laying of an egg. F or M in the individual identity indicates sex.

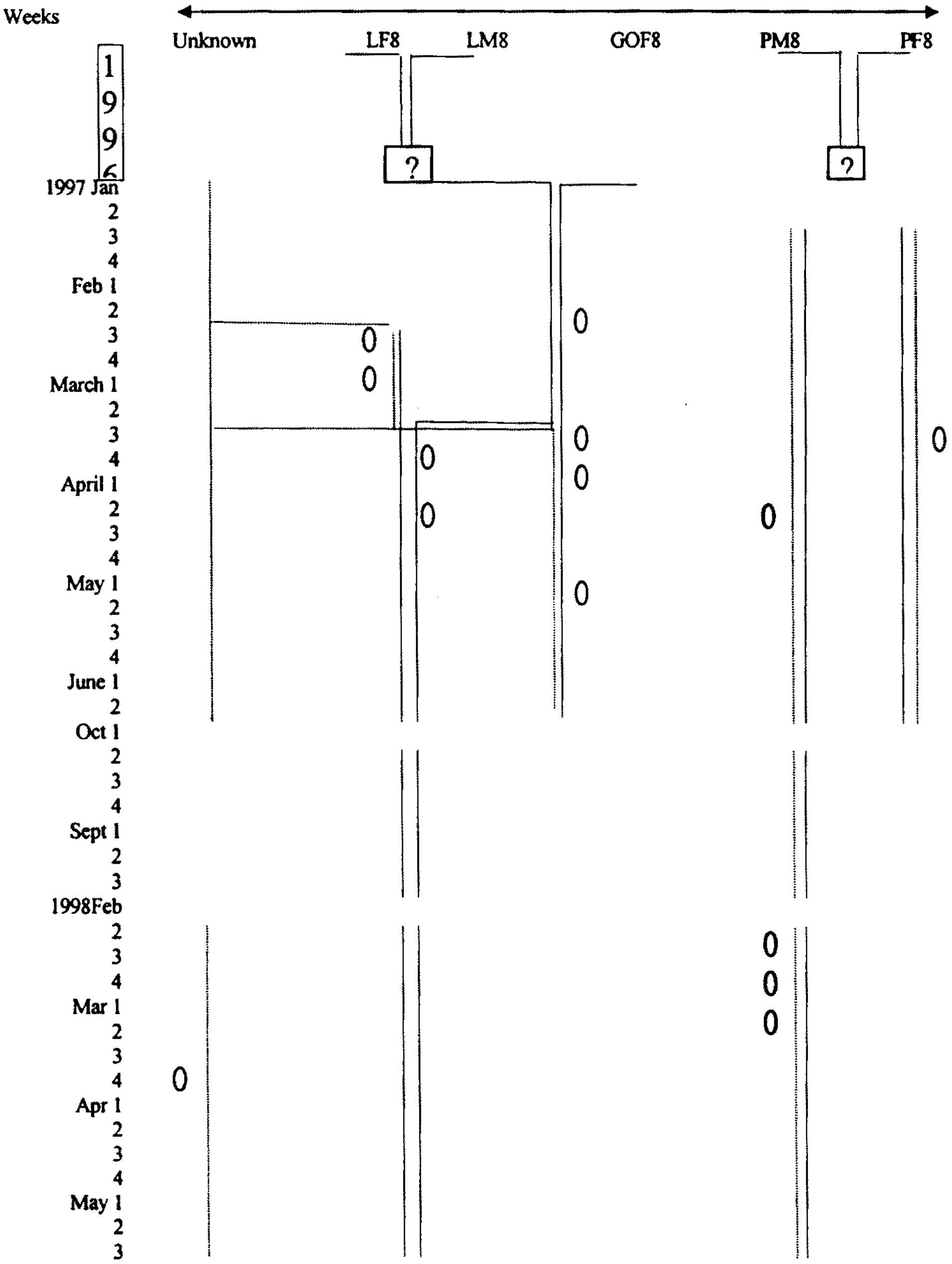


Figure 4.19. Time of possession on different mounds and a pair bonding. Dominant pair used more than a mound at a time (Gr9-Y9c). Megapode temporarily visits to the another mounds or changed the mound totally. Solid lines represents those birds known to work on mound 9, and dotted lines represents those birds that worked on other mounds as well whose ID is given in the box.

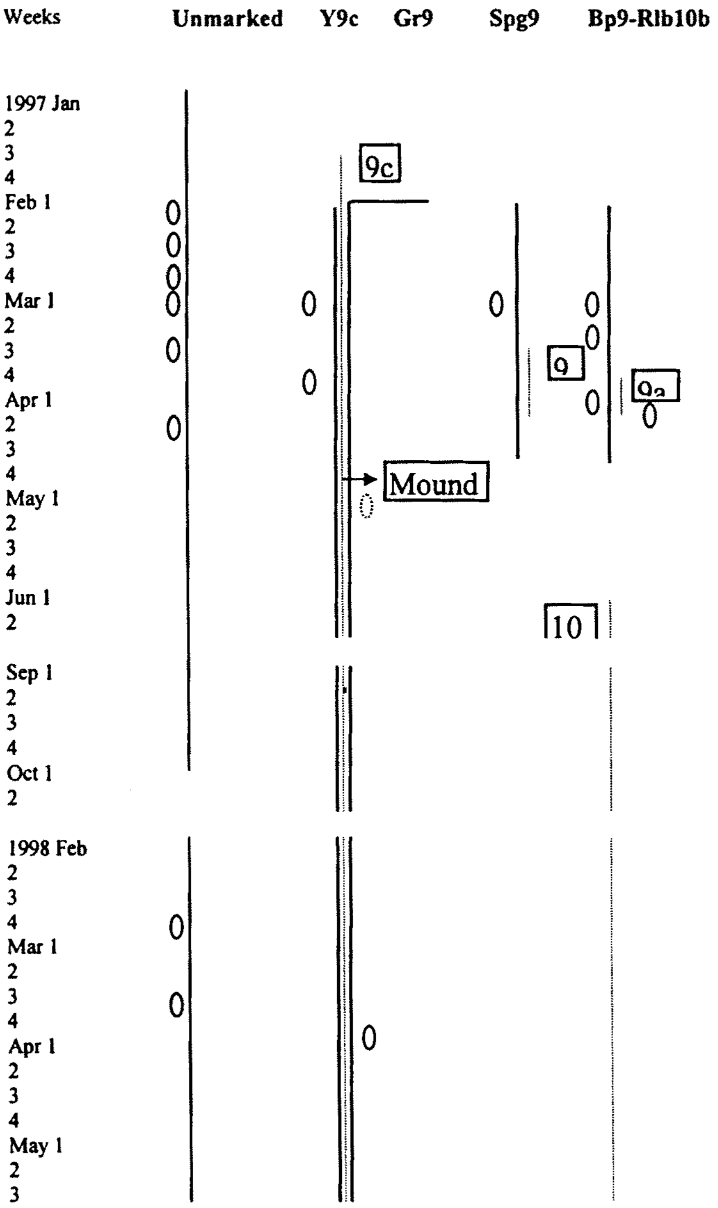


Figure 4.20. Mounds are used by more than one pair of megapode, and a pair may use more than one mound at a time. Solid line represents the pair's activity on Mound 3 and dotted line represents activity of the Mound 1 cluster (1, 1a & 1b). Continuity of possession as indicated by continuos lines was assumed when a pair was sighted with after breaks at the mound.

