COMPARATIVE ECOLOGY OF SYMPATRIC HORNBILLS (BUCEROTIDAE) IN THAILAND

BY

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CHAPTER 1

INTRODUCTION

GENERAL

Hornbills differ from other birds by the following anatomical characteristics; 1) the axis and atlas cervical vertebrae are fused, 2) the bill is surmounted by a casque, even in its simplest form as a low ridge, consisting in a distinct area on the skull that supports special tissue for growing the keratin sheath, 3) the median division of the kidney does not exist, and 4. the lashes on the upper eyelids are long and flattened (Johnson 1979, Kemp and Crowe 1985). Hornbills are presently classified in the families Bucerotidae (arboreal hornbills) and Bucorvidae (ground hornbills) in the order Bucerotiformes (Sibley and Monroe 1991). The name "hornbill" is derived from the fact that on their long curved bills, they are furnished with various forms of casques. The casque which magnifies the already large bill is usually hollow or filled with a spongy cellular tissue. Only the casque of the Helmeted Hornbill is solid and is the source of "hornbill ivory" (Smythies 1960, Kemp 1985) (Fig. 1-1). Due to the lack of under wing coverts hornbills emit a whooshing sound in flight.

There are 54 known species of hornbills distributed in tropical and subtropical regions of Africa and Asia (Kemp and Crowe 1985, Kemp 1988) (Fig.1-2). They are large in sizes varying from 40 to 150 cm in length. The general appearance of hornbills consists of an elongated body with a long neck, a small head and a large bill. The wing is broad and the tail is long. Feathers on the head are loose and voluminous. The legs are short and the toes are syndactyl. The plumage is only pigmented with melanin, ranging in colour from glossy black and white through grey and brown. The bill, casque, bare skin, feet and eyes may be varying from dull to bright colours. Males are usually larger than females and differ in the plumage, form or size of the casque, and colour of the bare skin (Kemp and Crowe 1985).

In Thailand there are 12 known species and two subspecies distributed throughout the country except around the central plain and the northeast (Smythies 1986, Lekagul and Round 1991). The species studied in this thesis are the Great Hornbill Buceros bicornis homrai, Wreathed Hornbill Rhyticeros undulatus, Oriental Pied Hornbill Anthracoceros albirostris albirostris, and Brown Hornbill Ptilolaemus tickelli austeni. The studied species strictly live in the evergreen of mixed deciduous forests which are distributed as shown in Figure 1-7.

In Thailand the forest area has been reduced from the original 80 % to 53 % in 1961, 39 % in 1973, and 25 % in 1978 (Humphrey and Bain 1990). Therefore the ranges of hornbills must inevitably have shrinked in relation to the remaining traces of forests that are suitable habitats because these birds are very sensitive to the fragmentation of habitats (Round 1988). In the following chapters, the results of nine years of study are presented with an emphasis on the following aspects: 1) the characteristics of nest site, nest tree and nest cavity, 2) breeding behaviours, 3) cooperative breeding, 4) food and feeding strategies, 5) home range and territory, and 6) flocking and roosting.

DESCRIPTIONS OF THE STUDIED SPECIES

Buceros bicornis homrai

Great Hornbill

Synonym: Dichoceros Bicornis, Buceros homrai, Buceros cavata.

Distribution: The subspecies ranges in Western Ghats and from Nepal and Bhutan to South China, Myanmar, Thailand and Vietnam (Fig. 1-3). In peninsular Malaysia and Sumatra it is replaced by nominated Buceros bicornis bicornis. A comparison of distribution of Great Hornbills in Thailand in the past (1974) with the latest (1991) is shown in Figure 1-4.

Description: Total length varies from 130-150 cm. Nominated bicornis is smaller (Deignan 1945). A large black and white hornbill with the head, neck, upper breast, vent and thigh are white. The head, side of neck, nape and a part of the white wing bar is painted yellow with preened oil. The face, chin and upper throat are black.

Both sexes look remarkably alike. The bill is long and curved. The anterior and tip of the upper mandible are bright orange whereas, the lower mandible is white. Both mandibles are stained yellow by preened oil as in the plumage. The casque is similar in shape for both sexes, being high and flat at the top and gradually curving forward and ending with two points. The male's casque is black at the junction of the front casque with the upper mandible and at the posterior edge. The female has some red on the rear casque.

The iris is red in males and white in females. The colour of the orbital skin in the male is black and in the female cherry red (Sanft 1960, Wildash 1968, King and Dickinson 1975, Medway and Wells 1976, De Schauensee 1984, Ali and Ripley 1987, Lekagul and Round 1991). (Plate 1-1).

Habitat: This species frequents forests that are both dense evergreen, moist deciduous forests and open park-like forests of scattered oaks from the plain level up to 1,500 m (Baker 1934, Medway and Wells 1976, Smythies 1986, Ali and Ripley 1987 Lekagul and Round 1991). Deignan (1945) found it was a common resident of primeval evergreen forests in northern Thailand.

Rhyticeros undulatus

Wreathed Hornbill

Synonym: *Buceros undulatus*, *Buceros javanicus*, *Buceros niger*, *Buceros annulatus*, *Buceros javanns*, *Buceros pusaran*, *Buceros subruficollis*, *Buceros pucoran*, *Rhyticeros undulatus ticehursti*.

Distribution: This species occurs from Assam to Myanmar, Thailand except central and northeastern parts, Laos, Vietnam, Malay Peninsula, Sumatra, Borneo, Java and Bali (Fig. 1-3). A comparison of distribution of Wreathed Hornbills in Thailand in the past (1974) with and the latest (1991) is shown in Figure 1-4.

Description: Total length reaches 120 cm in males. Two sexes are different. The adult male has the chestnut forehead, crown and nape. The face, side of neck and upper breast are buffy white. The hindneck throughout the rest of plumage (body and wing) are glossy black except for a pure white tail. The female has an entirely black plumage except for a pure white tail. Young birds resemble adults. The fledglings have a plumage resembling males.

The bill of adult and immature birds is ivory white. Fledglings have a greenish pale yellow bill. The casque is low and wreathed. The number of ridges on the casque relates to age as one ridge indicates one year old, but only up to a certain age. On the sides of the bill, both lower and upper mandibles are corrugated extending forward. The number of corrugation or ripples, may also be related to the age of the bird.

The adult male has a bright yellow gular pouch with a black stroke on each side of the pouch. In adult female the gular pouch varies from pale to bright blue, with black strokes on the sides of the pouch. Immature females have a yellowish green gular pouch for a few years before it turns to blue (pers. obs.). Fledglings have a gular pouch resembling those in males but with traces of black strokes on the sides of the pouch (pers. obs.). The orbital skin of both sexes is cherry red (Sanft 1960, Wildash 1968, King and Dickinson 1975, Medway and Wells 1976, Frith and Douglas 1978, Smythies 1986, Ali and Ripley 1987, Lekagul and Round 1991). (Plate 1-2).

Habitat: This hornbill is a forest species which frequents thicker cover of tall trees of evergreen forests, but it is not uncommon to see it in forest where oak tree are common. The species occurs in mixed deciduous forests from plain level up to 2,400 m (Baker 1934, Deignan 1945, Smythies 1986, Ali and Ripley 1987, Lekagul and Round 1991).

Anthracoceros albirostris albirostris

Oriental Pied Hornbill

Synonym: Buceros albirostris, Hydrocissa albirostris, Anthracoceros malabaricus, Anthracoceros coronatus.

Distribution: This subspecies occurs in the Himalayan foothills from Dehra Dun in Bihar through Nepal, Assam, Bhutan, Myanmar, south-eastern China (Yunnan and Guangxi Provinces), Indochina, Thailand to north-eastern areas of peninsular Malaysia along western off shore islands of Mergui archipelago, Phuket, Langawi Tarutau and Pulau Butang (Sanft 1960) (Fig. 1-5). Subspecies convexus occurs from southernmost Thailand through the Malay peninsula to Borneo, Sumatra and Java. A comparison of distribution of Oriental Pied Hornbills in Thailand in the past (1974) with the latest (1991) is shown in Figure 1-6.

Description: Total length varies from 70-89 cm in males; females are somewhat smaller. The colour of the bird is black and white . The outer tail feathers are black with extensive white tips, though the central pair tail feathers are entirely black. The wing tips are white which can be seen clearly in flight.

This species is strongly sexually dimorphic. The male has the bill and casque larger than in the female and different in shape. Both the bill and casque are ivory coloured. The female has black patterns both on the bill and casque, and the male has a larger convex casque compressed anteriorly. A black patch extends from the front top of the casque onto the upper mandible. (Plate 1-3).

Subspecies convexus is different from albirostris in that the outer tail feathers are entirely white. The female has no black pattern on the lower mandible as in the female albirostris. Both sexes have pale chalky blue orbital skins and lower cheek patches. (Frith and Frith 1983, Lekagul and Round 1991).

Habitat This species is common in tall lowland evergreen forests and is sometimes found in open forests from the plain level up to 1,400 m. It is also found in moist-deciduous forests, mixed bamboo and scrub-jungle or in secondary growth. (Baker 1934, Deignan 1945, Ali and Ripley 1987, Lekagul and Round 1991). This is a small hornbill and the most ecological tolerant of all hornbill species (Round 1988).

Ptilolaemus tickelli austeni

Brown Hornbill

Synonym: Anorrhinus austeni, Ptilolaemus tickelli indochinensis.

Distribution: This bird ranges from Assam, to Myanmar, South China, northern and north-central Thailand, Laos and Vietnam (Fig. 1-5). Subspecies tickelli occurs in southwestern (per. obs.), western Thailand and Tenasserim. A comparison of distribution of Brown Hornbills in Thailand in the past (1974) with the latest (1991) is shown in Figure 1-6.

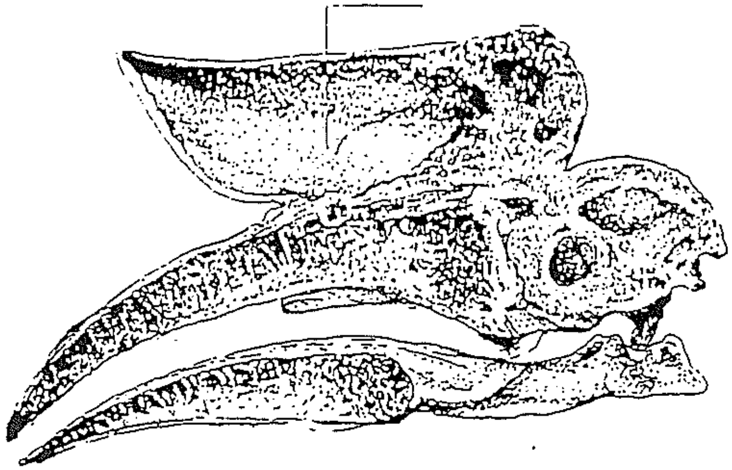
Description: The male is about 75 cm in length. The male has brown upperparts, and the throat especially the side of the cheek and upper breast are white or rufous. The underparts are rufous, but the thigh is buffy white. The primaries and alula are tipped white. The tail feathers are tipped white except the central pair. In the female, the upperparts are similar to the male, but the underparts are more dark brown . Fledglings have plumage similar to the male.

Both sexes have small ivory white bills, but they differ in the shape and size of the casque. The male has a rather long, low and laterally compressed casque and the base of the bill is orange. Female has a small low and arched casque. In immature males, the casque is rather round (pers. obs.). The fledglings have a greenish yellow bill without a casque and the tip of the bill is orange.

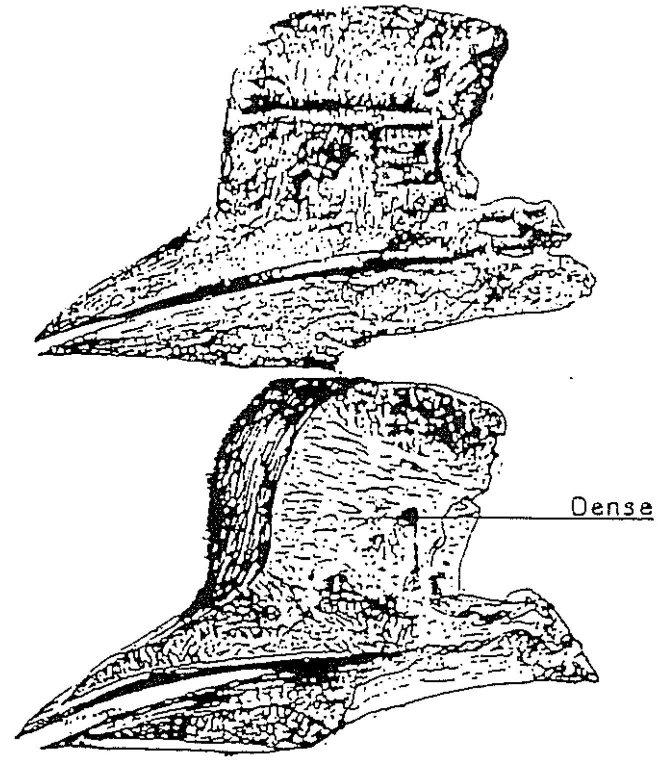
Both sexes possess a pale blue orbital skin. The fledglings have an orange orbital skin. (Plate 1-4).

In subspecies tickelli, the male is slightly different from the male austeni by having a rufous throat, but the female of this subspecies has a dark horny brown bill (Sanft 1960, Wildash 1968, De Schauensce 1984, Smythies 1986 Ali and Ripley 1987, Lekagul and Round 1991).

Habitat: This species is found in the dense evergreen forest of higher hills up to 1,500 m. However, it is not uncommon to see it in the forests of the plains and foot-hills. (Baker 1934, Deignan 1945, Smythies 1986, Ali and Ripley 1987, Lekagul and Round 1991).



Bill and casque of
<u>Bucaros</u> <u>rhinocaros</u>



Bill and casque of
<u>Rhinoolax</u> <u>vigil</u>

Fig. 1-1 Diagram showing the internal structure of two different types of casques. Left, Rhinoceros Hornbill (Buceros rhinoceros), and right, Helmeted Hornbill (Rhinoplax vigil).

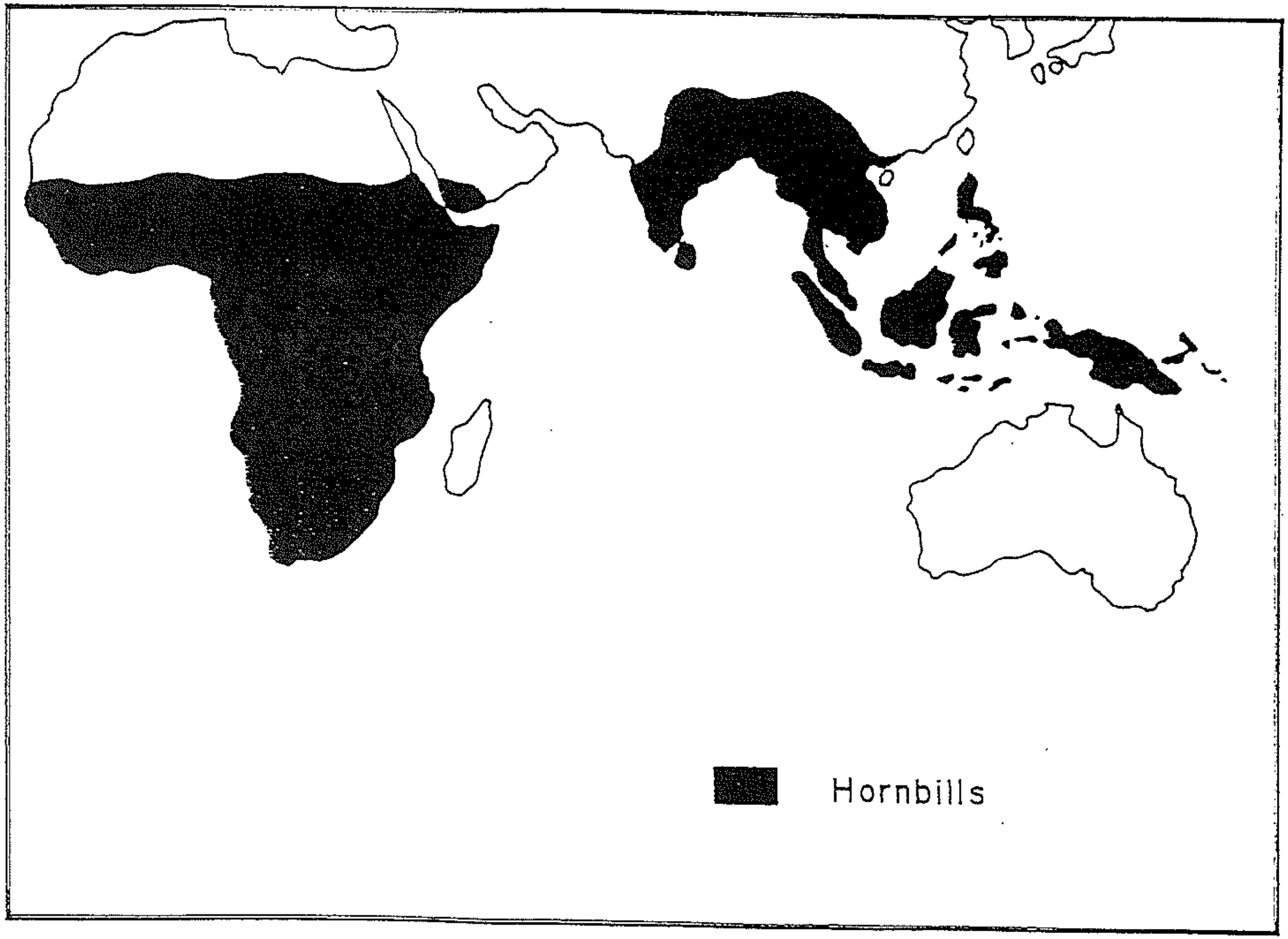


Fig. 1-2 World distribution of hornbills (Kemp 1979).

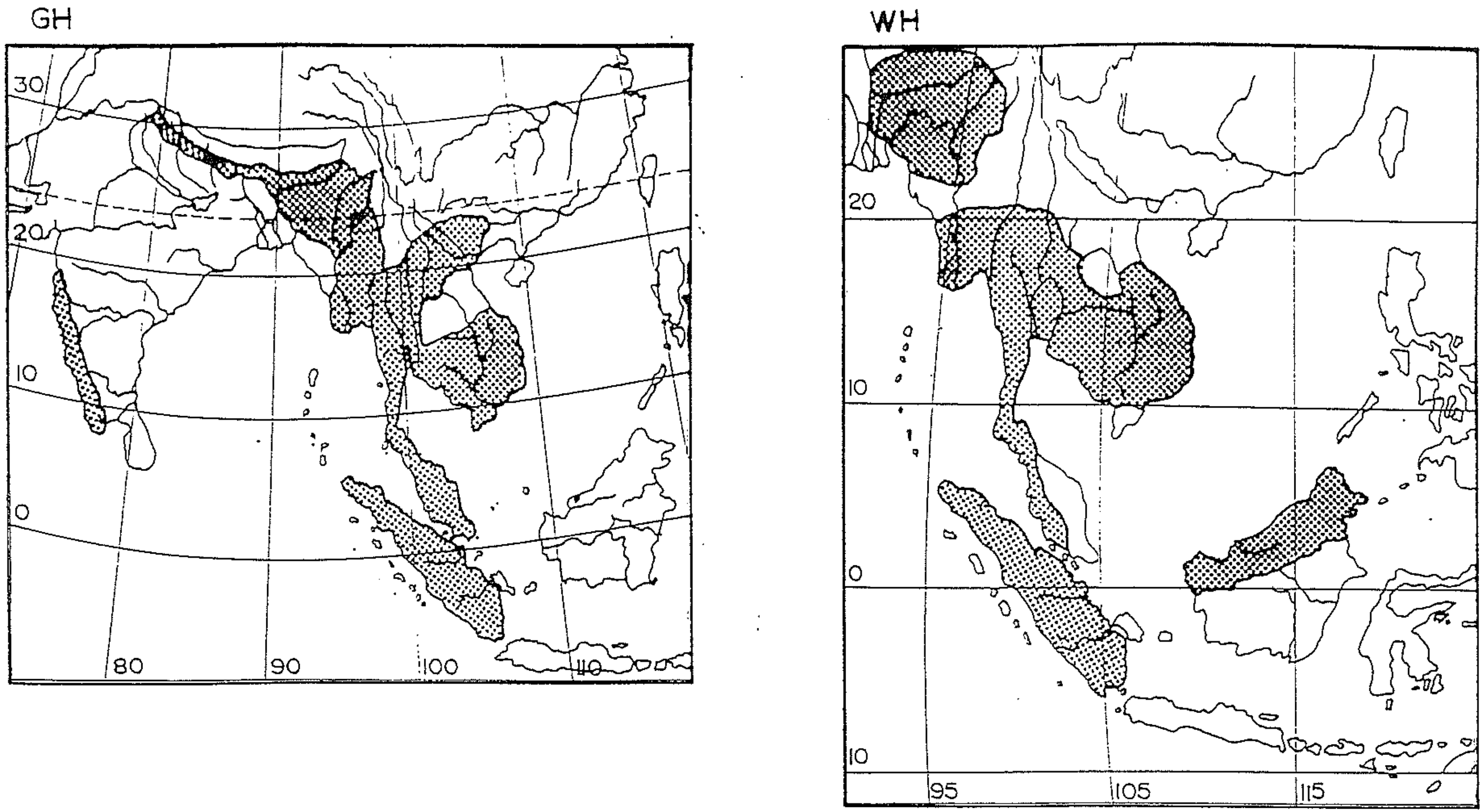


Fig. 1-3 Distribution range of Great Hornbill (GH, _Buceros bicornis_) and Wreathed Hornbill (WH, _Rhyticeros undulatus_) in the south and southeast Asia (Sanft 1960, Ali and Ripley 1987).

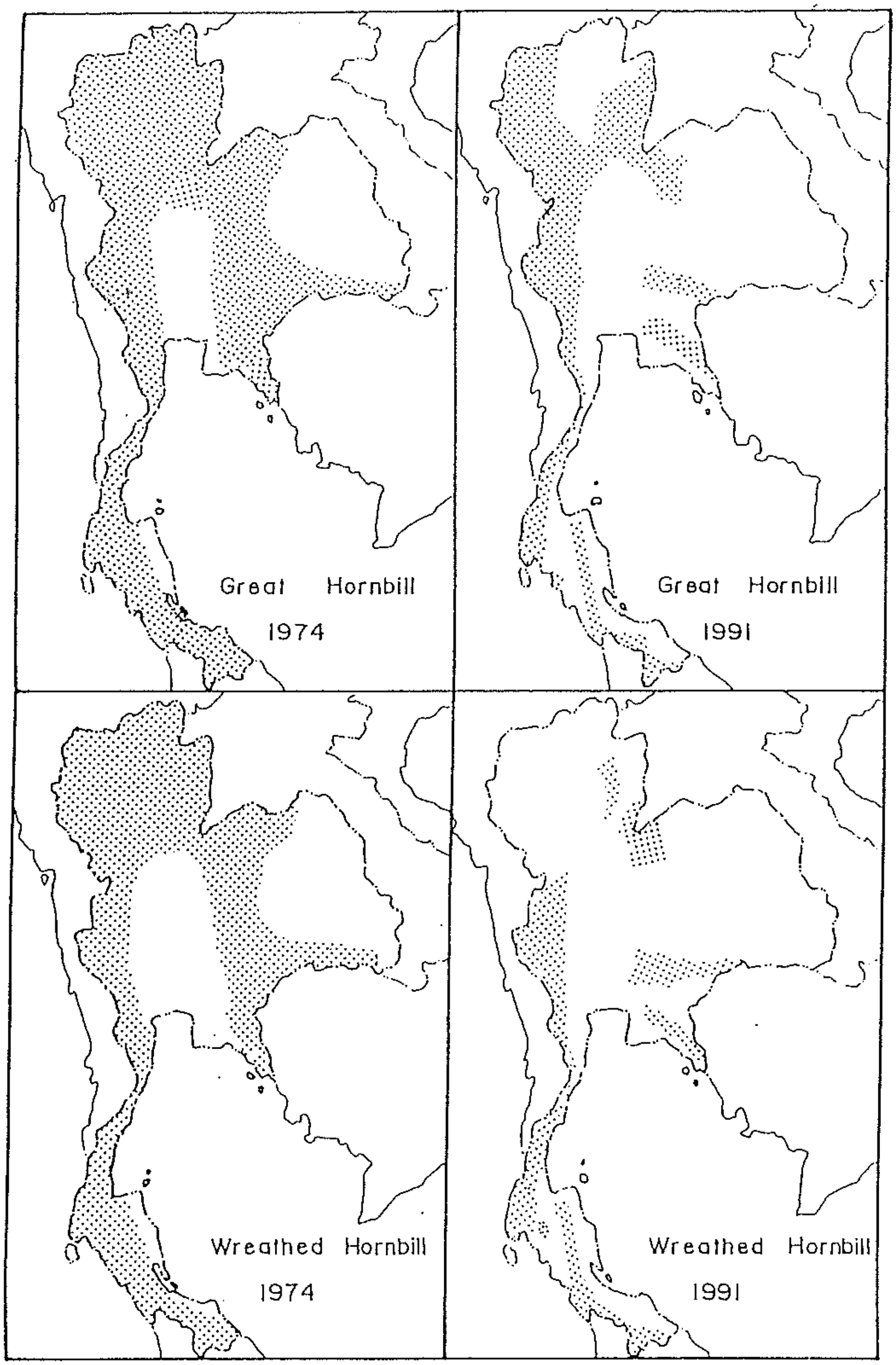


Fig. 1-4 Comparison of distribution of Great Hornbill (<u>Buceros bicornis</u>) and Wreathed Hornbill (<u>Rhyticeros undulatus</u>) in Thailand in the past (1974) (Lekagul and Cronin 1974) with the latest (1991) (Lekagul and Round 1991).

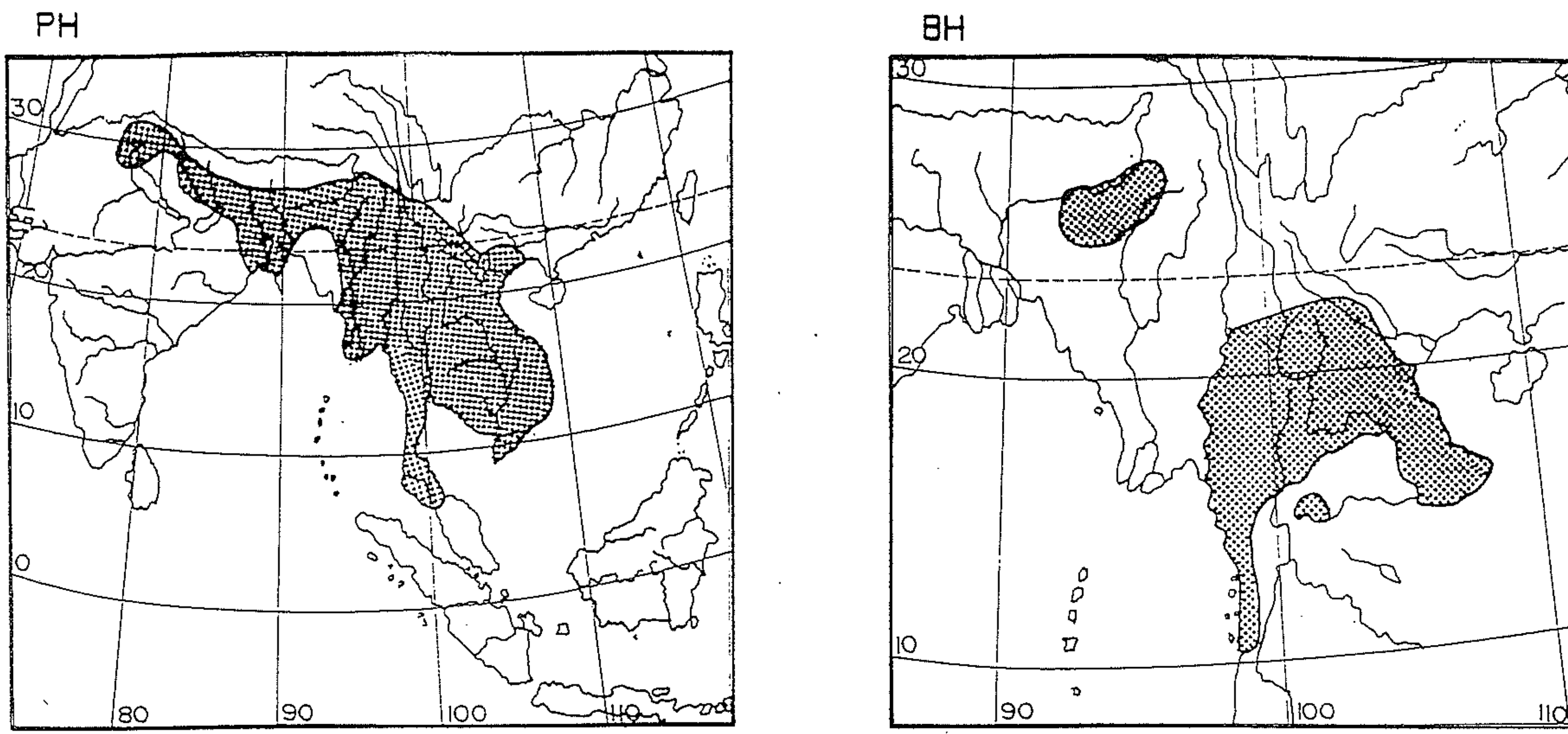


Fig. 1-5 Distribution range of Oriental Pied Hornbill (PH, Anthracoceros albirostris and Brown Hornbill (BH, Ptilolaemus tickelli) in south and southeast Asia (Sanft 1960, Ali and Ripley 1987).

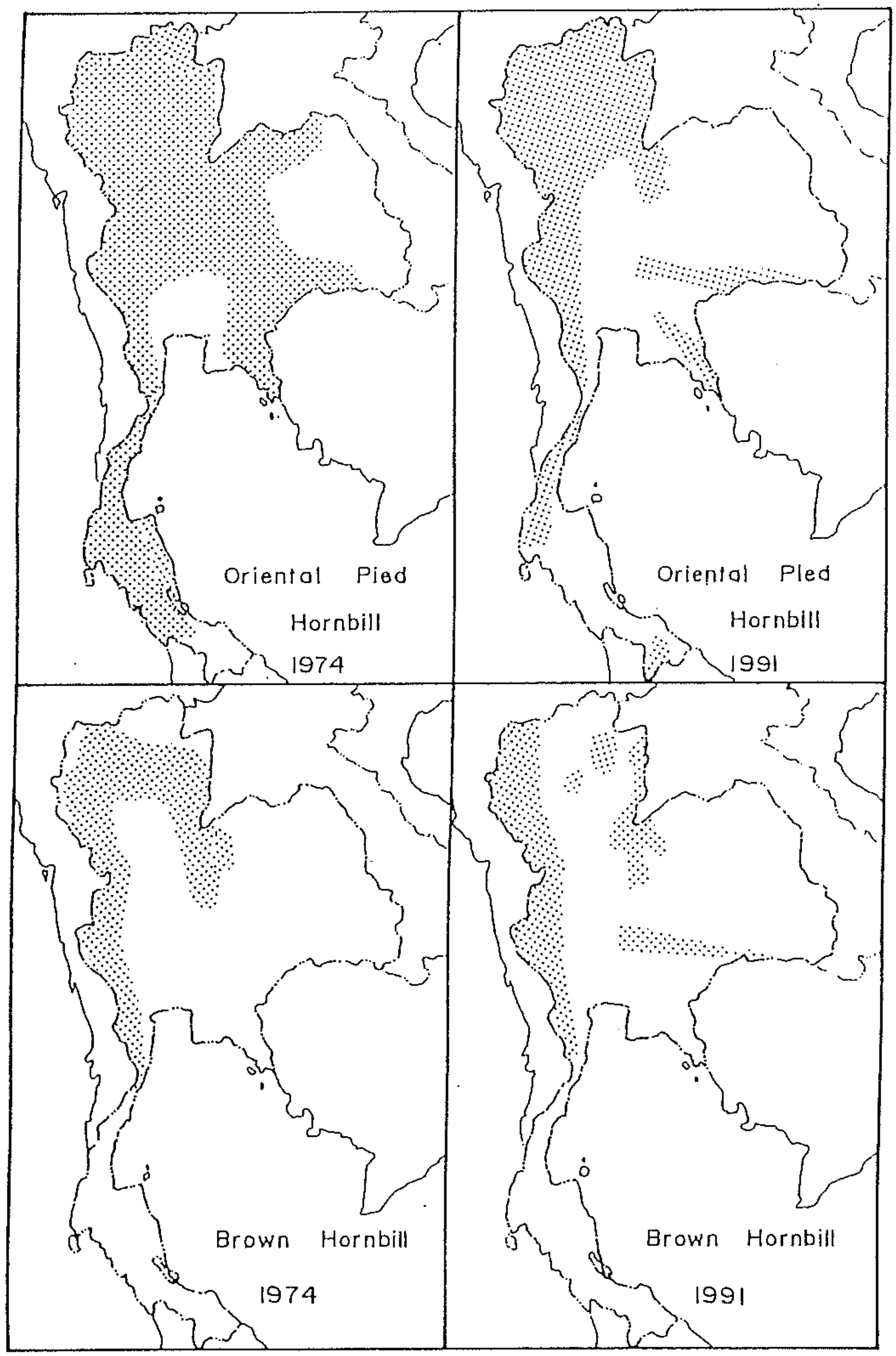


Fig. 1-6 Comparison of distribution of Oriental Pied Hornbill (<u>Anthracoceros albirostris</u>) and Brown Hornbill (<u>Ptilolaemus tickelli</u>) in Thailand in the past (1974) (Lekagul and Cronin 1974) with the latest (1991) (Lekagul and Round 1991).

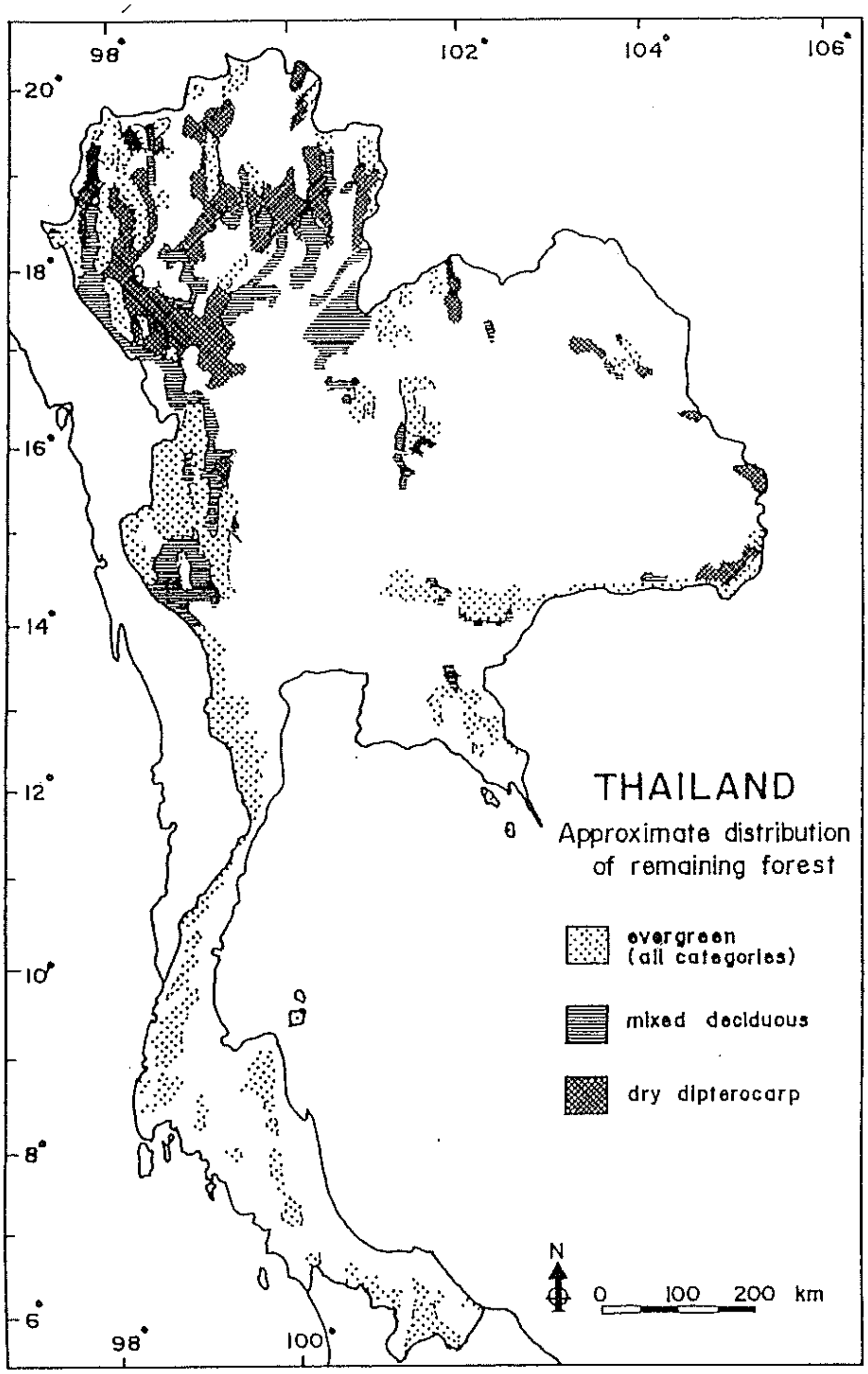
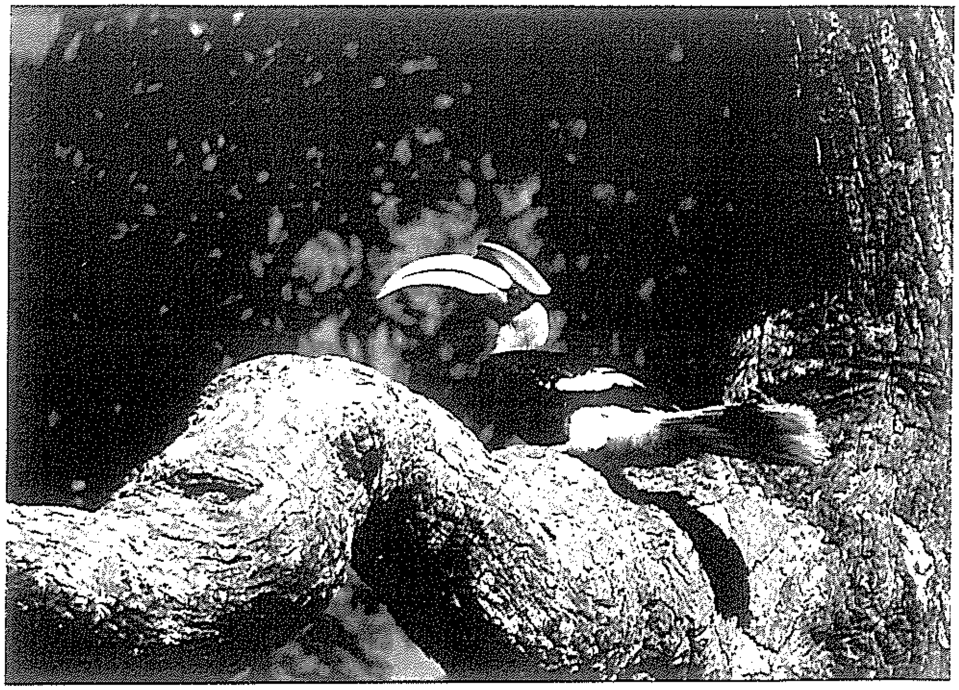


Fig. 1-7 Distribution of the three forest types which are habitats of hornbills in Thailand, especially the studied species from Lekagul and round (1991).