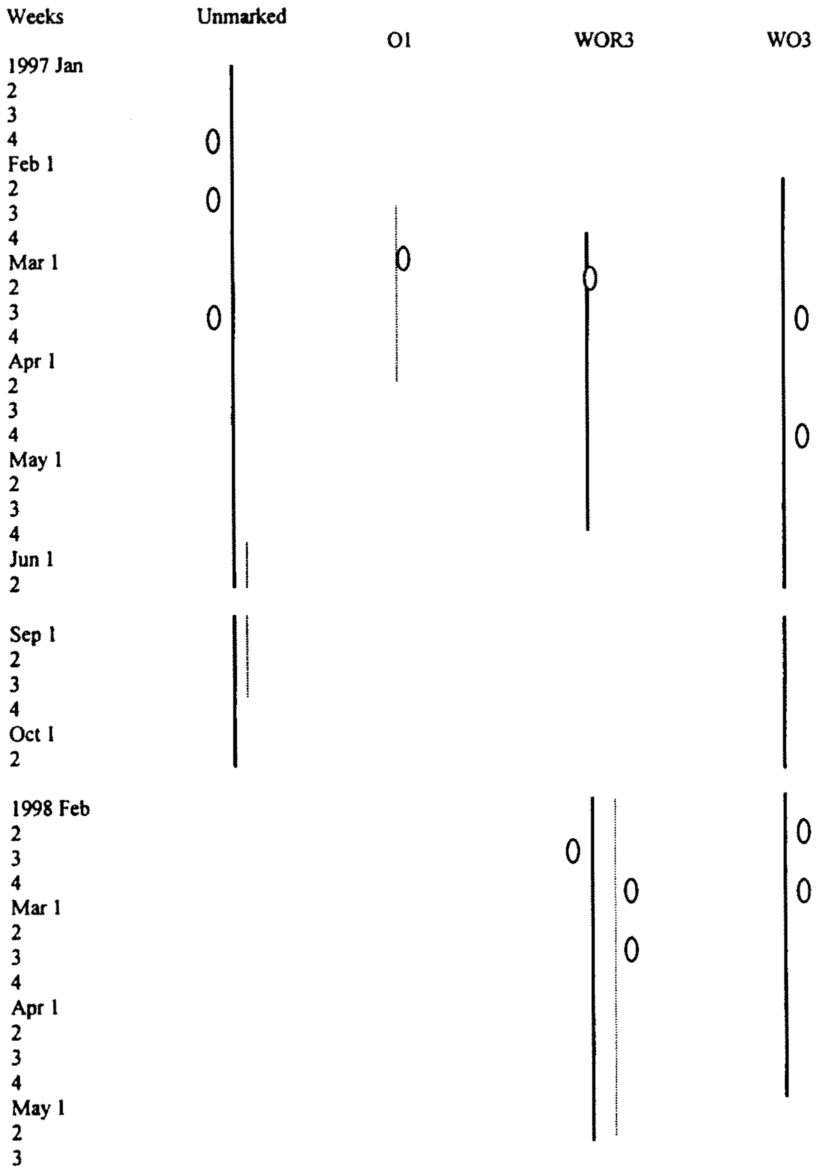
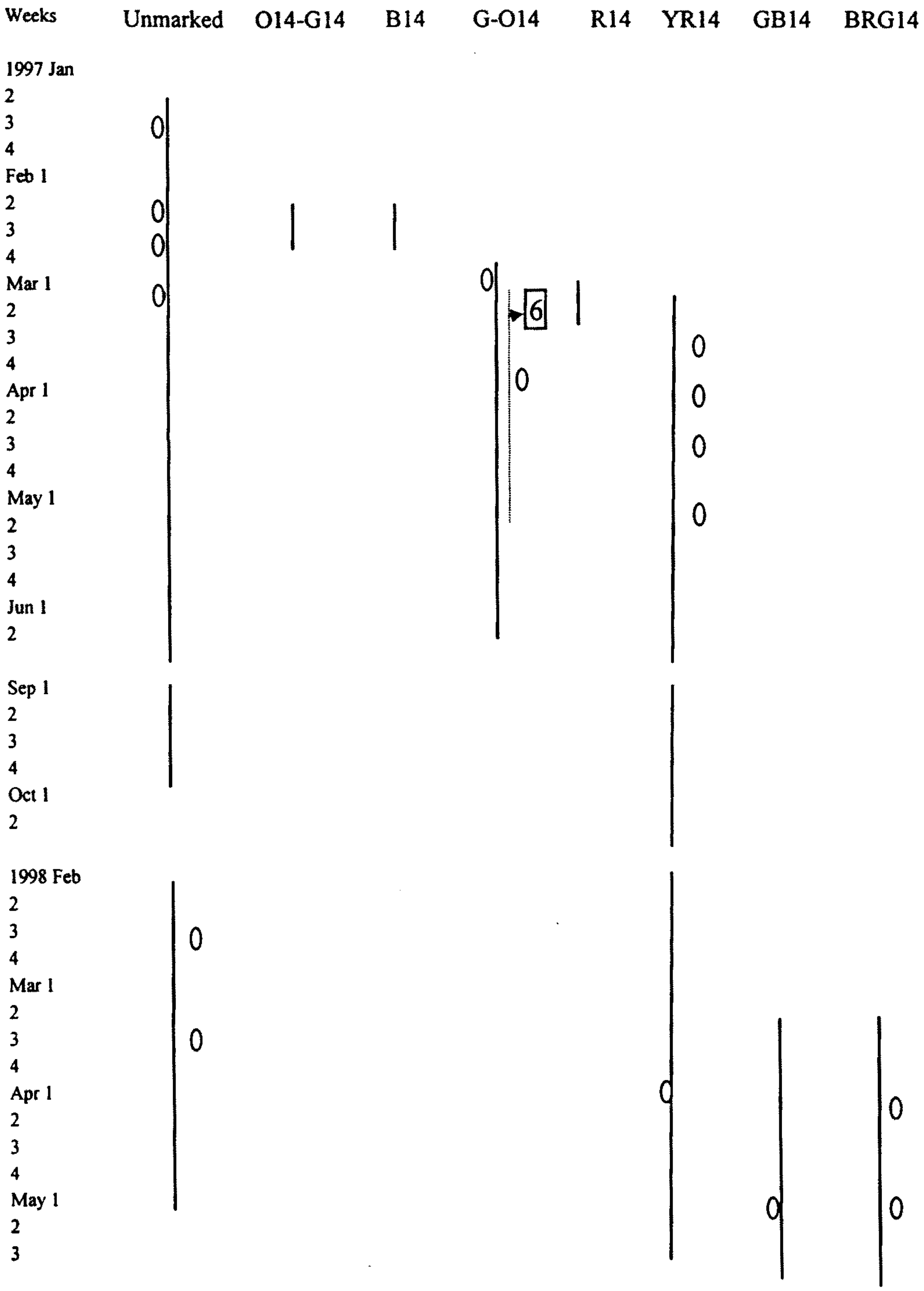


Figure 4.21. Time of possession of mound no.14 by the various pairs. At a time more than three pairs used this mound. Solid line represents birds that used mound No.14 and dotted lines represents birds that used other mounds as well.