Plate 1-1 Great Hornbill

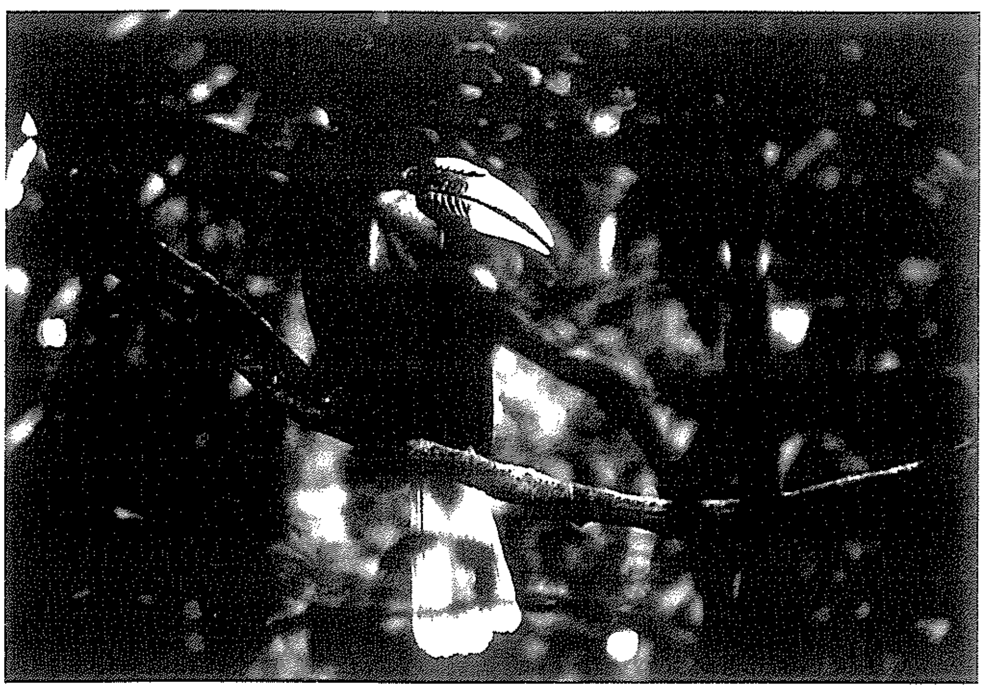


Male

Female

Plate 1-2 Wreathed Hornbill

Male



Female

Plate 1-3 Oriental Pied Hornbill

Male

Female

Plate 1-4 Brown Hornbill

Male

Female

CHAPTER 2

STUDY AREA AND STUDY SITE

GEOGRAPHIC LOCATION OF STUDY AREA

Khao Yai is situated in the eastern Dongrak range of the Korat plateau in central northern Thailand (14° 5'-35' N and 101° 5'-52' E) (Fig. 2-1). Khao Yai was designated as a national park in 1962, and covers an area of 2,168 square kilometers. The park incorporates forest and mountainous sections of Nakhon Ratchasima in the north and the east, Prachin Burin in the east, Nakhon Nayok in the south and Sara Buri in the west (Fig. 2-1) (Smitinand 1977).

PHYSIOGRAPHICAL FEATURES OF STUDY AREA

Except for low undulating land in the east, the park is generally mountainous varying from 250 to 1351 m a.s.l. The major peaks include the summit, Khao Rom (1,351 m), Khao Leam (1,326 m) and Khao Khieo (1,292 m) near the centre, Khao Sam Yot (1,142 m) and Khao Fa Pha (1,078 m) in the north-west, and Khao Kamphaeng (875 m) in the north-east. The majority of the park's area lies between 400m and 800m. The mountains in the north and the east are sloping gently, whereas slopes in the south and the west are steep.

The north-east is bounded by the long, wall-like Khao Kamphaeng, where underlying bedrocks comprise Palaeozoic sediments of the Kanchanaburi series. During the Permian period this was overlain by limestone and shale, forming the

Ratburi series. Granitic and grandioritic instrusions caused the Kanchanaburi and Ratburi beds foldings and uplifts to form mountains that subsequently eroded to form the red sandstone, shale, gypsum and salt Korat series which now forms the western edge of the Korat plateau. However, the substrate in most of the area within the paek comprises eroded rhyolitic flows from more recent volcanic activity (WCMC 1989, NPD 1987).

Soils in the bulk of the park are from the Kabin Buri, Chieng Mai, Chatturat, Korat, Khao Yai and Lam Narai series. These are mostly reddish-brown laterites, characterised by a sandy texture, with a moderate to good drainage and moderate soil fertility. The Pak Chong series soils, comprising a very fine clayey kaolinite of reddish-brown laterites are found to the north of the park and are generally found in deep, well-drained areas , with a high water-holding capacity but only moderate fertility. The Muak Lek series soils, found in the north and east, are loamy skeletals of non-calcic brown soils. This series is well-drained, shallow, of low fertility and highly susceptible to erosion (WCMC 1989, NPD 1987).

The forests in the park are watersheds for four major rivers, with an annual run-off discharge of about 1,889 million cubic meters. The Nakhon Nayok river covers a watershed area of 660 square kilometers in the west and south, Prachin Buri river covers 1,122 square kilometers in the south, east and the central regions, Lam Thakhong river covers 201 square kilometers in the north and around the park's headquarters, and Lam Phra Phloeng river covers a watershed area of 114 square kilometers in the north-east (WCMC 1989, NPD 1987).

VEGETATION IN STUDY AREA

The vegetation in Khao Yai is highly diverse. There are five types of forests in the park (Fig. 2-2):

1) **Dry mixed deciduous:** This type of forest occurs in the north-west between 400-600 m a.s.l. Typical tree species include Afzelia xylocarpus, Pterocarpus macrocarpus, and Lagerstroemia calyculata. The ground cover is composed of Bambusa arundinacea and several varieties of grasses.

2) **Dry evergreen forest:** This type of forest occurs along the east between 100-400 m a.s.l. and cover 26 % of the park area. The upper stories are composed of Dipterocarpus alata, D. turbinata, Shorea henryana, S. roxburghii, Hopea odorata and Tetrameles nudiflora. Understoried species include Aglaia sp., and Areca triandra. The ground cover is composed of plants belonging to the families Marantaceae and Zingiberaceae.

3) **Wet evergreen forest (tropical rain forest):** This type of forest covers more than 60% of the park area and it is found between 400-1000 m a.s.l. In the lower areas the vegetation is similar to the dry evergreen forest, but more members of Dipterocarpaceae trees are found. The canopy is typically three-storied with many epiphytes. Important canopy species include D. alata, D. gracilis, D. costatus, and Schima wallichii (Plate 2-1). The understory comprises

Lithocarpus annamensis, and Quercus fleuryi. The ground flora is similar to that of the dry evergreen forest but denser.

4) Hill evergreen forest: This type of forest is found on the mountain tops above 1,000 m a.s.l., where dipterocarps are replaced by gymnosperms Podocarpus sp., Lithocarpus sp. and Quercus sp.

5. Savanna and secondary growth: These types exist due to previous human settlements. It covers about 5% of the park area. Prevalent grass species include Imperata cylindrica, Neyraudia reynaudiana and Saccharum spontaneum. Some common secondary tree species are Hibiscus macrophyllus, Macaranga denticulata, etc. (Smitinand 1968, 1977).

CLIMATE IN STUDY AREA

The park experiences both the south-west and north-east monsoons and the distribution of rainfall is influenced by topography. The mean annual rainfall at the headquarters is 2,270 mm. The south and a limited area in the north-east tend to be wetter, with more than 3,000 mm in the Klong Tha Dan basin, below Khao Khieo and Khao Rom. The extreme west and south-east are driest areas with the mean annual rainfall of 1,600 mm.

Most precipitations fall during mid-May to October from the south-west monsoon, with an annual mean of 1,917 mm falling during this period at the Park's headquarters. The driest months are December and January when the average rainfall of the month is only 15 mm. The mean annual temperature is 23° C, up to 28° C in April and May and down to 17° C during December and January (NPD 1987). Climate zones of the park showing the temperature and precipitation are presented in Figure 2-3.

BIRDS IN STUDY AREA

Khao Yai supports a great diversity of birds. A total of 318 species have been recorded, most of these seen in the vicinity of the headquarters (CDC 1989). The bird fauna of Khao Yai is mainly composed of those lowland and submontane birds, which have fairly wide altitudinal ranges.

Some typical resident species inhabiting the evergreen forest of the headquarters area include the Silver Pheasant Lophura nycthemera, Vernal Hanging Parrot Loricurus vernalis, Green-billed Malkoha Phaenicophaeus tristis, Mountain Imperial Pigeon Ducula badia, Collared Scops-Owl Otus lempiji, bulbuls (including Pycnonotus jocosus, Criniger pallidus), Red-headed Trogon Harpectes erythrocephalus, barbets (including Megalaima faiostricta, M. incognita and M. asiatica), Golden-backed woodpecker Chrysocolaptes lucidus, Long-tailed Broadbill Psarisomus dalhousiae, Blue-winged Leafbird Chloropsis cochinchinensis, Asian Fairy Bluebird Irena puella, and four species of hornbills.

Khao Yai is a place for migratory birds, most of which are visitors from the north and inhabit the park from October to April. Among those migrants include the Haircrested Drongo *Dicrurus hottentottus*, Forest wagtail *Dendronanthus indicus*, Blue Rock Thrush *Monticola solitarius*, Black-naped Oriole *Oriolus chinensis*, and etc.

Common birds of prey are the Crested-serpent Eagle *Spilornis cheela*, Mountain Hawk Eagle *Spizaetus nipalensis*, and sparrow hawks (*Accipiter* spp.) (Kutintara and Pongumpai 1982, CDC 1989).

STUDY SITE LOCATION

The study site is situated in the north west of the park (approximately 14° 15'-30' N; 101° 20'-24' E) with an altitudinal range of 400-1,060 m a.s.l. The study site is crossed by Thanarat road which divides the study site into two sections, the east and the west (Figs. 2-2 and 2-4).

VEGETATION IN STUDY SITE

The study site is mainly covered with primary forests (about 60 square kilometers) described as tropical rain forest or wet evergreen forest and grassland and secondary growth (about 10 square kilometers). The forest consists of woody trees, woody climbers and vines. The upper story includes *Dipterocarpus baudii*, *D. gracilis*, *D. dyeri*, *D. costata*, *D. macrocarpus*, *Choerospondias axillaris*, *Eugenia* spp., *Podocarpus nerriifollius*, and strangling fig trees (*Ficus* spp.). The middle story includes *Polyalthia viridis*, *Gironniera nervesa*, *Slonea sigun*, and *Knema elegans*. The ground cover incluides *Strobilanthes cystolithigera*, *Calamus* spp., and plants of Zingiberaceae (Smitinand 1968, Treesucon 1984). The topographical distribution of forests and grasslands within the study site is shown in Figure 2-5.

CLIMATE

There was no weather station to collect climate data at the study site while this study was conducting. However, the climate data from nearby station (Nakhon Ratchasima Station) of Meteorological Department are available. Monthly precipitation, temperature and relative humidity of ten years are presented in Figure 2-6.

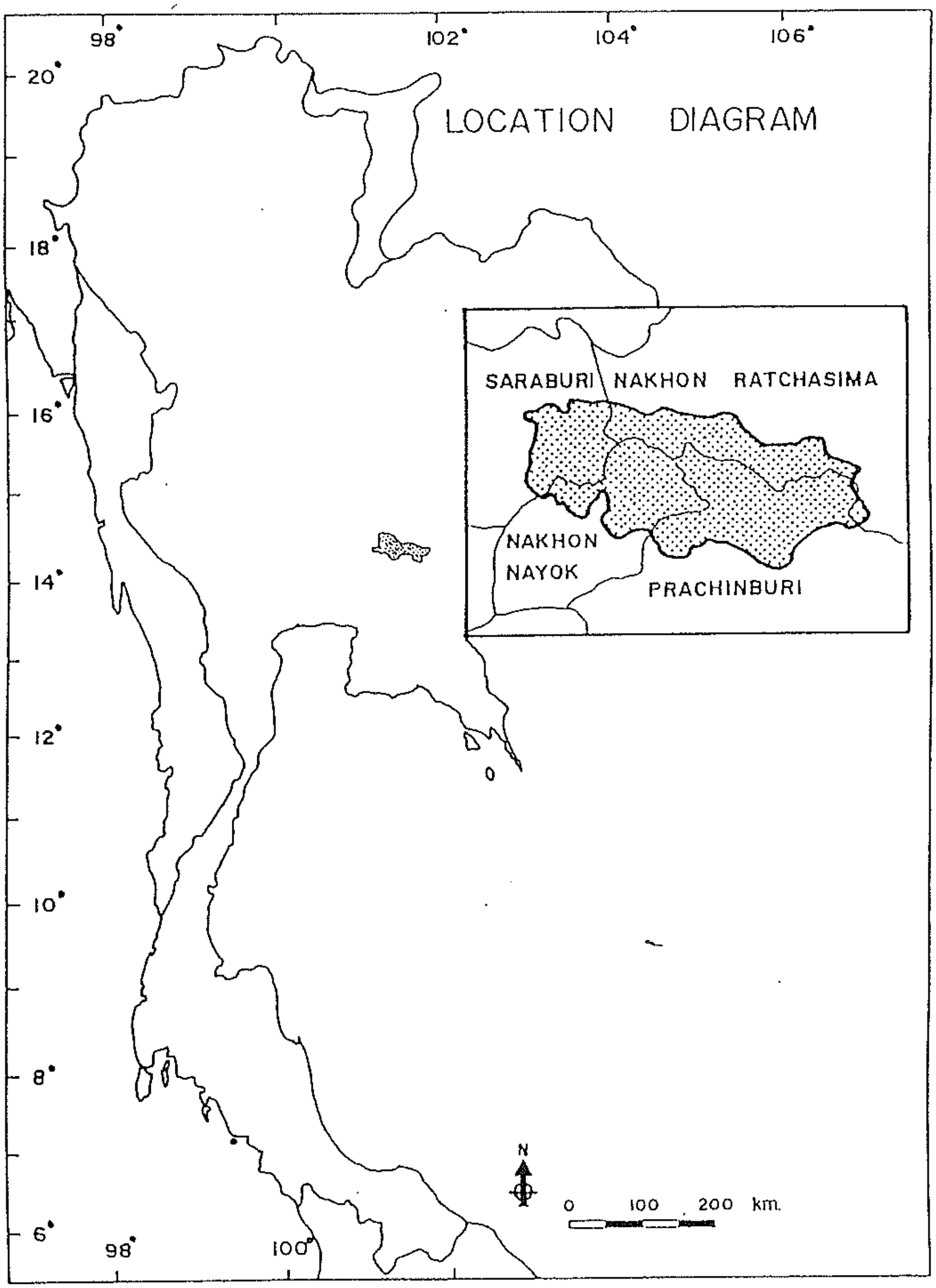


Fig. 2-1 Map showing location and boundaries of Khao Yai.

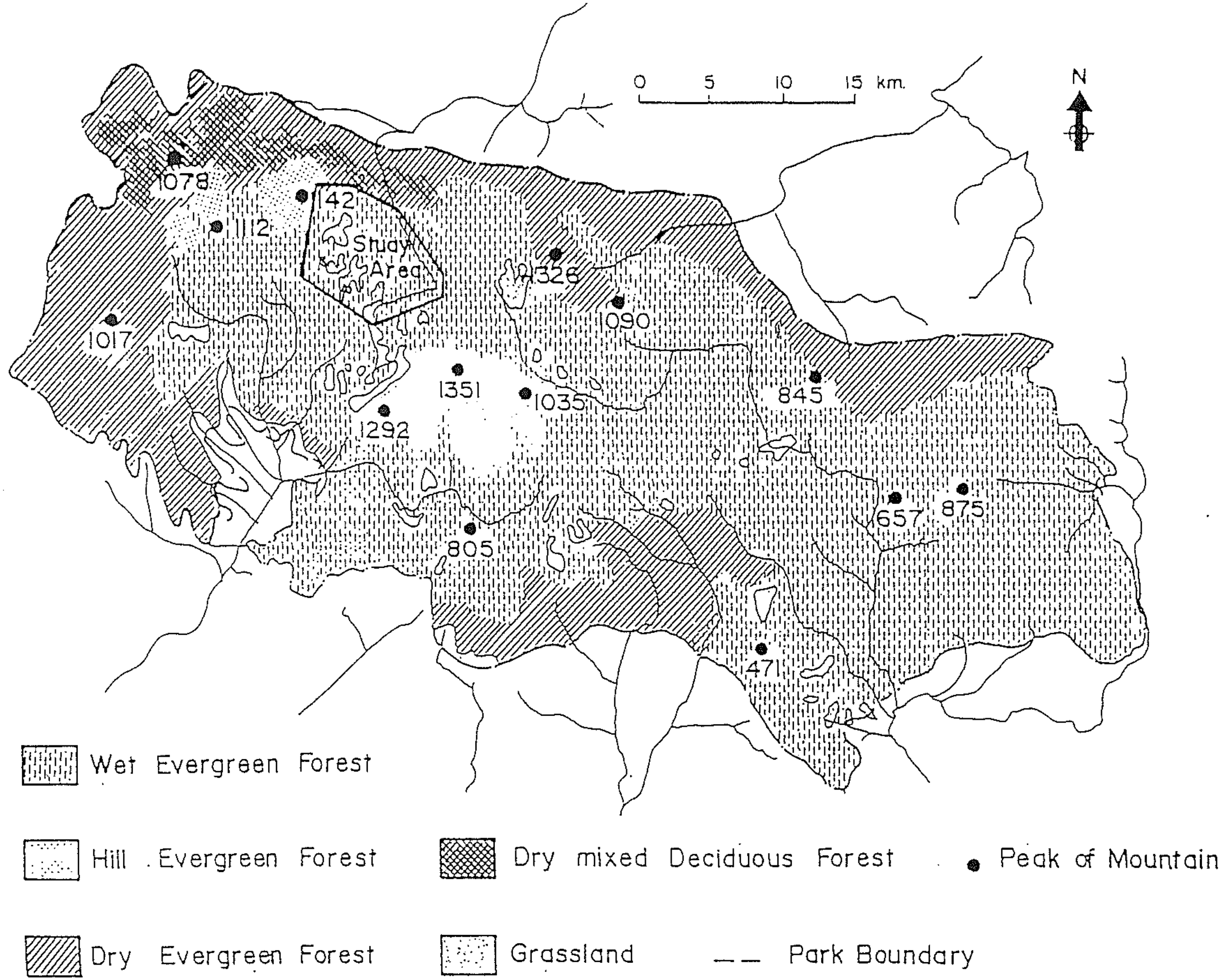


Fig. 2.2 Distribution of vegetation types and mountai[illegible]

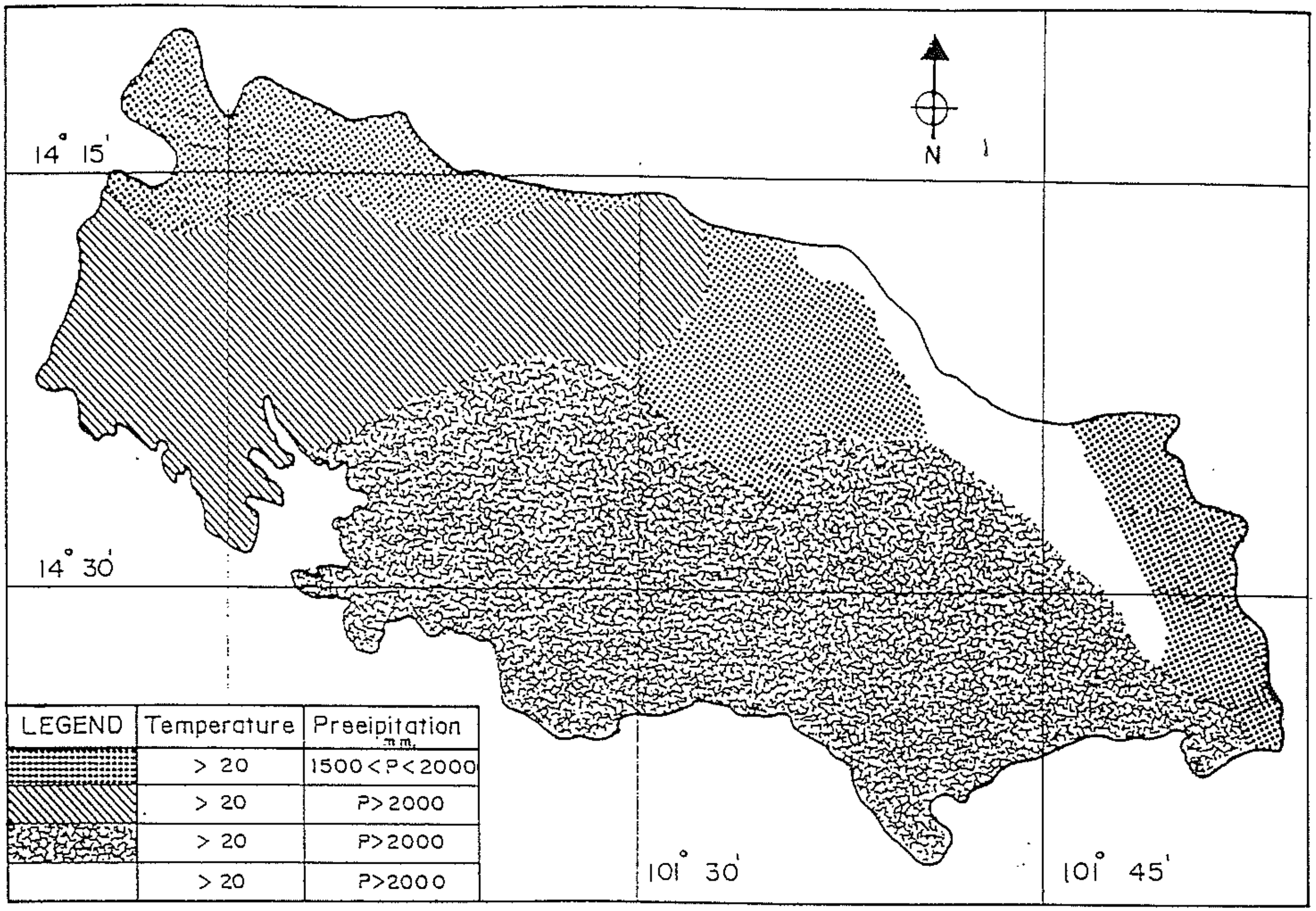


Fig. 2-3 Diagram showing zones of climate for temperatures and precipitation in Khao Yai.

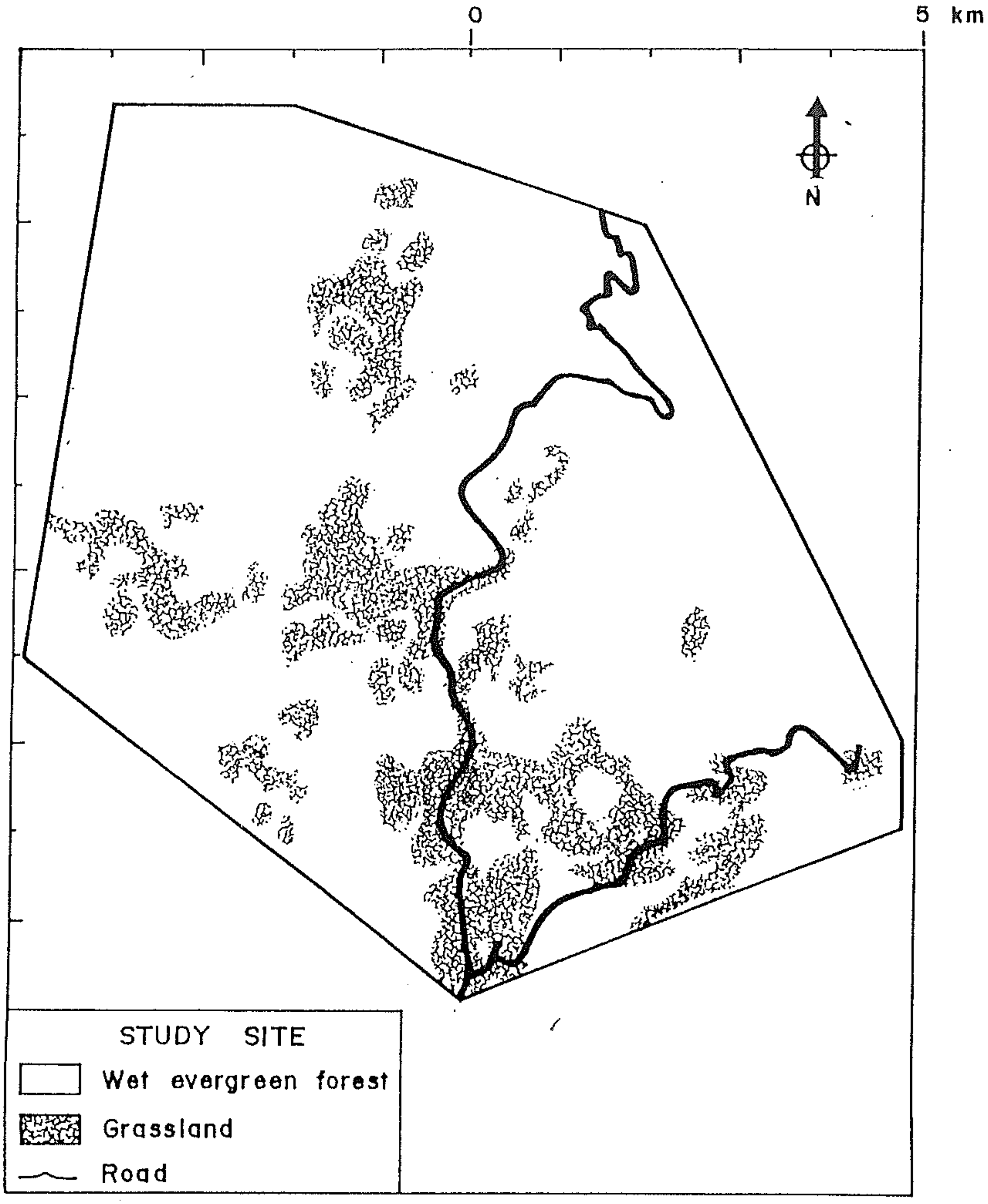


Fig. 2-4 Distribution of forest areas and grassland within the study site.

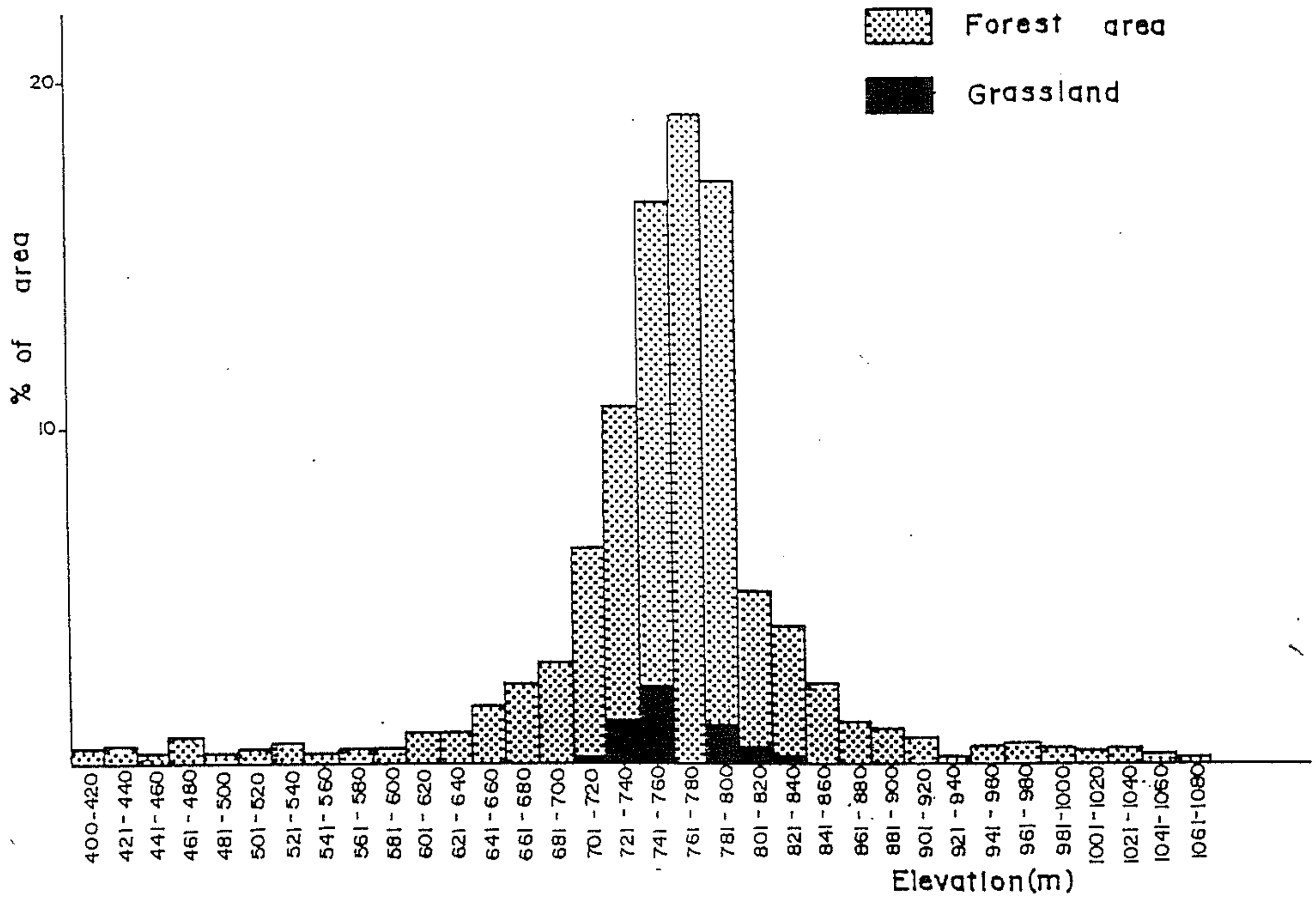
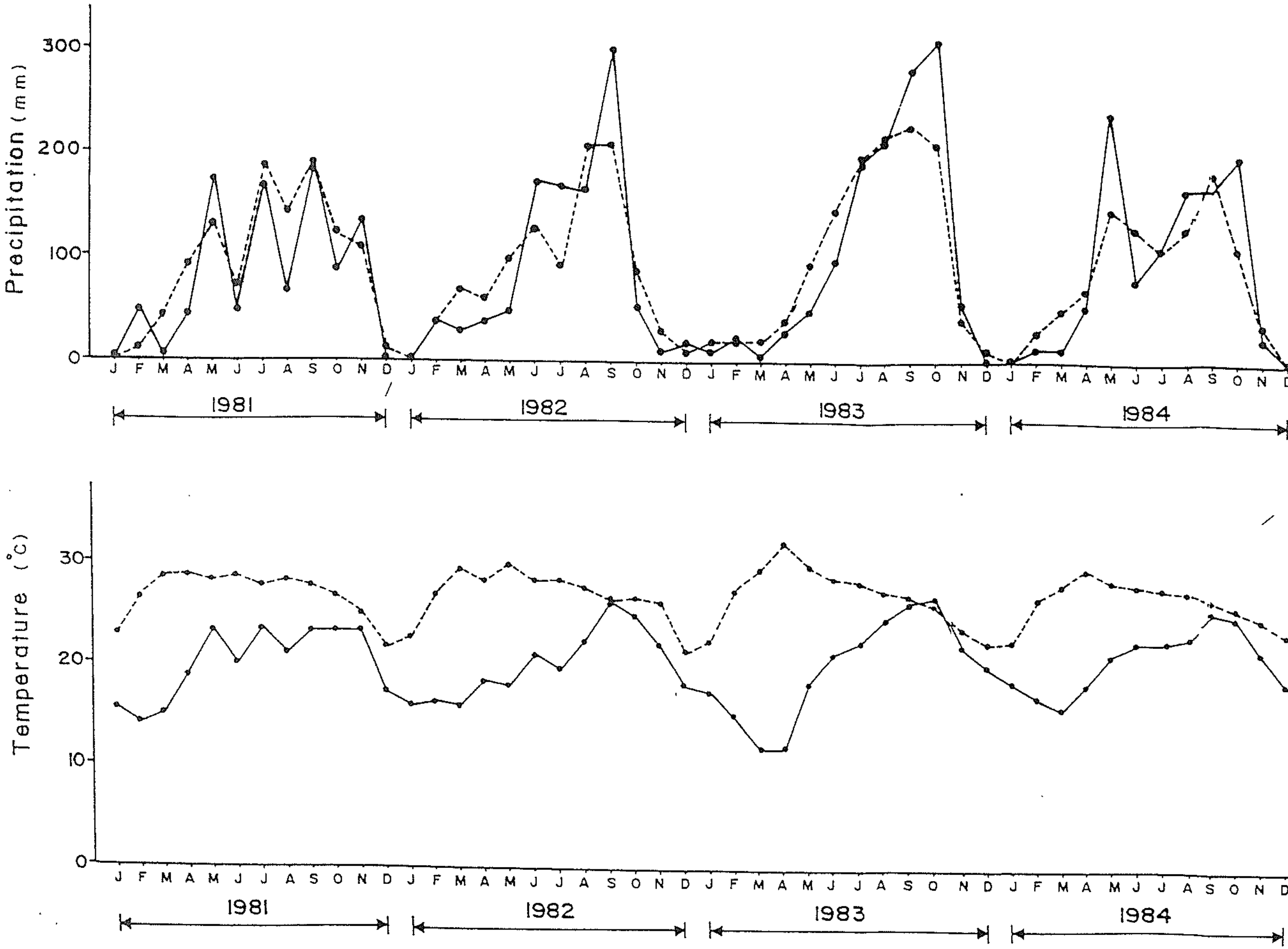
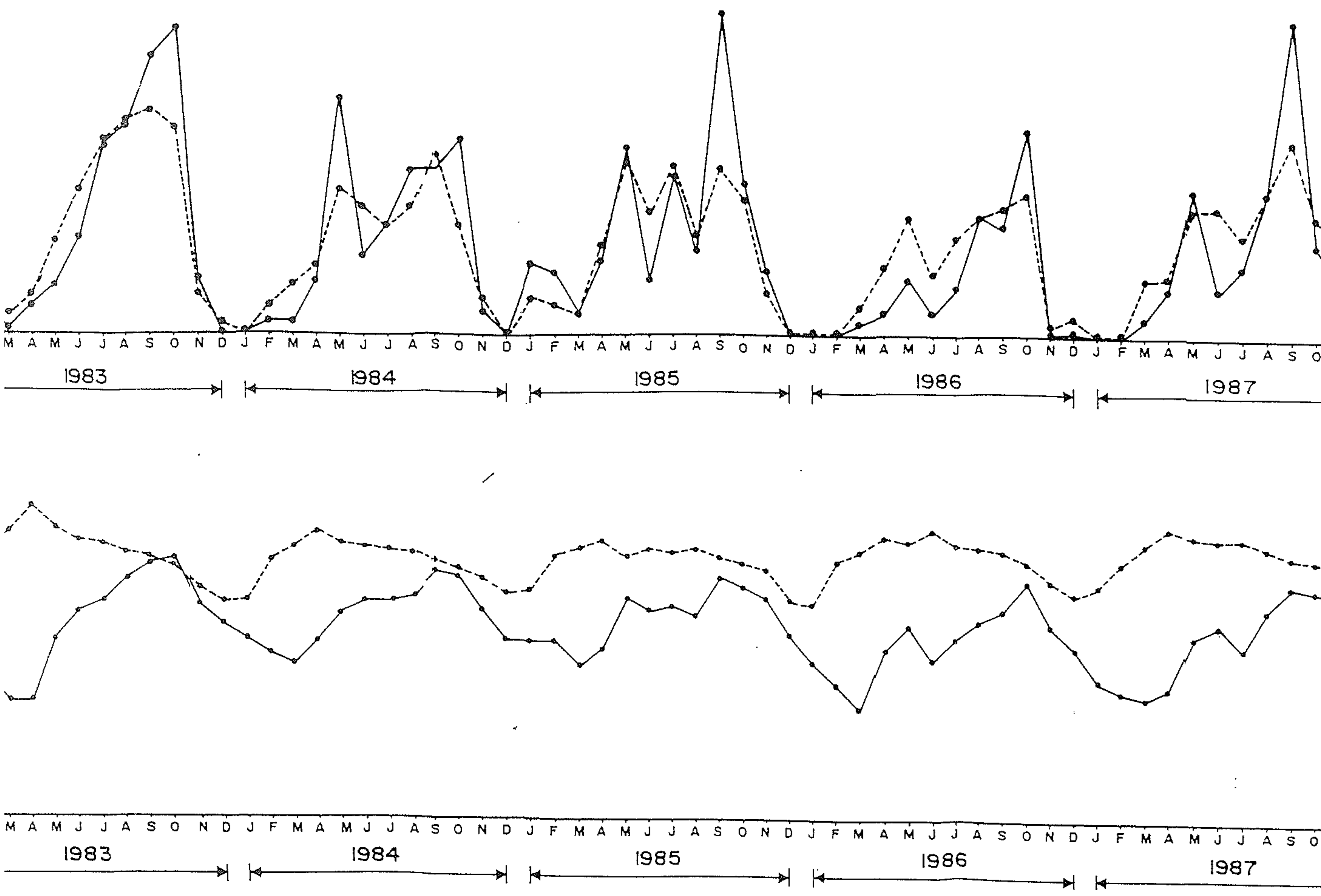


Fig. 2-5 Distribution of forests and grasslands at various altitudes.



Precipitation (mm)
0
100
200
300
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982
1983
1984
Temperature (°C)
0
10
20
30
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1981
1982
1983
1984


M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1983
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1983
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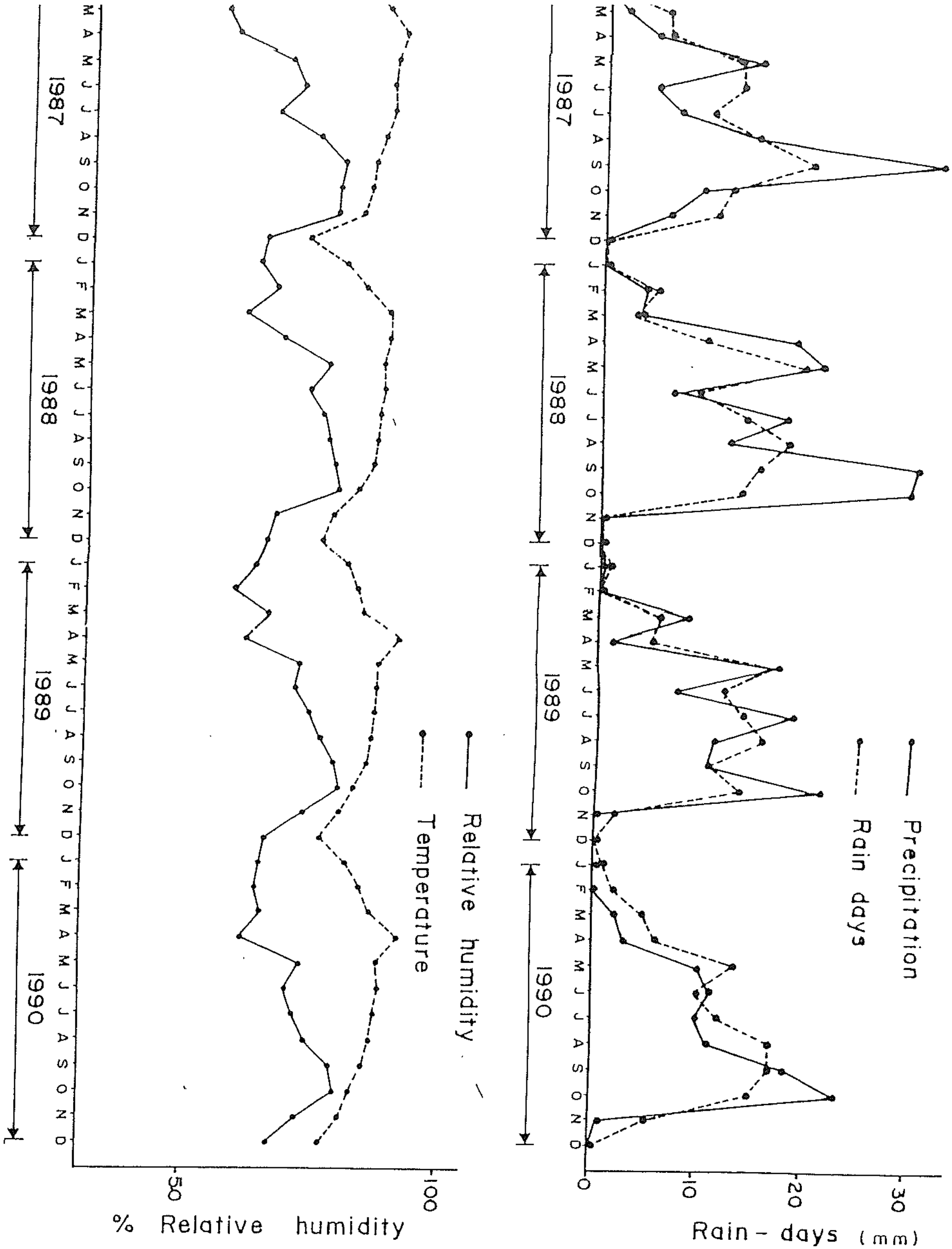


Fig. 2-6 Monthly data of precipitation, rain days, temperature, and relative humidity during 1981-1990 period measured at Nakhon Ratchasima

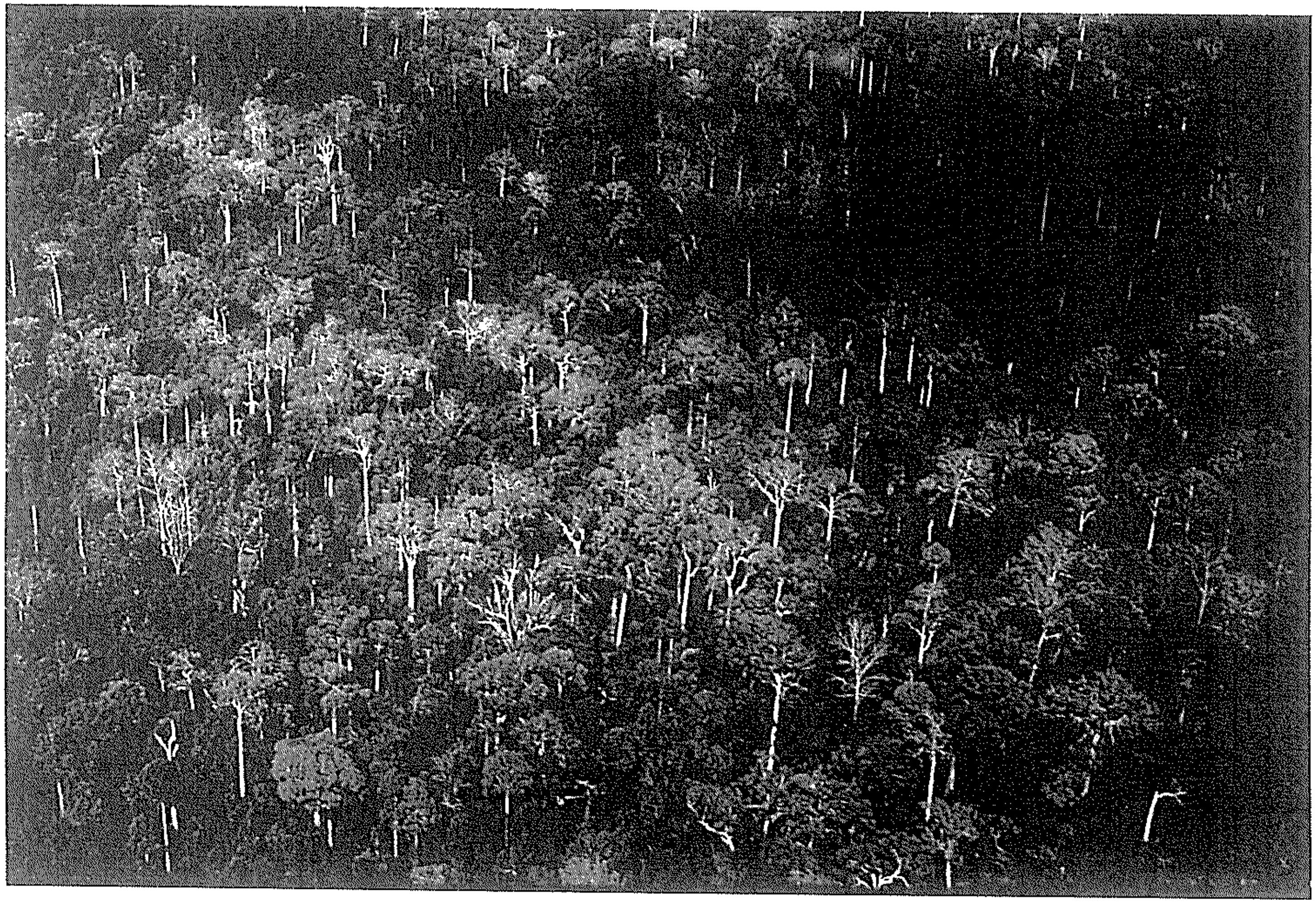


Plate 2 – 1 Habitat of hornbills at Khao Yai.

CHAPTER 3

NESTS OF HORNBILLS

INTRODUCTION

A nest is a special structure forming a place or receptacle in which the eggs and young develop. Nests are essential for most animals (Collias and Collias 1976) and were developed in accordance with evolution to help the parents meet the needs of the young. Nest types give important clues to the life of species because nests represent the essential requirements for reproduction and are thus directly relevant to the ecology (Collias and Collias 1984).

Hornbill nests are classified as one of the four categories described by Collias and Collias (1984) based on the evolutionary level and function as a place for incubating eggs, i.e. in an enclosed preformed cavity. Cavity-nesting has evolved in birds at virtually every stage of evolution. Early use of natural cavities was followed by special modification of the cavity. Cavity-nesting provides the shelter and energy conservation (Kendeigh 1961). According to Nice (1957) cavity-nesting birds are more successful in fledging their young than open nesting birds.

The shelter and safety provided by cavities, however, usually result in intense intra-and interspecific competition these cavities are limited in supply (Collias and Collias 1984). Aggressive competition for tree holes have been a profound force in the evolution of different size-classes among such birds as woodpeckers, corresponding to the different size entrance holes typical of each species (Collias and Collias 1984). The competition for nest cavity forces the European Nuthatches (Sitta europaea) plaster the hole entrance with mud to a smaller size so that the European starlings (Sturnus vulgaris) can not pass through. The nest entrance sealing behaviour in hornbills may have evolved along with the competition for nest cavity as well as with avoiding predators.

Hornbills are unable to excavate their own nest cavities as do other birds such as woodpeckers and barbets. They therefore must use available cavities in trees. The availability of nesting cavities of appropriate size, especially in forests disturbed by humans, could be an important population limiting factor.

The four species of hornbills studied, the Great, Wreathed, Oriental Pied, and Brown hornbills, inhabit a wide range of forest type habitat (Baker 1927, Deignan 1945, Medway and Wells 1976, Ali and Ripley 1987, Smythies 1986, Lekagul and Round 1991). A few information is available as to the nest site, nest tree, and requirements for nest cavity of each species, beyond the attempts to study quantitatively on nest trees and nest characteristics by Poonswad et al. (1987) and Liewviriyakit (1989). Madge (1969) described one nest cavity of the Bushy-crested Hornbill Anorrhinus galeritus in peninsular Malaysia.

Hussain (1984) briefly described the characteristics of two nests of the Narcondam Hornbill *Rhyticeros narcondami* on Narcondam Islánd in the Indian Ocean. Ali and Ripley (1987) reported of the use of trees in two genera, *Calophyllum* and *Cullenia*, by the Great Hornbill in South western India and Baker (1927) noted the Oriental Pied Hornbill in Burma (Myanmar) nested in trees of genera *Bombax*, *Lagerstroemia*, and *Dipterocarpus* Poonswad *et al*. (1987) reported several genera of nest trees used by hornills in Khao Yai such as *Dipterocarpus*, *Eugenia*, and *Cinnamomum*.

The information on nest site, nest tree species and nest cavity characteristics are very important for the prediction of future breeding success and population status of hornbills, hence management and conservation of these birds, would differ in different geographic regions and in different habitat types.

In this chapter, the nest site, nest tree and nest cavity characteristics of the four sympatric species of hornbill in Khao Yai are examined.

METHODS

Nest site and anecdote of nest cavity

Nest trees of all hornbill species were located either by following lone males from feeding sites or by inspecting large trees with visible cavities (Poonswad *et al* 1983). Active nests could be confirmed by the deposits of droppings, accumulations of nest debris, and seed regurgitates. All nest trees were then plotted on a contour grid map (1:50,000). The nests discovered between 1981 and 1991 (except 1986 and 1987) were monitored for use by hornbills or other animals as well as for their conditions.

The height of the nest tree was recorded and the position of the nest cavity in the forest strata was investigated using the classification proposed by Liewviriyakit (1989), i.e. top or the emergent layer (>25 m), the middle layer (15-24 m) and the lowest layer (4-14 m). Whether the nest cavity was in the tree trunk or in a branch was also recorded.

Nest density, distribution and aggregation

A total of 54 plots each of which is 1 Km^2, were established on the grid map (1:50,000). The area plotted includes grassland areas as well. Nest cavity located in each plot was counted regardless of current use. And the first occupant specie was identified for further analysis. The density, relative density, percentage frequency, and degree of aggregation were calculated as follows.

$$\text{Density} = \frac{\text{No. individuals}}{\text{Unit area}}$$

$$\text{Relative density} = \frac{\text{No. individuals of a species}}{\text{Total no. of individuals of all species}} \times 100$$

$$\text{\% Frequency} = \frac{\text{No. of sample plots where a species occurred}}{\text{Total no. of sample plots}} \times 100$$

For testing the degree of aggregation or clumping of nests for each species and all species in total, σ^2/x was modified from Zar (1984) (random distribution is expected when σ^2/x is close to 1.0 and aggregation is expected if σ^2/x exceeds 1.0).

Nest spacing

The distances between all nearest-neighbour nests, either of the same or different hornbill species, discovered during 1981-1985 were estimated and analyzed from the nest locations as located on the grid map (1:50,000). The distances were obtained by measuring the distance between the nests of the focus species to the nearest nests of the same species and to the nearest nests of the other three species. For example, a Great Hornbill nest no. 24 (G24) had G13 as its nearest-neighbour at a m, Wreathed nest no. 6 (W6) as nearest-neighbour at b m, Oriental Pied nest no. 18 (P18) as nearest-neighbour at c m, and Brown nest no. 12 (B12) as nearest-neighbour at d m. The focus nest and species were then changed until complete for all nests of all four species.

Nest tree and nest cavity characteristics

Once discovered, each nest tree was identified to genus or species. The diameter at breast height (dbh) is measured with a measuring tape. The height of the tree and of the nest cavity was measured using a Haga's Hypsometer. The shape and size of the nest entrance were determined from photographs and sketches (Fig. 3-1). The photographs were taken with a 35 mm camera equipped with 500 mm lens and measurements were made on the known image size at the film plane and the angle of coverage by the lens and distance from the camera to the nest entrance. The vertical dimension (VL) of the nest entrance was:

$$L = 0.048\ D(L'/B')(1/\cos\theta^2).$$

where L is the actual VL of the nest entrance, D is the distance between the camera and the nest tree, L' is the vertical length measured in the photograph, B' is the width of the photograph (Fig. 3-1 a & b), θ is the angle between the camera pointed at the nest against the horizontal (Fig. 3-1c). The horizontal dimension (HL) of the nest entrance was:

$$W = 0.07D\ (W'/C')(1/\cos\theta),$$

where W is the actual HL of nest entrance, W' is the nest entrance width measured in the photograph and C' is the width of the photograph.

The relative shape index of the nest entrance was obtained by dividing HL by VL (HL/VL).

The diameter of the nest tree at the height of the nest cavity (dnh) was occasionally measured directly, but at other times it was estimated by proportional comparison with the dbh. The orientation of the nest entrance was determined with a compass. A mean angle of orientation of each hornbill species was calculated from a method described by Batschelet (1981).

Interior dimensions of nest cavities were measured whenever possible. The dimensions measured were the depth from nest entrance to the opposite wall (D), the width between the rest two side walls (W), the height of the ceiling from nest floor (H), and the depth of the floor from the lower edge of nest entrance (F) (Fig. 3-2).

The nest cavities of each hornbill species were numbered in the order of discovery. If a nest was used by a different species in subsequent years, the cavity was allotted a second number in the sequence of the second species. For analysis of the characteristics of nest trees and nest cavities, such nests were included in the data for each species. The repeated data were only excluded if the nest was used by a different pair of the same species or when the total account was analyzed.

Study of physical environment of nest cavity and nest site

Inside nest cavity : A digital thermo-hygrometer was used to measure the temperature and humidity inside two nest cavities in living trees and those on the ground. The thermo-hygrometer has sensor probes of 1.5,20 and 50m in length. The 1.5 m cord probe was used on the ground, the 20 m cord probe was installed inside a Brown Hornbill nest (B13), and 50 m cord probe was installed inside a Great Hornbill nest (G9).

At the Great Hornbill nest : Measurements were made between 14 December 1991 and 6 May 1993. Every seven days measurements were taken at every hour between 7:00 and 17:00 hours and compared with the ground data obtained simultaneously. In addition, measurements was taken at one hour interval for 24 hours. This measurement was performed once a month in February, March and April 1993.

At the Brown Hornbill nest : Measurement were carried out between 3 January and 20 March 1992 in the same manner as at the Great Hornbill nest but with a 5 - 14 days interval.

There were some difficulties in obtaining data at these nest due to damage to the probes caused by the female hornbills and very high humidity inside the nest cavity.

Gradient of temperature and humidity in the forest habitat: Ambient measurements were recorded every 5 m above the ground to a height of 35 m along the tree trunk at about 7:00, 12:00 and 17:00 once a week between 6 July 1991 and 22 May 1993.

Abundance of potential large trees for nesting

A census of large trees was carried out in the forest throughout the study site. Three hundreds and two line demarcated 0.1 ha plots were laid along the east and west of the study site. The distance between lines was 250 m and the distance between plots was 400 m (Fig. 3-3a). All trees with a dbh greater than 40 cm (the minimum size used by nesting hornbills, see Poonswad et al. 1987) were counted and measured. Because the majority of nest trees belong to the genera Dipterocarpus and Eugenia (Poonswad et al. 1987), the large trees were then grouped into three categories for further analyses: Dipterocarpus, Eugenia and other trees. No attempt has been made to study altitudinal distribution of large trees.

Species composition of large trees

An investigation of species composition of large trees was carried out in a five square kilometer sector of the forested area located in the eastern side of the road which runs through the study site. Two hundred and fifty lines demarcating plots (each 0.1 ha) were laid within this area along east-west direction. The distance between lines was 250 m and the distance between plots was 100 m (Fig. 3-3b). All trees with a dbh greater than 40 cm were identified, counted and measured. Tree heights were also recorded.

RESULTS

Anecdote of nest cavity

A total of 80 nest trees were discovered during the 1981-1991 breeding seasons (except 1986-1987). The distribution of these nest trees is shown in Figure 3-4. The number of nests discovered each year is given in Figure 3-5. The discovery rate was highest in 1984 for all hornbill species and tended to decrease afterwards. The history of nest cavities used by hornbills and sometimes by other animals is shown in Appendix 3-1. It was found that competition for 29 nest cavities occurred and resulted in the changes of occupants (Appendix 3-1, see also Table 4-4 in Chapter 4). Twelve nests were used by more than one species or pairs in different year (Table 3-1 and Appendix 3-1).

The latest distribution of active nests is shown in Figure 3-6. Twenty six nest trees were lost during this study period due to various causes as shown in Table 3-2. Distribution and location of natural broken and poacher-cut nest trees is shown in Figure 3-7. The most important cause of nest loss was natural breakage, with an especially high damage rate in the Oriental Pied Hornbill nests.

Among 14 broken nest trees 50 % (7 trees) of these may have been broken in years 1986 and 1987. The breakage of nest trees as found in 1988 occured most likely in 1987. This could be related to thunderstorms occurred in the previous year, particularly in 1987 (Fig. 3-8).

Nest sites

The nests of all hornbill species were distributed in all three forest layers: top, middle and lower layers (Fig. 3-9). However, hornbills tended to select nests in the forest strata according to their body sizes. Statistical tests showed that the larger species (Great and Wreathed hornbills) preferred to nest in the middle and top, layers whereas the smaller species (Oriental Pied and Brown hornbills) nested in the middle and lower layers (χ^2 = 7.98, df = 2, P < 0.05). The highest number of nests (37 nests or 44.6 % of the total) of all hornbill species was found in the middle layer. The middle layer seemed to be the optimal nest site choice for the larger species and the suboptimal nest site choice for the smaller species. Among the 17 nests found in the top layer, 7 nests were used by Great Hornbills and 6 nests were used by Wreathed Hornbills amounting to 76.5% of the tatal. The Oriental Pied Hornbill seemed to have a wider preference for forest layers than in other three species (Fig. 3-9).

The majority of hornbill nests were found between 700 - 800 m a.s.l (79 % of total 80 nest trees). The altitudinal distribution of the nests are given in Table 3-3. There was a considerable overlap among the four species in the altitudnal distribution of nesting sites. However, Brown Hornbill seemed to favour higher altitudes and the Oriental Pied Hornbill lower (Mann-Whitney U-test, U = 92.0, $n1$ = 15, $n2$ = 29, P< 0.01).

Nest density, distribution and aggregation

Within fifty two plots of 1 Km^2 size, 75 nests were counted. These plots included patches of grassland. The density of nests of all four species was 0.98 nests per square kilometer, the nest density of Great Hornbills being highest (Table 3-4). Totally, nests of all species were aggregated (σ^2/x = 1.98, Table 3-3). The nests of only the Wreathed Hornbill were clearly distributed randomly, whereas those of the other species were found to be aggregated (Table 3-4).

Nest spacing

Greater nest spacing may occur intraspecifically, whereas different species can nest close to each other. The closest distance between two Great Hornbill nests was about 200 m. The closest distance between Great Hornbill nests and nests of any of the other three species was found to be as small as 30 m.

In general, as shown in Table 3-5 intraspecific nest spacing is significantly greater in the larger species (Great and Wreathed hornbills) than in the smaller ones (Oriental Pied and Brown hornbills). As for example the Great to the Great nest distances were greater than the Oriental Pied to the Oriental Pied nest distances ($t = 2.18$, $df = 47$, $P < 0.05$). Likewise, the Wreathed to the Wreathed nest distance was greater than both the Oriental Pied to the Oriental Pied and the Brown to the Brown nest distances ($t = 2.6$, $df = 34$, $P < 0.05$; $t = 3.39$, $df = 22$, $P < 0.05$, respectively). However, the Great to the Great nest distance was not significantly different from the Brown to the Brown. This confirmed the finding that the nests of the two smaller species studied were aggregated.

On the other hand, the intraspecific nest distances neither between two larger species nor between two smaller species were significantly different ($t = 1.4$, $df = 35$, $P > 0.05$, $t = 0.42$, $df = 22$, $P > 0.05$, respectively) (Table 3-

5). When considering the nearest-neighbour distance of species in the columns of Table 3-5 and Figure 3-10, statistic test showed differences in mean distance between nearest-neighbour nests which indicate that; Great Hornbills significantly avoided to nest close to the other Greats, but were able to nest close to the other species and at relatively similar distances ($F_{3,73}$ = 4.51, $P < 0.01$); Wreathed and Oriental Pied hornbills could become nearest-neighbours at similar distances to any focus species ($F_{3,73}$ = 0.959, $P > 0.05$ and $F_{3,73}$ = 0.812, $P > 0.05$, respectively) and oppositely, Great and Brown hornbills tended to nest close to each other but, on the other hand, significantly nested farther from other species ($F_{3,73}$ = 3.77, $P < 0.05$).

The number of nests of nearest-neighbour species to each focus species is shown in Table 3-5. No significant difference was found in the number of nearest-neighbour species nests to any focus species (Table 3-6). The Great Hornbill had the Oriental Pied Hornbill as the favourite nearest-neighbour species and vice versa. But the Wreathed Hornbill had neither the Wreathed nor the Brown hornbills as the nearest-neighbour species (Table 3-6). This indicated that the Wreathed Hornbill also avoided to nest close to each other as well as avoided to nest close to the Brown Hornbill (Table 3-5 in row).

Nest trees

The nests of the four hornbill species in the study site were found in 80 trees belonging to at least 13 genera

(Table 3-7). All nest cavities found were in living trees except for one nest of the Oriental Pied Hornbill, which was found in a dead tree of *Dipterocarpus* sp. All nests were in tree trunks except for one nest of the Wreathed Hornbill that was found in a large branch of a *Dipterocarpus* tree in 1984 (the branch broke in 1989).

The sizes (dbh) and heights of nest trees and the statistical tests for significant differences among different hornbill species are shown in Table 3-8.

It was obvious that the larger hornbill species used larger tree than the smaller ones, but they did not always use taller trees. Only the Wreathed Hornbill significanly used taller nest trees than the Brown Hornbill, but the differences in heights of nest trees for the rest of hornbill species were not statistically significant.

Nest trees were grouped into 3 categories, i.e. *Dipterocarpus*, *Eugenia*, and other trees (Table 3-9). The data strongly indicated that hornbills preferably selected *Euqenia* and *Dipterocarpus* trees for nesting, but there were no differences among the four hornbill species as to nest tree choice in these tree groups (Table 3-9).

Nest trees of genera *Dipterocarpus* and *Eugenia* had dbh significantly larger than other trees and the first genus was taller than either *Eugenia* or other trees (Table 3-10). *Eugenia* trees were significantly found at higher altitudes than the others (Table 3-10). Among 73 nest trees examined 14 nests (19.2 %) were located at a height of 25 m or

Nest cavity characteristics

As mentioned earlier, hornbills can not excavate their own nest cavities. All four species, however, were observed pecking the cavity entrance, removing old plaster, and scraping the rotting wood inside the cavity. In no case, however, hornbills could enlarge the nest entrance by pecking fresh wood by more than one cm.

A summary of nest cavity characteristics and statistical differences between the four hornbill species is presented in Table 3-8. There were significant differences among the four species in mean heights of nest cavity and nest tree, which tended to possitively correlate with the body size (Table 3-8). The Oriental Pied Hornbill, however, tolerated a wide range in heights of nest cavities (Fig. 3-9). The nest heights were significantly and possitively correlated with tree heights ($r_s = 0.803$, $n = 75$, $P < 0.001$) and with tree dbh ($r_s = 0.326$, $n = 73$, $P < 0.05$), hence, a high nest cavity was found in a large and tall tree. There was also significant correlation between VL and dbh ($r_s = 0.33$, $n = 59$, $P < 0.05$). This indicates that the greater vertical dimension is found at the larger size tree. There were no significant correlations between VL and any other variables nor between HL and tree height ($r_s = -0.06$, $n = 65$, $P > 0.05$; $r_s = 0.05$, $n = 65$, $P > 0.05$; $r_s = 0.23$, $n = 59$, $P > 0.05$; $r_s = 0.21$, $n = 65$, $P > 0.05$; $r_s = 0.08$, $n = 65$, $P > 0.05$, respectively).

The mean relative shape index of nest entrances and statistic tests are given in Table 3-8. The mean relative shape indices for all species were different from 1.0 (round entrances). Great Hornbills tended to use nests with vertically elongated entrances, whereas the other species tended to use nests with wide or close to round entrances (Table 3-8 and Appendix 3-2). Females of five Great, four Wreathed, two Oriental Pied and four Brown Hornbills were observed to enter the nest with struggle. Hence, they used as small dimension of nest entrance as can be. There were no correlations between relative shape index and nest heights, tree height and dnh (r_s = 0.158, n = 63, $P > 0.05$; r_s = 0.01, n = 63, $P > 0.05$; rs = 0.17, n = 58, $P > 0.05$, respectively).

Over the years there have been considerable changes in the shape of nest entrance (Appendix 3-2). Most nest entrances became narrower with years, whereas only in a few nests they were enlarged (G22, WS, B8).

Dimensions of interior nest cavity of all four hornbill species are given in Table 3-12.

Hornbills showed no specific nest entrance orientation. The distribution and mean angle (Ø) of nest entrance orientation of all four hornbill species are shown in Figure 3-12. By ANOVA there was no significant difference among the mean angles of nest entrance orientations of these four hornbill species ($F_{3, 79}$ = 0.02, $P > 0.05$).

Physical environment

Before the imprisonment (see Chapter 4) period, the temperatures inside the nest cavity and on the ground were more or less the same and relatively stable, although the relative humidity was slightly different (Fig. 3-13). After the female was imprisoned there was only slight difference between the temperatures inside nest cavity and on the ground. This pattern was similar in both Great Hornbill (G9) and Brown Hornbill (B13) nests.

The temperature inside nest cavities was constant for 24 hours, whereas on the ground, the temperature slightly changed during the day time except in April which when it was found high but constant through 24 hours (Fig. 3-14). The means of twenty-four hour temperatures inside the nest cavity were 21.9° C in February, 25.6° C in March and 26.9° C in April. The mean temperatures on the ground were 19.1° C, 23.3° C and 21.6° C for the respective month. Relative humidity was different by the hour during the day time both inside the nest cavities and on the ground. But in April the humidity was uniformly high both inside the nest cavities and on the ground.

The gradients of temperature and humidity inside the forest showed no differences as a function of the height from 0 - 35 m above the ground (Fig. 3-15) as well as no differences neither during the breeding season nor the non-breeding season (Fig. 3-15). Hence, this evergreen forest regulates quite a constant condition throughout the year.

DISCUSSION

Nest sites

Hornbills in Khao Yai have a limited choice in their selection of nest sites due to their inability to excavate their own nest cavities. The wider altitudinal range of nest sites in the two smaller species, the Oriental Pied and Brown hornbills, can be explained partly by a wider habitat selection in the presence of competitors (Rosenzweig 1991). The four hornbill species in the study site live sympatrically and there are overlaps in timing of the onset of breeding (Chapter 4), although the two larger species usually begin breeding about one month earlier than the two smaller species (Poonswad et al. 1987). Therefore, competition may be avoided by nesting at relatively lower or higher altitudes than the larger species which already had established their nesting.

Among the four species, the nests of the Brown Hornbill were located relatively lower to the ground (Baker 1927, Ali and Ripley 1987) and those of the Wreathed Hornbill relatively higher. The nest height preferences may be related to their feeding strategies and daily activities. Brown Hornbills feed less on fruits (60% of total diet) and most daily activities are performed in the middle and lower stories. Wreathed Hornbills on the other hand, feeds almost entirely on fruits (95 % of total diet) the main food being fig which needed to obtain from the higher canopy. (Poonswad et al. 1987, Liewviriyakit 1989).

The presence of the smaller hornbill species seems to have little influence on the larger ones, but the presence of larger ones may force the smaller ones to be more restrictive in their habitat use. This type of competition is known as "asymmetrical competition" (Lawton and Hassell 1981). However, it will be important to examine whether the distribution of food and large trees influences the altitudinal distribution of the nests. This should be useful as an indicator to predict the distribution of nest sites of a particular species in an area. Unfortunately, there is no study on altitudinal distribution neither of large trees nor of food trees.

Factors which may have an effect on intraspecific nest spacing are (1) the difference in the breeding onset between the larger and the smaller species, the larger hornbills began nesting earlier than the smaller one, (2) the degree of nest aggregation which is lower in the larger species than in the smaller species, and (3) dominant behaviours, which are most easily observed in Great Hornbills that are able to nest close to any species except to conspecific.

Nest trees

In the present study hornbills (tend to) nest in the trunks of living trees and such the cas was observed by Madge (1969), Kemp (1976), Hussain (1984) and Poonswad *et al*. (1987). There were reports of the use of dead trees by Oriental Pied Hornbills (Baker 1934) and one Southern Pied Hornbill *Anthracoceros albirostris convexus* in a dead

Koompassia exelsa in peninsular Malaysia (Pan 1987, see Frith and Frith 1983 for the scientific name of the Southern Pied Hornbill). It would be interesting to know whether hornbills prefer to nest in living or dead trees if suitable cavities are available. The use of dead trees by the Oriental Pied Hornbills may be an indication of a shortage of suitable nest sites. Unfortunately, there was no observation on the differences of physical environments between cavities in living and dead trees. The essential conditions for egg incubation are proper heat, humidity, oxygen, and carbon dioxide pressure (Drent 1975, McFarland 1981). It may be postalated that optimal conditions, are avialable in cavities in living trees through chemical reaction processes, such as respiration or photosynthesis. The measurements of the temperature inside the nest cavities in living trees showed a considerably constant condition and the constant temperature may also provide the regulation of other factors necessary for egg hatching (McFarland,1981). Relatively high humidity in a living tree may prevent the eggs from losing much water which is one of the most important conditions for egg hatchability (Drent 1975).

In Khao Yai, hornbills tended to select the largest and tallest trees, and also tended to prefer trees of genera *Dipterocarpus* and *Eugenia*. The followings are the possible reasons for these choices.

1. Hornbills seem to be attracted by tall and large trees of various genera that are abundant. Among all nest trees *Dipterocarpus* were tallest and largest (largest in

dbh). This genus usually emerges to form the top canopy of the forest (Whitmore 1989, Liewviriyakit 1989, Manokaran et al. 1991). They may be easily subjected to storms which break branches off and cause wounds and cracks in the trunks. Through these wounds, these trees, particularly Dipterocarpus are susceptible to certain fungi Ganoderma spp. and Cryptoderma spp. These fungi eventually cause heart and butt rot (Chalermponse 1985), and as a consequence, a cavity is formed. These processes may occur to other emergent trees as well, but may not be as frequent as in Dipterocarpus trees.

As Baker (1927) noted that the Burmese Pied Hornbill A. albirostris favoured trees of genera Bombax, Lagerstroemia and Dipterocarpus, which towered high above the surrounding forest of small deciduous trees or secondary growth. Johns (1982) observed a Rhinoceros Hornbill Buceros rhinoceros using a cavity in an emergent Shorea pauciflora. Pan (1987a) reported the nest of a Southern Pied Hornbill at a height of 50 m in Koompassia exelsa. Although most Eugenia trees in the study site were not as high as Dipterocarpus trees, those Eugenia trees which served as nest trees were very large in diameter. Thus, it is very likely that large and tall trees attract nest seeking hornbills.

2. Besides using large and tall trees, hornbills obviously used trees that were in abundance and trees of genera Dipterocarpus and Eugenia were common trees in this forest. Liewviriyakit (1989) who studied the plant

community surrounding nest sites in Kao Yai provided the data for the relative abundance of various kinds of trees. Kemp (1976) found no preference for particular tree species for nesting in three species of Tockus Hornbills, which used tree species that were most abundant. Hussain (1984) reported that Narcondam Hornbills mostly nested in trees of the genera Sideroxylon and Sterculia, both of which are common in the moist evergreen forests on Narcondam Island.

3. Both Dipterocarpus and Eugenia trees are of durable hardwood (Uphof 1968) and may survive longer than other trees. If a particular species of trees chosen for nesting survives longer than other kinds of trees, that particular one would be used at proportionately higher frequency.

Nest cavities

The four hornbill species selected the entrances of nest cavities according to their body sizes. No other studies are available for comparison of the nest characteristics of these species except for a few short notes and some measurements of nest cavities made by Deignan (1945) and Ali and Ripley (1987) for the Great, Johns (1982) for the Rhinoceros, Madge (1969) for the Bushy-crested and, Pan (1987) for the Southern Pied hornbill. The measurements of nest entrance sizes reported by those authors are within the ranges of the Great, Oriental Pied and Brown hornbills' in this study.

Hornbills preferred to use cavities with narrowest entrance possibly to reduce time, energy and materials consumption during entrance sealing. Baker (1934) observed female Great Hornbills used holes with a narrow entrance. As well as Moreáu (1937) observed hornbills of the genus Tockus (Lophoceros) used cavities with entrances that were just large enough for the female to enter. Those observations are similar to what had been observed in this study.

Table 3-1. Twelve nest trees which were used by different hornbill species in Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Tree genus	dbh (cm)	1st found species	2nd species or pair use	3rd species or pair use	Remarks
Cinnamomum	70	PH (1984)	BH (1990)	-	
Dipterocarpus	150	GH (1985)	WH (1988)	-	
Dipterocarpus	97	BH (1984)	GH (1988)	-	
Dipterocarpus	65	GH (1984)	PH (1992)	-	
Dipterocarpus	68	PH (1984)	BH (1992)	-	
Eugenia	120	WH (1981)	GH (1984)	-	
Eugenia	80	WH (1984)	WH (1991)	-	
Eugenia	78	BH (1983)	PH (1984); BH (1984)	WH (1989)	nest entrance was artifi enlarged in 1988 (see te
Eugenia	54	WH (1981)	GH (1982)	-	
Nephelium	90	WH (1982)	PH (1984)	-	
Unknown	127	WH (1981)	PH (1990)	-	
Unknown	55	PH (1981)	BH (1992)	-	

Table 3-2. Accumulative number of nest discovery and nest loss and the known causes of nest loss.

	1981	1982	1983	1984	1985	1988	1989	1990	1991	Total
Accumulative no. nest discovery	13	20	31	61	69	74	76	79	80	80
Accumulative no. nest loss	1	1	1	4	5	21	23	25	26	26
Cause of nest loss										
Nest tree breakage	1	0	0	1	1	7	2	2	0	14
Nest tree cut by poacher	0	0	0	0	0	4	0	0	0	4
Nest entrance closed or narrow	0	0	0	0	0	4	0	0	1	5
Nest floor sinking	0	0	0	2	0	1	0	0	0	3
Annual nest loss	1	0	0	3	1	16	2	2	1	26
% Accumulative nest loss	7.7	5.0	3.2	6.6	7.2	28.4	30.3	31.6	32.5	32.5

Table 3-3 Altitudinal distribution of 89 nest sites of the four sympatric hornbill species in the study site.

	Hornbill species			
	Great	Wreathed	Oriental Pied	Brown
Altitude (m)				
Range	660-850	640-880	670-840	740-870
Mean	770.7	774.1	756.6	800.7
SD	41.7	56.7	36.4	41.8
N	28	17	29	15

Table 3-4. Density, frequency and degree of aggregation of nests of four sympatric species of hornbills within 52 plots (52 km^2) measured in 1991. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

	GH	WH	PH	BH	Total
No. of nests	18	6	17	10	51
No. of plots occupied by species (from total 52 plots)	12	6	12	8	28
Frequency of occurence %	35.7	12.7	33.7	19.4	53.8
Nest density/km^2	0.35	0.12	0.33	0.19	0.98
Relative nest density (%)	35.7	12.2	33.7	19.4	100
Degree of aggregation (σ^2/x)	1.34	0.83	1.39	1.26	1.98

Table 3-5. Range, mean and SD of distances between nearest-neighbour nests of various hornbill species.

GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill and BH = Brown Hornbill.

Nest of focus species	Total nest no.	Nearest-neighbour distance of species (m)											
		GH			WH			PH			BH		
		Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
GH	25	160-2320	1001.6	611.0	70-2920	919.6	718.8	5-2800	749.6	702.5	20-2920	1374.8	1035.6
WH	12	70-1240	615.0	451.7	610-4040	1421.7	944.2	240-1780	836.7	584.4	260-4420	1792.5	1217.0
PH	24	5-1340	552.3	399.6	160-3970	1141.3	876.1	200-1280	667.1	451.8	100-2760	1544.4	844.2
BH	12	20-1400	498.3	457.9	180-2320	964.2	746.2	190-1900	992.5	666.9	100-2200	565.0	767.4

Table 3-6. Number of focus species nests whose nearest-neighbours are of various species. GH = Great Hornbill, WH = Wreathed HOrnbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Focus species	Nearest-neighbour species				Total by hornbill size
	Larger sp.		Smaller sp.		
	GH	WH	PH	BH	
Larger sp.					
GH	4	5	10	6	37
WH	8	0	4	0	
Smaller sp.					
PH	10	4	6	4	36
BH	3	1	2	6	
Total by size	35		38		73

Ho: Number of nests of larger (GH and WH) or smaller (PH and BH) as nearest neighbours of the larger focus species and smaller focus species are not different. ($\chi^2 = 0.12$, df = 1, $p>0.05$)

Table 3-7. Number and percentage of tree genera that were originally used by hornbill species in Khao Yai.
GH = Great Hornbill, WH =Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill

Tree genus	No. of trees used by hornbill species				Total
	GH	WH	PH	BH	(%)
Dipterocarpus	9	7	9	2	27 (33.8)
Eugenia	7	5	4	5	21 (26.2)
Cinnamomum	3	0	2	1	6 (7.5)
Altingia	1	0	2	0	3 (3.8)
Choerospondias	0	0	0	3	3 (3.8)
Lithocarpus	2	0	1	0	3 (3.8)
Tetrameles	1	1	1	0	3 (3.8)
Gironniera	0	0	2	0	2 (2.5)
Nephelium	0	1	0	1	2 (2.5)
Alstonia	0	0	0	1	1 (1.2)
Ficus	0	0	1	0	1 (1.2)
Pterospermum	0	0	1	0	1 (1.2)
Unknown	2	1	3	1	7 (8.8)
Total	25	15	26	14	100

Table 3-8. Summary of characteristics of nest tree, nest site and nest cavity of four hornbill species in Khao Yai with their body masses (Kemp 1979) and statistical tests of difference between species. GH = Great Hornbill, WH = Wreathed Hornbill, BH = Brown Hornbill, PH = Indian Pied Hornbill, DBH = Diameter at breast height, DNH = Diameter at nest hole height, VL = Vertical dimension of nest entrance, HL = Horizontal dimension of nest entrance.

	Species and approx. body mass				Kruskal-Wallis Test corrected for ties			Mann-Whitney U-test significant level		
	GH 3,000 g	WH 2,500 g	PH 1,000 g	BH 900 g	H	*n*	*P* df=3	U	*n*1, *n*2	*P<.05, ***P*<.01
Nest tree										
dbh (cm)										
Range	54-157	54-267	46-135	51-109				46.5	26, 15	GH & BH**
Mean	110.5	119.8	80.4	76.8	22.13	81	<.01	122.5	26, 23	GH & PH**
SD	24.8	47.4	26.1	15.3				52.0	17, 15	WH & BH**
N	26	17	23	15				105.5	17, 23	WH & PH*
Tree Height (m)										
Range	17-46	22-46	13-50	13-36						
Mean	29.4	31.5	26.5	24	8.001	81	<.05	59.5	17, 15	WH & BH**
SD	8.1	7.4	8.4	6.6						
N	27	17	22	15						
Nest cavity										
Nest Height (m)										
Range	10-36	10-36	2-45	7-27						
Mean	19.1	21.1	15.8	12.9	12.46	81	<.01	45	17, 15	WH & BH**
SD	7.7	7.7	9.5	5.8				100	27, 15	GH & BH**
N	27	17	22	15						
dnh (cm)										
Range	40-100	40-100	40-100	40-100				83.0	25, 13	GH & BH**
Mean	78.1	74.3	55.7	63.5	21.54	71	<.01	76.5	25, 20	GH & PH**
SD	15.8	17.6	15.8	15.2				42.5	11, 20	WH & PH**
N	25	11	20	15						
VL (cm)										
Range	15-72	14-43	8-50	9-44				65.5	24, 14	GH & BH**
Mean	37.2	22.8	21.9	18.6	13.69	71	<.01	121.5	24, 20	GH & PH*
SD	17.8	9.1	12.3	9.3						
N	24	13	20	14						
HL (cm)										
Range	7-26	9-26	6-16	6-18				61.0	13, 20	WH & PH*
Mean	13.3	14.2	10.3	10.5	8.25	71	<.05			
SD	5.1	4.9	2.8	3.4						

Table 3-8. (cont.)

	Species and approx. body mass				Kruskal-Wallis Test corrected for ties			Mann-Whitney U-test significant level		
	GH 3,000 g	WH 2,500 g	PH 1,000 g	BH 900 g	H	*n*	*P* df=3	U	*n*1, *n*2	**P*<.05, ***P*<.01
HL/VL										
Range	0.14-1.18	0.23-1.50	0.18-1.50	0.25-1.44	2.4	71	>0.05			
Mean	0.5	0.7	0.6	0.7						
SD	0.3	0.4	0.4	0.4						
N	24	13	20	14						

Table 3-9. Frequency of hornbill nests in different genera of trees, and frequency of tree genera in 302 plots. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Tree genera	Hornbill species[1]				Freq. of tree genus[2]	
	GH	WH	PH	BH	as nests	in plots
Dipterocarpus	9	7	9	2	27	103
Eugenia	7	5	4	5	21	42
Other	9	4	13	7	33	1,321
Total	25	5	26	14	80	1,466

[1]Ho: Tree genera and hornbill species assort independently; χ^2=5.99 $P > 0.10$, df = 6.

[2]Ho: Total frequencies of tree genera used as nests do not differ from frequencies in plots; χ^2= 186.606, $P < 0.01$, df=2

Table 3-10. Nest tree genera, size (dbh), height, and height of nest cavity found on them and altitude where they were found. dbh = diameter of tree at breast height.

	Nest Tree			Kruskal-Wallis Test corrected for ties				Mann-Whitney U-test significant level	
	Dipterocarpus (1)	*Eugenia* (2)	Others (3)	H	n	P df = 2	U	$n1$, $n2$	* P < 0.05 ** P < 0.01
dbh (cm)									
Range	65-150	52-157	48-267						
Mean	106.9	100.8	88.0						
SD	26.7	20.2	42.7	8.54	73	<.05	178.5	22, 30	(1) & (3)**
N	22	21	30				204	21, 30	(2) & (3)*
Tree Height (m)									
Range	18-50	14-35	13-36						
Mean	35.3	26.3	24.1	24.55	73	<.001	77.5	22, 21	(1) & (2)**
SD	8.2	5.4	5.4				85	22, 30	(1) & (3)**
N	21	21	31						
Nest Height (m)									
Range	10-45	7-25	2-20						
Mean	25.4	15.0	12.8	24.66	73	<.001	80	22, 21	(1) & (2)**
SD	9.2	4.1	5.0				-193	22, 30	(1) & (3)**
N	21	21	31						
Altitude (m)									
Range	640-880	730-850	720-870						
Mean	752.2	793.6	767.7	9.72	80	<.01	148.1	22, 21	(1) & (2)**
SD	53.2	38.4	37.7				216.5	21, 30	(2) & (3)*
N	26	22	33						

Table 3-11. Frequency, percentage, rank of abundance and mean size (dbh and height) of twelve most common species of 42 identified genera/species in 250 sampling plots. *Genera/species known to be nest tree.