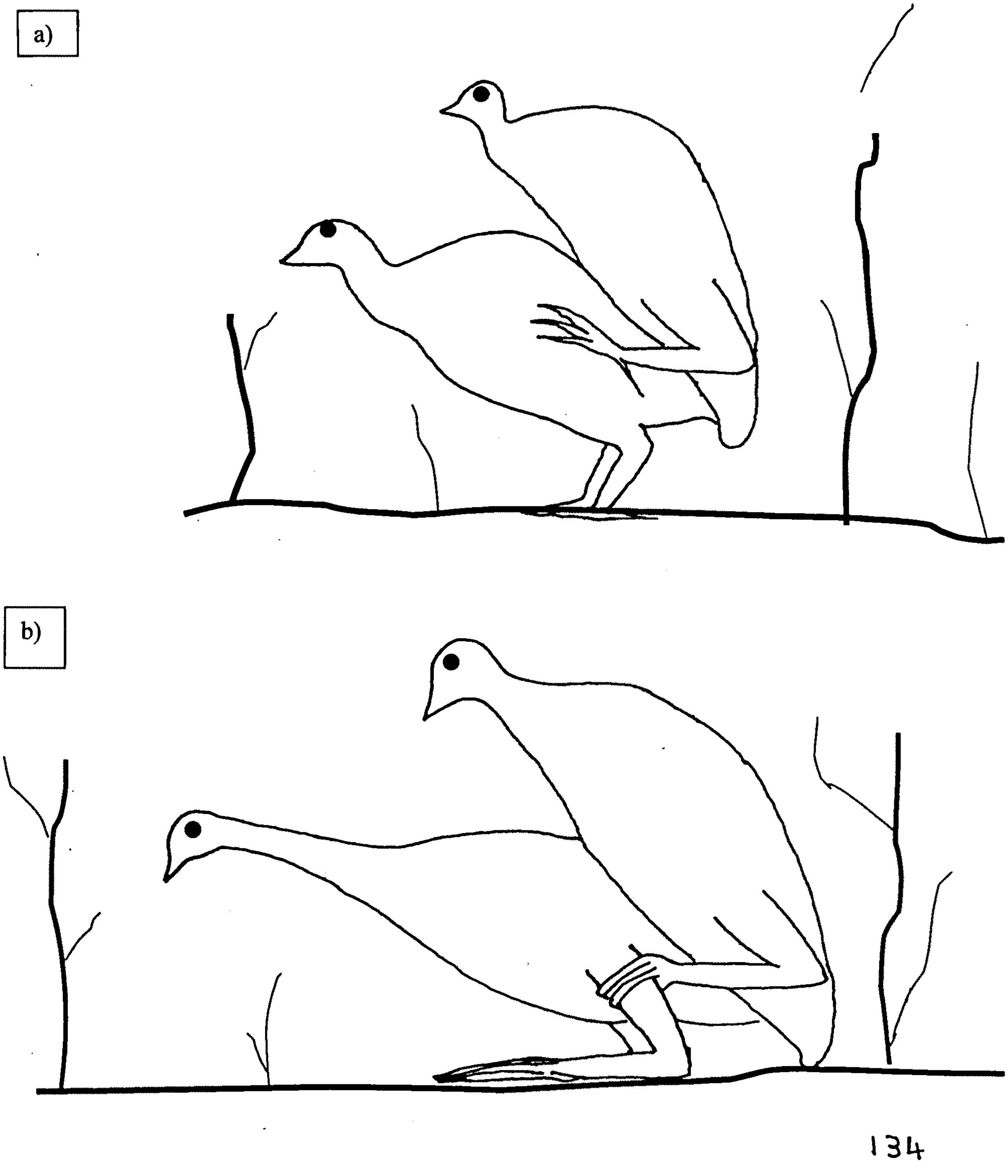


Intra-pair displays between male and female megapodes were not observed. However, on one occasion the male exposed food 2-3 times while working on the mound and the female came up and ate it.

4.3.12. Extra-pair copulation

Extra-pair copulation was observed at least eight times. In the one instance in 1997 when this was observed, the male of one pair copulated or attempted copulation six times with the female of another during a fight that lasted about 45 minutes, and during which it continually chased the female including onto trees. Their respective partners were calling but neither fought nor attempted mating. In 1998, extra-pair copulation was seen twice, in both instances as a part of physical fights. One of these was between two pairs who were then joined by an unpaired bird. Whether the unpaired bird copulated was not known. The second instance was between nine birds that included three pairs and three unpaired birds, two of which were males and one a female. In this instance the fight was initiated between a pair and an unpaired female who was raped by the male of the pair. While raping, the male chased the female and held her leg with his claws. During raping, the wings of male were extended and their tips pressed against the ground for balance (fig 4.22). Another pair then joined them, whose male raped both the paired and unpaired females. Two more unpaired males then joined these, and then by one more pair. During this action males of the pairs tried to protect their respective partners from other males but it was not effective. Copulation took place apparently indiscriminately for about an hour. In at least five other instances, rape was attempted but copulation was not observed.

Figure 4.22. Mating posture of the megapodes. a) while normal mating male sit or stand on the back of his partner but b) during the raping male hold the running female's hind limb and then mate.



4.3.13. Hierarchy

A hierarchial system exists in this species, especially where there is multiple-pair use of the mound (Fig 4.18- 4.21). The dominant pair expresses their supremacy over the others by warning (calls), chasing, fighting. Hierarchial system was evidenced by:

Mound No. '9c' was constructed by a solitary male ('Y9c', on 4-Feb-1997). Later this unpaired male paired with 'Gr9', which was attached to mound '9'. Both mounds were very close together. After pair formation the 'Y9c-Gr9' pair used both mounds ('9c' and '9'). During this time the 'Y9c-Gr9' pair was dominant over those two mounds and chased other pairs. But the same birds, when unpaired, were chased by unmarked pair(s) of mound '9'. After a few weeks (on 1-March-1997) the 'Y9c-Gr9' pair was chased by the 'SPG9' pair during which time the 'SPG9' pair was laying eggs in the mound. During this time both pairs fought each other very often, however the 'SPG9' pair was dominant over 'Y9c-Gr9'. One more pair (BP9) used mound 9 for egg laying. These 'Y9c-Gr9' and 'BP9' pairs did not show more aggressiveness when they met each other on the mound (on 21-March-1997 both pairs worked on the different side of the mound without any agonistic interaction). Along with the 'Y9c-Gr9', 'BP9' and 'SPG9' pairs, one more solitary bird used mound 9 during March and April (1997) but this unpaired bird was chased by all the pairs of mound 9. Once, two solitary birds met each other on mound '9' when both fought and separated within 3 minutes.

In 1996, at mound '8', the Payu pair was dominant over the others. There was no observation of the fight between the Payu pair and the Loong pair in 1996. In 1997, the

Loong pair was dominant over the others in all the seasons. The Payu or other beta pairs were disturbed from the mound by the calls of the Loong pair, even though they were far away from the mound. Usually both partners of a pair actively participated in the fights, however in 7 incidences, the female Loong alone chased the intruders while the male Loong was silent. The alpha pairs usually used to call from the top of the mound but subordinate pairs did not. There were no observations of solitary birds calling from the mound.

4.4. DISCUSSION

4.4.1. Territoriality

The term territory is broadly defined as an area guarded against other individuals of the same species, as has been defined by Odum and Kuenzler (1955) and Hinde (1956).

4.4.2. Establishment of the territories

Aggressive behaviour is an important element of initial territory establishment in many birds (Yasukawa 1979). Territories were usually established during February and March, resulting in more territorial calls and fights. Territories are successfully formed by the breeding pairs, while unpaired birds roamed without distinct territory boundaries, which is consistent with the presence of 'floaters' in other species (Eckert and Weatherhead 1987). The maintenance of the territories was possible only by the pairs.

4.4.3. Function of the territories

Statistically there was no significant variation in the territorial size of the Nicobar Megapode, because some pairs had large sized territories in the dry season but small in the wet season, and others had small sized territories in the dry season but larger ones in the wet season. However, compared to the dry season, the territory of the Nicobar Megapode was smaller in the wet season. Food does not appear to be a limiting factor in the Nicobar Megapode between seasons, as territory size did not change significantly. This indicates that the primary function of a territory is to gain access to a mound (Frith 1959; Jones 1990a).

In the absence of information about the resource level, this study could not attach clear ecological meanings to the variations in territory size in the Nicobar Megapode. However, according to Shoener (1968) territory size has been positively correlated with the food density of the area, and birds living in poorer habitats may have to establish larger territories to obtain sufficient resources (Wiens 1973). If the territory size of the Nicobar Megapode was small in the dry season, it means that an egg-laying megapode need not spend much energy to increase the territory size, but in the wet season (egg laying not observed) too, the size of the territories were small. It is thus assumed that the habitat (breeding ground) of the Nicobar Megapodes is naturally rich in food (cf. Shoener 1968, Wiens 1973), which are enough for breeding and non-breeding pairs.

4.4.4. Territorial period, maintenance and fidelity

As long as a pair (excluding the alpha pair) was using a mound for egg laying it was called the territorial period of that pair. An egg-laying pair could maintain their territory at the mound only up to the last egg laid, or maintain their territories in the non-egg-laying period. But slight changes were observed in the size and location of the territories of some pairs during the dry and wet seasons. The mound is the most important structure in the territory of an individual or a pair. Alpha pairs tended to show mound fidelity or territorial fidelity throughout the year, but others (the beta pair) did not.

4.4.5. Territories of paired and unpaired megapodes

Most egg-laying pairs were dominant over non-egg-laying megapodes. Dominance in the Nicobar Megapode was not permanent, and appeared to be a function of mound occupancy. In some species of birds, competition among males/females for territories results in some individuals not acquiring territories. These unsuccessful competitors consequently exist as `floaters' and rapidly fill vacancies created by the removal of successful territory owners (Orians 1967). The factors that determine whether an individual will be an owner or a floater remain unclear (Orians 1967). In the case of the Nicobar Megapode, the floaters appear to be unpaired birds who were unable to get a partner. One hypothesis is that floaters are competitively inferior to territory owners and could explain why Shombabh remained unpaired for so long. Theoretical analysis of animal contests, on the other hand, predict that owners may be successful at defending their territories against intruding floaters due to asymmetries unrelated to fighting ability (Rohwer 1982).