Tree genera/species	Frequency in plots	%	Rank of abundance	Mean size ($\bar{X}$+SD) dbh (cm)	Mean size ($\bar{X}$+SD) Height (m)
*Lithocarpus spp.	144	16.1	1	57.9±16.3	28.6±4.8
*Dipterocarpus spp.	111	12.4	2	71.5±25.1	35.1±6.6
*Choerospondias axillaris	91	10.2	3	62.3±17.3	29.2±6.0
Sapium baccatum	52	5.8	4	70.2±21.3	29.6±5.4
Anthocephalus chinensis	50	5.6	5	70.7±18.2	31.5±6.2
Sloanea sigun	36	4.0	6	59.2±18.9	28.4±7.4
*Eugenia spp.	32	3.6	7	58.0±17.7	29.8±5.9
Polyalthia evecta	25	2.8	8	53.1±14.0	27.6±5.4
Paramichelia bellonii	24	2.7	9	68.3±20.9	30.6±4.9
*Cinnamomum glaucescens	18	2.4	10	69.3±30.8	30.7±6.5
Amoora gigantea	17	1.9	11	63.9±24.5	34.1±9.4
Schima wallichii	15	1.7	12	63.3±18.2	29.0±3.5

Table 3-12. Interior nest cavity dimensions of four hornbill species. D = Depth from entrance to the opposite wall; W = Width of cavity; H = Height of ceiling; F = Floor level from the lower edge of entrance. G = Great Hornbill, W = Wreathed Hornbill, PH = Oriental Pied Hornbill, B = Brown Hornbill. ( )= Tree # as refer in Appendix 3-1.

Nest code (Tree #)	D(cm)	W(cm)	H(cm)	F(cm)	Remark
G2(T2)	70	50	>200	0	
G4(T4)	30	32	39	6	
G20(T41)	42	50	200	7	
W3(T7)	65	46	>200	3	
W4(T15)	45	35	94	14.5	Female digged (1982)
W10(T48)	46	45	>200	0	
P4(T11)	40	23	>200	7	
P5(T12)	45	25	30	0	
P6(13)	45	30	170	0	
B1(T19)	40	32	>200	0	
B2(T20)	46	40	110	17	

Avg 46.727

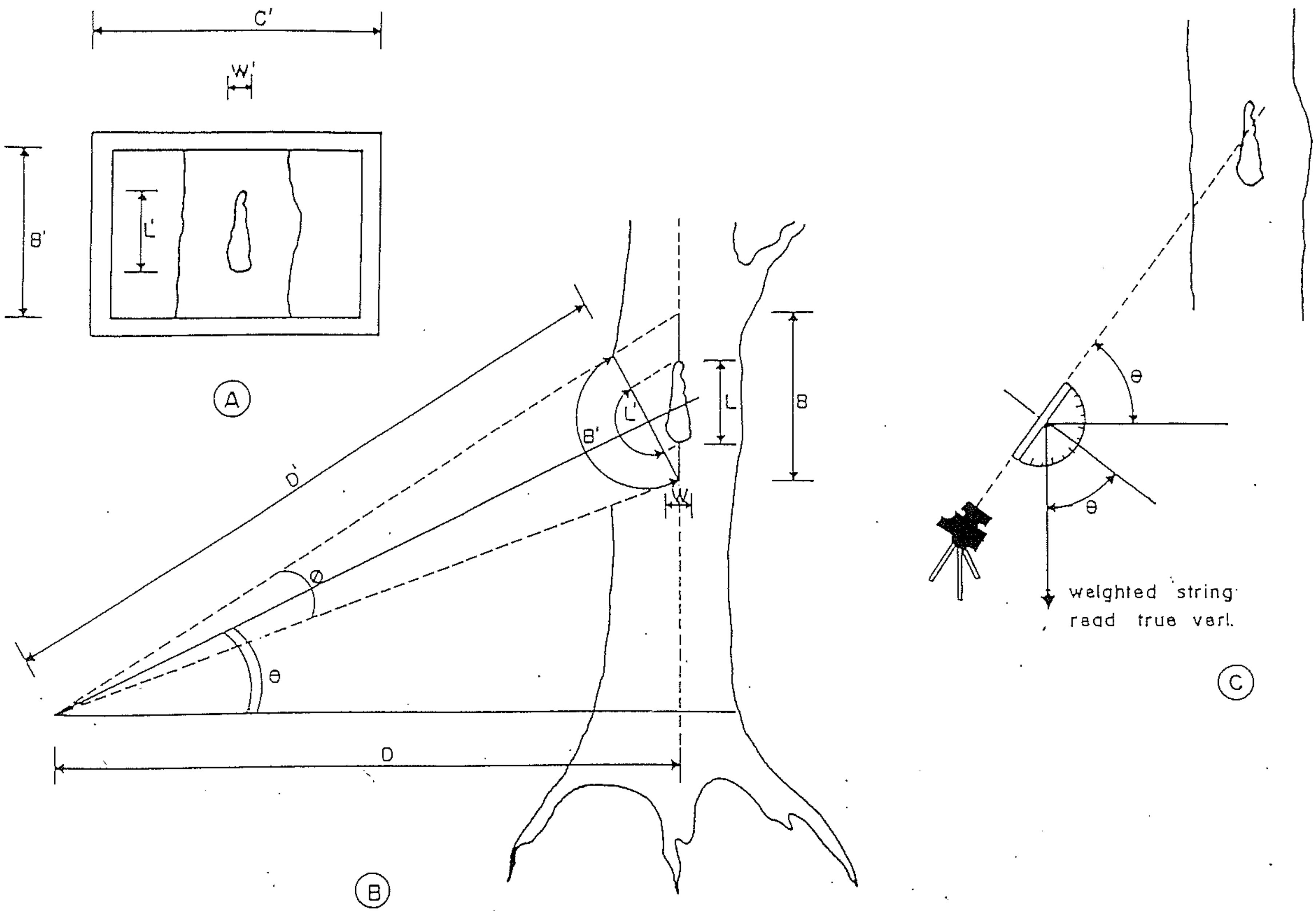


Fig. 3-1 Diagram showing sketch and calculation of shape and size of the entrance of hornbill nests using photographs

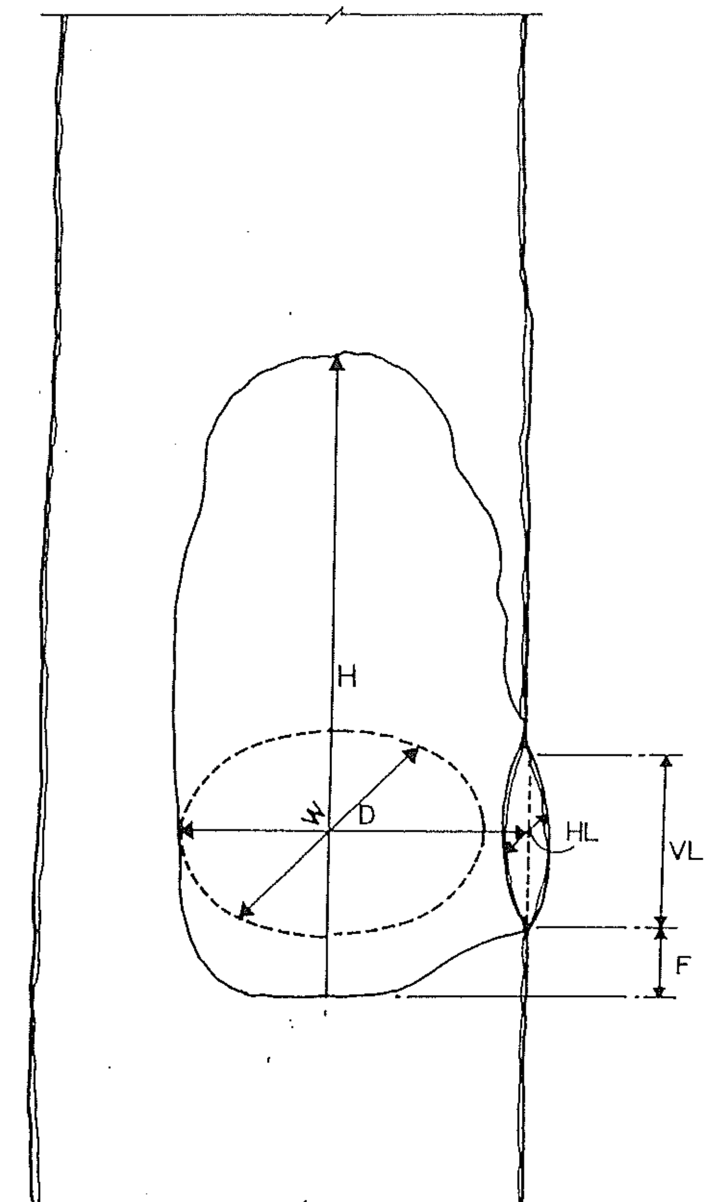
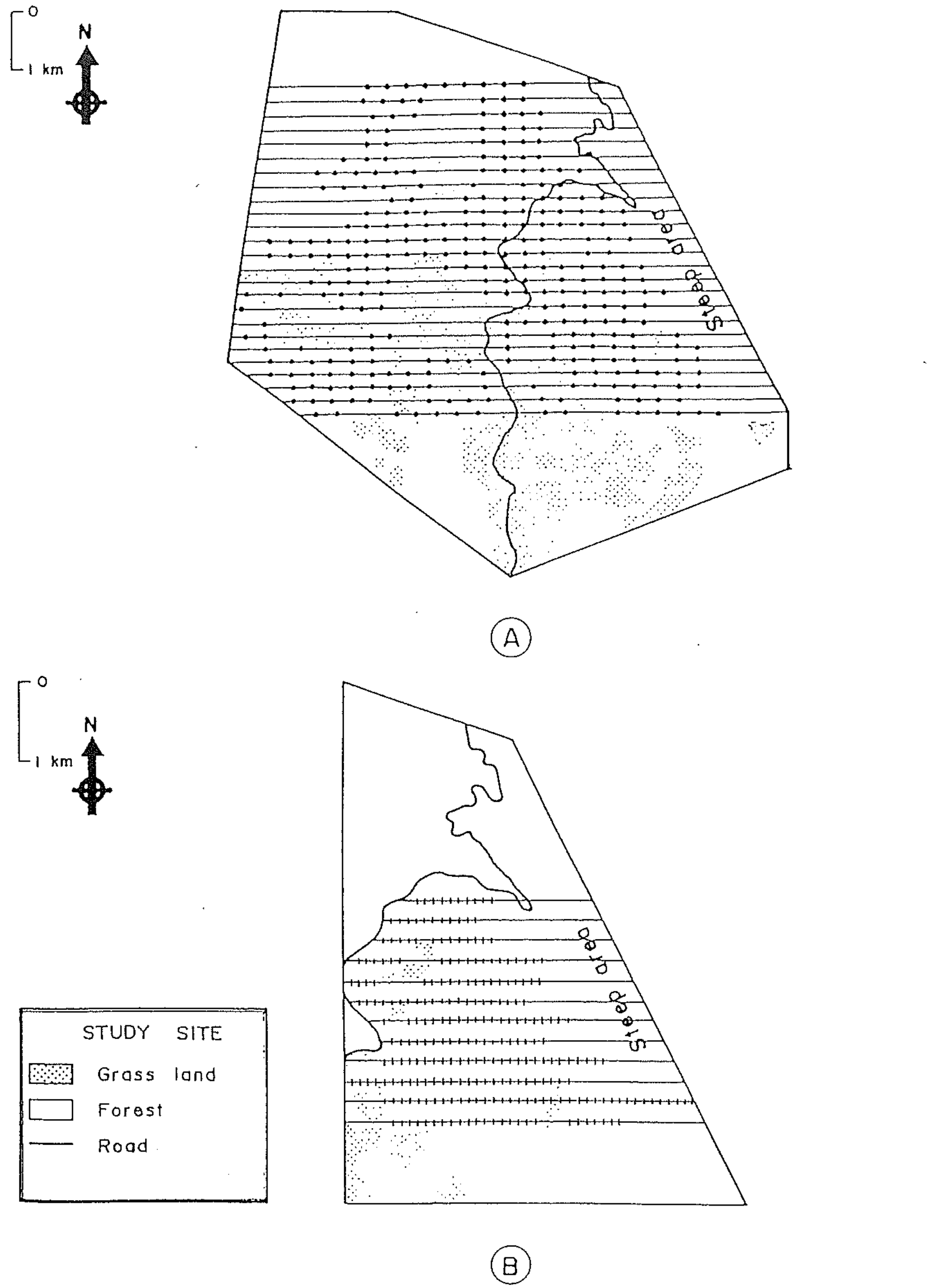
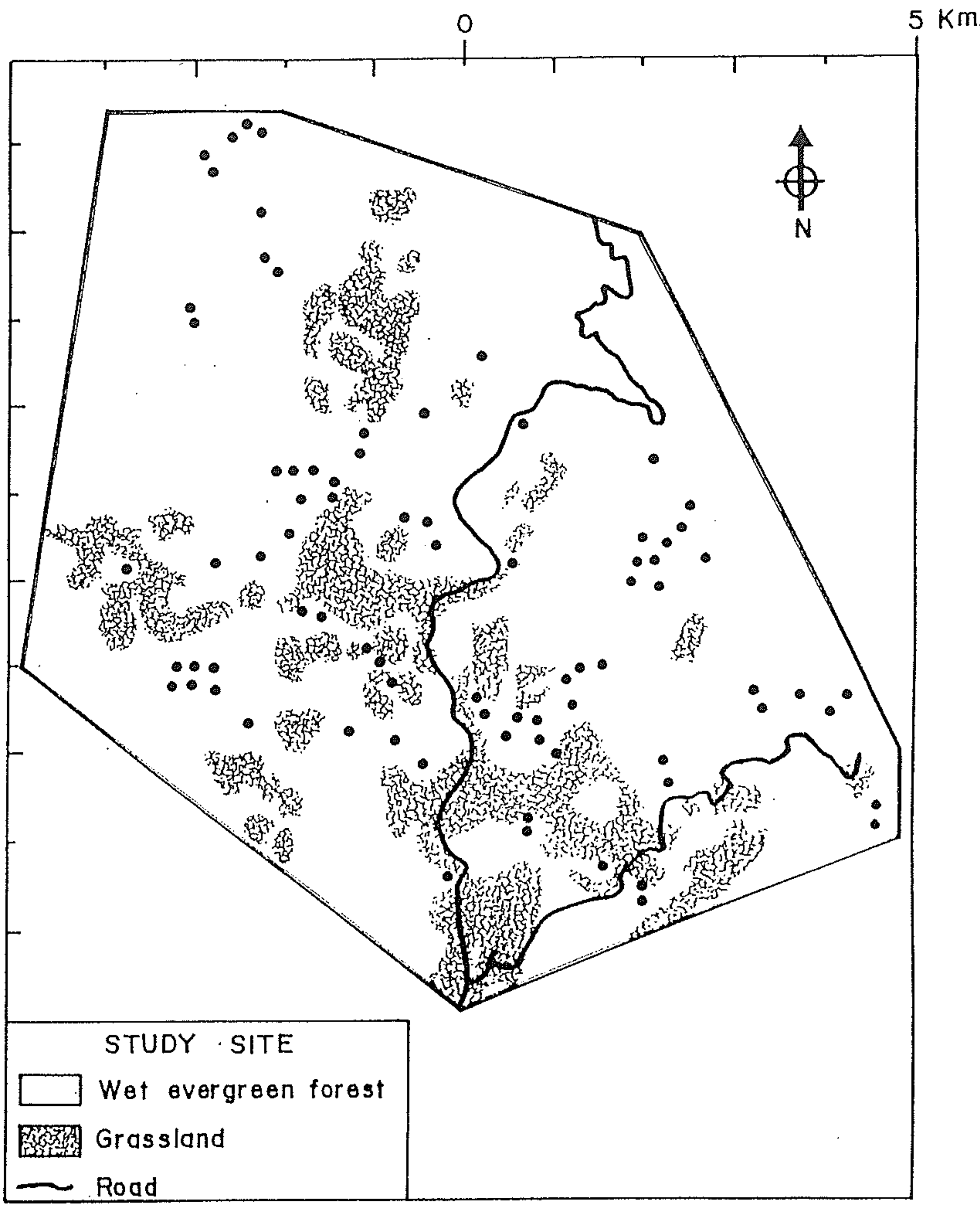


Fig. 3-2 Diagram of an interior nest cavity showing different dimensions.



ig. 3-3 (A) Three hundred and two line plots (each 0.1 ha) to study the abundance of large trees (dbh $\geq$ cm) within the study site. (B) Two hundred fifty



. 3-4 Location and distribution of 80 nest trees (black dots) of four hornbill species in Khao Yai during 1981-1991.

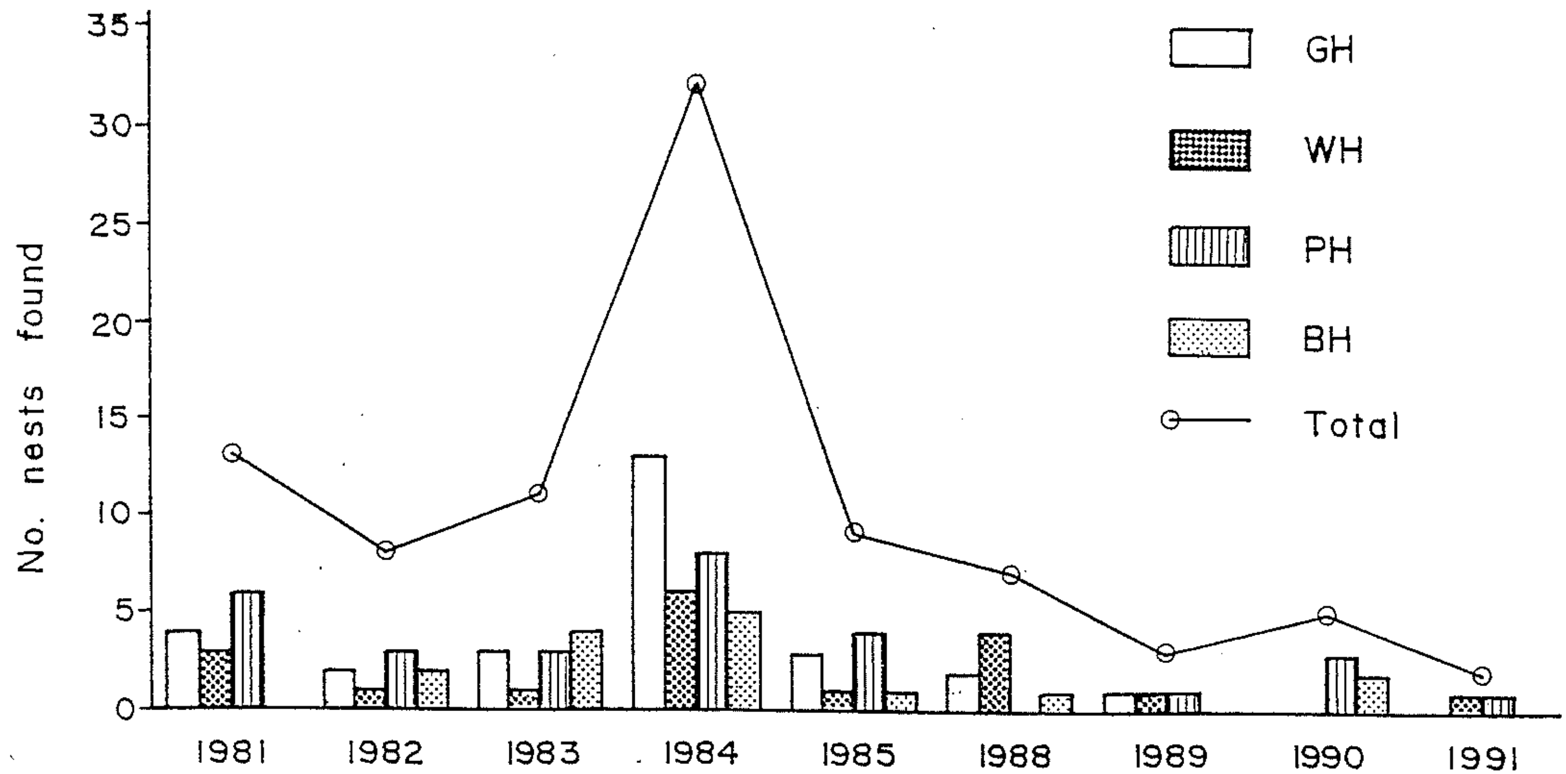


Fig. 3-5 Numbers of hornbill nests disovered in Khao Yai during 1981-1991.

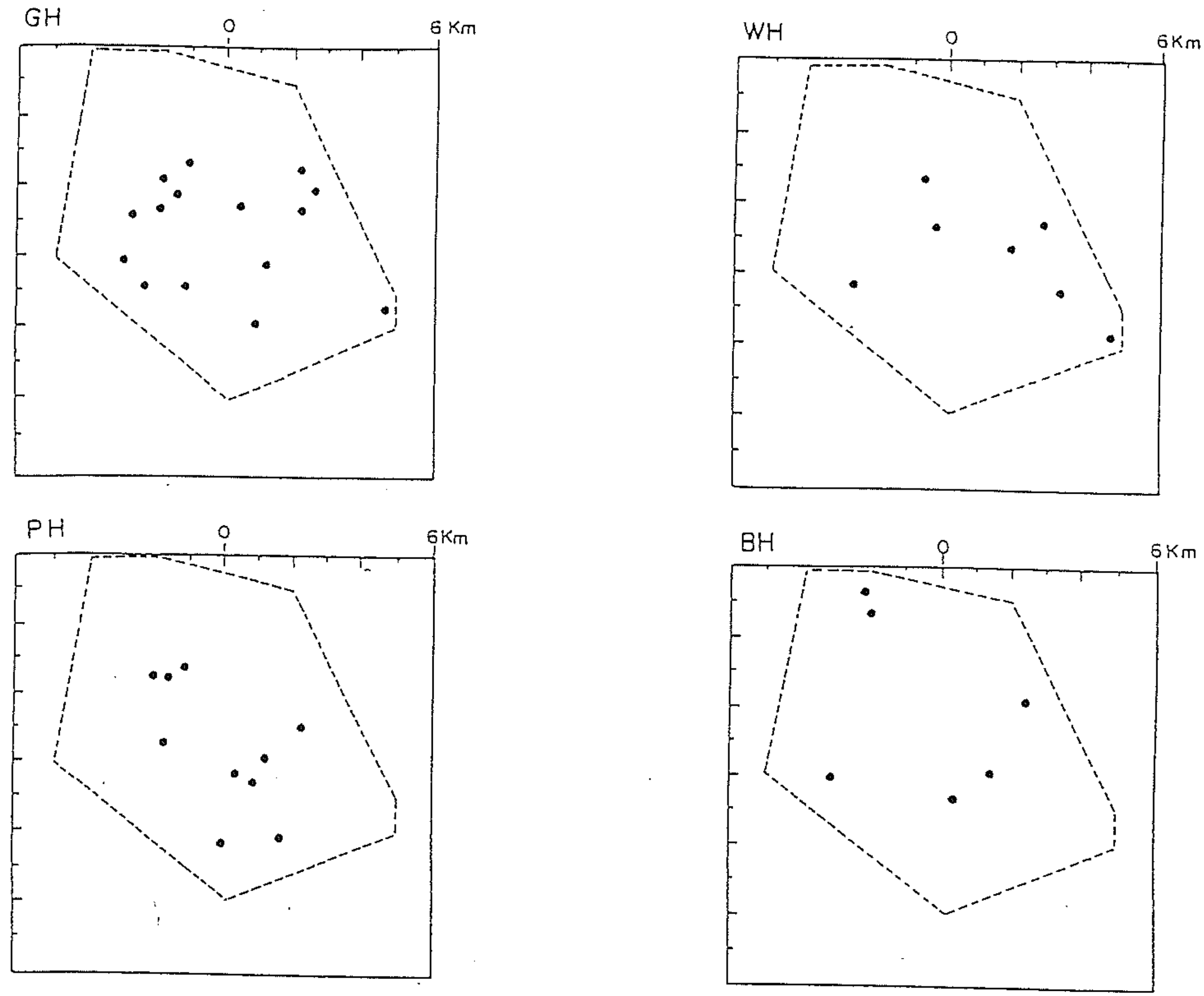


Fig. 3-6 Current active nests (black dots) of four hornbill species in Khao Yai in 1991 breeding season.

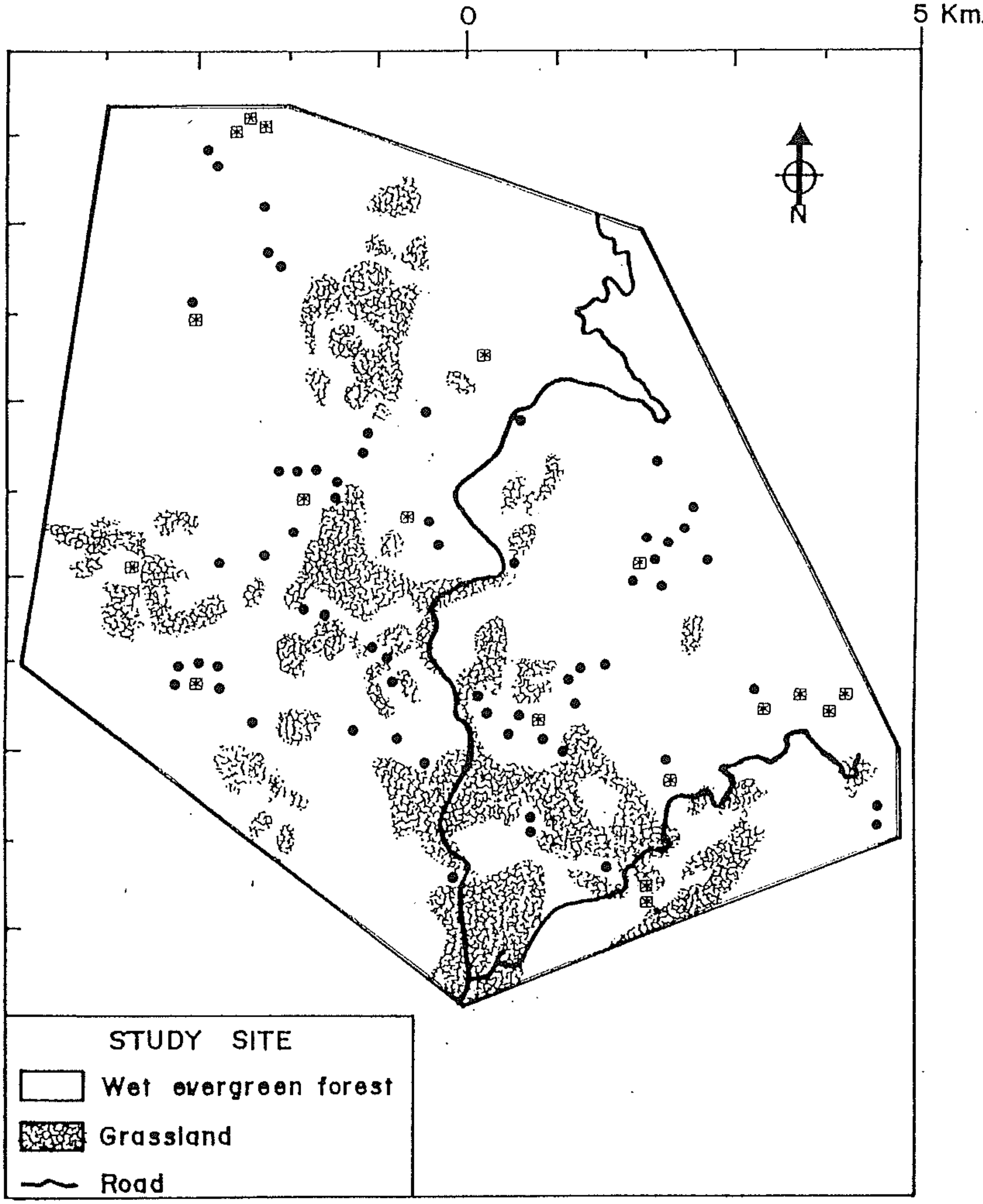


Fig. 3-7 Location of broken and cut nest trees (square with asterisk) of four hornbill species in Khao Yai between 1981 and 1991. Black dot = remained nest tree.

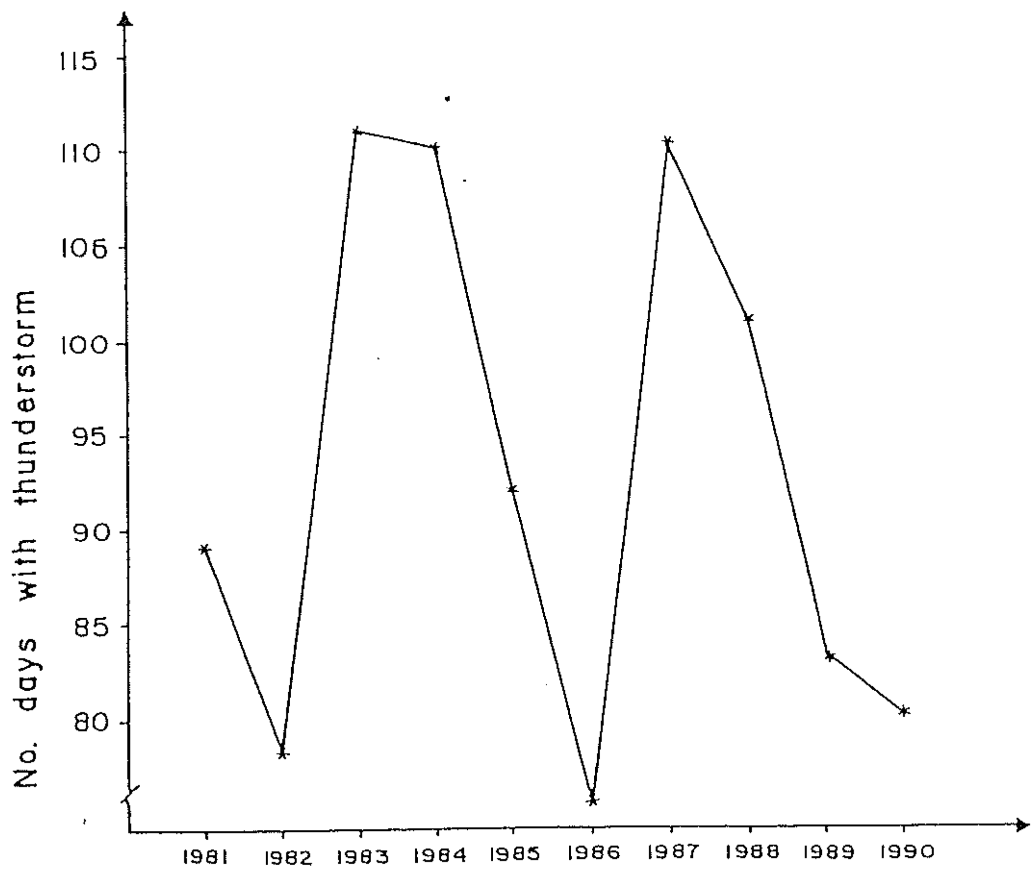


Fig. 3-8 Annual frequencies of thunderstorms in Nakhon Ratchasima Province during 1981-1990.

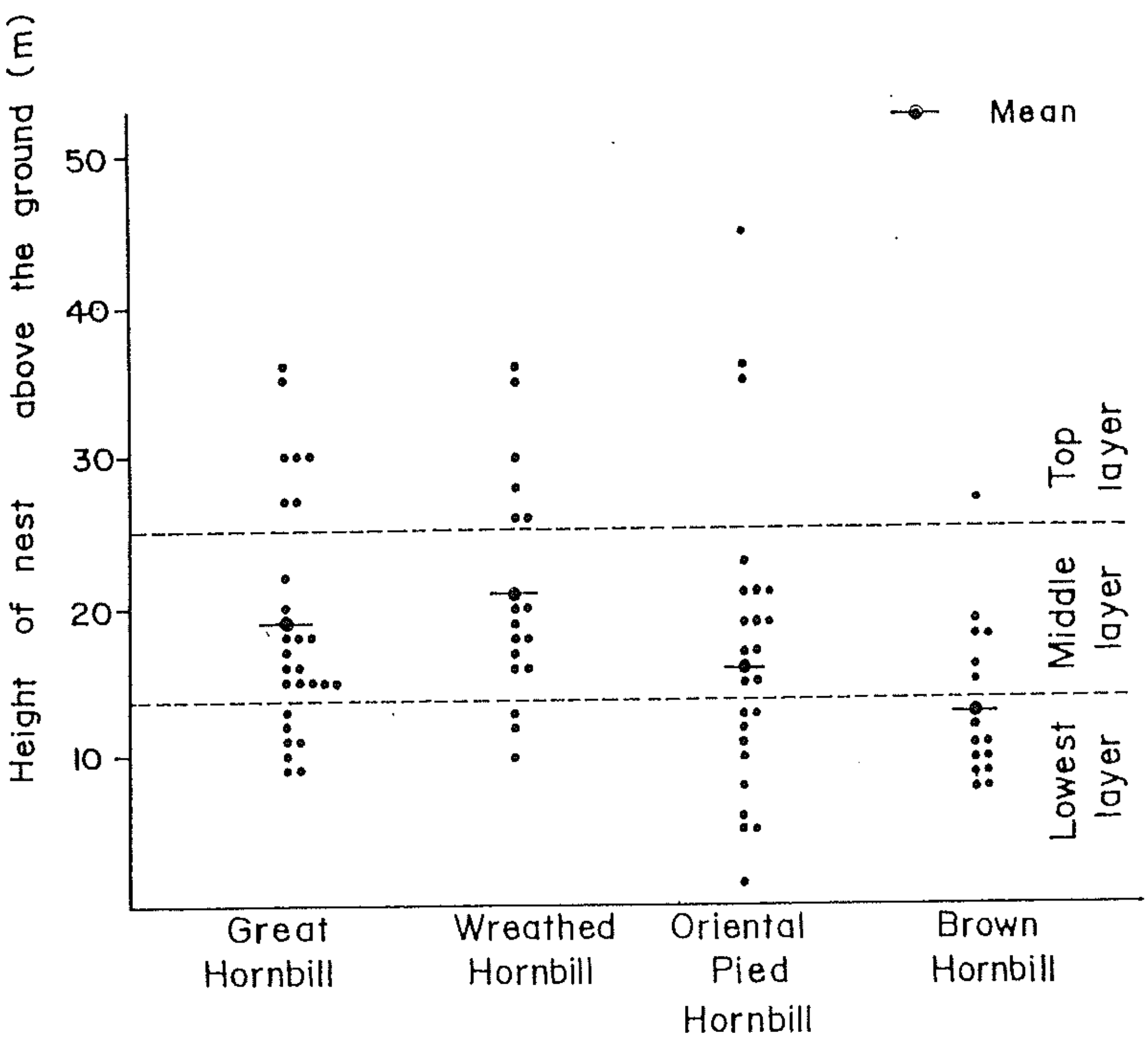


Fig. 3-9 Nest heights of four sympatric species of hornbills.

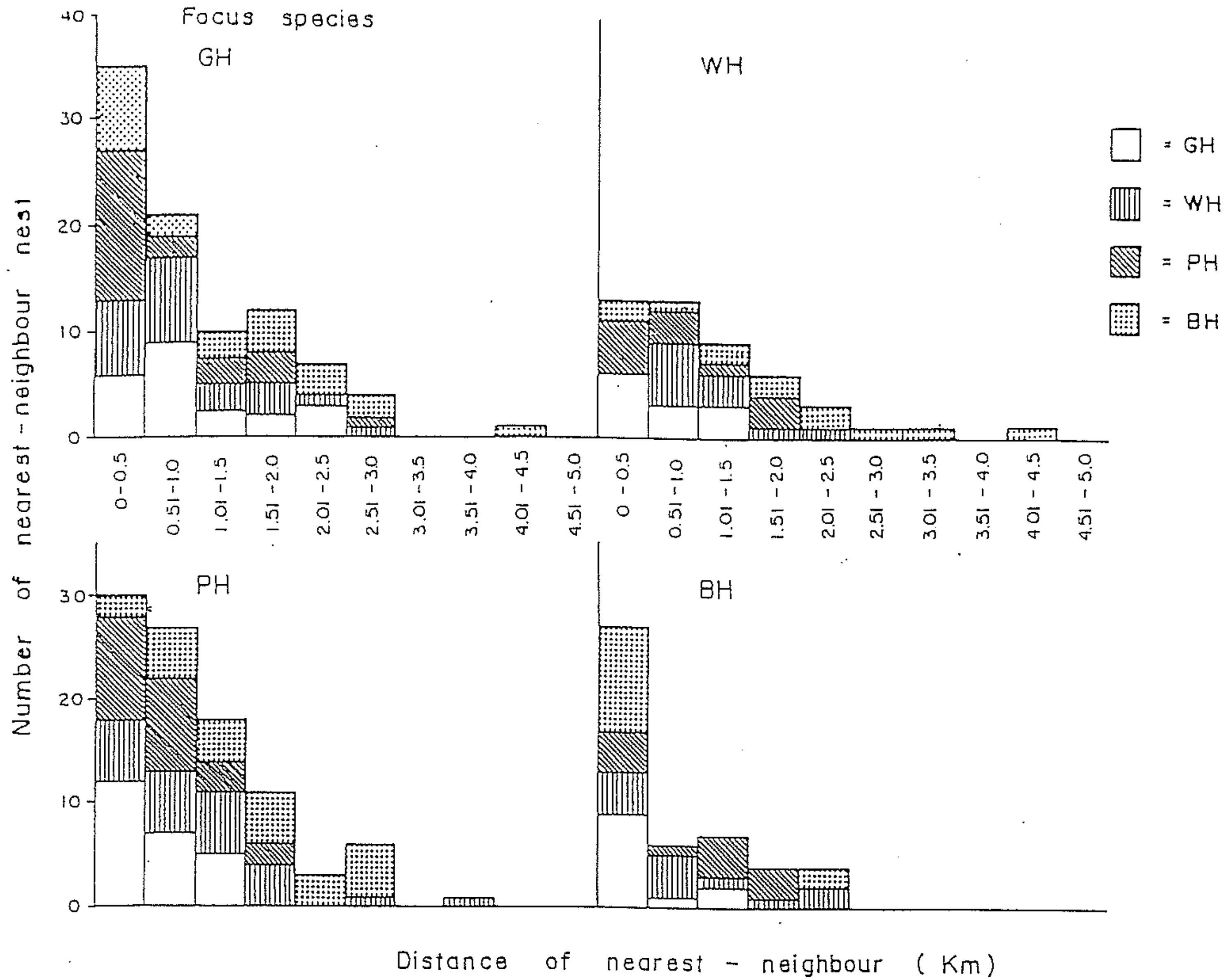
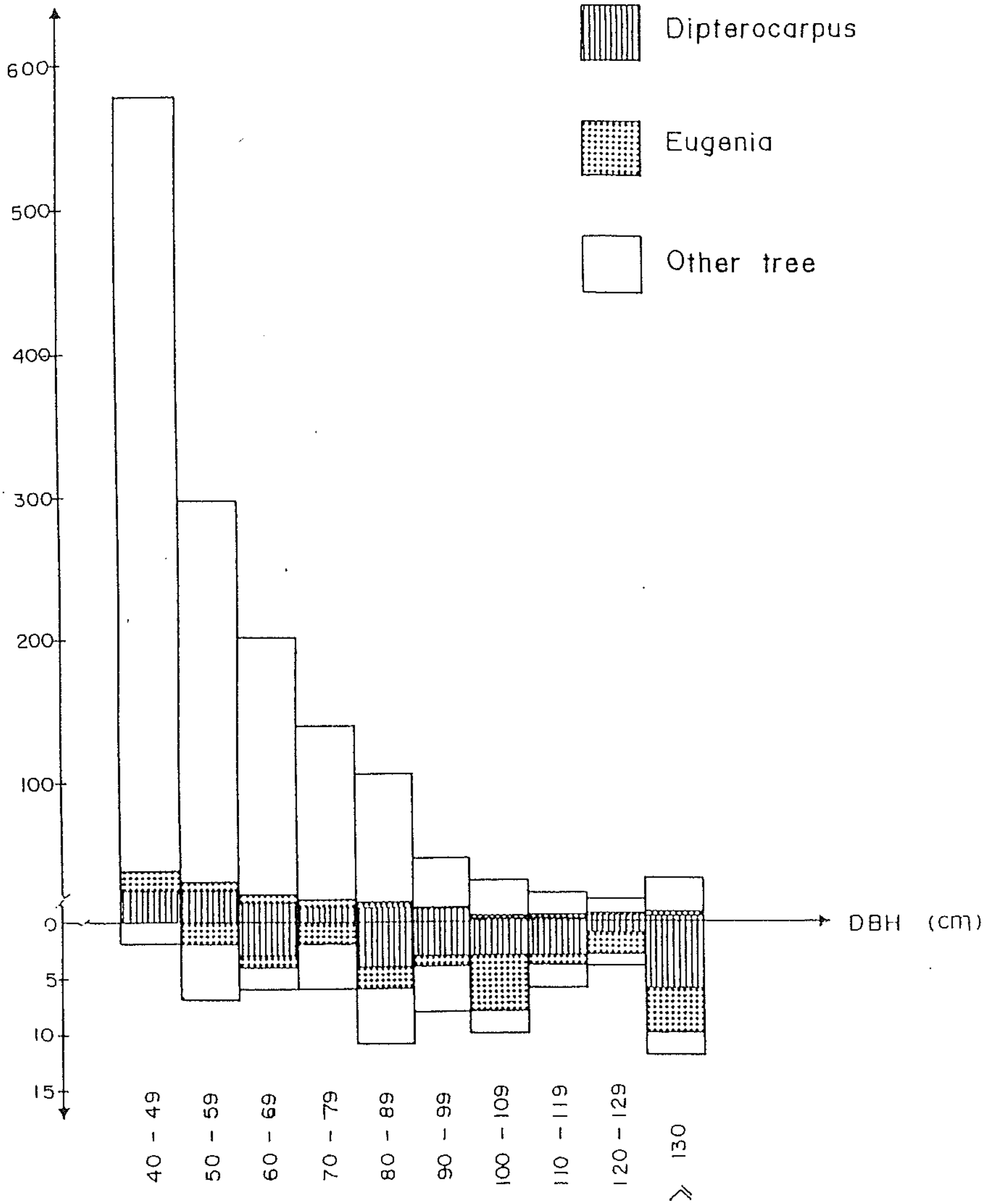


Fig. 3-10 Frequency and distance of various nearest-neighbour species to each focus species of hornbills. GH = Great Hornbill, WH = Wreathed Hornbill,



[.] 3-11 Comparison of frequency of trees of various size (dbh) found in 302 sample plots and frequency of nest trees of various size used by hornbills.