4.4.6. Is the Nicobar Megapode monogamous?

Most bird species are monogamous because of the necessity of biparental care of the young (Lack 1968, Oring 1982). Of these, 50% of bird species have long term partnerships (Lack 1968). Furthermore, recent ideas about monogamy in birds suggests that there is no monolithic mating system, but it is often, though not necessarily, associated with some level of biparental care, and monogamous individuals may or may not engage in extra-pair fertilisation (Black 1996). Generally mound-building megapodes are monogamous (Jones *et al.* 1995). Most sightings of the Nicobar Megapode were pairs while working on the mound and elsewhere, and they exhibited synchronous behaviours such as duetting and the joint defence of territories and mounds. This is consistent with other species in the group, where mound building megapodes are thought to be monogamous (Jones *et al.* 1995). Of the five colour-marked pairs, two remained together throughout the study. Two changed partners, one of which was brief, and the fate of the fifth pair was not known. Even though long-term partnerships in the Nicobar Megapode probably exists for only 40% of all partnerships, the pairing behaviour of the Nicobar Megapode confirmed that they are largely monogamous, even though temporary pair bonds, change in partner and extra-pair copulation were present.

In conclusion, there are even species in which some populations are purely monogamous while others are highly polygynous (Ford 1983) and the high rate of promiscuous matings observed in Australian Brush-turkeys is likely in dense populations where females are able to encounter many males (Jones 1988). Temporary pair bonds, change in partners and extra-pair copulation that occurred in the Nicobar Megapode was likely because of the dense population (because of the clumped distribution of the Nicobar Megapode towards the coastal forest). However, as the sample size is small (only five colour marked pairs) the persistence of pair bonds within the species is still unclear.

4.4.7. Why is there a monogamous mating system in the Nicobar Megapode?

Megapodes, particularly those belonging to the genus *Megapodius*, are believed to be distinctly monogamous as most species exhibit features associated with monogamy such as monomorphism, virtually inseparable pairs and duetting (Jones *et al.* 1995). It was thought that monogamy may be inevitable in mound building species since high paternal investment could only be expected where male parental care benefits their own progeny (Smith 1984). Monogamy in this group, however, is an anomaly as female emancipation from parental care, and the presence of resources (e.g. the incubation mound) that can be dominated by males, should result in a polygynous mating systems (Orians 1969), and promiscuity has been documented for certain sexually dimorphic species (Jones 1989a&b, Jones *et al.* 1995). The formation of partnerships in the Nicobar Megapode could be for the following reasons:

1) *Continuous incubation:* Megapode eggs are relatively very large (20% of the females' body weight (Jones *et al.* 1995)) and a female typically lays from about 12 to 30 eggs per season (Jones *et al.* 1995), but in the case of the Nicobar Megapode the clutch size is small and female lay one to four eggs at the intervals of 15 days (see chapter 3) over a breeding season of many months. The Nicobar Megapode works continuously and would need more energy. It is likely that energy may not be provided by a single individual, and it therefore requires partnerships.

2) *Resource defence:* More of the population of the Nicobar Megapode is distributed in the coastal forest than in the interior (Dekker 1992, Sankaran 1995a, b), and selecting particular habitats for the construction of the mound (see Chapter II), leads to competition. Unpaired birds may not be able to establish their own territories and defend the mound against pairs. For successful defence of the resources (mound and foraging areas), partnerships are probably essential to this species.

4.4.8. Partnerships, reuniting and partners change

Though the Nicobar Megapode exhibits the characteristics of permanent pair bonds which are consistent with several other species of mound building megapodes (Crome and Brown 1979; Jones *et al.* 1995) (Fig 4.18 to 4.21), 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 observed. This could indicate that the pair bond in this species, and possibly other mound building megapodes, might be far less permanent than was thought.

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. That access to mounds 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 serve as precopulatory display to strengthen or reinforce pair bonds (this lack of courtship display is apparently consistent in most megapodes) (Jones 1990, Jones *et al.* 1995, Black 1996). The separation and reuniting of the L8 pair may be explained by the 'better option hypothesis' (Ens *et al.* 1993) where either sex may change partners to improve access to or defence of resource

4.4.9. Role of unpaired birds

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 the absence of space within which to establish a territory or the inability to build a new mound, which appears to be a key function of pair formation. The frequent fights between unpaired birds and pairs, and the intra-sex fights that took place during such encounters, may indicate that solitary birds were attempting 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 the males of pairs. Also, solitary females have been observed laying eggs. It is not known whether unpaired males and females copulate, though a very brief pair bond was formed between two such individuals. Thus the presence of unpaired birds, or 'floaters', may be an alternate breeding strategy. Unpaired males may intrude and fight with males of a pair so as to force divorce by usurpation (Minton 1968) or even if unsuccessful in forming pair it may increase chance of breeding by raping the female.

4.4.10. Are megapodes sharing their mound?

That more than one pair of the Nicobar Megapode use a mound at any given time especially during the peak period of egg laying raises the question of whether this species actually shares their resources or not (Fig 4.18 to 4.21). Nest robbing is common in communal breeders (Mexican Jay: Brown 1963, Australian Magpie; Carrick 1963 and Groove-billed Anis; Vehrencamp 1977). Breeding megapodes may act destructively toward the eggs of others that are in their communal incubation mound. Of the 30 mounds studied more than one pair used a mound. In two instances the pair that was working on the mound kicked out eggs of other bird(s). Though it could be hypothesised that such behaviour is related to dominance (Brown 1963), the absolute indifference of megapodes to eggs within or on the mound indicates that this was merely chance. In the Nicobar Megapode, on one occasion two pairs worked on a mound at a time when both were beta pairs. Except for this, the Nicobar Megapode did not allow any one of their counterparts to use the incubation mound when working.

It is easy to say that the Nicobar Megapode do not share their mound with counterparts since alpha pairs did not allow beta pairs to use their mound, who do not allow their subordinate pairs or unpaired birds to use the mound. Since dominance (alpha pair status) in the Nicobar Megapode was not permanent, most of the users of an incubation mound have a chance to become an alpha pair. Thus, though frequently repulsed, it is in the interest of subordinate pair to attach themselves to a mound, not only because they can lay eggs, but could also become dominant pairs and gain uninterrupted access to the mound. Therefore it is very difficult to conclude whether the Nicobar Megapode share their mounds with counterparts or not. In Papua New Guinea, both *Megapodius freycinet* and *Talegalla jobiensis* laid eggs in a mound (Dwyer 1980), which is again confusing the mound sharing behaviour in the megapodes.

4.4.11. Hierarchy

4.4.12. 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. Subordinate pairs may shift territories to occupy a different mound (BP9 in fig. 4.9). Dominant pairs may also lay in more than one mound (G-O14 in fig. 4.10, Y9c-Gr9 in fig 4.9). 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.

4.5. CONCLUSION

In general, the Nicobar Megapode was territorial throughout the year. Hierarchy varies temporally and spatially. Alpha pairs were more likely to show mound and territory fidelity than Beta pairs. Territories overlapped where a large number of pairs used a mound. The average size of the territory was 0.8 ha. A major function of the territory of the Nicobar Megapode was to protect the mound from neighbours or strangers. Both partners of a pair equally defended their territory from others.

Nicobar Megapodes are largely monogamous. However, temporary pair bonds, change in partner and extra-pair copulation are present in this species. Unpaired megapodes tried to steal the mate from an existing pair and it leads to changes in partnerships, extra-pair copulation and temporary pair bonding. An egg-laying pair is dominant over a non-egg-laying pair. The dominant rank in the society of the Nicobar Megapode was not permanent. Dominance status appears because of the mound rather than the territory. The Nicobar Megapode is whether sharing the mound with counterparts or not is unclear.

Chapter V

FOOD AND SOME FEEDING ECOLOGY OF THE NICOBAR MEGAPODE

5.1. INTRODUCTION

Megapodes forage by scratching and raking among the debris on the ground, opportunistically taking food items as they are exposed (Jones *et al.* 1995). Different types of food items have been reported, including both fauna and flora (Cleland 1912, Booth 1986). In general, megapodes are omnivores. Leaf-litter invertebrates and seeds are the major food items of megapodes, though the Australian Brush-turkeys *Alectura lathami* feed on fruit in the tree canopy as well (North 1914; Gill 1970; Brookes 1919).