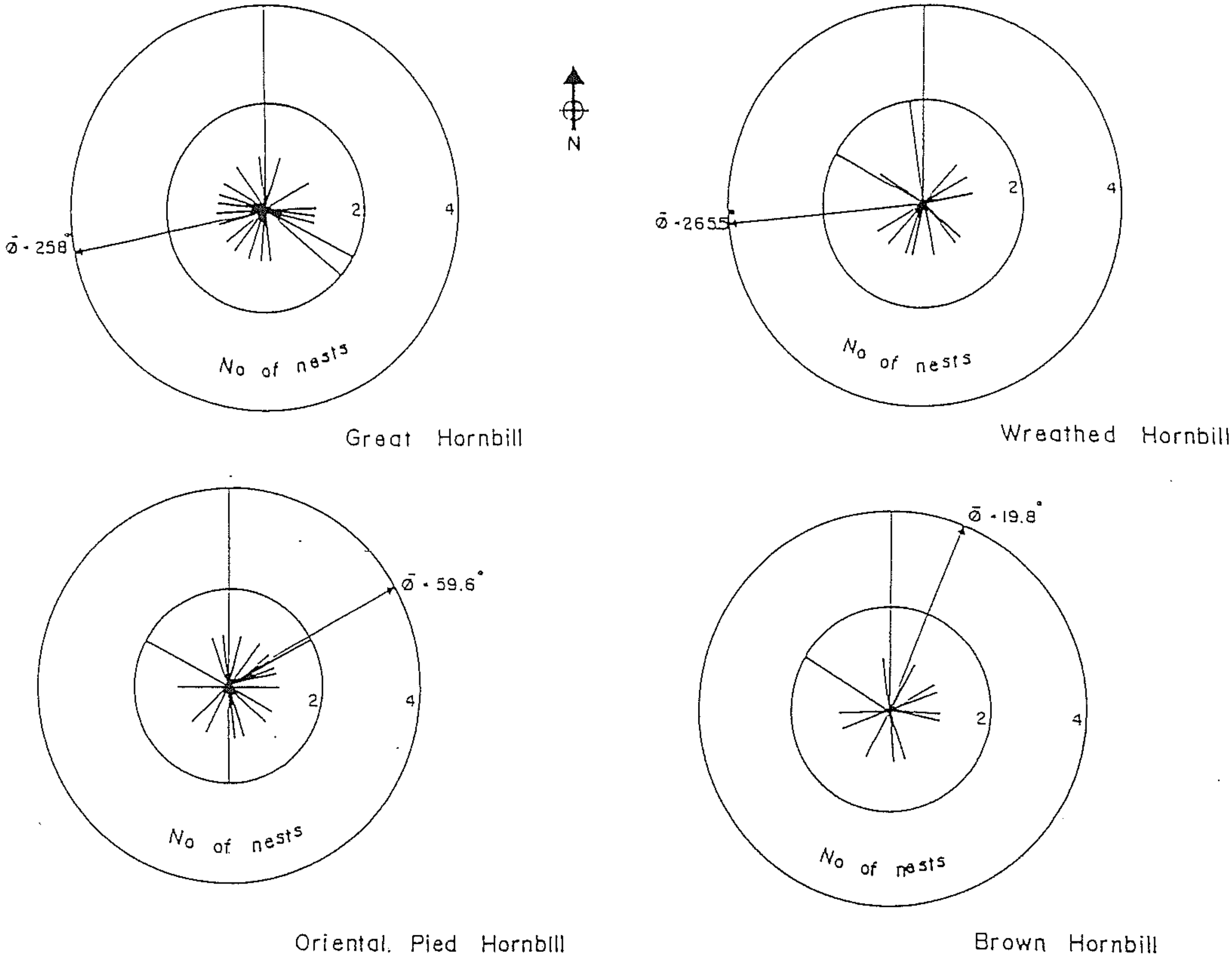


Fig. 3-12 Distribution of nest entrance orientation of four
sympatric species of hornbills in Khao Yai

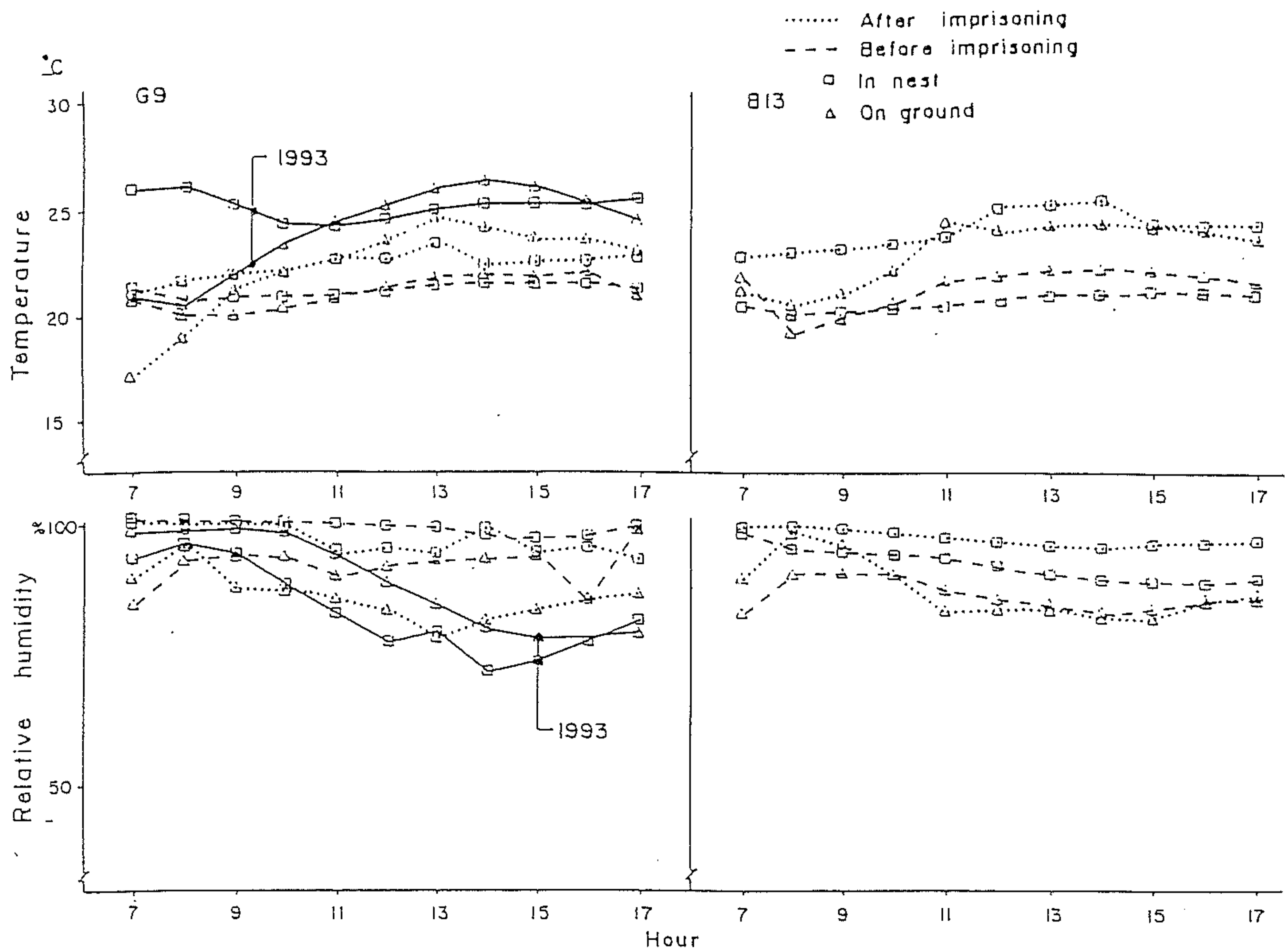


Fig. 3-13 Temperature and relative humidity patterns measured inside two nest cavities and on the ground at an hour interval before and after imprisonment period of females Great (G9) and Brown (B13) Hornbills during 1992 breeding season. otherwise stated

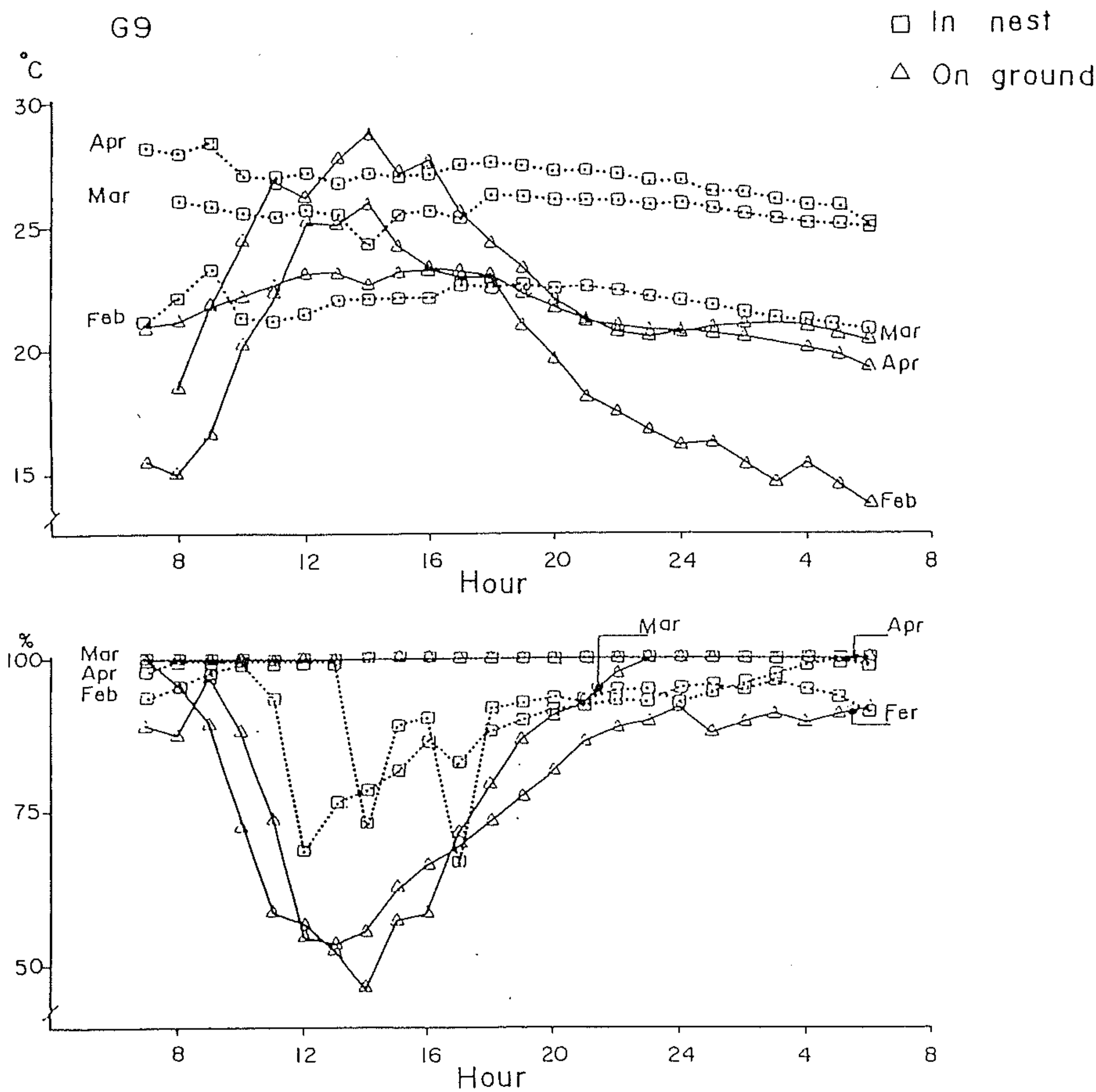


Fig. 3-14 Monitoring of temperature and relative humidity inside a nest cavity of Great Hornbill (G9) for 24 hours in comparison with those on the ground in 1993 breeding season.

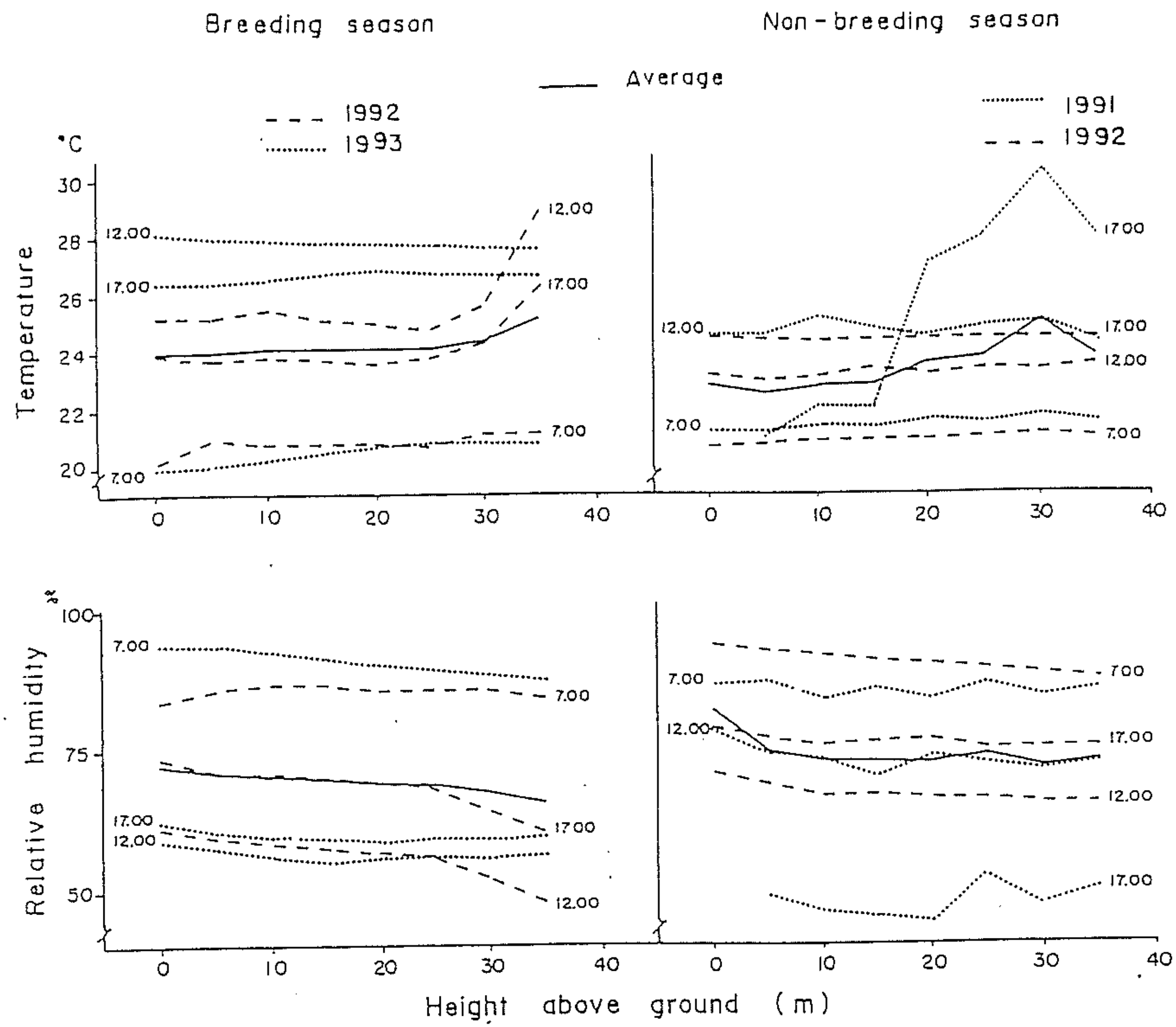
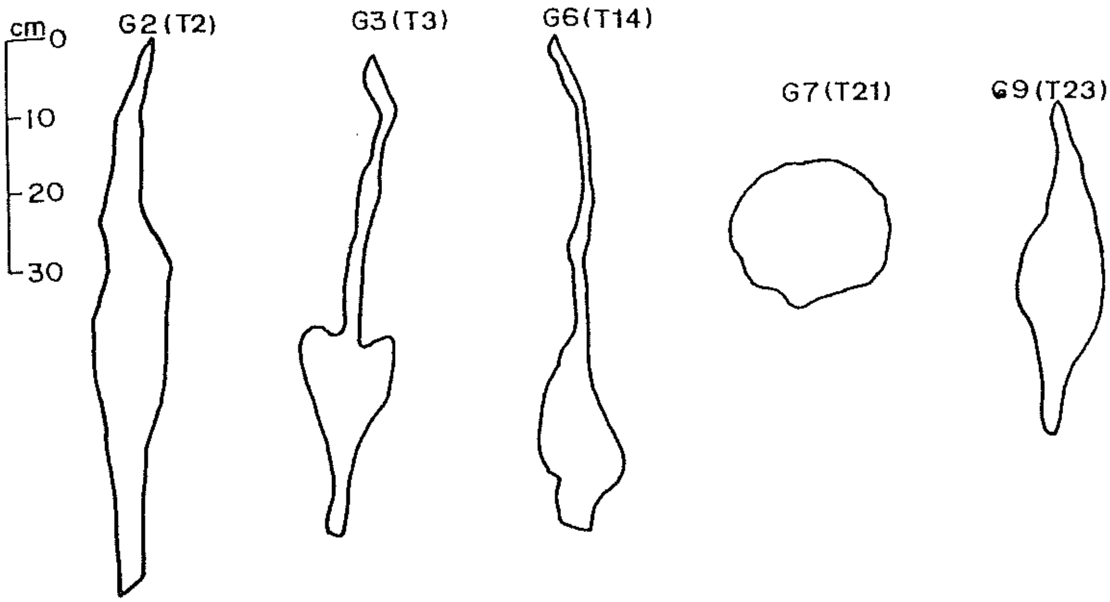


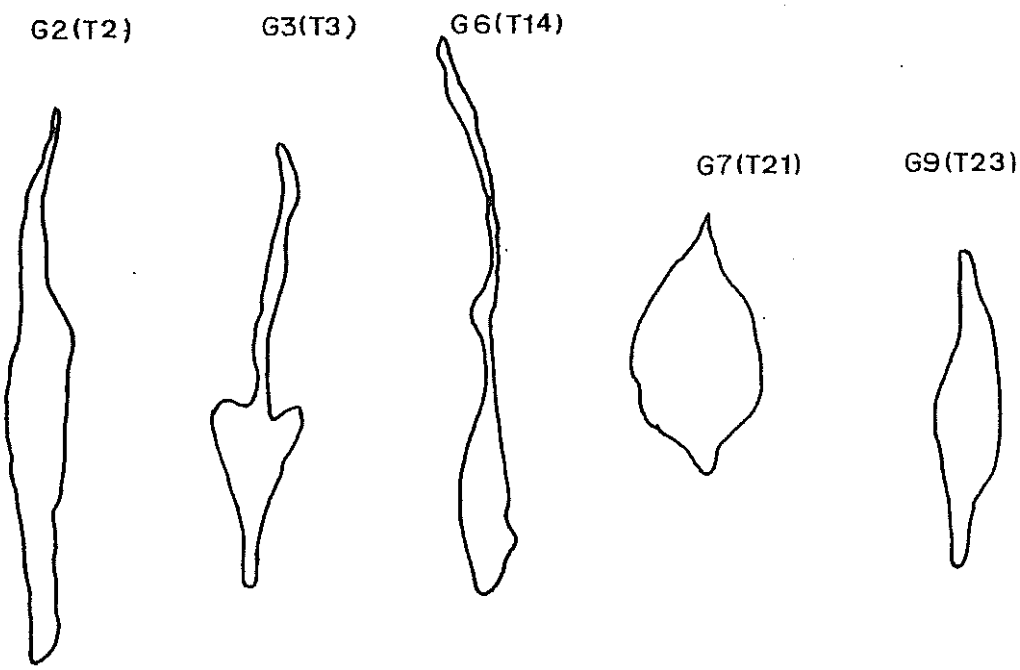
Fig. 3-15 Gradient of temperature and relative humidity in the forest at 865 m a.s.l in Khao Yai.

Appendix 3-2 Comparison of shapes of nest entrances of four hornbill species studied in Khao Yai between November 1984 and November 1992. G2 indicates hornbill species and nest code, (T2) indicates number of nest tree referred in Appendix 3-1

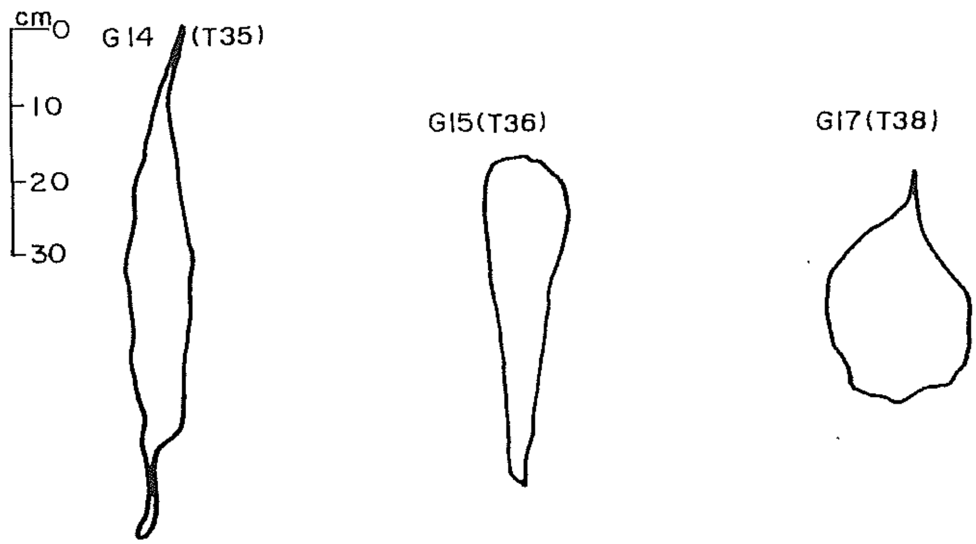
GREAT HORNBILL (1:10 Natural Size)
(measured November 1984)



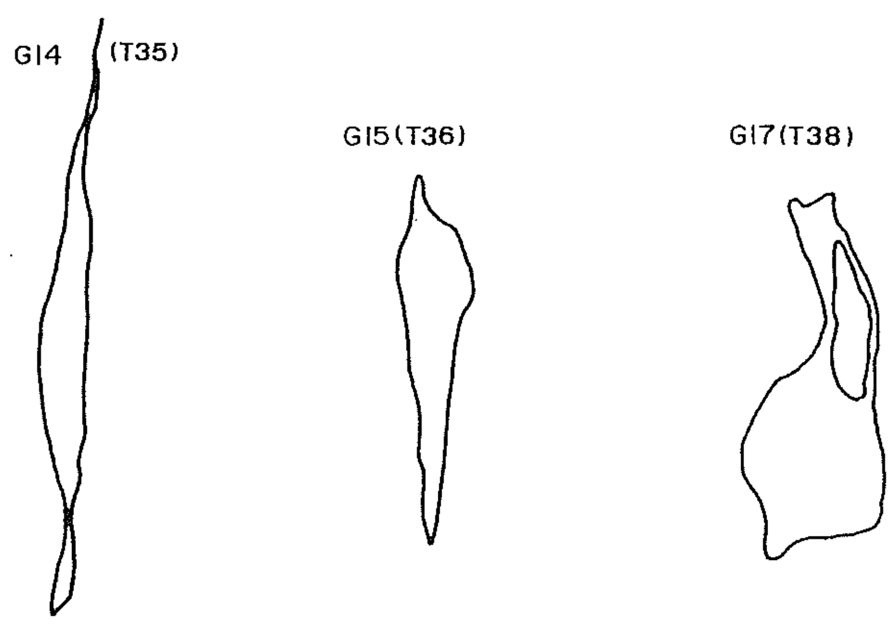
GREAT HORNBILL (1:10 Natural Size)
(measured November 1992)



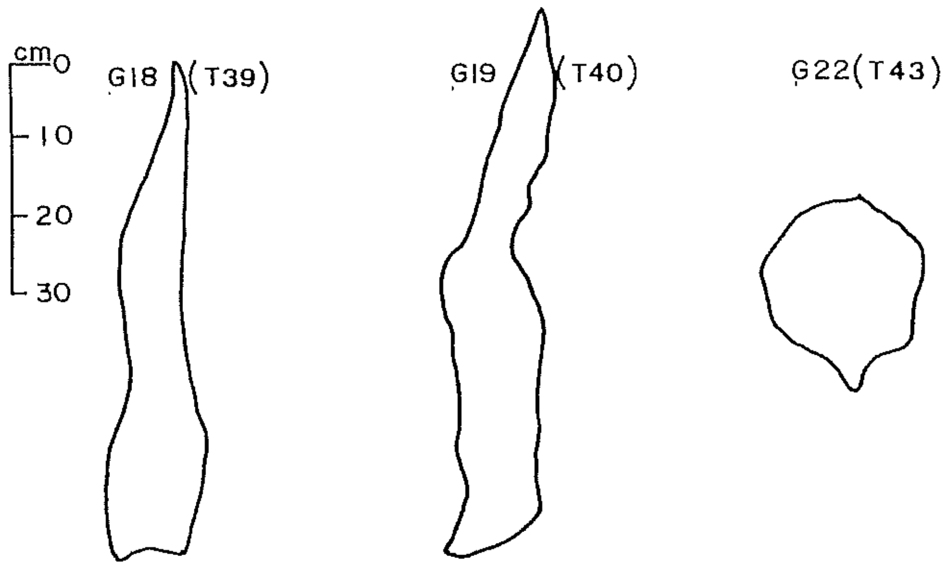
GREAT HORNBILL (1 : 10 Natural Size)
(measured November 1984)



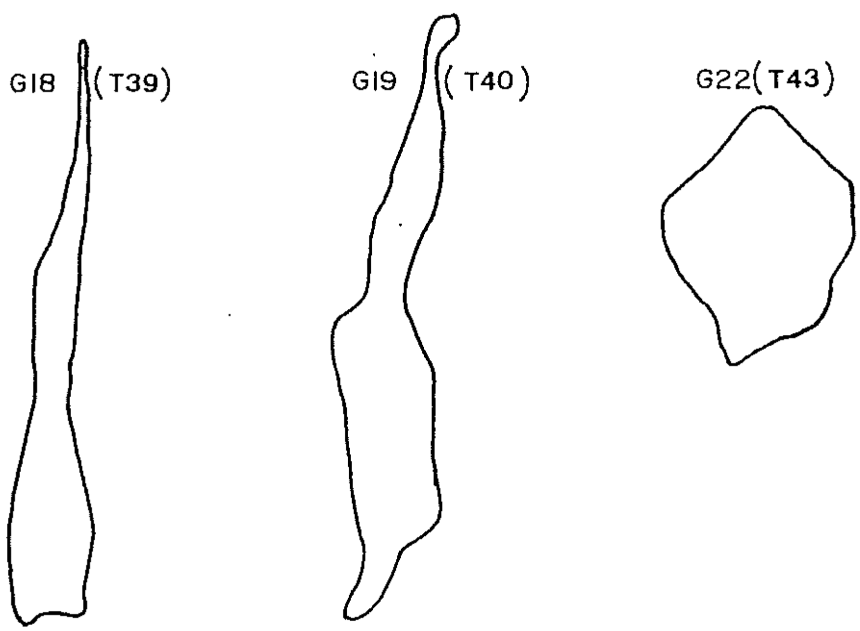
GREAT HORNBILL (1 : 10 Natural Size)
(measured November 1992)



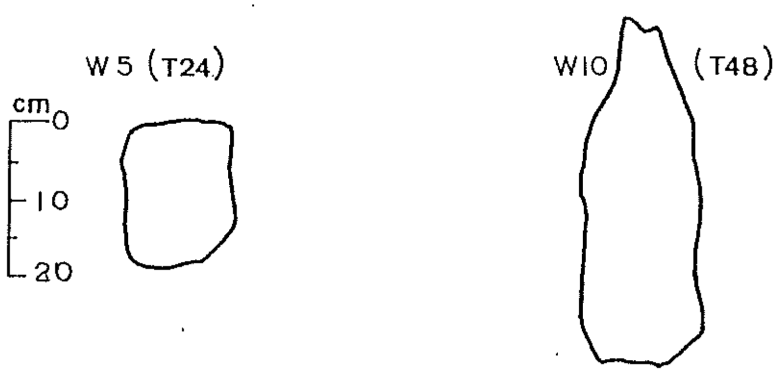
GREAT HORNBILL (1 : 10 Natural Size)
(measured November 1984)



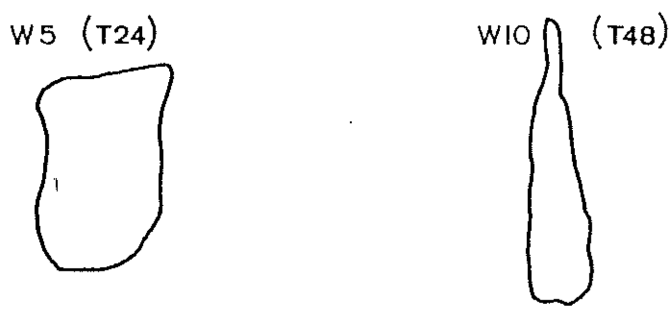
GREAT HORNBILL (1 : 10 Natural Size)
(measured November 1992)



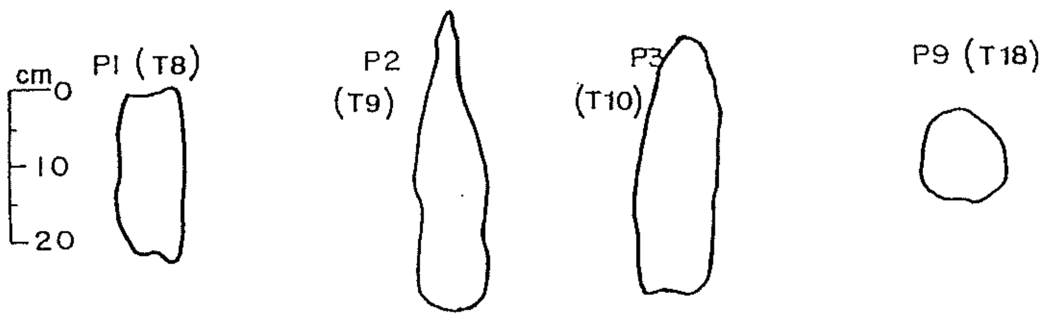
WREATHED HORNBILL (1 : 10 Natural Size)
(measured November 1984)



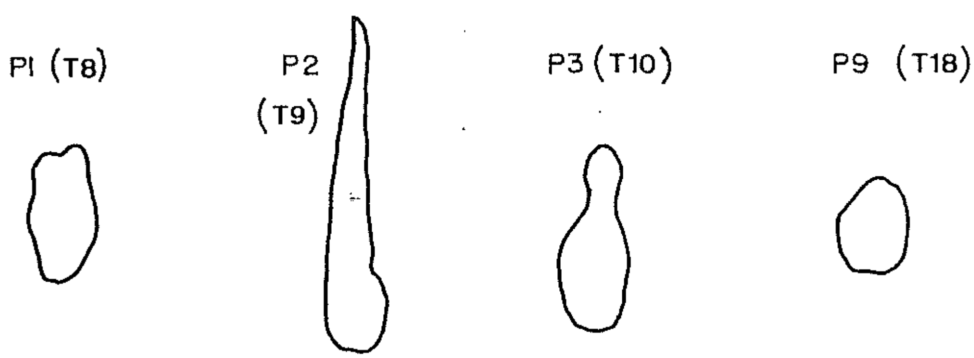
WREATHED HORNBILL (1 : 10 Natural Size)
(measured November 1992)



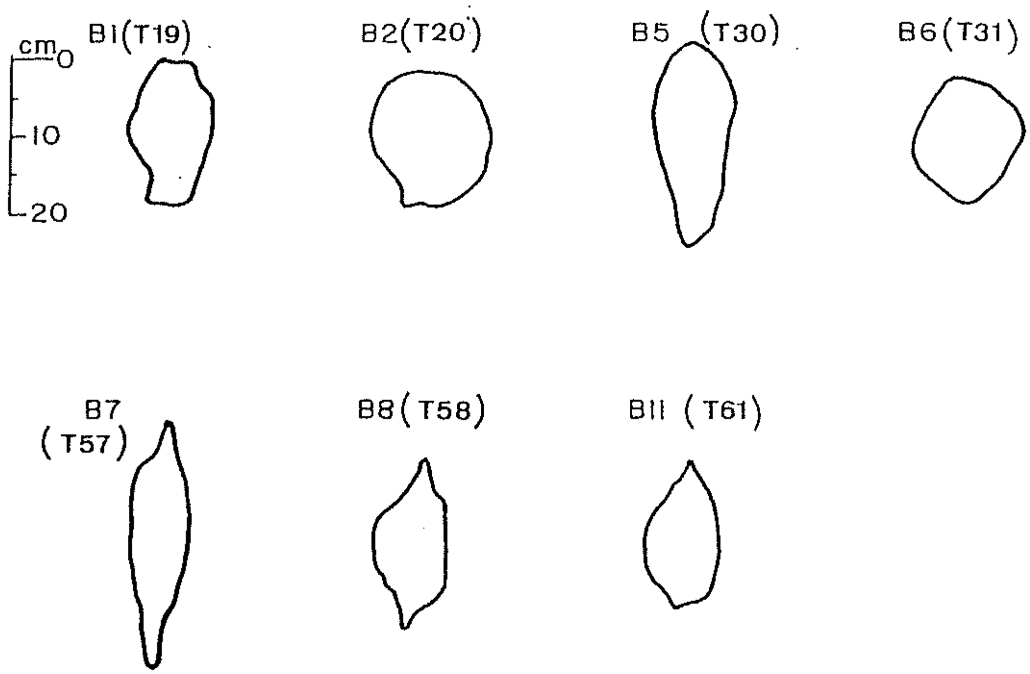
INDIAN PIED HORNBILL (1 : 10 Natural Size)
(measured November 1984)



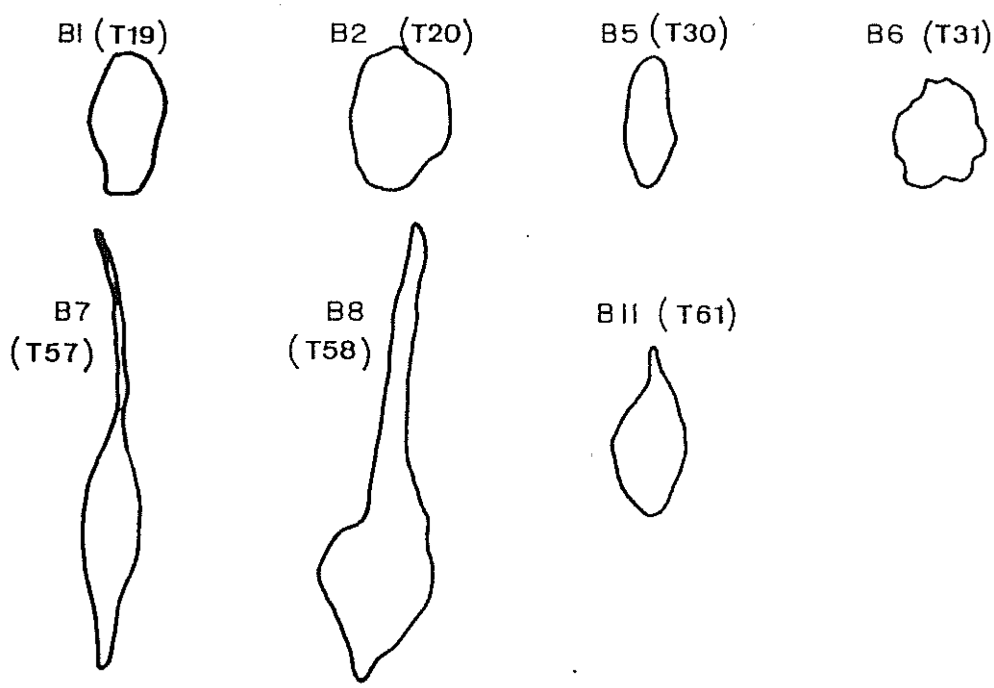
INDIAN PIED HORNBILL(1 : 10 Natural Size)
(measured November 1992)



BROWN HORNBILL (1 : 10 Natural Size)
(measured November 1984)



BROWN HORNBILL (1 : 10 Natural Size)
(measured November 1992)



Appendix 3-1. History of hornbill nest cavities during 1981-1991 in Khao Yai National Park. G = Great Hornbill, W = Wreathed Hornbill, P = Oriental Pied Hornbill, B = Brown Hornbill, S = Successful breeding, U = Unsuccessful breeding, NTB = Nest tree Book, NFS = Nest floor sink, FLD = Nest floor flooded, NEC = Nest entrance closed, NN = Nest entrance narrow, NTC = Nest tree cut by poacher, KC = King cobra, FLS =n 'a0 Red giant flying squirrel, OWL = Owl , X = No entering, - = No data.

Tree #	First occupant species	Year found	Hornbill species use									Remarks
			1981	1982	1983	1984	1985	1988	1989	1990	1991	
1	G	1981	X	NTB								
2	G	1981	G/U	G/U	X	G/S	X	NFS				
3	G	1981	G/S	G/S	G/S	G/S	G/U	G/U	G/U	G/S	G/S	
4	G	1981	G/U	X	X	BEE	X	NTB				
5	W	1981	W/S	W/U	X	G/S	G/S	G/S	G/S	G/S	G/S	
6	W	1981	W/S	G/U	X	G/S	G/U	G/S	G/S	G/S	G/S	
7	W	1981	W/S	W/U	X	X	X	NN	-	P/S	P/S	
8	P	1981	P/S	P/U	P/S	P/S	P/S	P/S	-	P/U	X	
9	P	1981	P/S	P/S	X	P/S	X	X	X	X	X	
10	P	1981	P/U	P/S	X	P/S	P/S	X	P/S	P/U	P/S	
11	P	1981	P/S	P/S	FLD	KC	X	-	P/S	P/S	P/S	
12	P	1981	P/S	X	X	NTB						
13	P	1981	P/S	P/S	X	X	P/S	P/S	-	-	-	
14	G	1982		G/S	X	NFS						
15	W	1982		W/U	X	P/S	P/S	P/S	P/S	P/U	X	
16	P	1982		P/S	P/S	P/S	P/S	NEC				
17	P	1982		P/S	X	X	-	-	-	-	-	
18	P	1982		P/S	P/S	P/S	P/S	-	P/S	P/U	P/S	
19	B	1982		B/S	B/S	X	X	X	X	X	X	
20	B	1982		B/U	X	NFS						
21	G	1983			G/S	G/S	G/S	X	G/S	G/S	G/S	
22	G	1983			G/S	G/S	X	X	G/S	G/S	G/S	
23	G	1983			G/S	G/S	G/U	G/S	G/S	G/S	G/S	
24	W	1983			W/S	W/U	X	X	X	X	X	

Appendix 3-1. (cont.)

Tree #	First occupant species	Year found	Hornbill species use 1981	1982	1983	1984	1985	1988	1989	1990	1991	Remarks
26	P	1983			P/S	P/S	P/S	NTB				
27	P	1983			P/S	-	-	-	-	P/S	P/S	
28	B	1983			B/S	B/S	B/U	NTC				
29	B	1983			B/U	B/S	X	B/S	W/S	W/S	W/S	
30	B	1983			B/S	X	X	OWL	X	B/S	B/S	
31	B	1983			B/S	B/S	B/S	NN	X	X	X	nest entrance was enlarged in 1988
32	G	1984				G/S	G/U	G/S	G/S	X	X	
33	G	1984				G/U	X	G/S	G/S	G/S	G/S	
34	G	1984				G/S	G/S	NTC				
35	G	1984				G/S	G/U	X	G/S	G/S	G/S	
36	G	1984				G/S	G/S	X	X	X	G/S	
37	G	1984				G/S	G/U	NEC	NEC	NTB		
38	G	1984				G/S	X	G/S	G/S	G/S	G/S	
39	G	1984				G/S	X	X	G/S	G/S	X	
40	G	1984				G/S	G/S	G/S	G/S	G/S	G/S	
41	G	1984				G/S	X	NTC				
42	G	1984				G/S	G/S	NTC				
43	G	1984				G/S	G/S	G/S	G/S	G/S	G/U	
44	W	1984				W/S	W/S	W/U	W/U	W/U	W/S	
45	W	1984				W/U	W/S	G/S	NTB			
46	W	1984				W/S	W/S	W/S	W/S	-	W/S	
47	W	1984				W/S	W/S	NTB				
48	W	1984				W/S	FLS	NTB				
49	W	1984				W/S	W/S	NEC				
50	P	1984				P/-	-	-	-	BEE	P/S	
51	P	1984				P/S	P/S	-	-	B/S	X	
52	P	1984				P/-	-	-	-	-	NEC	
53	P	1984				P/-	-	-	P/S	P/S	P/S	
54	P	1984				P/-	-	-	-	NTB		
55	P	[illegible]				[illegible]				[illegible]		

Appendix 3-1. (cont.)

Tree #	First occupant species	Year found	Hornbill species use									Remarks
			1981	1982	1983	1984	1985	1988	1989	1990	1991	
56	P	1984				P/S	X	NEC				
57	B	1984				B/S	B/S	X	B/S	B/S	X	
58	B	1984				B/S	B/S	G/S	G/S	G/S	G/U	
59	B	1984				B/S	B/U	NTB				
60	B	1984				B/S	B/S	X	-	B/S	B/S	
61	B	1984				B/S	X	B/S	B/S	B/S	B/S	
62	G	1985					G/S	W/U	W/S	W/S	W/S	
63	G	1985					G/U	G/S	G/S	G/S	G/S	
64	G	1985					G/S	-	X	X	G/S	
65	W	1985					W/S	-	W/S	X	W/S	
66	P	1985					P/S	NTB				
67	P	1985					P/-	NTB				
68	P	1985					P/S	P/S	P/S	P/S	-	
69	B	1985					B/U	B/S	B/S	B/S	B/S	
70	G	1988						X	X	G/S	G/S	
71	W	1988						W/S	W/S	W/S	W/S	
72	W	1988						W/S	W/S	W/S	W/S	
73	W	1988						W/S	X	X	X	
74	B	1988						B/S	B/S	B/S	B/S	
75	G	1989							G/-	-	-	
76	P	1989							P/S	-	P/S	
77	P	1990								P/S	P/S	
78	P	1990								P/S	P/S	
79	B	1990								B/S	B/S	
80	P	1991									P/S	

CHAPTER 4

BREEDING BEHAVIOURS OF HORNBILLS

INTRODUCTION

Breeding is the part of the life cycle of birds which relates most intimately to the environment. In other organisms, there may be a very restricted time-span for favourable conditions as for example, cold-blooded animals are capable of interrupting their reproductive cycles at different stages of egg, embryonic or larval development by inserting states of rest or encystment (Immelmann 1971). These animals are therefore capable of distributing the whole cycle into different favourable conditions, allowing the adjustment of physiologically important functions to favourable periods of the year. Because of its serious physiological demands, reproduction must be a period when stress is minimum and survival of parents and young is maximum. Birds, however have developed great adaptations to the changes in environmental conditions.

The majority of birds have definite breeding seasons with almost regular intervals, at approximately the same time every year (Immelmann 1971). Lack (1968) pointed out that the period of egg laying is subjected to geographical area rather than to particular species or family. In temperate zones most species start laying eggs in spring and have young in late spring to early summer (Lack 1950). In contrast, in tropical regions there is no particular pattern of breeding season due to greater heterogeneity of ecological complexes and breeding activity of various species may be observed throughout the year. Furthermore, geographical variations in the period of reproduction tends to be much greater than in the temperate zone (Baker 1938, Lack 1954, 1968, Miller 1960).

Breeding time of the hornbill species examined in this study in different geographical areas is shown in Appendix 4-1. The differences may indicate the availability of particular stimuli in certain seasons. An escapable question is what is the trigger for the onset of breeding in these hornbills in Khao Yai?

In this chapter, therefore, I investigate 1) the beginning of the breeding season, 2) different phases in the breeding cycle, which includes pre-nesting, nest sealing, imprisonment, egg-laying and incubation, and fledging), and 3) breeding behaviours.

METHODS

Pre-nesting phase

Known cavities of 23 nests of the Great, 15 of the Wreathed, 17 of the Oriental Pied and 11 of the Brown hornbills were visited prior to the beginning of the breeding season, at intervals of 1 to 30 days, from 1981 to 1991 (except 1986, 1987). Actual observations were made at nests by using binoculars and/or a spotting scope. The observation period at a nest varied from 1 to 8 hours per observation day with a total of 298 hours. All behaviours of the breeding pairs performed at the nest site were recorded.

Attempts to identify individual breeding pairs returning to the nests of previous years were made using photographs and sketches of the head parts, bill casques, etc., combined with behaviours and positions when feeding. Intra- and interspecific competition were also investigated. The key parts which assisted in more accurate individual identification were as follows.

Great Hornbill: The shape of the casque, the pattern of black colour on the front part of the casque, and the proportion of the bill and the casque.

Wreathed Hornbill: Identification of individuals was made by counting the number of ridges on the casques, as well as the shape of ridges. Besides, as noted by Frith and Douglas (1978), it was possible to estimate the age of each individual based on this character since one ridge indicates one year of age, although the number of ridges does not increase with age any more at a certain age.

Oriental Pied Hornbill: The shape of the casque, the pattern of black colour on the front part of the casque, and the patterns and colour of the facial skin.

Brown Hornbill: The shape of the casque, the proportions of the casque and the bill, the mark and colour of the orbital skin, and the patterns of varying colour of plumages on the upperparts and throat.

Whenever a breeding male was trapped for radio-tagging, extra marking was made using colour paint on the bill and/or the casque. All materials brought by the male or used by the female were identified while observing sealing behaviour. Nest plaster was collected from the nests of all four species at the end of breeding cycle. Except for the Great Hornbill, the plaster was collected at two different stages, i.e. after the emergence of female and at the fledging of chicks.

Composition of plaster

The composition of plaster was analysed by breaking it and soaking in water. Then the separated materials were examined under a dissecting microscope. The plaster was also ground and weighed in a 17 cc container.

Phases of breeding cycle

To determine the imprisoning, egg laying, incubating and fledging periods, the observations were made at an interval of 1 to 4 days. The behaviours of both breeding males and females were recorded throughout the breeding season from 7:00 to 17:00 hours.

Analysis of weather data

The weather data from 1981 to 1990 were obtained from the Meteorological Department at Nakhon Ratchasima Station. Cumulative precipitation, average temperature and relative humidity at different times of the year were analysed with reference to various phases in breeding cycle, i.e. onset of breeding (November to December), imprisoning phase (January to March), entire breeding cycle (January to May), and non-breeding season (June to October).

RESULTS

Availability of nest cavities

The most important factor for breeding of hornbills was the availability of suitable nest cavities (see Chapter 3). The cumulative number of nests found, nest losses and annual existing nests during 1981-1991 (except 1986 and 1987) are presented in Table 4-1 Nest trees was most abundant in 1985. The numbers of nests in existence seemed to be stable from 1988 onward. The percentage of nest existence was highest in 1983 and began to decline since. In 1988, there was a remarkable declining in nest existence (Table 4-1).

Nest reuse

All four species were observed to reuse nest cavities year after year. Ratios of nest reuse by hornbill species and by year from 1982 to 1991 (except 1986, 1987) are given in Table 4-2. Great Hornbill reused the previous nest cavities most (0.7), whereas Wreathed and Brown hornbills reused nest cavities at the lowest ratio (0.54). Annual reuse by all four species was markedly low in 1983 (0.26), whereas the nest reuse ratio for the four species combined was 0.62 (Table 4-2).

Among 80 nest trees examined in the nine years of the study, only 6 nest trees (7.5 %) were reused for more than 5 consecutive breeding seasons by the same pair (4 Great, one Wreathed and one Brown hornbills), regardless of breeding success (see also Appendix 3-1 in Chapter 3).

Pre-nesting phase

Breeding occurrs once a year for all four species of hornbills and begin in the dry season (Fig. 4-1). Before female hornbills were imprisoned in a nest cavity, the breeding pair had to prepare themselves and the nest cavity. The pre-nesting phase is defined as the period during which a breeding pair showed attempts to nest, prior to imprisonment of the female. This phase included various activities such as nest visiting, courtship displays, nest preparation, copulation, and nest sealing, and extended from the end of December to mid February in the two larger species and from late January to late March in the two smaller ones.

Nest visiting or nest searching was usually performed by the pair or by the male, although females were also seen seeking nest cavities in the Wreathed Hornbill (3 cases). Flocks of Brown Hornbills were observed visiting the nests with the breeding pair(2 cases). The larger and smaller species of hornbills differed in the nest visiting period.

The larger species (Great and Wreathed hornbills): These two species (13 pairs and 6 pairs, respectively) began to visit or seeking for nest cavities as early as the first week of January until the last week of that month.

The smaller species (Oriental Pied and Brown hornbills) These two species had a longer seeking period than the larger species. Oriental Pied Hornbills (5 pairs) were observed visiting nest cavities as early as mid January until early March. The Brown Hornbills (7 pairs) were observed visiting nest cavities as early as the last week of January until late February.

In all cases (13 Great, 6 Wreathed, 5 Oriental Pied and 7 Brown hornbill pairs), either males or females or both were seen inspecting inside nest cavities by sticking their heads into the cavities.

The identification of the pairs was rather difficult, because breeding males were identified but females were not easily recognized individually. Observation of the females during this period very short and difficult, because they mostly either stayed secretively and quietly on a bushy branch or inside the nest cavity.

Examining photographs, sketches and various behaviours, it was known that the breeding pairs of the Great, Oriental Pied and Brown hornbill breeding pairs remained the same throughout the study period once they occupied the nest cavities.

Courtship display

Courtship display was observed in all species and was often seen at the nest sites. The behaviours included 1) the male flew around the nest tree and frequently flew from a perch to the nest cavity, which observed in 12 Great, 3 Wreathed, 5 Oriental Pied and 3 Brown hornbill pairs as if to persuade the female to inspect the nest cavity, 2) the male pecked the nest entrance, which observed in 10 Great, 5 Oriental Pied and 3 Brown hornbill pairs as if to enlarge it for the female to enter, 3) the male fed the female, which observed in all species except the Wreathed Hornbill (number of pairs same as in 2), and 4) the male stayed in body contact with the female, and rubbed his bill with hers, which was observed in Great (4 pairs) and Oriental Pied hornbills (2 pairs). The courtship display of the female was observed in the Great Hornbill; she beat her bill on the side of a branch as if she were practicing sealing of the nest entrance. The courtship feeding of the Great Hornbill did not occur daily at the nest site, sometimes observed in fruiting fig trees. However, the above described behaviours may be similar in all hornbills. Since they were secretive when breeding, (only breeding pairs within the nest sites) it was observed that in the presence of other hornbill species or other pairs, no courtship display were performed. But the breeding pair turned to show nest territory defending behaviours instead (see Chapter 7).

Preparation of nest cavities

This activity was performed mostly by the females in all four species. Before the nest entrance was sealed, the female removed the old remaining plaster, entered the cavity and then threw out nest debris of the previous year. The nest debris included fruit seeds, food remnants, old feathers, rotten wood dust, and some other unidentified items. The level of the nest floor was adjusted and the nest wall was scraped as well as excavated. This period lasted in a few days to one week, perhaps depending on the frequency of work of the female at the nest.

Copulation

Copulation took place during the periods of nest cavity preparation and nest sealing. Most copulation occurred either on the nest tree or on an adjacent tree. Therefore, it was difficult to observe. However, the copulation of 2 pairs each the of Great, Oriental Pied and Brown hornbills were observed. No copulation was observed for the Wreathed Hornbill. Hence, the Wreathed Hornbill may copulate in a more secretive environment, such as in the top of dense canopy away from nest trees. Copulation was performed in a similar manner in all three species observed.

In the case of the Great Hornbill, copulation was seen for two consecutive days while the female practised sealing outside the nest cavity. The male chased her from branch to branch and after she stopped escaping, the male pressed her down with his beak and stepped on her back. There was no bill beating while copulating. The copulation took about - 10-15 seconds. Copulation may occur as many as four times in a day. This frequency of copulation was observed in a pair of the Brown Hornbill. The male copulated with the female while she intermittently emerged from nest sealing work.

It was still unknown whether the day of imprisoning related to copulation. The period from copulation to imprisonig varied greatly. Two females of the Great and one of the Brown hornbills, were imprisoned a few days after the latest copulation was seen. But another female of the Brown Hornbill was imprisoned one month after copulaton was observed.

Two cases of the Oriental Pied Hornbill, copulation and imprisoned dates were recorded. In the first case, copulation was observed on 26 February and the female imprisoned on 10 March, about 2 weeks after copulation. In the second case, the latest copulation was observed on 18 February, and the female was imprisoned on 20 February.

Nest sealing

The nest sealing activity was performed entirely by the female (15 pairs of Great, 7 Wreathed, 10 Oriental Pied and 9 of Brown hornbills were observed). Some males (4 Great, 5 Oriental Pied and two Brown hornbills) were observed to supply plaster materials, i.e.bark, mud, rotten wood, and fruits.

Great Hornbill: Males supplied chewed tree bark, pieces of rotten wood and fruits. No mud was brought in.

Wreathed hornbill: Males were observed bringing only fruits to females.

Oriental Pied Hornbill: Males brought mud to females in all observed cases. One breeding male was observed bringing pieces of dry mud, on up to 20 trips in one day. At two nests the males were seen digging dry mud from the bank of a creek or struggling to remove the mud from the roots of a fallen tree. At 12 nests males brought some pieces of dry mud to females even during feeding of the brood. During such periods the females of these nests were observed plastering nest entrances.

Brown Hornbill: Males were observed to supply females the materials similar to those of the Great Hornbill.

While the female was sealing the nest entrance, the male usually stayed to accompany her and fed her intermittently. During this study, the sealing process of all species took 3 to 10 days or even longer. The female may not come to seal the nest entrance everyday. When she came, she spent about 1 to 2 hours for sealing. She occasionally imprisoned herself temporarily several times before she was permanently imprisoned.

Composition of plaster

The materials used in nest plastering varied with the species. However, it was found that the plaster of all species consisted chiefly of four kinds of material: 1) mud, 2) wood dust, 3) tree bark and pieces of wood, and 4) food debris. The proportion of these materials varied according to the species (Fig. 4-2).

Great Hornbill: From an analysis of plaster samples collected at two periods, it was found that the materials used and the proportions of different materials in the samples were very similar. at a glance, the plasters was hard and tough but crumbly in some parts and not homogenous. It was rather light with weight of 0.5 g/cc on average (14 samples). Every sample contained wood dust, pieces of wood and food debris in relatively equal proportion, but very little mud was incorporated.

Wreathed Hornbill: The plaster consisted of a large amount of wood and food debris with a smaller amount of wood dust and mud. The average weight was 0.5 g/cc and the plaster was hard and crumbly and not homogenous (8 samples).

Oriental Pied Hornbill: The plaster was as hard as rock and were rather homogenous. It was the heaviest, with weight 0.8 g/cc on average (7 samples), and was consisted of about 90% of mud.

Brown Hornbill: The plaster was similar to that of the Wreathed Hornbill. It was hard and weighed 0.4 g/cc on average (4 samples). The proportions of wood dust, wood pieces and food debris were roughly equal.

Besides the four main components, the plaster sometimes contained pieces of old feather and stone fruit seeds, indicating that nest debris was also used. Food debris consisted mainly of fig seeds, old fruit skins, and insect parts, which suggested that faeces and food regurgitates had sometimes been incorporated. Direct observations confirmed the use of faeces in the plastering process.

Competition for nest cavity and nest abandonment

Competition usually occurred during the nest visiting and nest sealing periods, which were the most critical period for nest abandonment. However, competition for tree cavities with the invaders, which attacked the imprisoned females, was also observed during the egg incubation and chick raising periods, particularly in Brown Hornbills (3 cases).

It was found that competition over tree cavities was rather common (45.4 %) and may result in nest abandonment (53.3 % of the competed nests) (Tables 4-3 and 4-4). Among the four sympatric species of hornbills, both intra- and interspecific competition were observed. Competition mostly occurred interspecifically (23 nests or 79 % of a total of 29 nests). This resulted in 43 % of the 23 cases of abandoned nests (Table 4-4). Intraspecific competition was observed in Wreathed (3 cases) and Brown hornbills (2 cases). In all cases vigorous fighting was observed, but in two case of the Wreathed Hornbill fighting cause nest abandonment. Fighting between individuals of the same species occurred in such a way that the invading females insistently and fiercely attacked the imprisoned females and cracked the nest plaster. In one case in the Wreathed Hornbill, the invading female attacked the breeding male as well. Attacking by the invading female must have been vigorous as bill beating sounds were heard at least within 100 m.

Competition for nest cavities occurred not only among hornbills but also between hornbills and other cavity-inhabiting animals and insects. These were bees (Apis sp.), resinous bees (Trigona sp.), monitor lizards (Varanus sp.), Red Giant Flying Squirrels (Petaurista petaurista), and King Cobra (Ophiophagus hannah)(Table 4-4).

The followings are anecdotal information on cavities for which competition was observed. (see also Appendix 3-1):

T4 was used by a pair of the Great Hornbill in 1981, and the chick was removed by a child but died after being returned to the nest. In the following breeding season (1982), the pair examined the site but did not attempt to nest as the nest hole was occupied by resinous bees.

At T5, in the 1982 breeding season, two female Wreathed Hornbills competed with each other. Fighting occurred between the breeding male and an intruding female. This resulted in nest abandonment in 1982 and 1983. In 1984, the Great Hornbill competed with the Wreathed Hornbill and the former species has taken this nest cavity until the present.

At T6 in 1982, the Great Hornbill competed with the Wreathed Hornbill, and the Great occupied the nest but the breeding was unsuccessful. In 1983, the Great and Wreathed hornbills competed again at this nest and disturbed each other, resulting in nest abandonment.

At T7 in 1984, the nest was visited by the pairs of the Oriental Pied and Wreathed hornbills which disturbed each other and neither used the nest. Until 1988, the original nest entrance was narrow. In 1990, however, a pair of the Oriental Pied Hornbill used this nest cavity by entering through the artificial observation hole which was made in 1982.

T8 was visited in two consecutive breeding seasons (1988 and 1989) by two pairs of hornbills, Oriental Pied and Brown hornbills, which disturbed each other. The pair of Oriental Pied Hornbill visited the site consistently and showed insisting, aggressive and territorial behaviours more than the Brown Hornbill. From photographs and sketches of this Oriental Pied pair, it was believed to be the former occupant, and eventually they occupied the nest. The cavity was occapied by _Varanus_ sp. during the non-breeding season of 1984. But, finally, when the pair of Oriental Pied Hornbill visited the nest at the beginning of the breeding season 1985, the lizard was expelled by the female and the pair eventually nested with successful breeding.

At T24 in 1984, two pairs of the Wreathed Hornbill were seen competing each other. The two females were imprisoned after one another. The first female entered on 9 February and remained either inside or outside the nest cavity until 26 March, before deserting the nest. The second female, which was identified by a different number of ridges on the casque, behaved in the same manner and stayed from 4 to 14 April and deserted the nest as well. This cavity was vacant after that event until 1991.

T29 was occupied for about one month by a pair of Oriental Pied Hornbill during early breeding season, in 1984 but a female Brown Hornbill was found imprisoned later in the same season. From 1989 to 1991 a pair of Wreathed Hornbill occupied this site.

T33 was visited by Great, Wreathed, Oriental Pied and Brown hornbills in 1985. All species were seen inspected the inside of the nest cavity. The Brown Hornbill female even began to seal, but did not complete the sealing and resulted in nest abandonment later in that year. It was interesting to note that this nest entrance was large enough for the male and female of Brown Hornbills to enter the cavity at the same time.

At T70, in 1988, a pair of the Great Hornbill was observed attacking a Oriental Pied Hornbill female which was sealing this nest cavity and resulted in nest abandonment.

The dbh of nest trees which competition occurred were studied. The range and mean $\pm$ 1SD of dbh of the competed and non-competed nest cavities were; 51-150 cm, 86.54 ± 26.29 cm (n = 24) and 46-267 cm 103.29 ± 37.58 cm (n = 49) respectively. For dnh, the results were; 40-210 cm, 67.41 ± 34.68 cm (n = 22) and 40-250 cm, 78.8 ± 36.16 cm (n = 45) respectively. The nest cavities that had competition were significantly smaller than the non-competition nests at the mean size of dbh and dnh (U = 420.0, $n1$ = 24, $n2$ = 49, $P < 0.05$; U = 345, $n1$ = 21, $n2$ = 45, $P < 0.05$, respectively). Hence nest cavities with means of dbh 86.5 cm and dnh 67.4 cm are the sizes which may accommodate females and broods of all four species.

It is interesting to note that there was no intra-specific competition for nest cavity had been observed between the Great or Oriental Pied hornbills.

The annual nest cavity abandonment ratio for all four hornbill species due to all causes (including disturbances by humans and arboreal animals such as Yellow-throated Marten Martes flavigula) was highest in 1983 (0.45) and lowest in 1984 (0.14) (Table 4-5). Among the four hornbill species, the Wreathed Hornbills abandoned nest cavities most frequently when either a competition or disturbance occurred. Interspecific agonistic interactions are shown in Table 4-6. The winner for nest cavities was the Great and the loser was Wreathed hornbills. Oriental Pied Hornbills did not lose or gain.

Female imprisonment

There was a clear relationship between the imprisonment of female hornbills and dry day. The majority of females of all four species were imprisoned on days with no or little rain (Fig. 4-3).

The larger species: The Great (n=28) and Wreathed (n=13) hornbills had the same peak period for imprisonment, i.e. 11-20 January. In these two larger species female imprisonment occurred one month earlier than in the two smaller species (Fig. 4-4a).

The smaller species: The peak of the imprisonment period was 11-20 February in the Brown Hornbill (n = 12) and 21-28 February in the Oriental Pied Hornbill (n=14).

Among these four species the imprisoning period overlapped for about one month long, from 21-31 January until 11-20 February (Fig. 4-4a). The highest frequency (mode) of imprisoning occurred on 17 January (n=7), 14 January (n=5), 20 February (n=5), and 18 February (n=6), for the Great, Wreathed, Oriental Pied and Brown hornbills, respectively.

Pre-laying phase, egg laying and clutch size

The pre-laying phase is defined as the period from the imprisonment of female to egg laying. The exact egg laying dates were known from one nest of the Oriental Pied Hornbill in 1984 and 1985 breeding seasons and one nest of the Wreathed Hornbill in 1982. The female Oriental Pied

Hornbill was imprisoned exactly on the same day, on 20 February, in both years. In these years, the first egg was laid on the same day, on 27 February. In 1984, the female laid the second and third eggs on 29 February and 4 March respectively. But in 1985, the second egg was laid on 2 March. Therefore, the egg laying interval ranged from 2 to 3 days. The pre-incubation phase of the Oriental Pied Hornbill took exactly 7 days.

In 1982, a Wreathed Hornbill female laid the egg on 20 February; thus, the pre-incubation phase was 9 days. But she abandoned the egg on 25 February, since the male ceased to feed her for unknown reasons for 2 days before she emerged. Thus, the incubation period for the Wreathed Hornbill is still unknown.

The clutch size seemed to be correlated inversely with the size of hornbills, i.e. the larger species had smaller clutch sizes. The known clutch size of the Great and Wreathed hornbills was only one (n=3 and n=2 respectively). The biggest clutch size of the Oriental Pied Hornbill was 3 eggs (recorded from 2 nests). The clutch size of the Brown Hornbill was 2-3 eggs (from 2 nests).

Egg incubation

The incubation period is defined as the period from the completion of egg laying to the day chick hatching. The exact period of egg incubation was known from one nest of the Oriental Pied Hornbill in two breeding seasons. The incubation period of 2 clutches (5 eggs) ranged from 24 to and 24 March. In 1984, three chicks hatched on 23, 26 and 29 March and in 1985 two chicks hatched on 26 and 28 March. Thus, these Oriental Pied Hornbills hatched around week 5 after female imprisonment.

The incubation period of the other species is unknown. However, the dates when sounds made by chicks of these species were first detected varied from the first week of March to the first week of April. But there were also records of chick sounds detected late in April. Thus, on average, chicks of the Great and Wreathed hornbills must have hatched around week 7 or 8, and for the Brown Hornbill around week 4, after female imprisonment.

Clutch sizes and incubation periods of the four hornbill species reported from elsewhere are compared with results in the present study in Appendix 4-2.

Nestling phase

The nestling phase is defined as the period from the chick hatched to chick fledging. It varied in 58 to 97 days for the Great, 62 to 112 days for the Wreathed, 44 to 53 days for the Oriental Pied, and 66 to 71 days for the Brown hornbills.

Emergence of the female

The usual emergence of female from the nest occurred before chick fledging in all Great Hornbill nest observed. The emergence dates varied from 25 March to 13 May, with a peak being between 1-10 April. Thus female Great Hornbills emerged about 40 days after chick hatching. A single chick (n = 23 nests) was observed to reseal the nest entrance by itself immediately after the female emerged. The materials used were food brought by the parents mixed with its own feces. Although I did not observe either the male nor female bring any piece of wood to the chick, wood and tree bark were found incorporated in the nest plaster. The speed at which the chick resealed the nest entrance is given in Figure 4-5. The speed of resealing was remarkably high on the day just after female emerged.

It was unusual for the female Oriental Pied and Brown hornbills to emerge before the young fledged (known only in one nest for each species). In these two cases, the nest entrances were not resealed by the chicks.

Chick fledging

Behaviours of the female may indicate the approach of fledging from a few hours up to few days before the actual emergence occurred. She may begin to crack the nest plaster and then reseal it. Sometimes she may thrust herself out as if to test whether she can pass through.

The order and interval of emergence was always the same. The female usually emergeed first, followed by a chick or chicks (Oriental Pied and Brown Hornbills have more than one chick in a nest). However, the chicks emerged first in several cases (4 Wreathed, 5 Oriental Pied and 3 Brown hornbills) . In at least 5 cases of the Oriental Pied Hornbill, the females emerged up to 20 days before the last chick fledged. The chicks of the same brood may fledge on different days depending on their growth.

The fledging time counted from cracking of the plaster to chick emerging, may take from a few hours up to 2 weeks. Chicks of all four species usually fledged before noon (n = 31). The earliest fledging time was before 6.00 am (1 nest of Wreathed Hornbill) and the latest fledging time was about 11.00 am (2 Great and 1 Oriental Pied hornbill nests) It seemed that chicks avoided fledging on rainy days (Fig. 4-6).

The fledging period was similar in all species (Fig. 4-4a). The mode of fledging dates for the Great, Wreathed, Oriental Pied and Brown hornbills was the same, on 18 May. (n = 6, 4, 4 and 3, respectively). The schedule of chick fledging of individual species was as follows:

Great Hornbill: The earliest date of fledging was between 21 and 30 April and the latest was 14 June.

Wreathed Hornbill: The earliest and latest dates of fledging were 7 May and 28 June, respectively.

Oriental Pied Hornbill: The earliest and latest dates of fledging were 14 April 11 June, respecttvely.

Brown Hornbill: The earliest and latest dates of fledging were 2 May and 16 June, respectively.

Breeding cycle

The breeding cycle is defined as the period from female imprisonment to fledging of the young. The means and SD of the period for all four hornbill species are given in Figure

4-4a and 4-4b. The Wreathed Hornbill had longest breeding cycle of about 18 weeks (129.3 ± 11.4 days) on average and the Oriental Pied Hornbill had shortest of about 12 weeks (82.9 ± 6.8 days) on average.

All phases in the breeding cycle of these four sympatric hornbill species can be summarized as follows (see also Fig. 4-1):

1. The pre-nesting phase varied from 1 week to 3 weeks, for all four species.

2. The pre-laying phase, which was known for the Wreathed and Oriental Pied hornbills, took about 1 week (9 and 7 days, respectively).

3. The incubation phase took about 7 weeks for the two larger species and about 4 weeks for the two smaller species after the female was imprisoned.

4. The nestling phase took 8 to 13 weeks for the Great, 9 to 16 weeks for the Wreathed, 6 to 8 weeks for the Oriental Pied, and 9 to 10 weeks for the Brown hornbills.

5. The fledging phase may take from a few hours up to two weeks.

Breeding success

Any nesting attempt in which at least one chick fledged was defined as "successful breeding", regardless of mortality that may occur after the fledging. Breeding success was indicated by the ratio of successful pairs to the total of known breeding pairs (Table 4-7). In total, breeding success of all four hornbill species was rather high (0.87). The Wreathed Hornbill had the lowest breeding success (0.78). There was no significant difference between breeding successes of the larger and the smaller species (χ^2 = 2.824, df = 1, $P > 0.05$). The annual breeding success ratio was lowest (0.59) in the 1982 breeding season and highest (0.95) in 1991.

Chick production

Throughout the present study, 66 pairs of the Great and 27 pairs of the Wreathed hornbills produced only one chick per breeding pair. The Oriental Pied Hornbill produced 1 to 2 chicks per breeding pair with an average of 1.5 chicks per pair (n = 12). The Brown Hornbills produced the highest number of chicks, varying from 1 to 3 chicks per breeding pair, with an average of 2.6 chicks per breeding pair (n=15).

From the average annual existing nest cavities of the four hornbill species, the annual expected number of chicks produced by each species within the study site was derived and is shown in Table 4-8. The Brown Hornbills produced the highest number of chicks annually (19.9 chicks).

Predation and mortality

Predation on breeding hornbills or chicks during the breeding season seems to be highly improbable due to protective habit of sealing the nest entrance. However, predation was actually observed at a Brown Hornbill nest, which had two chicks but no helpers (see cooperative breeding below).

fledged. After the female emerged, the chicks did not reseal the entrance as do Great Hornbill chicks. The chicks were later killed by a Yellow-throated Marten *Martes flavigula*, which are apparently an important enemy of breeding hornbills. They were observed to climb up on 5 Brown, two Great and one Wreathed hornbill nests. At a Wreathed Hornbill nest a marten caused nest abandonment by disturbing the pair and the chick was killed later. A marten also killed a Great Hornbill chick , before the chick resealed the nest entrance after the emergence of female.

Large-billed Crows *Corvus macrorhynchos* were observed to attack newly fledged Oriental Pied Hornbills (reported by a park officer). One newly fledged Great Hornbill was attacked by an unknown enemy very late at night (reported by a ranger). After inspection of the wound, it was clear that the chick may have been attacked by a very large night bird of prey. The most probable nocturnal bird of prey in this area is the Spot-bellied Eagle Owl *Bubo nipalensis*, which is a resident bird within the study site.

Poaching of hornbills in the National Park area was not intense but has been reported. Records of mortality and causes of death of the four hornbill species are shown in Table 4-9. During nine years of observations, the known minimum mortality rate was 3+ hornbills per year.

Age of breeding hornbills

It was difficult to determine the ages at which hornbills breed. In this study, only the ages of breeding Wreathed Hornbills were determined. Numbers of ridges on the casque of breeding Wreathed Hornbills were recorded for both males and females, and they were found to vary from 3 to 10 (13 males, 6 females). The greatest number, 10 ridges, was recorded from only one male. This number indicated that the male was at least 10 years old. Five males had 6 ridges, three males had 5, three males had 4 and one male had 3. The youngest breeding male was thus estimated to be 3 years old.

The number of ridges on the casques of 6 breeding females varied from 3 to 7. The youngest female imprisoned had 3 ridges. Two females had 6 ridges and three had 7 ridges. The breeding pair may be of same age (1 pair) or of different age (2 pairs), and a pair could be one to two years different in age (3 pairs).

Parental care strategy

Although hornbills are well known for their brood caring by males, the parental care of hornbills differs with species. From my observations it was found that there were 3 types of parental care.

Father care: This type of caring strategy was observed in the Wreathed and Oriental Pied hornbills, in which only breeding males took care of the female and brood throughout the breeding cycle. The duties included feeding the female and brood, chasing invaders (territory defence), and cleaning the front of the nest cavity. In only one pair of the Oriental Pied Hornbill, in which the female emerged shortly before the chick fledged, did the female help her mate feed the two chicks. However, the feeding by the female was not frequent.

Biparental care: This type was observed only in the Great Hornbill, and the female emerged ahead to help her mate feed the brood (only one chick). Feeding to the chick by the emerged female is regular and frequent in this type of care (see also Chapter 6). After female emergence, both the male and female shared duties in caring for the chick, in the same manner as the male in Type I.

Cooperative care: This type was observed in the Brown Hornbill. The observations at 12 nests had shown that breeding males normally had other individuals helping at the nests. However, not every breeding pair had nest helpers and the number of nest helpers varied from 1 to 5 individual males, with an average of 2.3 helpers per breeding pair (N=21 pairs). The helpers participated in feeding the brood, guarding the nest, and chasing intruders.

Time budget of the breeding male hornbill

After female imprisonment, the major activities of males included foraging, feeding the female and brood, and nest guarding. The proportion or percentage of the daily time budget spent by a breeding male on these activities is time budget spent by a breeding male on these activities is summarized in Figure 4-7. Time spent at the nest site and absent from the nest site was not significantly different between the larger and the smaller species (χ^2 = 3.34, df = 1, $P > 0.05$). When the male was absent from the nest site, it was likely that he was on foraging and travelling from the nest to the food source. As the breeding male came into the nest site, he may either feed or may not feed the brood. If he did not feed, he behaved as if he came to stay guarding the nest, by sitting on a high perch in the nest site or on a perch near the nest cavity.

All four species spent similar time on feeding, although. Brown Hornbills spent slightly longer time for it (3.23 %). It should be noted that the smaller species fed the brood immediately upon arrival at the nest and left the nest site as soon as feeding was finished without wasting time or doing other jobs.

DISCUSSION

Onset of breeding

In Khao Yai the drought after 5 months of heavy rain was an important stimulus for the onset of breeding and later imprisonment of female hornbills. These dry months before the imprisonment should secure drier conditions of the nest cavity, rather than to be related to the availability of nest plaster materials as it was explained earlier by Poonswad et al. (1987).

A nest of the Oriental Pied Hornbill was flooded with water and resulted in nest abandonment. It is apparent (Appendix 3-1, in Chapter 3) that hornbills need drier nest cavities. The hypothesis is supported by Kemp (1976), who also suggested that flooding could cause nest abandonment in Tockus hornbills. Furthermore, Moreau (1936) observed that the Silver-cheeked Hornbill, Bycanistes brevis used tree bark as lining material to protect eggs from the damp conditions on the nest floor. In another case, an imprisoned female Wreathed Hornbill was observed regurgitating stone fruit seeds inside the nest, perhaps to cover the damp nest floor (Poonswad et al. 1983).

On the other hand, Kemp (1973) observed that rainfall appeared to be an important factor which made mud available as nest plaster material, as well as being related to food supply and thus affecting the onset of breeding African Tockus spp. North (1942) suggested that the availability of suitable nesting materials may stimulate the nest sealing behaviour in African hornbills.

The drought may also be related to flowering of wild fruit trees which eventually producing fruits during the breeding season. Unfortunately. there was no intensive study of whether flowering and fruiting of trees in Khao Yai was related to the drought and/or preceding-year rain. However, Smitinand (1977) reported 22 species of trees and 23 species of shrubs in Khao Yai flower in the dry season, i.e. February and March. It is believed that drought, short day-length and low temperature are important stimuli for flowering of many trees in tropical forest (Garner and Allard 1923, Coster 1925, 1926, Webb 1958 and Schulz 1960). Such conditions occur from November through February in Khao Yai area (Fig. 2-6, Chapter 2).

Besides physical environmental factors, McClure (pers. comm.) suggested that the onset of breeding be stimulated by visualization of others as often the case of colonial breeding breeding birds.

Difference in timing of breeding season

The breeding season of Asian hornbills in different geographical areas is likely to be affected by distinct seasonal changes, either from wet to dry or from dry to wet. These changes are brought about by monsoons, though there is no distinct seasons in Malay Peninsula. But in Malaysia, birds particularly hornbills still do not breed at any time of the year. This should strongly indicate that there must be other factors influencing the onset of breeding, two of which could be the long breeding cycle or the long time for which the chick is dependent , and the most abundant food period. The seasonal changes may trigger food production, such as the fruiting of wild trees, and increase the abundance of invertebrates including insects (Kemp 1973, Whitmore 1984) and the availability of plaster material (Kemp 1973).

Latitude seems to have an effect on the timing of onset of hornbill breeding season. Breeding starts earliest in tropical regions north of the equator, next in subtropical regions and last in tropical regions south of equator. This is, perhaps, related to seasonal changes in such regions. In Sumba Island, Indonesia, the Sumba Hornbill Rhyticeros everetti begins to breed in September (Juhaeni, pers. comm.), which is the rainy season there.

These hypotheses are partly supported by Thompson (1966) who observed that the majority of birds in North Borneo bred in the driest months, June to August. In contrast, the breeding season of birds from other tropical regions such as East Africa was found to coincide with rainy seasons (Immelmann 1971, Kemp 1973). As for hornbills, rainfall means providing the plaster material and food supplies (Kemp 1973).

Intra- and interspecific competition for nest cavities

Competition observed throughout the present study made it clear that there was a shortage of suitable cavities within the study site. Some unsuccessful breeding pairs kept staying near the nest sites or visited their nests in the non-breeding season (Poonswad and Tsuji, in press). This should indicate early reservation of the nest sites by the breeding pairs.

Competition for nest cavities was more intense between hornbills of similar size. The reasons for this would be that the species with similar size may have 1) similar basic requirements for nest sites and 2) similar breeding cycles, especially the imprisoning period. The overlap of these basic biological and ecological requirements would inevitably cause interaction to a certain degree.

When competition occurs between the larger and smaller hornbill species, the larger one is usually dominant over the smaller one (McFarland 1981) and the former has a better chance in the competition as shown in the previous section.

Nest sealing

Hornbills are good example of sharing roles between males and famales in nesting. My observations as well as those reported by Baker (1927), Moreau (1941), North (1942), and Ali and Ripley (1987), confirmed that the role of the male is to supply materials including fruits, but never sealing the nest. On the other hand, Porrit and Riley (1976) observed both sexes worked on plastering in the

Brown-cheeked Hornbill, though the male appeared to do most of the work.

The main material used by Asian and African hornbills to seal the nest entrance is faeces and mud (Baker 1927, Kemp 1973,1979, Ali and Ripley 1987). This was the case of the Oriental Pied Hornbill in this study. On the other hand, Moreau (1937) reported that the Yellow-billed Hornbill *Tockus melanoleucos* and Silver-cheeked Hornbill seldom used faeces to plaster the nest. Extra materials used for sealing observed in this study seemed to be those which are abundant or easily obtained.