Alelctura lathami, are primarily solitary while foraging, although large numbers will congregate at localized rich food resources. Wide range of seeds, fruits berries, and other vegetable matter with invertebrates such as beetle larvae, and even frogs, grasshoppers are taken by this species (Cleland 1912; Bravery 1970), but in captivity it took mice, tadpoles, and snails (Coles 1937). Malleefowl *Leipoa ocellata* diet mainly contained fruits, buds and seeds of shrubs (Frith 1962) and herbs (Benshemesh 1992). Also fungi, ants, and termites were eaten when available (Jones *et al.* 1995). Booth (1986) recorded seeds of *Cassytha melantha, Dodonacea bursariifolia, Enchylaena tomentosa,* and Zygophyllum spp. and invertebrates such as ants, bees, beetles, cockroaches, dragonflies, grasshoppers, spiders, and wasps. Green cabbage was commonly eaten in spring and arthropods in autumn (Brickhill 1987). Stomach contents of Maleo *Macrocephalon maleo* consisted of different types of snails, whipscorpion (Jones *et al.* 1995) and the seed of highly poisonous *Pangium edule.*

Polynesian Megapode *Megapodius pritchardii ate* land snails, centipedes, worms, crabs, cockroaches, termites, ants, coconut, and fruits (Todd 1983; Weir 1973). Seeds of *Colubrina asiatica*, Hymenoptera, Lepidoptera, Coleoptera, Diptera, Arachinida, snails and other vegetable matters were eaten by the Micronesian Megapode *Megapodius laperouse* (Stinson and Glass, 1992; Jones *et al*. 1995). Dusky Megapodes *Megapodius freycinet* ate snails and beetles (Jones *et al.* 1995). Orange-footed Megapode *Megapodius reinwardt* feed on centipedes, snails fruits, grubs, worms, ants, young snakes, millipedes, scorpions, seeds, earthworm (Banfield 1913; Ashby 1922; Macgillivary 1914, Jones *et al.* 1995). In literature, there is no information about the chicks feeding activities but in captivity they fed on a variety of live foods and will peck at anything unusual (Jones *et al.* 1995).

The environmental features of incubation sites may influence the foraging activities of the birds (McFarland 1981). The nutritional requirements of males and females are likely to differ markedly. Comparisons of fecundity in species where females forage alone and those where males accompany them would be of interest, particularly in a species where males enhance the females' feeding success by locating and bringing food items (Jones *et al.* 1995).

Information about the food and foraging behaviour of the animals is essential for both *in-situ* as well as *ex-situ* conservation. In literature, there was no detailed information about the food of the Nicobar Megapode; however, stomach contents of Nicobar Megapode specimen from Tillanchong contained a beetle *Scarabus plicatus* and a snail *Helicina zelebori* (Ali and

Ripley 1983). This study gives some more information about the food and foraging behaviour of the Nicobar Megapode.

5.2. OBJECTIVE

1. To identify the food items of the Nicobar Megapode.
2. To find out temporal variations in foraging activity in the Nicobar megapode

5.3. RESULT

5.3.1. Seasonal distribution of foraging activity

The Nicobar Megapodes forage by scratching and raking among the debris on the ground, opportunistically taking food items as they are exposed. Foraging patterns significantly varied between the years (K-W test, $\chi^2 = 9.23$, df=2, $p<0.01$), probably due to the significant variation in the precipitation (K-W test, $\chi^2 = 7.81$, df=2, $p=0.02$). More precipitation reduced the foraging activities of the Nicobar Megapode ($r=-0.46$, $p=0.05$). In 1998 foraging was greater (10 %/month) than other years (3.6% / month in 1996, 4.8% / month in 1997) as that was a drought year. The peak period of foraging in 1996 was February (23 %) but less in June (9 %) (Fig 2). In March 1997, more foraging activities was recorded (25%) but it was low in June. In 1998, more foraging activity was seen during March and April. Compared to summer, foraging was very low in the rainy season during September and October 1996 (Fig 5.1).

5.3.2. Foraging and egg laying

The Great Nicobar Island received normal summer precipitation during the year 1996 and 97 but not in 1998. Therefore 1996 and 1997 data was used for checking whether there was a correlation between amount of the foraging activity and egg laying. Foraging significantly influenced the egg-laying of the Nicobar Megapode ($r=8.18$, $p<0.001$). However, if the 1998 data was included, then there was no significant correlation between the foraging and egg laying. February, March and April were good time for the egg laying megapodes and during this period more foraging took place. However, in 1998, foraging was more but egg laying was low (Fig 5.2).

5.3.3. Food

The Nicobar Megapode eat soil invertebrates, flying insects, vertebrates and vegetative matter. The stomach content of eight number of Nicobar Megapode contained cockroach, beetles, ants, lizards, snails, grasshoppers, hermit crab, seed of *Macaranga peltata*, and rotten vegetative materials. A megapode was observed chasing an agamid lizard on the ground, megapodes have been observed feeding on the tissue of dead red crabs on the ground.

Apart from rotten vegetative matter, the seed of *Macaranga peltata* was the only major vegetative material in the stomach of the birds (Table 5.1). Cockroach and snails were the major animal food items.

Figure 5.1. Seasonal distribution of foraging activity.

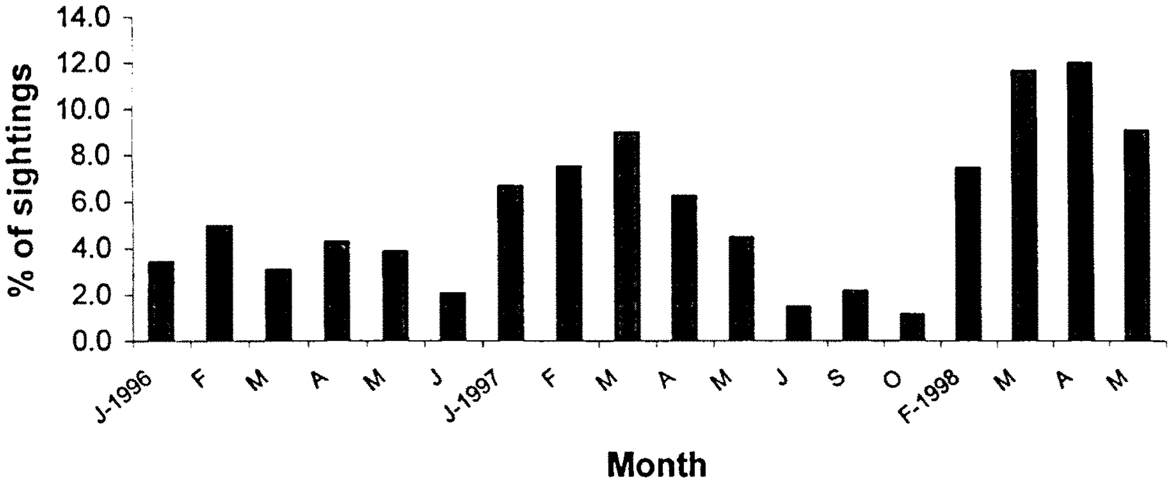
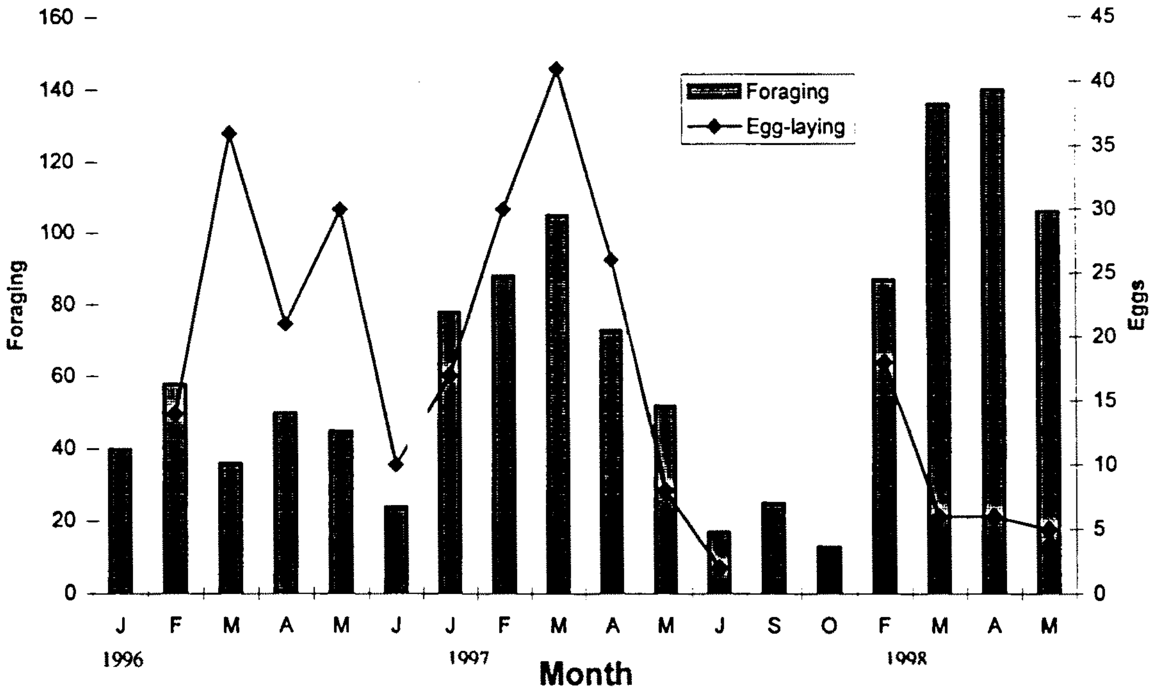


Figure 5.2. Relationship between the foraging and egg laying. Though percentage of foraging activity was greatest in 1998, less number of eggs were laid in that year.



Some of the beetles were identified in the study area as the food of megapode are *Anomala andamanica, Anomala rhodomela, Alissonotum piceum, Parastasia luteola, Heteronechus lioderes, Rhyssemus germanus, Aphodius moestus, Holotrichia nicobarica, Apogonia nicobarica, Anomala varicolor*, and *Dasyvalgus insularis*. The Nicobar Megapode was also observed eating centipedes, butterflies, moths, termite and tadpoles of frog. Like many other birds, megapodes ingest grit in order to help break down their food. Drinking of rainwater has been observed occasionally in the Nicobar Megapode.

Table 5.1. Food and its preference by the Nicobar Megapode. Both volumetric as well as Occurrence methods were compared.

Food item	Volumetric	Occurrence
	rank 1	rank 2
Macaranga peltata	1	1
Dictyoptera (cockroaches)	2	2
Snails	2	3
Litters	3	2
Beetles (*Microserica nicobarensis* etc)	4	4
Ants	4	4
Unidentified	4	3
Grasshopper	4	5
Pauropodans	5	5
Hermit crab	5	5
Reptile scale	6	6

Stomach contents of two-deceased chicks were analyzed. Of these, one chick, which was partially eaten by hermit crab, contained only one type of seed that could not be identified. Another chick, which might have been killed by a raptor, contained nothing in its stomach.

5.2.4. DISCUSSION

Breeding capability of the animals will be dependent upon the quality and quantity of the nutrition of those animals (Immelmann 1971, Goth and Vogel 1996). Generally during the breeding season, birds give more importance to the nest building, incubation and parental care of young than foraging (Immelmann 1971). In other cases where breeding occurs throughout the year equal importance is given to both breeding and foraging (Immelmann 1971). The nutritional and energetic requirements of female megapodes appear to necessitate prolonged periods of foraging (Jones *et al.* 1995), which inevitably means that the female must spend significant amounts of time away from the incubation site. However, in the case of the Nicobar Megapode both male and female equally worked on the mound and spent time equally on the foraging ground. Males of the Nicobar Megapode did not help the female for foraging except on one occasion when a male located food for his partner. This may indicate that food is not a limiting factor in the Nicobar Megapode.

Rainfall and egg production might be linked via food availability (Goth and Vogel 1996). Rainfall is the major environmental factor regulating the foraging behaviour of the megapode and also there was significant relationship between the foraging and the egg laying of the Nicobar Megapode. Frequent rains can increase the number of invertebrates in the soil litter of tropical forests (cf Goth and Vogel 1996) and this may also be the case in the Nicobar Islands. Since the Nicobar Megapode feed mainly on invertebrates, the production of eggs may be linked to rainfall patterns. During extremely dry weather (1998), egg laying was low and birds spent more time for foraging, probably due to less food abundance.

5.4. CONCLUSION

The Nicobar Megapode is omnivorous. Cockroaches, snails, and seeds of *Macaranga peltata* were the most preferred food of this bird. Both male and female of a pair equally spent time in foraging. Rainfall and egg production was linked via food availability. Frequent rains during dry season increased the egg production of the Nicobar Megapode.

Chapter VI

The process of hatching and notes on the chick of the Nicobar Megapode

6.1. INTRODUCTION

Super precocial chicks of megapodes hatch at distances varying between about 20 cm and one meter or more beneath the surface of the incubation site (Jones *et al.* 1995). In order to emerge from the incubation site they must dig their way to the surface, a process they perform without any assistance from the adult (Frith 1959, Jones *et al.* 1995). The time taken in moving from the level of hatching to the surface varies according to the depth, the compaction of the substrate, the nature of the substrate, and energy reserves of the individual hatchlings (Jones *et al.* 1995). The behaviour of the Nicobar Megapode's chick is virtually unknown. Here, a 'chick' refers to both hatchlings and fledglings. 'Hatchling' are those chicks working their way out of the egg and up to the surface. Once at the surface and out in the open, it was called fledgling (Heij et al. 1995).

6.2. RESULTS AND DISCUSSION

In 1998, totally seven eggs were monitored. Of these, in three eggs a crack was observed longitudinally after 65.33 (±SE1.86) days from the day of egg laying or approximately ten days prior to the hatching (Table 6.1).

Table 6.1. Date of egg laying, cleaving and hatching of three monitored eggs.

Egg	Laid on	Cleaving on	Hatched on
1	06/02/98	12/04/98	22/04/98
2	07/02/98	12/04/98	23/04/98
3	07/02/98	18/04/98	28/04/98

The hatching and emergence of chicks from the mound was observed in five cases. The climb of the hatchling from the egg chamber to the surface is a long process that can take up to 83.8 hours (SE=12.7, max=118, min=48; table 6.2), and the mean rate of movement was about 1.25cm per hour (SE=0.07, n=5). Movement of the hatchling is effected by two factors. First, the breathing of the hatchling results in contraction and expansion of the body, which loosens and allows soil to trickle down on either side of its body from the top. The legs are then flexed and the hatchling is then pushed up a little. The average rate of leg kicks of the hatchling was 2.7 kicks /hour. The average rate of leg kicks of the hatchling, just after the time of hatching was 1.8 kicks/hour, after an hour the leg kicks rate increased to 2.6/hr. When the hatchling was at the surface layer of the mound the leg kicks rate was higher (4.6/hr).

Table 6.2. Date of egg laying, hatching, place of egg laying and time taken by a hatchling to reach the surface from where they emerged.

Egg	Laid on	Hatched on	Depth of egg chamber (cm)	Duration*
1	17/01/97	01/04/97	126	96
2	21/01/97	13/04/97	138	118
3	09/02/97	21/04/97	103	95
4	04/02/97	26/04/97	93	62
5	06/02/98	22/04/98	95	?
6	07/02/98	23/04/98	102	?
7	07/02/98	28/04/98	56	48

*Duration of time taken by a hatchling to cross the distance between egg chamber and mound surface.

Chicks invariably left the mound soon after reaching the surface, and sighting of the chicks on the mound was difficult. Successful hatching was also indirectly noticed by observing the hatching hole on the incubation mounds whose surface was damp. When the surface of the mound was dry, the hatching hole could not be seen due to the shifting of sand. The morphometric characters was measured for 17 chicks (Appendix II).

6.2.1. Activities of hatchling

Totally 22 chicks were sighted in the study area, of these 17 chicks were captured and were released at the same place. As soon as the chick emerged out from the mound they performed both body and leg preening. All moved towards the forest. Once, within seven seconds a chick flew 53 meters with a stop. Another chick, as soon as it emerged out from the mound, flew and perched on a branch that was 73cm high from the ground. Chicks make alarm calls when handled. Identifying chicks on the forest floor was difficult because of their camouflage on the ground. Chicks showed alarm behaviour even on seeing a tree shrew *Tupaia nicobarica*.

6.2.2. Fate of chick

All the chicks sighted in the field were on or near the incubation mounds. None of the chicks were sighted away from the mound, though, local people reported sighting chicks in the interior forest too. During the study period, just three juveniles were sighted and all of them were unpaired birds. Six deceased chicks were sighted in the study area, of these four were observed being eaten by a Nicobar Serpent Eagle, Nicobar Shikra and hermit crabs (Table 6.3, see chapter 7).

Of the 22 chicks observed, in five an opaque membrane was present over the eye which rendered the bird blind. Three of these were cured, by immersing them in seawater, while the other two died. Considering how alert the chicks are, it is likely that those preyed upon by the predators were also born with the eye disorder.

Table 6.3. Six chicks killed/eaten by the various predators belongs to various groups.