Silver-cheeked Hornbills of Africa use tree bark as lining material after chick hatching (Moreau 1936) instead of plaster material as was used by the species studied here. Lining materials used by the studied species were regurgitated seeds and moulted feathers.

Breeding strategy

Hornbills are monogamous. The breeding strategy of hornbills may have evolved through their mating system, as well as their incubation and parental care requirements. In the breeding biology of hornbills, constraints which do not allow hornbills to breed other than monogamously are 1) the inability of the male to care for more than one set of a female and a brood, 2) the inability of a single parent to feed fledglings (Wittenberger and Tilson 1980), and 3) the importance of the male's contribution to parental care to breeding success (Oring 1982). In order to overcome these constraints in hornbills, they must either pair for life and share parental care (Oring 1982) or raise more fledglings successfully by having nest helpers (Brown 1978) as in the case of Brown Hornbills (Poonswad et al. 1986)(see Chapter 5).

Moreover, as a cavity-nester, hornbill has advantages over other birds. Besides avoidance of predators, the female can conserve energy by incubating an egg or eggs inside tree cavity and save a food source for chicks by imprisoning herself into a cavity while she incubates eggs and raises chicks (Mc Farland 1981). Then the female should use little energy, and adequate nutrition during incubation can be ensured by having her mate feed her. This latest behaviour enhances and strengthens the pair bond (McFarland 1981). In terms of male investment, this cavity-breeding strategy will assure the breeding male that he puts all his energy and efforts into his own offspring.

Breeding success and parental care

Although cavity-nesters breed more successfully than open nesters (McFarland 1981), hornbills produce relatively low number of offsprings per year. Factors which may influence the low productivity are: 1) Hornbill chicks are large in size, and need long parental care (Poonswad et al. 1986). The large-sized hornbills such as the Great Hornbill needs biparental-care in order to feed the growing chick efficiently. 2) Food may be an important factor which influences the parental care type, and leads to raising only one chick or no more than one plus the female. It could be a harmful work load for the male involved in father-care if there are more than two chicks. This was evidenced in the case of a Black Hornbill *Anthracoceros malayanus* at Jurong Bird Park that raised 3 chicks plus fed the female. The male died just a few days before the chicks fledged (Saad, pers. com.). It was therefore surprising that the Oriental Pied Hornbill raised more than one chick with high breeding success while feeding a female. The male must have had high ability in obtaining food and/or their feeding strategies might have allowed them to raise more than one chick (see also Chapter 6).

The cooperative-care type in hornbills no doubt enhances breeding success and chick production. This type of parental care may be related to a complicated social organization and demography or else of the species. (see also Chapter 5).

Table 4-1. Annual number of nests found, cumulative number of nests found, nest loss and annual number of nests existing and percentage of annual remaining nests of four hornbill species in Khao Yai during the 1981 - 1991 breeding seasons (no data for 1986 and 1987).

	1981	1982	1983	1984	1985	1988	1989	1990	1991
Annual no. nest found	13	7	11	30	8	5	2	3	1
Cumulative no. nests	13	20	31	61	69	74	76	79	80
Cumulative no. nests lost	1	1	1	4	5	21	23	25	26
Annual no. nests existing	12	19	30	57	64	53	53	54	54
% Nest existence	92.3	95.0	96.8	93.4	92.8	71.6	69.7	68.4	67.5

Table 4-2. The re-use of nest cavities by four sympatric hornbill species in Khao Yai during 1981-1991 breeding seasons (no data for 1986 and 1987).

Annual re-use ratio = No. nests used / No. suitable nests in previous year

	1981	1982	1983	1984	1985	1988	1989	1990	1991	Average	Individual species re-use ratio
Great Hornbill	4	2/3	1/5	6/8	12/21	11/23	16/17	15/18	16/18	9.9/14.1	0.70
Wreathed Hornbill		2/3	0/3	1/4	5/8	2/9	6/8	5/10	7/7	3.5/6.5	0.54
Oriental Pied Hornbill		5/6	3/9	7/12	11/18	--- No observation------				6.5/11.3	0.58
Brown Hornbill		0	1/2	3/5	6/10	3/11	4/9	6/7	6/9	4.1/7.6	0.54
Total		9/12	5/19	17/29	34/57	16/43	26/34	26/35	29/34	20.3/32.9	0.62
Annual re-use ratio		0.75	0.26	0.59	0.60	0.37	0.76	0.74	0.85	0.62	

Table 4-3. Competition for tree cavities resulted in nest abandonment in 1983, 1984, 1985, 1988 and 1991 at Khao Yai. GH = Great Hornbill; WH = Wreathed Hornbill; PH = Oriental Pied Hornbill; BH = Brown Hornbill.

	GH	WH	PH	BH	Total
(1) No. tree cavities observed	23	15	17	11	66
(2) No. nest competition seen	6	10	6	8	30
(3) No. suitable nests abandoned due to competition	4	7	4	1	16
% Nest competition (2)/(1)	26.1	66.7	35.3	72.7	45.5
% Competed nest abandoned (3)/(2)	66.7	70.0	66.7	12.5	53.3

Table 4-4 Summary of competition for tree cavities among four sympatric species of hornbills and between hornbills and other animals in Khao Yai observed during 1981 to 1991 (except 1986, 1987).
GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Tree #	Year found	1st sp. occupied	Species of interaction			Result followed Competition				Remarks
			Intra-specific	Inter specific	Other sp.	Nest Abandoned	1st sp. continued	Competitive sp. cont.	Fighting coccurence	
4	1981	GH			*Trigona*	/				
5	1981	WH	/	GH		/		/	/	
6	1981	WH		GH*		/		/		*See also text
7	1981	WH		PH*		/				*See also text
8	1981	PH		BH*	*Varanus*	/	/			*See also text
9	1981	PH		WH						
10	1981	PH		WH			/			
11	1981	PH			King cobra	/				
15	1982	WH		GH,BH		/				
19	1982	BH		WH			/			Female WH attacked the imprisoned female
20	1982	BH		WH		/				
21	1983	GH		WH			/			
24	1983	WH	/			/			/	
29	1983	BH		PH,WH*						*See also text
30	1983	BH		WH			/			
31	1983	BH	/				/		/	
33	1984	GH		BH,PH WH		/	/			*See also text
44	1984	WH	/					/		
45	1984	WH	/	GH			/	/		
46	1984	WH		GH			/			
48	1984	WH			*Petaurista* sp.	/				
50	1984	PH			Apis sp.	/				
51	1984	PH		BH				/		
58	1984	BH		GH				/		
61	1984	BH	/				/			
62	1985	GH		WH				/		
69	1985	BH		PH			/			
70	1988	GH		PH*		/				*See also text
73	1988	WH		BH		/				

Table 1-5. Annual number of nest abandonments of four sympatric hornbill species due to all causes observed during the 1982-1991 breeding seasons at Khao Yai (no data for 1986 and 1987).

	1982	1983	1984	1985	1988	1989	1990	1991	Average	Nest abandonment ratio
Great Hornbill										
No. nests abandoned	1	4	2	8	5	2	3	2	3.4	0. 21
No. known existing nests	5	8	21	23	17	18	18	18	16.0	
Wreathed Hornbill										
No. nests abandoned	3	3	1	3	2	2	3	2	2.4	0.33
No. known existing nests	3	4	8	9	8	9	8	9	7.3	
Oriental Pied Hornbill										
No. nests abandoned	1	6	3	3	1	1	2	3	2.5	0.22
No. known existing nests	9	12	18	16	3	8	13	11	11.3	
Brown Hornbill										
No. nests abandoned		0	2	4	5	3	1	3	2.6	0.30
No. known existing nests		5	10	11	9	7	9	9	8.6	
Annual										
No. nests abandoned	5	13	8	18	13	8	9	10	10.5	0.25
No. known existing nests	17	29	57	59	37	42	48	47	42	
Annual nest abandoned ratio	0.29	0.45	0.14	0.31	0.35	0.19	0.19	0.21	0.25	

Table 1-6 Competition resulting in a change of occupant species observed at 54 existing suitable cavities discovered during 1981-1991 which were subsequently used for nesting by four hornbill species. + indicates species occupied more cavities; - indicates species lost cavities. GH = Great Hornbill; WH = Wreathed Hornbill; PH = Oriental Pied Hornbill, BH = Brown Hornbill;

Known former occupant species	Available suitable cavities known occupied by species from discovery	Won from other hornbill species	Lost to other hornbill species	Lost to other animals	Total loss or gain	Net current no. suitable cavities available to species (from Appendix3-1)
GH	25	+4	-1	-1	+2	19
WH	15	+2	-6	-1	-5	9
PH	26	+2	-1	-1	0	18
BH	14	+1	-2	0	-1	8

Table 4-7. Annual breeding success ratios of 269 breeding pairs of four hornbill species observed during 1981-1991 breeding seasons at Khao Yai (no data for 1986 and 1987). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

	1981	1982	1983	1984	1985	1988	1989	1990	1991	Total	Mean breeding success/pair
GH											
No. known breeding pairs	3	4	4	19	15	12	16	15	16	104	0.87
No. successful pairs	2	2	4	18	9	11	15	15	14	90	
Success ratio	0.67	0.50	1.0	0.95	0.6	0.92	0.94	1.0	0.88		
WH											
No. known breeding pairs	3	3	1	7	6	6	7	5	7	45	0.78
No. successful pairs	3	0	1	5	5	4	6	4	7	35	
Success ratio	1.0	0	1.0	0.71	0.83	0.67	0.86	0.8	1.0		
PH											
No. known breeding pairs	6	8	6	15	13	2	7	11	8	76	0.91
No. successful pairs	5	7	6	14	13	2	7	7	8	69	
Success ratio	0.83	0.88	1.0	0.93	1.0	1.0	1.0	0.64	1.0		
BH											
No. known breeding pairs	-	2	5	8	7	4	4	8	6	44	0.89
No. successful pairs	-	1	4	8	4	4	4	8	6	39	
Success ratio	-	0.50	0.8	1.0	0.57	1.0	1.0	1.0	1.0		
Total											
No. known breeding pairs	12	17	16	49	41	24	34	39	37	269	0.87
No. successful pairs	10	10	15	45	32	21	32	34	35	233	
Annual breeding success ratio	0.83	0.59	0.94	0.92	0.78	0.88	0.94	0.87	0.95	0.87	

Table 4-8 Annual expected number of hornbill chicks of four hornbill species produced from average annual existing nest cavities within study site during 1981-1991 at Khao Yai (no data for 1986 and 1987). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

A = Average annual existing nest cavities (from Table 4-5)	B = Breeding success ratio (from Table 4-7)	C = Average no. chick(s) per successful pair	Annual expected no. of chicks in study site AxBxC
GH = 16.0	0.87	1	13.9
WH = 7.3	0.78	1	5.7
PH = 11.3	0.91	1.5	15.4
BH = 8.6	0.89	2.6	19.9

Table 4-9. Records of motality and causes of death of four hornbill species in study site and adjacent area known during the period of 1981-1991 (no data for 1986). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Year	Hornbill species	No. of hornbill found dead	Cause	Remarks
1981	GH chick	1	Human disturbance	Removed a chick from a nest
1981	GH adult female	1	Unknown	
1982	WH chick	1	Male abandoned nest	With unknown reason
1983	WH (unidentified sex and age)	15+	Poaching	Reported by park officers
1983	PH fledgling	1	Accident while fledging?	Found under nest hole
1984	WH fledgling	1	Unknown	
1984	PH immature	1	killed by human	Using a slingshot
1984	PH chick	2	Ant	Ants attacked inside the nest
1985	BH chick	2	Killed by a marten	
1987	BH chick	unknown	Poaching	Cutting nest tree
1987	GH chick	1	Poaching	Cutting nest tree
1987	BH immature	1	Unknown	
1988	WH chick	1	May be starvation	Nest was deserted by male
1990	PH chick	1	Human disturbance	
1991	GH chick	1	Parent birds abandoned first and later marten preyed on chick	Abandonment was caused by human disturbance

Figure 4-1 Summary of periods during when various phases in the breeding cycle occurred in relation to rainfall (data derived from Meteorology Department at Nakhon Ratchasima Station between 1981 and 1990). GH=Great Hornbill, WH=Wreathed Hornbill, PH=Oriental Pied Hornbill, BH=Brown Hornbill.

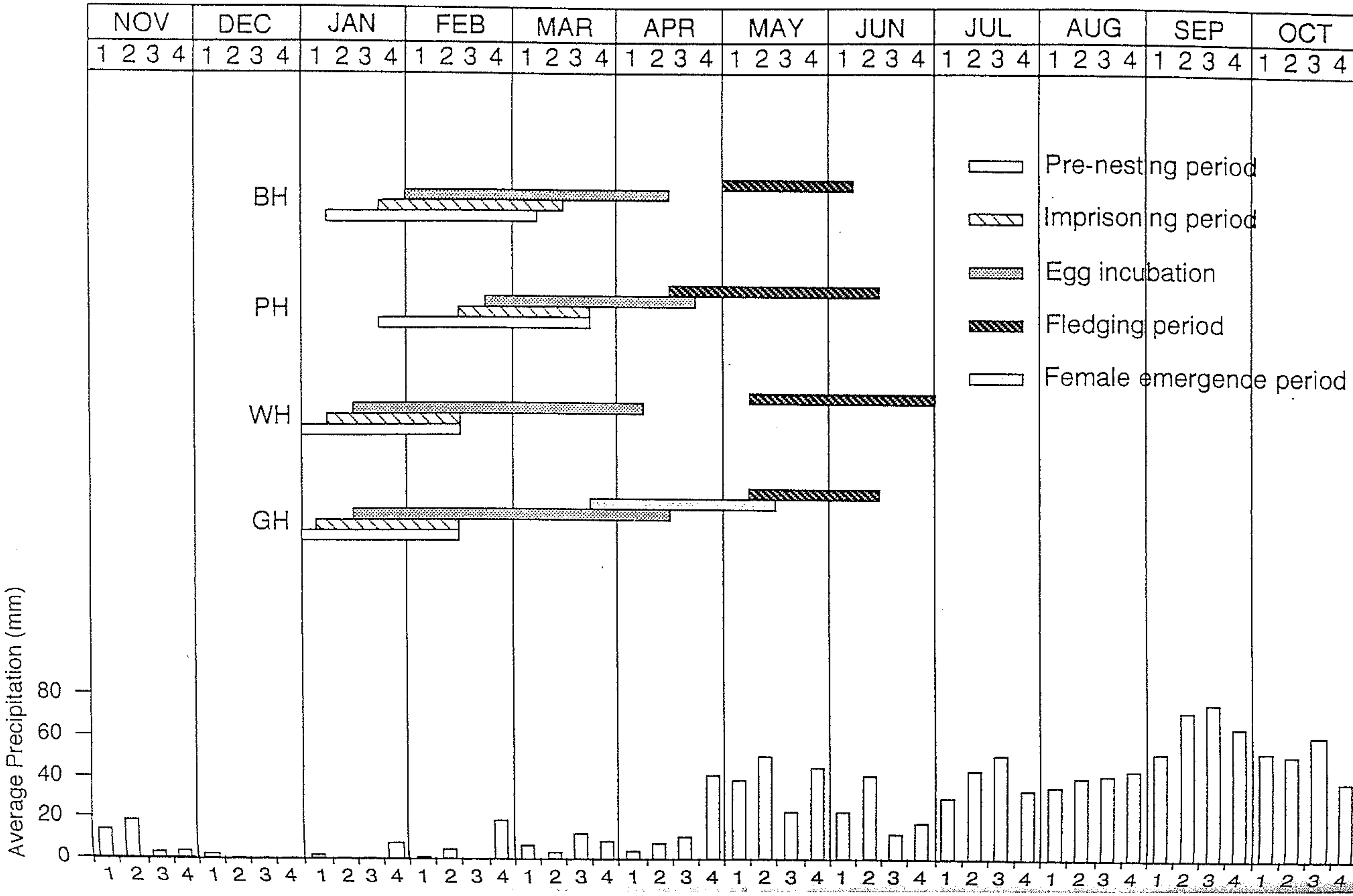
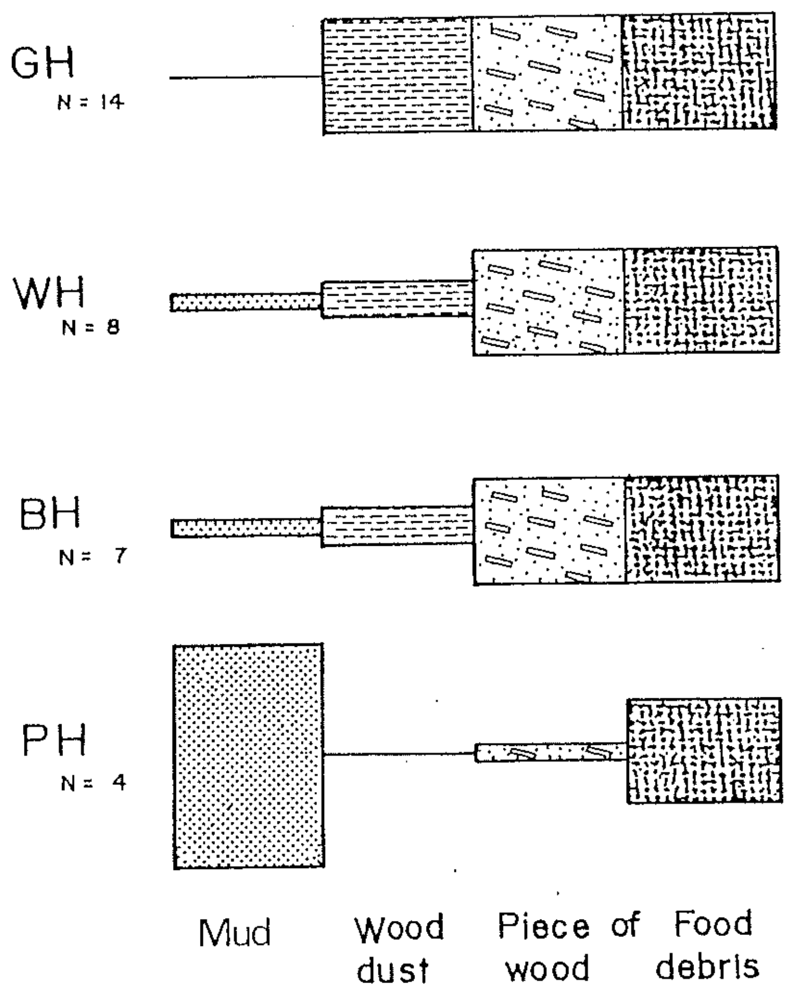


Fig. 4-2 Composition of nest plaster in four hornbill species in Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.



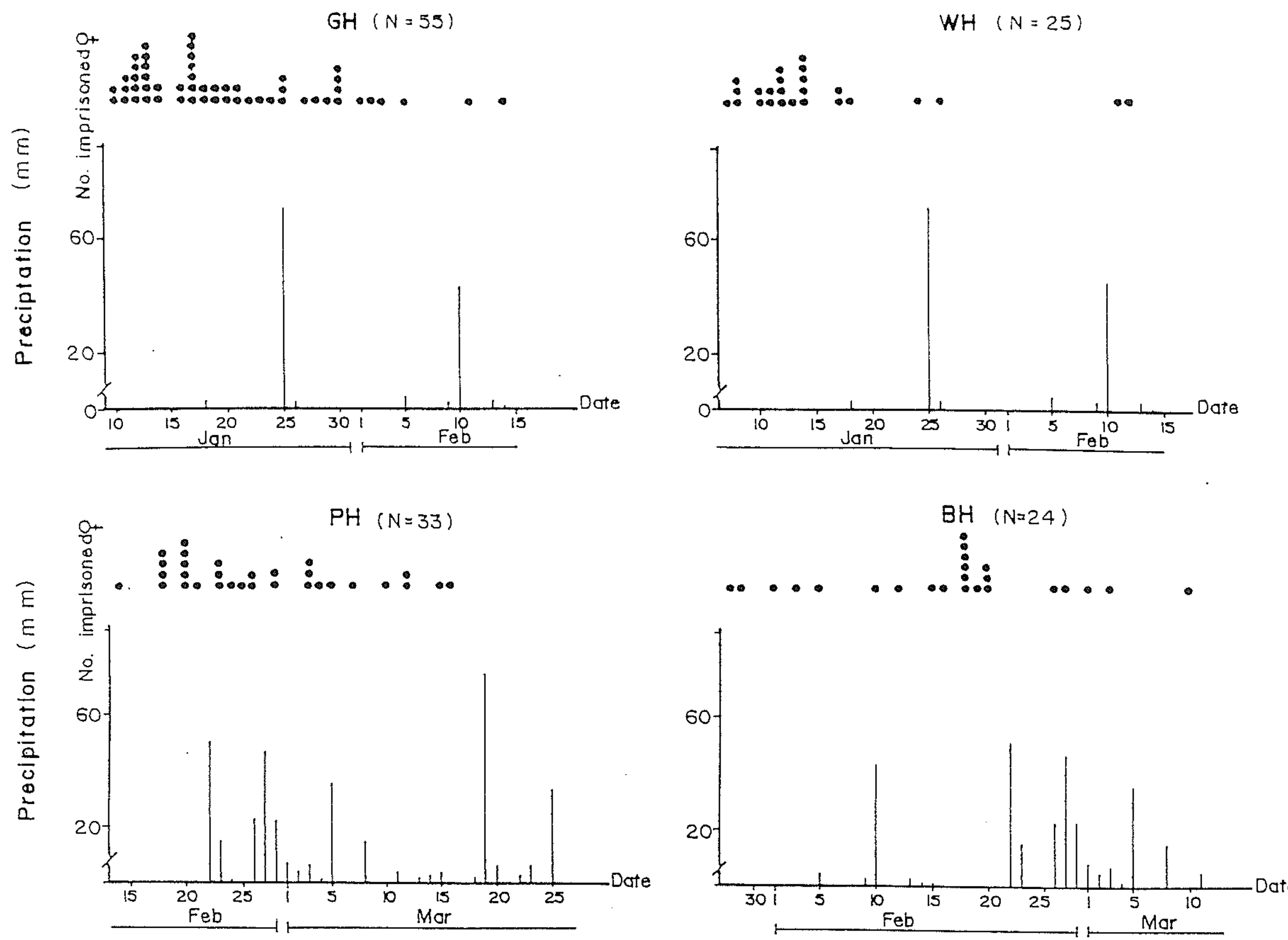


Fig. 4-3 Imprisoning dates of female hornbills in Khao Yai in relation to rainfall.

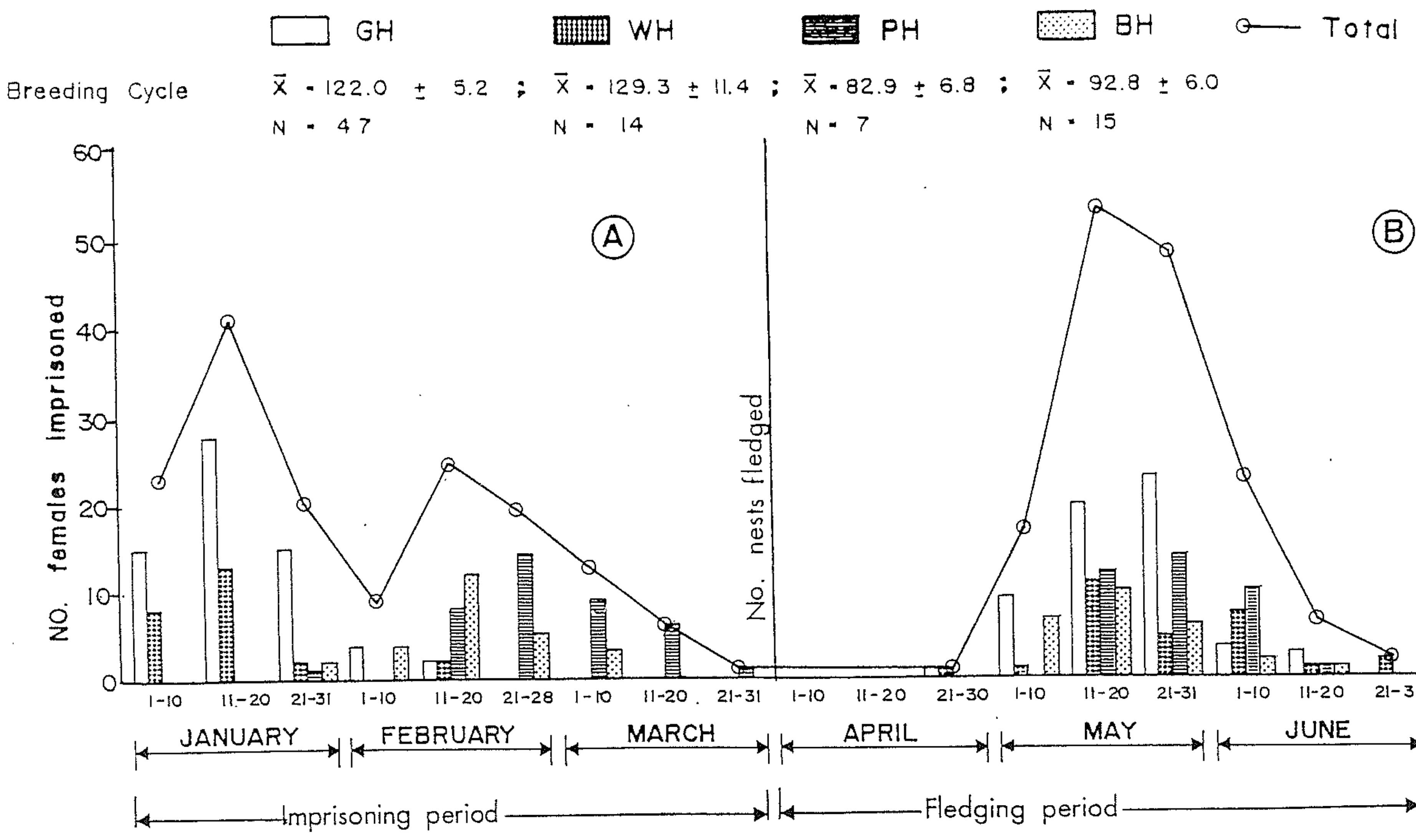


Fig. 4-4 Duration of peak imprisonment of females (A) and fledging of chicks (B) of Great (GH Wreathed (WH), Oriental Pied (PH) and Brown Hornbills (BH) and the total of all females imprisonment during the period of 1981-1991 (no data for 1986 and 1987) in Khao Yai.

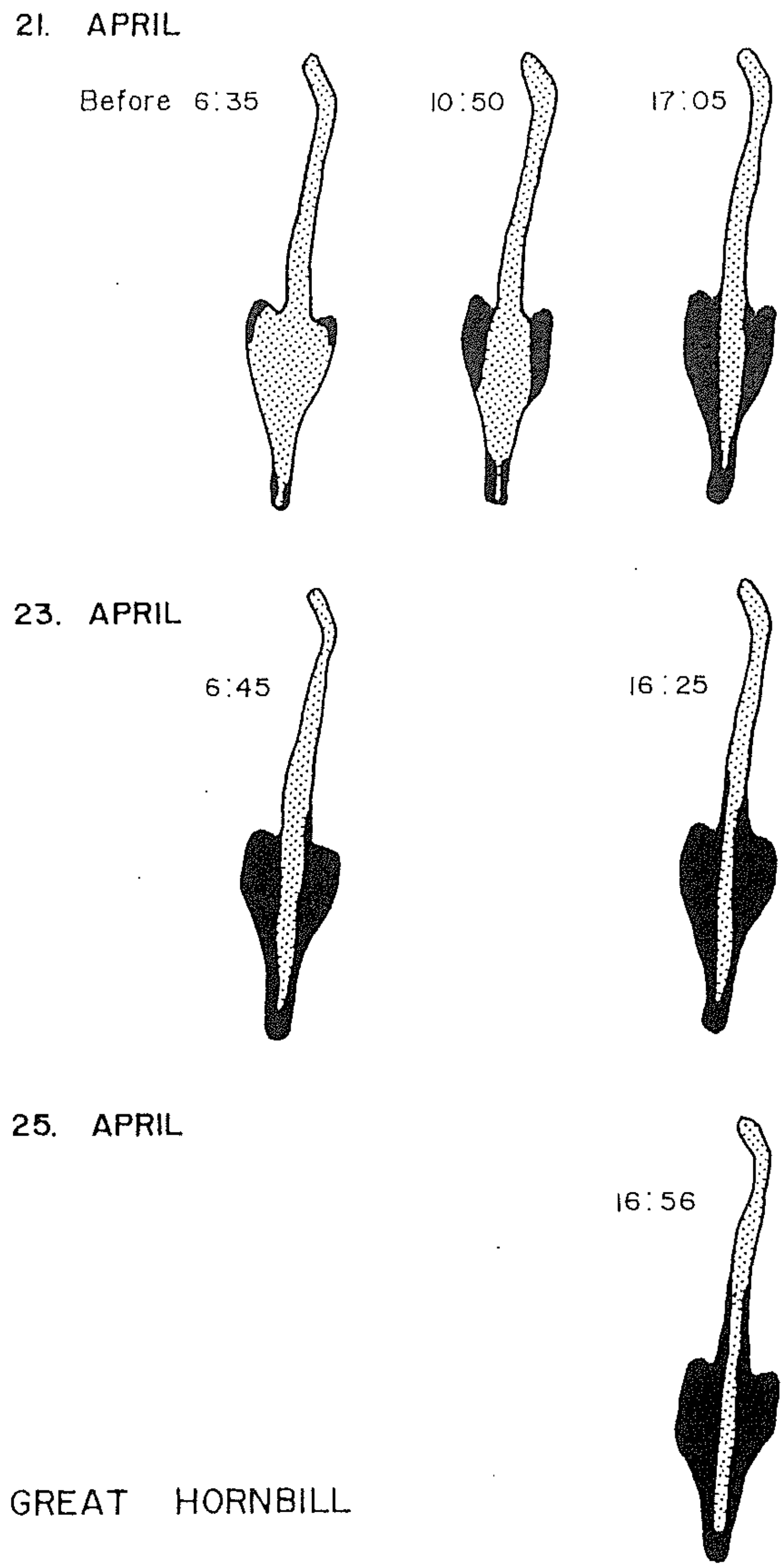


Fig. 4-5 The speeds of nest resealing by a Great Hornbill chick after the female emerged.

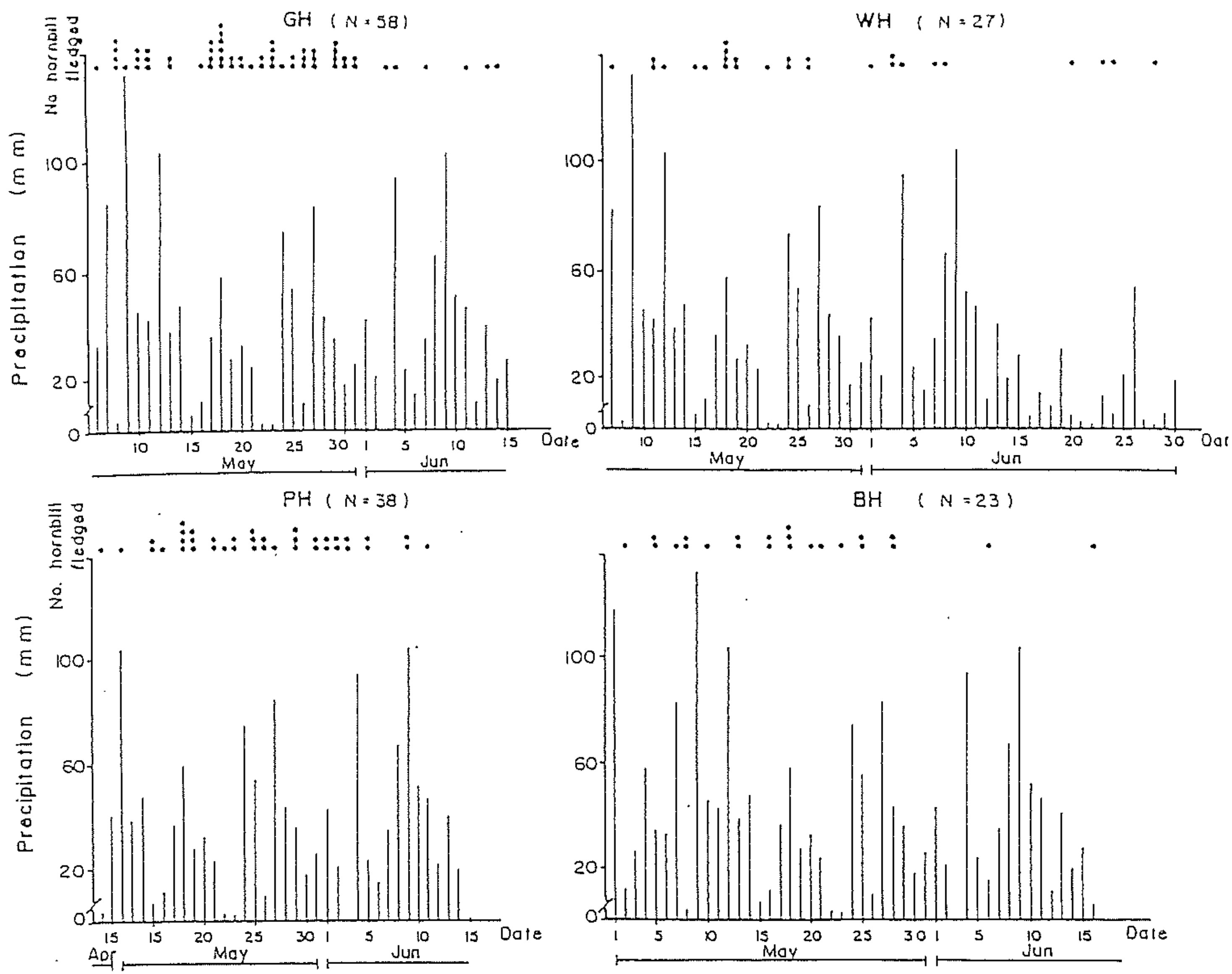


Fig. 4-6 Fledging dates of four hornbill species in Khao Yai in relation to rainfall. GH = Great Hornbill, WH = Wreathed Hornbill, .

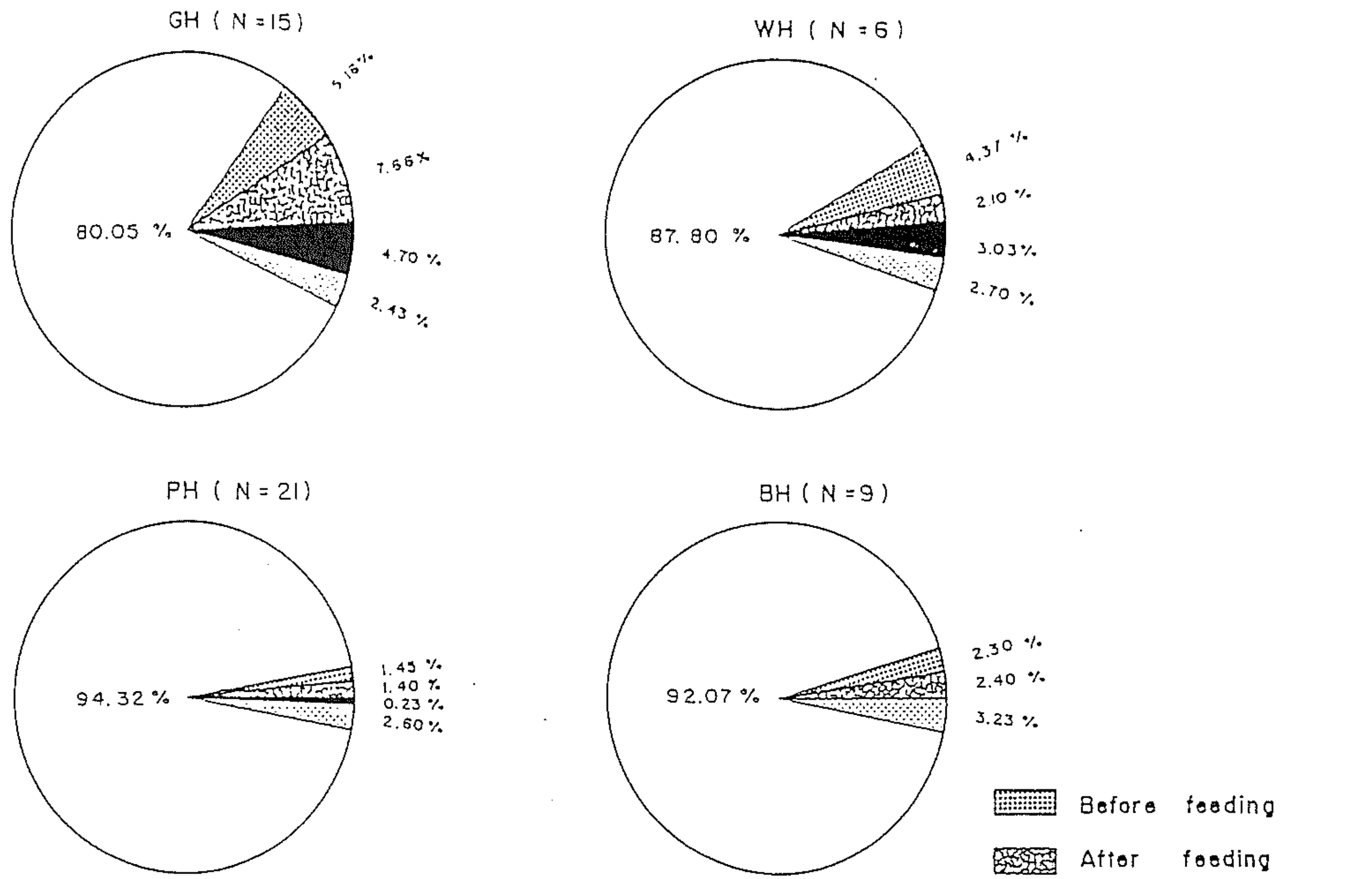


Fig. 4-7 Time budget of breeding males of four hornbill species during the breeding seasons of 1981-1955 in Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Appendix 4-1. Comparison of breeding cycles of the four hornbill species studied at Khao Yai compared with those in other geographical areas.

Hornbill sp.	Locality	Breeding season	Egg incubation	Nestling	Reference	Remarks
Great Hornbill *Buceros bicornis*	Khao Yai	Jan - Jun	Feb-Mar	Apr-May	Present study	
	Himalaya Region	Feb - Apr	-	-	Baker 1927,1934 Ali and Ripley 1987	
	East Himalaya	-	May	-	Baker 1934	
	Burma(Mayanma)	Jan - Apr	-	-	Smythies 1986	
	South Sumatra	-	Nov	Dec-Jan	Wallace 1962	
Wreathed Hornbill *Rhyticeros undulatus*	Khao Yai	Jan - Jun	Feb-Mar	Apr-May	Present study	
	Assam, India	-	Apr-Jun	-	Sanft 1960	
	West Java	-	Jul-Sep	-	Hoogerwerf 1949 Sanft 1960	
	Tenasserim, Burma	Feb - Mar	Mar-Apr	-	Baker 1927	
Oriental Pied Hornbill *Anthracoceros albirostris*	Khao Yai	Feb - May	Mar	Apr-May	Present study	
	Pegu and Tenasserim, Burma	-	Mar	-	Baker 1934, Smythies 1986	
	Assam, Cachar and Kuman, India	-	Mar-May	May	Baker 1927	
	Central Java	-	Nov	-	Hoogerwerf 1949	Subspecies *A.a.conve*
	Perak, Malaysia Peninsula	-	-	May	Pan (1987)	" "
Brown Hornbill *Ptilolaemus tickelli*	Khao Yai	Feb - May	Mar	Apr-May	Present study	
	Assam, North Cachar, India	Apr - Jun	-	-	Baker 1927,1934, Ali and Ripley 1987	
	Tenasserim,	Feb - May	-	-	Sanft 1960	

Appendix 4-2. Comparison of clutch sizes and incubation periods of four hornbill species at Khao Yai with data from other geographical areas.