Hatchling	**Date of sighting**	**Killed / eaten by**
1	12/04/96	Nicobar Shikra
2	01/05/97	Nicobar Hawk-Owl?
3	03/05/97	Nicobar Crested Serpent Eagle
4	12/05/97	Nicobar Shikra
5	23/04/98	Hermit Crab
6	22/04/98	Cat or Nicobar Hawk-owl?

6.2.3. Miscellaneous

In mound No.9, an adult bird kicked out an emerging-hatchling from the mound while digging a pit. There was no reaction between the adult birds and the chicks. The kicked-out-chick left the mound after taking a short rest.

In mound No.7, a pair, while digging a pit kicked out a 72 days old embryo from the egg chamber. Embryo was not fully developed and hence died.

Chapter VII

PREDATORS IN THE BREEDING GROUND OF THE NICOBAR MEGAPODE

7.1. INTRODUCTION

Mound building megapodes spend day after day on the mound, collecting leaf-litter from the forest floor to build their mound and regulating the incubation temperature of the mound (Frith, 1956; Clark 1964; Jones *et al.* 1995). The presence of the birds on the mound for a prolonged period makes adult megapodes highly susceptible to predation, especially during the breeding season. Mound building megapodes are therefore not sympatric with predatory mammals, such as felids or canids (Dekker, 1990). Dekker (1990) states that the megapodes do not occur on the mainland of Southeast Asia, Greater Sunda Islands and Andaman Islands where mammalian carnivores are found in wide variety. After egg laying, burrow-nesting megapodes do not take care of the nest site to regulate the incubation temperature, returning only to lay another egg (Todd 1983; Dekker 1990), because of this behaviour the chances of predation upon the burrow-nesters is less than the mound builders.

Indigenous plants and animals are now at risk because of introduced species in at least 78 major island groups of the world (Atkinson 1989). The introduction of predators, either deliberately or unintentionally, by settlers within the last 200 years has devastated a number of island faunas and exterminated megapodes from most of the west Polynesian islands (Steadman 1993). The commonest and most problematic introduced predators for megapodes are cats and dogs. Red fox *Vulpes vulpes* is the major threat to the Malleefowl

Leipoa ocellata in southern Australia (Jones *et al.* 1995). In this chapter predators of the Nicobar Megapode in the breeding ground are described.

7.2 RESULTS AND DISCUSSION

The Nicobar Megapode was preyed in three stages as eggs, chicks and adults (Table 7.1). Eggs were mainly preyed upon by the Monitor Lizards. Apart from the Monitor Lizards, predation by human being was also observed.

Table 7.1. Predators of the Nicobar Megapode.

Name of the Predators	Information from tribal	In references	This study	Target
Human	+	+	+	E,A
Monkey	+			A
Wild Boar	+	+	+	E
Feral Dog	+	+	+	A
Feral Cat	+	+	+	A
Rat	+			C*
Sea Eagle	+	+		C
Serpent Eagle	+	+	+	C
Shikra	+		+	C
Hawk Owl			+	C
Monitor Lizard	+	+	+	E,C
Python	+	+	+	C,A
Rat Snake	+	+		C
Hermit Crab	+		+	C*
Red crab (*Gecarcoidea* spp.)	+	+		C*
Robber Crab	+	+		C*
Red Ants	+	+	+	C*

E: Egg, A: Adult, C: Chick, C*: Deceased or sick chick

7.2.1. Monitor Lizard

Monitor lizard, the primary predator of megapodes, was common in the study area. There was a close relationship between the megapodes' activities and the monitor lizard's presence on the mound. Monitor lizards were more active on the mound during morning (seven to 10 hrs) and evening (15 to 17 hrs). Monitor lizard arrived at the mound not only for feeding on the eggs of the megapode but also to lay its own. Monitor lizard sightings on the mound was very low in 1997 but it was high in 1996 and 1998 (Fig 7.1). Main breeding season of the *Varanus salvator* is October and November although breeding has been known to occur throughout the year (Horn and Visser 1989).

During the study period 11 eggs of monitor lizard were unearthed from a mound, and were reburied in the ground, where temperature never goes up beyond 28°C. All those eggs successfully hatched. However, there was a difference in the incubation periods between the eggs hatched in the mound (265 days) and the control (305 days). Similarly, the incubation period of *Varanus salvator* reported by varied between 222 and 327 days (Horn and Visser 1989, Andrews and Gaulke 1990).

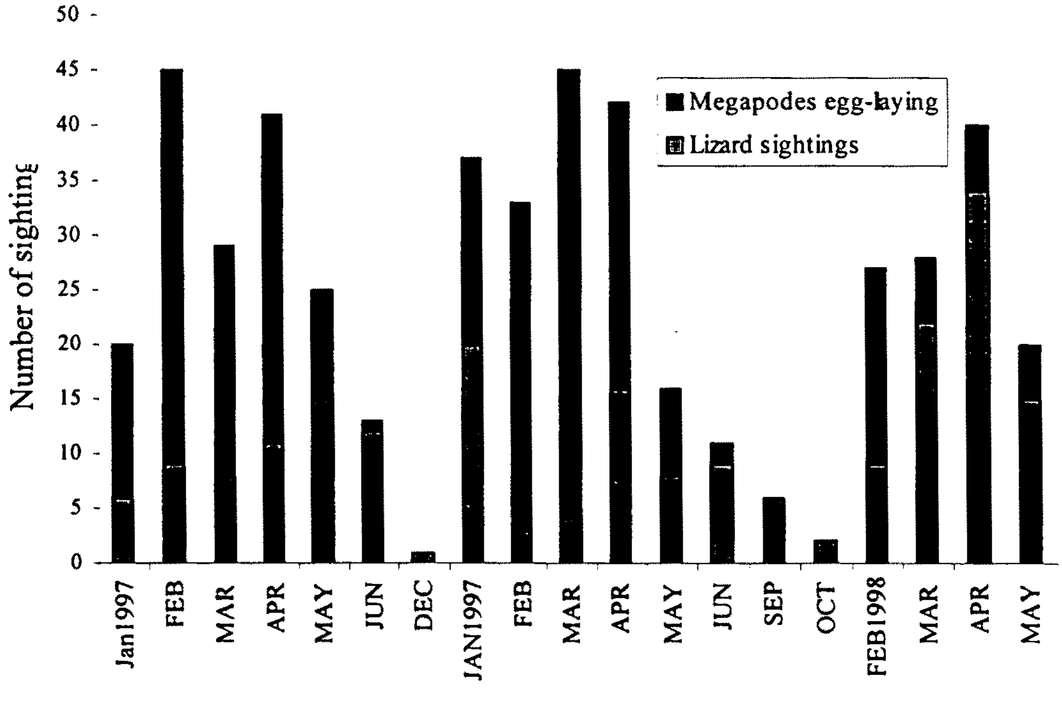
Monitor Lizards only preyed upon eggs of the Nicobar Megapode but not on the adult. This was evidenced from several observations when both monitor lizards and the Nicobar Megapode worked on the mound together, displaying neither threat nor avoidance behaviour.

7.2.2. Other predators

7.2.2.1. *Man*

Both tribal and settlers (from the mainland) ate the meat of megapodes. Interview with many tribal indicates that at least once he/she have tasted the meat of the megapode. Egg collection was very less in the Great Nicobar Island because it is a time consuming process. Compared to Nicobarese,

Figure 7.1. Mound arrival patterns of the *Varanus salvator* and egg laying of the Nicobar Megapode during the study period.



Shompens were actively involved in the egg collection (Seetharaman pers. comm). Settlers were involved in both hunting and collection of eggs.

7.2.2.2. *Birds*

Birds such as Shikra, Nicobar Hawk-Owl, Nicobar Crested Serpent Eagle, Andaman Serpent Eagle, White bellied Sea Eagle are the possible predators of the chicks of the Nicobar Megapode. Twice the chicks of the megapode were observed to be eaten by the Shikra and once by Nicobar Crested Serpent Eagle.

7.2.2.3. *Snakes*

In Nicobar Islands, the Reticulate Python and Cat snakes are widely distributed, but were not observed eating chicks or adult megapode. However, tribals and mainlanders have observed adult megapode being eaten by the Reticulate Python. It is possible that rat snakes can also prey upon megapode chicks or adult.

7.2.2.4. *Introduced Animals*

Dogs and Cats were introduced into the Nicobar islands by the travellers from other neighbouring islands like Sumatra, Java etc. or from the mainland India. Both tribal (Nicobarese only) and mainlander used dogs for hunting the Wild Boar. There were some feral populations of both dogs and cats on the island, the latter is more common. The dogs and cats were not observed preying upon megapodes, though dogs have been observed occasionally chasing megapodes at the mound and elsewhere.

7.2.2.5. *Invertebrates*

Four chicks were observed being eaten by the hermit crabs and red ants (n=4). In one observation, the hatchling coming out from the mound was caught by hermit crabs and eaten. The robber crab and the red crab were observed on the mound but were not seen preying on megapodes.

Tribal and mainlanders reported that the Crab Eating Macaque and several species of rats preyed upon the chick and adult megapode.

7.3. CONCLUSION

The Nicobar Megapode nesting grounds had a wide range of potential predators. *M. n. abbotti* could be preyed upon at three stages eggs, chicks and adults. Monitor lizard *Varanus salvator,* raptors, man, python, cat, dog and some invertebrates preyed upon the eggs or chicks or adult megapodes. Monitor lizard not only fed on the eggs of the megapode, but also laid its own in mound.

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Appendix I. Classification of family Megapodiidae.

Genus	Species	Sub-species	Distribution	Total species
Megapodius	*Megapodius pritchardii*		Mariana and Palua Islands	13(28)
	Megapodius laprouse	*M. l. laperouse*	Nivafo'ou , Tonga	
		M. l. senex		
	Megapodius nicobariensis	*M. n. nicobariensis*	Nicobar - India	
		M. n. abbotti		
	Megapodius cumingii	*M. c. gilbertii*	Philippines to Sulawesi	
		M. c. cumingii		
		M. c. dillwyni		
		M. c. pusillus		
		M. c. tabon		
		M. c. talautensis		
		M. c. sanghirensis		
	Megapodius bernsteinii		Banggai and Sula	
	Megapodius tenimberensis			
	Megapodius freycinet	*M. f. freycinet*	North Moluccas	
		M. f. oustaleti		
		M. f. quoyii		
	Megapodius geelvinkianus			
	Megapodius forstenii	*M. f. forstenii*		
		M. f. buruensis		
	Megapodius eremita		Karkar to Solomon	
	Megapodius layardi		Vanuatu	
	Megapodius decollatus			
	Megapodius reinwardt	*M. r. reinwardt*	Kangean to North Australia	
		M. r. tumulus		
		M. r. yorki		
		M. r. castanonotus		
		M. r. macgillivrayi		
Macrocephalon	*Macrocephalon maleo*		Sulawesi	1(1)
Talegalla	*Talegalla cuvieri*	*T. c. cuvieri*	West Irian	3(8)
		T. c. granti		
	Talegalla fuscirostris	*T. f. fuscirostris*	South New Guinea	
		T. f. occidentis		
		T. f. aruensis		
		T. f. meyeri		
	Talegalla jobiensis	*T. j. jobiensis*	Noth New Guinea	
		T. j. longicauda		
Aepypodius	*Aepypodius arfakianus*	*A. a. arfakianus*	Upland New Guinea	2(3)
		A. a. misoliensis		
	Aepypodius bruijnii		Waigeo	
Alectura	*Alectura lathami*	*A. l. lathami*	East Australia	1(2)
		A. l. purpureicollis		
Leipoa	*Leipoa ocellata*		Australia	1(1)
Eulipoa	*Eulipoa wallacei*		Mollucca	1(1)

Appendix II. Morphometric characters of adult, chick and egg of Nicobar Megapodes.

Bird	Structure	mm/gram*	n
Adult female	Tarsus	72.45 ±SE 0.56	6
	Wing	231.2 ± 3.99	6
	Culmen	27.8 ± 0.25	6
	Weight	783.5 ± 28.48	6
Adult male	Tarsus	73.69 ± 0.85	11
	Wing	243.45 ± 3.15	11
	Culmen	27.44 ± 0.34	11
	Weight	758.09 ± 25.42	11
Chick	Tarsus	25.6 ± 1.14	17
	Wing	87.96 ± 1.7	17
	Maxillary	18.3 ± 0.3	17
	Weight	63.9 ± 3.9	17
Egg	Length	83.6 ± 0.73	36
	Width	49.0 ± 0.3	36
	Weight	109.4 ± 5.8	36

* Weights are in gram and lengths are in mm

Appendix III. Vertebrate fauna of study area (excluding fish)

Checklist of Amphibians.

Common name	Scientific name	Endemicity
Nicobar Frog	Rana nicobarensis	+
Tree Frog	Rhacophorus leucomystax	
Indian Toad	Bufo melanostictus	
Nicobar Toad	Bufo camortensis	+

Checklist of Reptiles of Nicobar Islands

Common name	Scientific name	Endemism
Smith's Gecko	*Gekko smithii*	
Stripeheaded Gecko	*Lepidodactylus lugubris*	
Whitelipped Garden Lizard	*Calotes mystaceus*	
Andaman Water Monitor	*Varanus salvator andamensis*	+
Skink	*Mabuya rudis*	
Bronzeback Skink	*Spehenomorphus maculata*	
Nicobar Tree Skink	*Dasia nicobarensis*	+
Tree Skink	*Dasia olivacea*	
Tiwari's Bronze back	*Dendrelaphis humayuni*	+
Reticulated Python	*Python reticulata*	
Amphibious Sea Snake	*Laticauda laticaudatus*	
Boie's Water Snake	*Xenochropis trianguligerus*	+
Dogfaced Water Snake	*Cerberus rhynchops*	
Green Tree Snake	*Dendrelaphis cyanochloris*	
Yellowstriped Trinket	*Elaphe flavolineata*	
Green Sea Turtle	*Chelonia mydas*	
Hawksbill Turtle	*Eretmochelys imbricata*	
Leatherback Turtle	*Dermochelys coriacea*	
Malayan Box Turtle	*Cuora amboinensis*	
Olive Ridley Turtle	*Lepidochelys olivacea*	
Saltwater Crocodile	*Crocodylus porosus*	

Kingfisher			
Nicobar Dwarf Kingfisher	*Ceyx erithacus macrocarus*		+
Nicobar Storkbilled Kingfisher	*Halcyon capensis intermedia*		+
Blackcapped Kingfisher	*Halcyon pileata*		
Nicobar Collared Kingfisher	*Todiramphus chloris occipitalis*		+
Nicobar Greenbreasted Pitta	*Pitta sordida abbotti*		+
Swallow	*Hirundo rustica*		
Brown Shrike	*Lanius cristatus*		
Nicobar Blacknaped Oriole	*Oriolus chinensis macrourus*		+
Grey or Ashy Drongo *	*Dicrurus leucophaeus*		
Nicobar Racket Tailed Drongo	*Dicrurus paradiseus nicobariensis*		+
Andaman Glossy Stare	*Aplonis panayensis tytleri*		+
Nicobar Hill Myna	*Gracula religiosa halibrecta*		+
Nicobar Paradise Flycatcher	*Terpsiphone paradisi nicobarica*		+
Nicobar Blacknaped Monarch Flycatcher	*Hypothymis azurea nicobarica*		+
Dark Thrush *	*Turdus obscurus*		
Redthroated Pipit	*Anthus cervinus*		
Forest Wagtail	*Motacilla indica*		
Greyheaded Yellow Wagtail	*Motacilla flava*		
Grey Wagtail	*Motacilla cinerea cinerea*		
Nicobar Olivebacked Sunbird	*Nectarinia jugularis klossi*		+
Nicobar Yellowbacked Sunbird	*Aethopyga siparaja nicobarica*		+

Checklist of Mammals of Nicobar Islands

Common Name	Scientific name	Endemicity
Nicobar Leafnosed Bat	*Hipposideros diadema nicobarensis*	+
Indian Flying Fox	*Pteropus giganteus*	
Nicobar Flying Fox	*Pteropus melanotus melanotus*	+
Nicobar Crabeating Macaque	*Macaca fascicularis umbrosa*	+
Nicobar Wild Pig	*Sus scrofa nicobarica*	+
House Rat	*Rattus rattus alexandrinus*	
House Rat	*Rattus rattus holchu*	+
Nicobar Tree Shrew	*Tupaia nicobarica surda*	+

* represents new records to Great Nicobar ,'+' sign indicates yes Source: Tikadar and Das (1985), Pande *et al.* (1991), Rao (1996), Pande *et al.* (1991), Das (1994), Abdulali (1964 & 1967) Ali and Ripley (1983) Sankaran (1995), Grimmett *et al.* (1998) and Sankaran (1998).