Hornbill species	Clutch size	Incubation period (days)	Reference
Great Hornbill	1 - 2	40	Choy (1980)
Buceros _bicornis_	1 - 2	Unknown	Ali and Ripley (1987)
	1, 2 or 3 (rare)	31	Baker 1927
	1	approx. 40	Present study
Wreathed Hornbill	2 - 3	Unknown	Baker 1927
Rhyticeros _undulatus_	-	35 - 42	Kemp 1979
	1	approx. 40	Present study
Oriental Pied	2 - 3	Unknown	Ali and Ripley 1987
Hornbill	2 - 3	24 - 27	Present study
Anthracoceros _albirostris_			
Brown Hornbill	3 - 4 up to 5	24	Baker 1927
Ptilolaemus _tickelli_	2 - 3	Unknown	Present study

CHAPTER 5

COOPERATIVE BREEDING

INTRODUCTION

Hornbills are best known for their unique nesting habits. In general, the female seals herself into a nest cavity, leaving only a narrow vertical opening. Through this opening, the female and chicks are fed by the male and the brood deficates. The female either remains in the nest cavity throughout the breeding cycle, or emerges to help her mate feed the chicks, depending on the species (Poonswad et al. 1983).

The social life of hornbills involves simple cooperation in caring for young between the male and female in a monogamous pair bond as in the Great Hornbill (Poonswad et al. 1983). This bond is believed to last for life (Moreau and Moreau 1941) and remains intact both during and outside the breeding season.

Social behaviour is complicated by cooperative breeding in some hornbills such as in *Anorrhinus galeritus* and *Tockus birostris* (Madge 1969, Kemp 1979). The adult male is aided in feeding the female and young by others which are believed to be close relatives of the family.

In this chapter, I present the results of observations on the cooperative breeding in the Brown Hornbill. These observations involve (1) relationships between breeding pairs and nest helpers; (2) roles of breeding males and nest helpers during the nesting period, and (3) relationships between nest helpers at different nests.

METHODS

Individual identification of breeding males and helpers

In order to observe behaviours during the breeding season, nests of Brown Hornbills were located by following foraging flocks or lone males, and nest location were mapped on a grid map scale 1:50,000. An observation blind was built near each nest. Observations were made with 8x30 binoculars or a 20X and 40X spotting scope. The determination of social relationships is based on observations during 1982 through to 1985 breeding seasons. Nest helpers were individually recognized by the following characteristics: (1) the shape and size of casques and marks on them, (2) marks on the orbital skin, (3) plumage colouration patterns, and (4) individual behavioural characteristics. Recognition of individual breeding males and nest helpers was aided by photographs and sketches.

Marking of nest helpers

To study the relationships between nest helpers of two different nests, B1 and B5 (the breeding pairs will be coded according to the year in which the female imprisoned as 83B1 and 83B5) which were about 1 km apart, two nest helpers of 83B1 and one helper of 83B5 breeding pairs were captured in 1983 in a 210 mm mesh mist net and were marked using coloured plastic collars and casque paints. The tail feathers were stained using picric acid, melachite green and brilliant blue. The marked nest helpers were observed at two nests on the same day. In the same year three nest helpers of a third nest, B3 (83B3 breeding pair which was located in a completely different region of the study site from the former two nests, were captured and marked. B3 nest was about 50 m apart from B4 nest (or 83B4 breeding pair) where no helper or breeding male were marked.

In order to prevent starvation of broods by abandonment of if the breeding male and nest helpers, capturing for marking was done when the broods were sufficiently grown up, i.e. close to the fledging time.

Weights of the food fed to females and broods were determined by the method described in Chapter 6.

RESULTS

It was very difficult to study the cooperative breeding system in Brown Hornbills. Constraints included 1) difficulty of capturing birds for marking, 2) difficulty in following marked birds, and 3) the marked birds seldom returned to the former nest in the following year. Although data were collected for sereral years and may not be of the same groups of helpers, they demonstrated the relationships between helpers and breeding pairs, the type of nest helpers, and the role of nest helpers.

Nest helpers

There were 12 nests of Brown Hornbills found during the 1982 to 1985 breeding seasons. The distribution of nests during these period is shown in Figure 5-1, regardless of nest loss in later years. It was observed that there were other males assisted the breeding male, besides the breeding male attending the nest for various activities. These non-breeding males are called "nest helpers" or "helpers" throughout this chapter (see Types of nest attendants discussed in the following pages). The numbers of nest helpers of 20 breeding pairs observed in various years varied from 1 to 5 individuals. When considering of the age classes of the helpers, they could be either the offsprings or siblings of the breeding pair (Appendix 5-1). The number of nest helpers of a nest varied through different stages of the breeding cycle, which takes 13 to 14 weeks (Chapter 4). Seven nesting pairs, one in 1983, two in 1984 and four in 1985, had no nest helpers (Table 5-1). Among these seven breeding pairs without helper, three pairs bred successfully with unknown number of chicks, the rest did not succeed in breeding.

Portraits of nest helpers at different nests and in different years at the same nests are presented in Appendix 5-1. Although the exact age of helpers could not be determined, it was possible to distinguish yearlings from adults by a round and shorter casque which yearlings possess. Nest 82B1 had four helpers which were categorized at least in three age classes of immatures. Helper no. 1

seemed to be youngest, helpers nos. 2 and 3 seemed to be the same age, and helper no. 4 was oldest (Appendix 5-1). Helpers of 84B6 breeding pair were of at least three different ages. Helpers nos. 1 and 2 were the same age and they were younger than helper no. 3. Helper no. 4 seemed to be oldest (Appendix 5-1). The helpers of 85B7 breeding pair seemed to be older than the helpers of the former two nests. They could be the siblings of the breeding pair (Appendix 5-1) because 85B7 breeding pair had no helper with round casque which indicated that no young of the first year age became helper.

Number of nest helpers and the breeding cycle

During the breeding season, the number of nest helpers was differed significantly with weeks after the female was imprisoned ($F = 5.29$, $df = 3$, $P < 0.01$). It was also found that the average number of nest helpers increased significantly as the breeding cycle progressed ($r = 0.356$, $n = 116$, $P < 0.01$). (Fig. 5-2).

Types of nest attendants

Brown Hornbills that visited their nests were not all nest helpers. These nest attendants can be divided into 5 different types.

1. True nest helpers. This type was called the true nest helper or simply nest helper (helper), consisted of all males of different ages which visited the nest and participated in feeding the nesting female and the brood

regularly although not on every visit. In this study, nest helpers were not always younger than the breeding male.

2. Watchers. They were also other males that visited the nest frequently with nest helpers(type 1), but the nest helpers did not allowed these males to feed the nesting female even they tried to.

3. False nest helpers. This type mostly consisted of unpaired females that visited the nest and sometimes fed the nesting female in the absence of nest helpers. They were usually not allowed to feed if the nest helpers were present and actually they were chased away by the latter.

4. Nest visitors. This type consisted of males visited once in a while to the nest with nest helpers without participating in feeding. These visitors were probably the members of the main foraging flock.

5. Intruders. The intruders were females which found visited the nests (observed at 5 nests) in the absence of nest helpers, but they sometimes came in pairs. When in pairs, the intruding male was observed trying to feed the nesting female. The intruding female showed aggressive behaviours by attacking the nesting female, cracking and removing the nest plaster. Once, the nest helpers arrived only the female was chased away, and the male still could join the flock. This male would have been a nest helper to this breeding pair. Some of those female intruders were still immature, judging by their very small casques.

Roles of breeding males and helpers in cooperative breeding

The role of breeding males at the nest was consistent, whereas that of nest helpers was intermittent. During the breeding season, breeding males and nest helpers assume the following roles.

1. **Nest sealing.** When the breeding season began this activity was performed by the pair (7 pairs). They looked for a nest cavity or returned to an old nest cavity with or without a company of helpers. The male performed courtship displays as described in Chapter 4. The breeding male was observed to supply plaster materials as already described in Chapter 4. There was no helper participation at this phase of breeding.

2. **Feeding.** The breeding male and nest helpers played the most prominent role in this aspect. Feeding by the breeding male was not uniform, but on average it was greatest at week 9 of the breeding cycle (Fig. 5-3a). Food fed per helper on average was also greatest at week 9 and decreased toward fledging (Fig. 5-3b) which was similar to that of the breeding male.

It was obvious that the breeding male's workload was high when he was without helpers and the workload was clearly decreased when he had helpers (Fig. 5-4). The average feeding load of the breeding male decreased by 16.5 % if he had a helper. Further the average feeding load decreased 46 % if he had two helpers. An increase in the number of nest helpers more than two seemed not to reduce the workload of the male. However, it was found that the number of nest helpers significantly affected the amount of total food provided (Fig. 5-3b) ($F = 5.804$, $df = 4$, $P < 0.01$). On the other hand, the nest helpers supplied food as much as 60 % of the total amount of food fed to the brood.

During the feeding activity at the nest, it was observed that a dominant-subordinate hierarchy existed. The dominant bird was the breeding male as it was expected, but in one case, at 84B6 nest, the oldest helper showed aggressive behaviour to the breeding male by snatching food from the breeding male or other helpers to feed the nesting female. Sometimes, this aggressive helper flew against the others preventing them from feeding the female. However, the dominant one did not always feed more.

3. **Chick raising.** Nest helpers did not play any role in chick production directly, but most likely affected indirectly. Although the number of nest helpers did not increase with the number of chicks ($r_s = 0.6417$, $n=9$, $P > 0.05$) (Table 5-2), the nests which had a high number of chicks tended to have more helpers (Table 5-2). There were only 3 out of 7 pairs had successful breeding when without helper. At 85B3, which had two chicks and no helpers, the chicks were killed by a marten because the female emerged before chick fledging. When the fledging time approached, nest helpers were observed to perform a behaviour as if they were training the chicks for calling notes (seen at 3 nests).

One of the helpers would do this after feeding, or went back to the nest only for this purpose. He perched near the nest and began to call, and the chick then repeated the calls.

4. Nest sanitation. Hornbill nests are kept clean by the females, and the broods squirt their faeces through the nest entrance. Besides the nesting female, who was observed to remove the chick's faeces that remained inside or in front the opening, the breeding male was also observed to remove faeces or food debris which remained in front of the opening after feeding. This duty was observed only to be performed by the breeding pair.

5. Nest territory defence. Brown Hornbills annouced their nest territories, although such nest territories were not clearly marked. Usually the breeding male and nest helpers annouced the nest territory within a radius of about 100 m from the nest tree (see also Chapter 7) by making loud calls. If the intruders were of the same species, the nest helpers attacked and chased the intruders away. The flying displays and wing beat noises of the helpers were observed when the intruders were very close to the nest (within 5 m from the nest). They otherwise only called to annouce their presence.

Relationships among nest helpers of different nests

The monitoring of marked breeding males and nest helpers yielded unsatisfactory results due to the fact that 1) the coloured plastic collars might have dropped off because they were not well hooked, and/or 2) the aluminum leg bands were too difficult to spot. However, the colour marks lasted until at least the end of the breeding cycle. Therefore, it was possible to determine that nest helpers of four pairs which were about 50 m (83B3 and 83B4) and 1 km (83B1 and 83B5) apart helped only at their nests. In 1984, both 83B1 and 83B5 did not nest, but 83B3 used the same nest (B3) with one helper without any mark on it. In the 1985 breeding season, at least one helper of 83B3 was observed to help at different nest(85B7 breeding pair), which located farther than 1 km from the former nest, whereas at B3 nest in the same year 85B3 breeding pair had no helper. Whether this was a coincidence or 85B3 breeding pair actually lost all former helpers was unknown.

DISCUSSION

From this study, it may be concluded that the cooperative breeding in the Brown Hornbill could have been derived from the following reasons.

1) Cooperative breeding in Brown Hornbills may indicate poor or weak breeding strategy in the species. This might be due to either the quality of breeding males or the quality of habitats. The males in this case may have less ability compared with the males of the Oriental Pied Hornbill, which live sympatrically. The latter species could successfully rear 1 to 2 chicks and feed the female, with a high rate of breeding success (Chapter 4). This

hypothesis is at least partially supported by the increase in the number of helpers as the breeding cycle progressed.

As the chick grow, requirements for both feeding and the protection from predators may increase, especially when the fledging period approaches. If the male is without helpers, all of these activities would cause a higher stress to the breeding male. In addition, Lewis (1982) also showed that in Sparrow Weavers (Plocepasser mahali), the helpers began to participate in feeding only after chicks hatched for a period of time. It can be interpreted that after chick hatching the breeding pair needs helpers.

It is interesting to investigate whether the number of nest helpers has any correlations with the habitat quality index. The index could be abundance or shortage of nest cavities plus food, and the presence of predator.

2) Why do only males help? The cooperative breeding in the Brown Hornbill seems to be different from those of the Bushy-crested (Madge 1969 and pers. obs.) and White-crowned hornbills, Berenicornis comatus, (pers. obs. at one nest). The two latter species have both sexes as helpers. In Bushy-crested Hornbills the helpers are of different ages. I agree with Ricklefs (1975) who suggests that cooperative breeding has evolved in a demographic context such that the number of yearlings greatly exceeds adult mortality. Demographic patterns in terms of sex ratio are likely to be applicable to the Brown Hornbill breeding system, where only males are helpers. It was probable that the sex ratio in the current population was skewed toward

the males by having more than one age class of males as helpers (see also chick production in Chapter 4). The study of demography of the Florida Scrub Jay (Aphelocoma caerulescense) by Woolfenden and Fitzpatrick (1984) may partially support this findings. They found that the ratio of males to females was actually even, but such a ratio increases according to the age of helpers. They explained that the increase in sex ratio (male>female) was due to the delayed reproduction of males and early dispersal of females seeking breeding vacancies, thus resulted in a change of sex ratio in the flocks. In this study, it was not known whether females dispersed earlier for breeding vacancy or not, but it was observed that females may look for nest cavities (as intruders) before reaching maturity.

Role of helpers

For many species the role of the helpers is mostly feeding the nestling and/or fledglings and defending territory. This seems to be the case with the nest helpers of the Brown Hornbill. They did not participate in nest building as the helpers of the Azure-winged Magpie (Cyanopica cyana) do (Komeda et al. 1989).

In this study, the number of helpers was not significantly correlated with the number of chicks produced. Ligon (1981) reported a similar case in the Green Woodhoopoe (Phoeniculus purpureus). The nest helpers would have a significant effect on the survival of the chicks. In order to ensure the survival of more chicks, more nest helpers would be required to supply sufficient food. Otherwise starvation may cause death in the nestlings (Kemp 1976). Therefore by having more helpers the chicks could fledge more successfully.

Length of time of being a helper and relationship between the male and the helper

Duration of a male being a helper may depend on pairing opportunity and the availability of nest cavity. The Brown Hornbills in this study seemed to serve as helpers for at least 2 to 3 years.

It was most likely that helpers of the Brown Hornbills were either offspring (82B1, 84B6) or sibling (85B7) of the breeding pair. Furthermore in the case of false nest helpers, they possibly were the offsprings of the nesting pair because she occasionally visited the nest with the breeding male (pers. obs.).

Table 5-1 Numbers of breeding pairs, numbers of breeding pairs with helpers and the percentages observed in Brown Hornbills between the 1982 and 1985 breeding seasons at Khao Yai.

	1982	1983	1984	1985	Total
No. breeding pairs	1	5	7	7	20
No. breeding pairs with helpers	1	4	5	3	13
% breeding pairs with helpers	100	80.0	71.4	42.9	65.0

Table 5-2 Number of chicks and nest helpers recorded of various breeding pairs between the 1982 and 1985 breeding seasons at Khao Yai.

Breeding pair	No. chicks	No. helpers	Remarks
82B1	2	5	
83B1	3	4	
83B3	3	5	
83B5	3	4	
83B6	3	5	
85B3	2	0	(see text)
85B6	3	4	
85B7	1	2	
85B8	3	3	

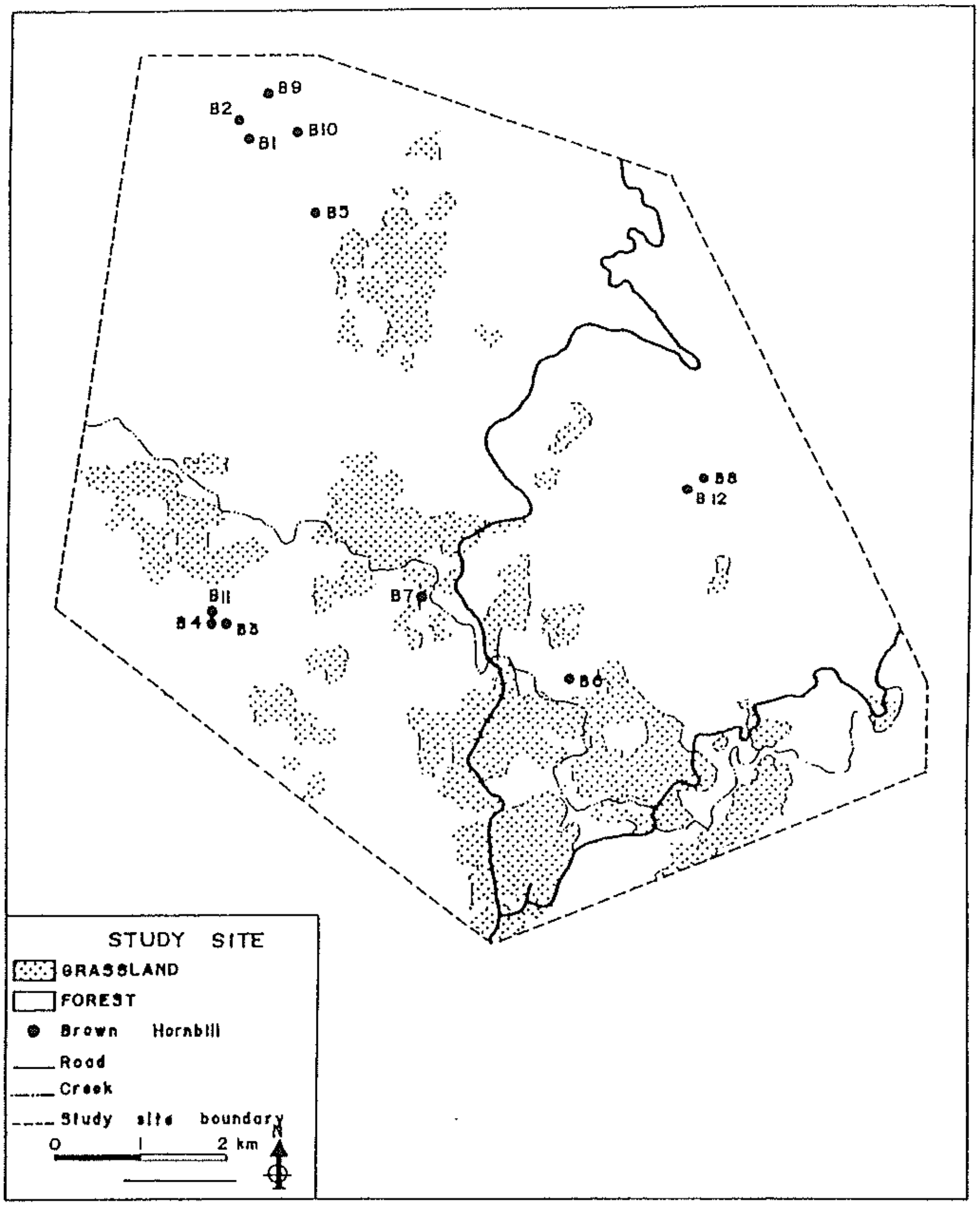


Fig. 5-1 Distribution of nests of Brown Hornbills found between 1982 and 1985 in Khao Yai.

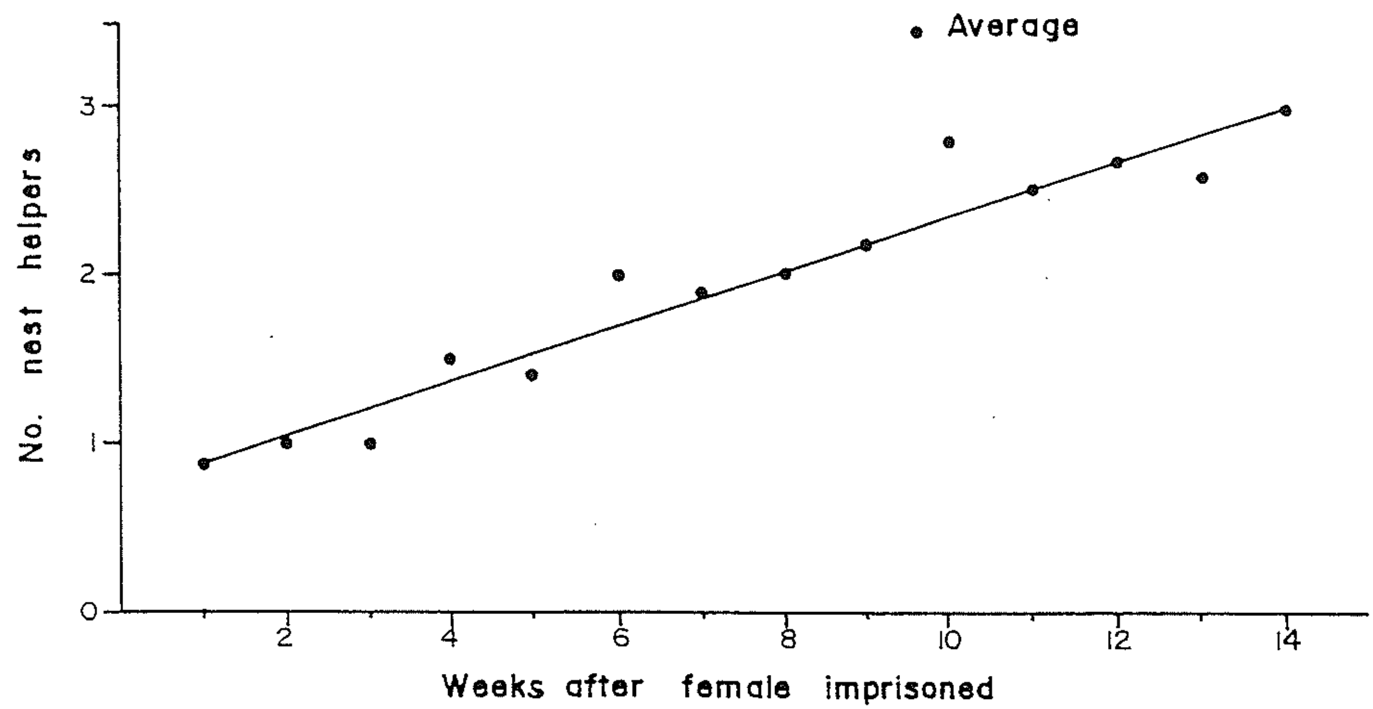


Fig. 5-2 Weekly change in average number of helpers after the imprisonment of the female Brown Hornbill in Khao Yai observed during 1982 to 1985.

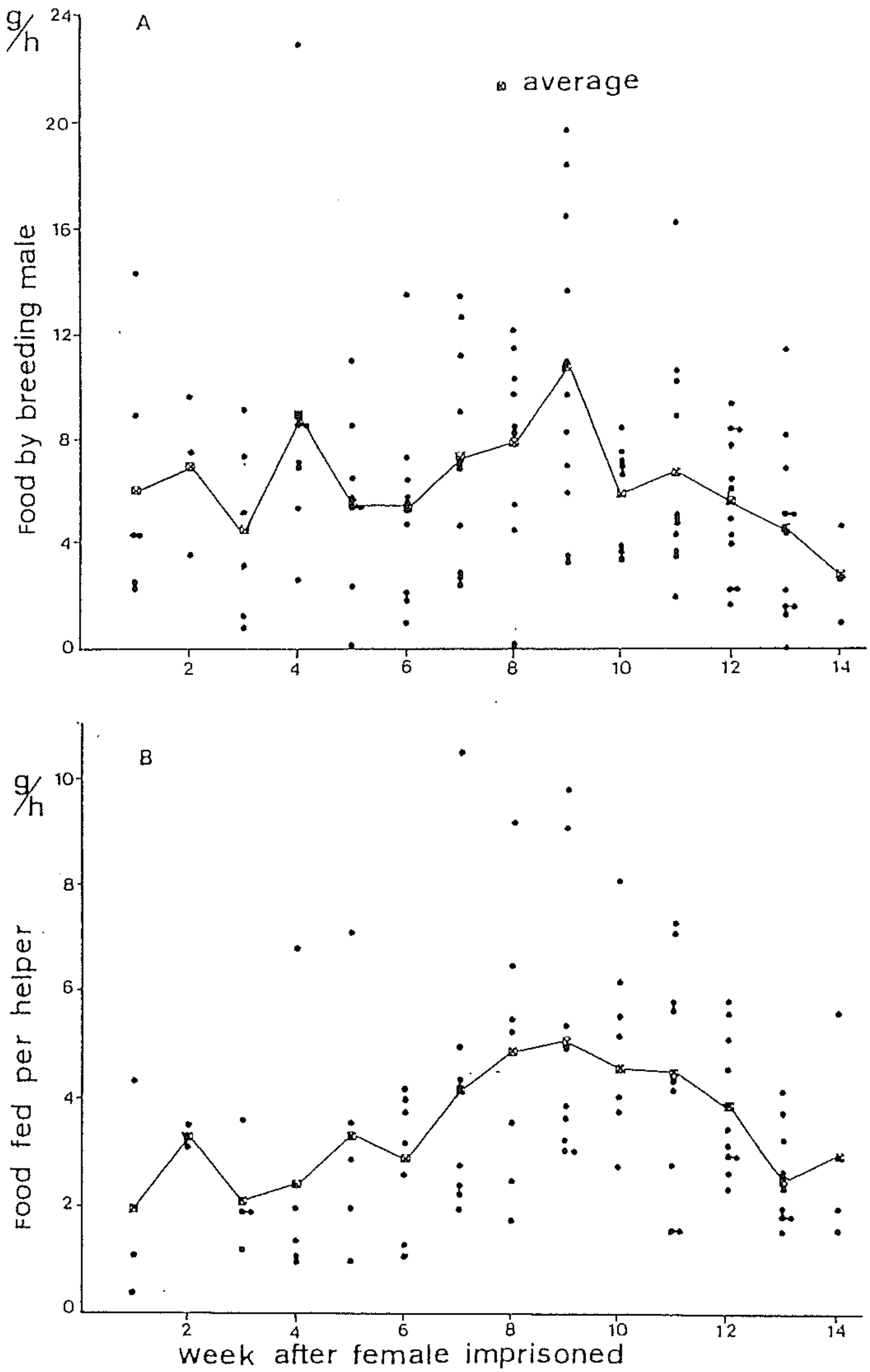


Fig. 5-3 Weekly changes in the amount of food fed to the brood and its average after female was imprisoned: By the

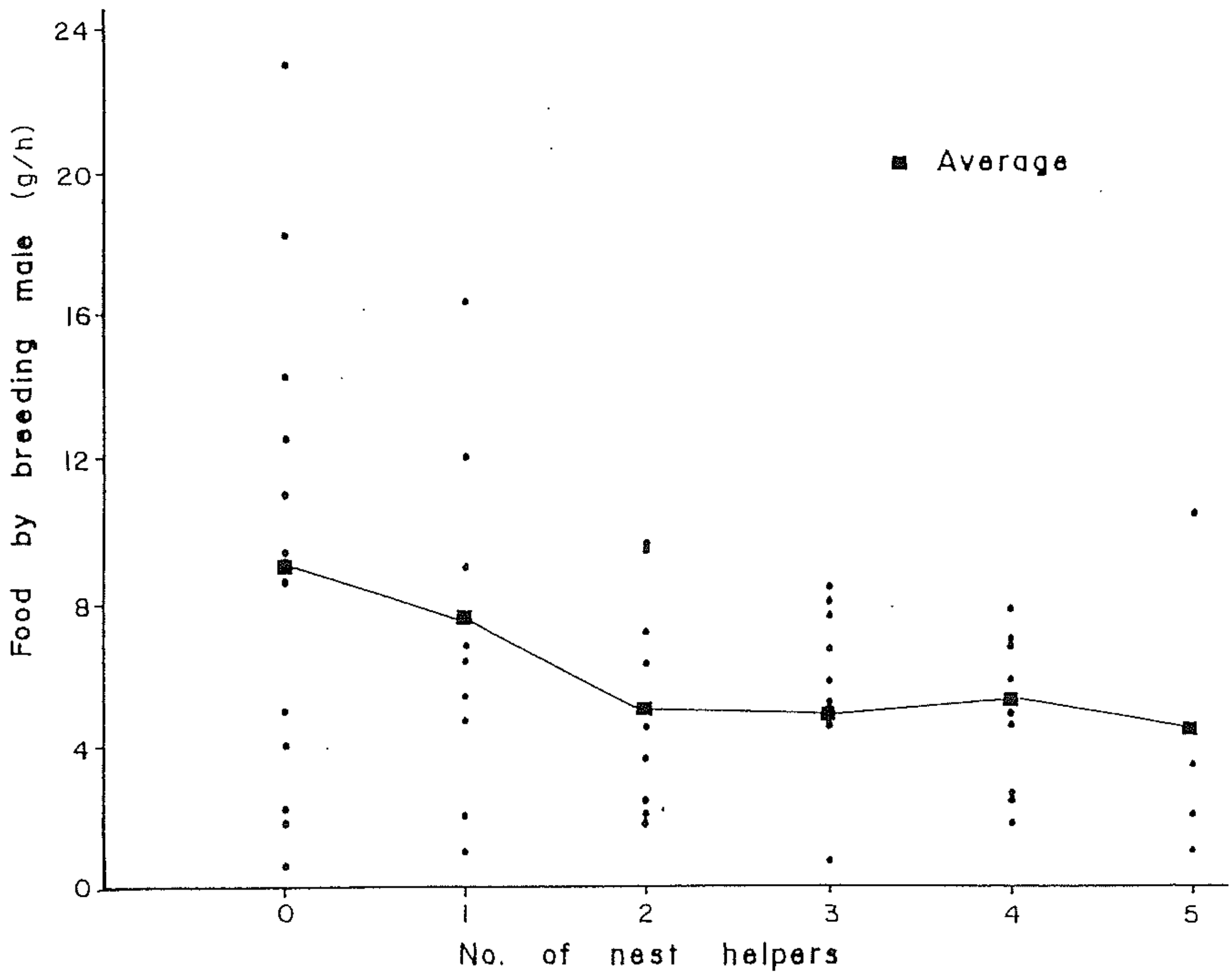
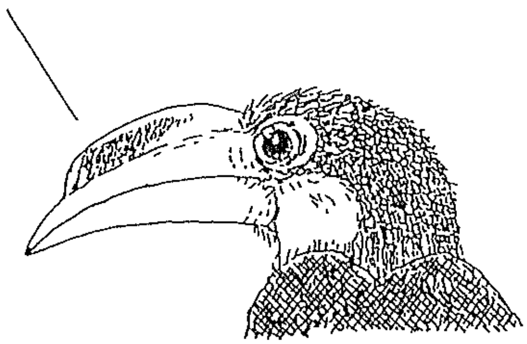


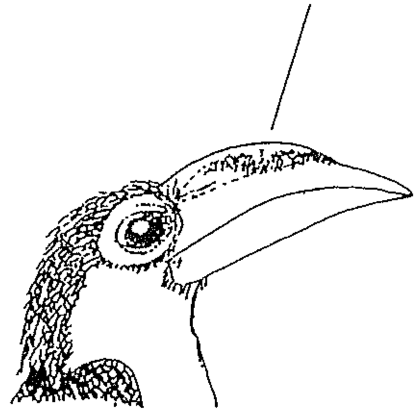
Fig. 5-4 Weekly changes in the average amount of food fed by the breeding male when the number of nest helpers increased.

Appendix 5-1 Portraits of breeding males and nest helpers of different ages from various nests of Brown Hornbills in three different years, 1982, 1984 and 1985 in Khao Yai.

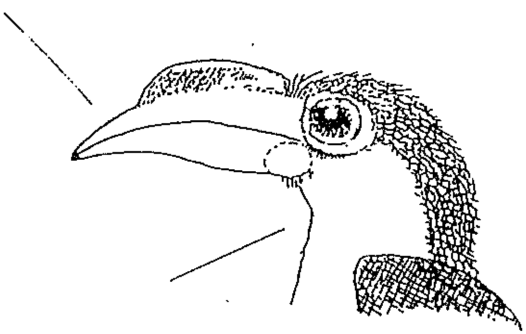
NEST NO. 82B1



BREEDING MALE



HELPER NO.1



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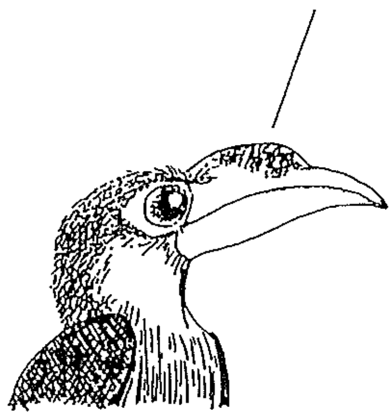

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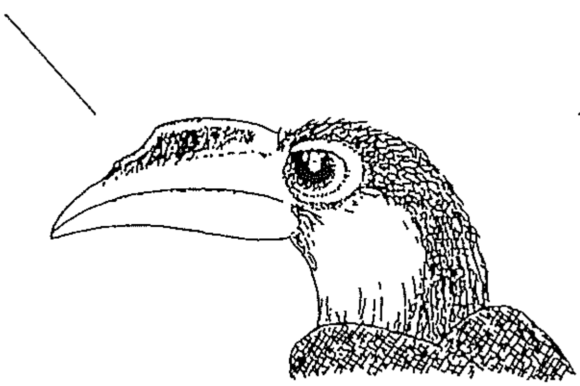
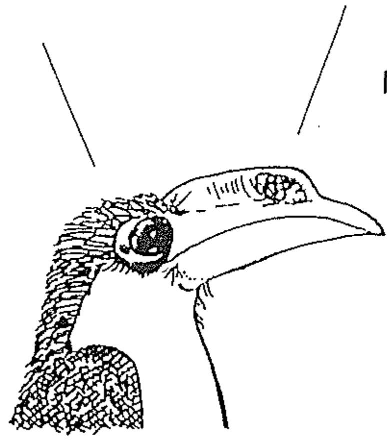
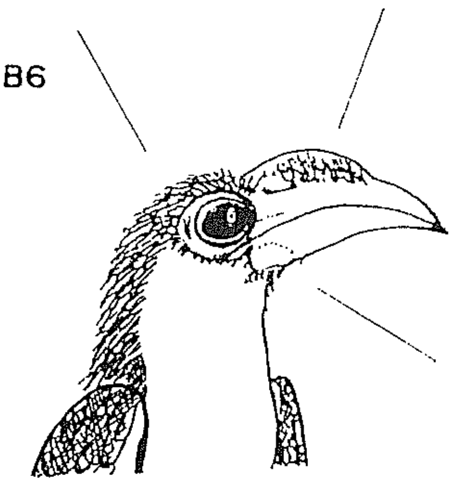


HELPER NO. 4

NEST NO. 84B6



BREEDING MALE



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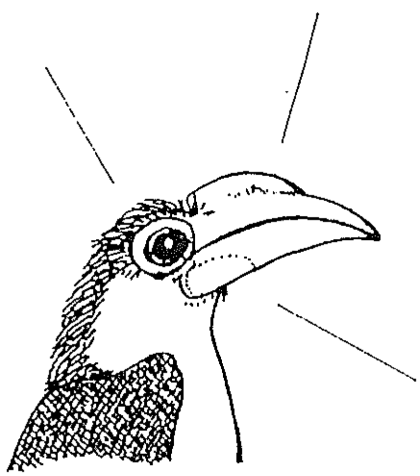

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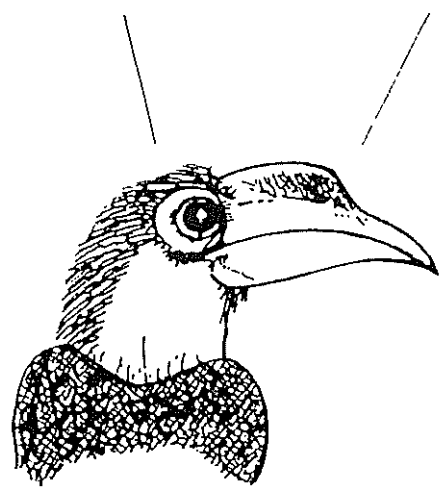

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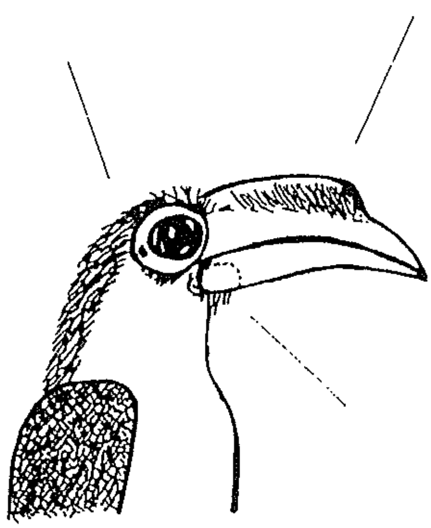

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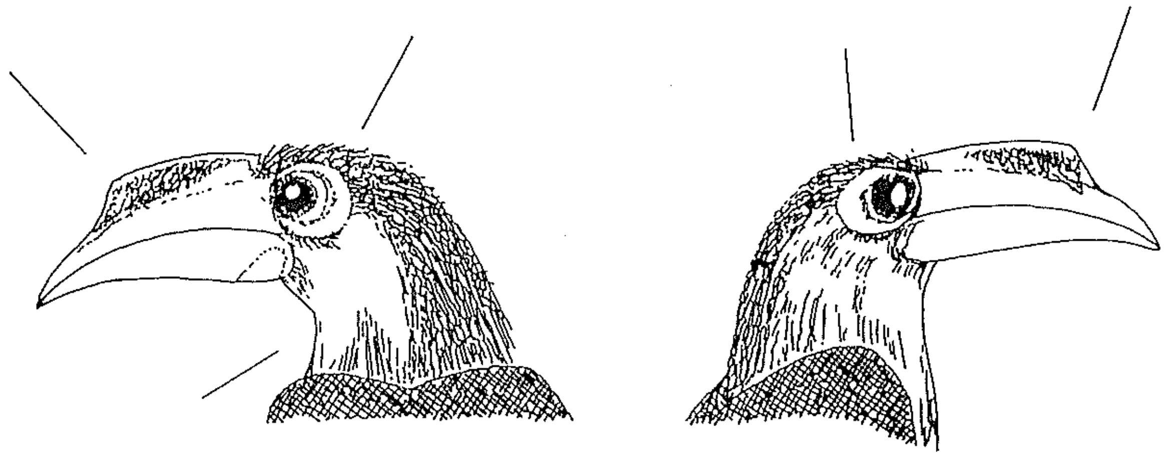
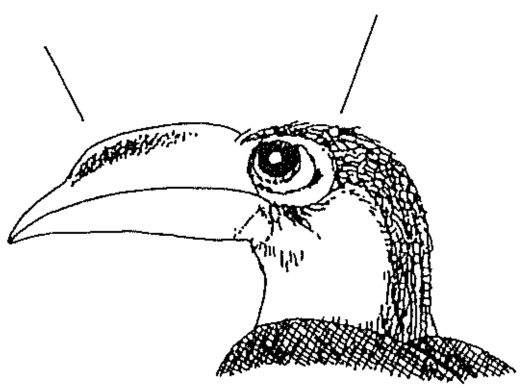


BREEDING MALE



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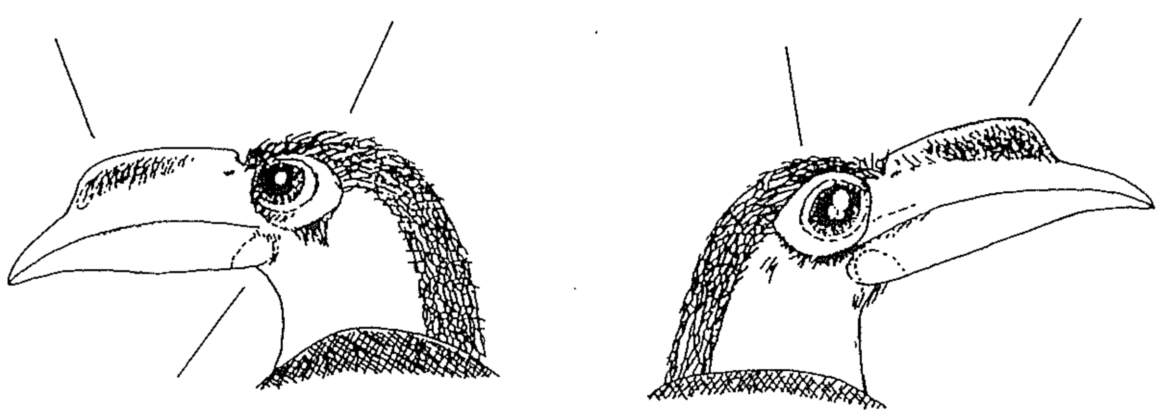


BREEDING · MALE

CHAPTER 6

FOOD AND FEEDING

INTRODUCTION

Feeding is one of the most essential activities of all animals, so there is no doubt that most animals are dominated by their never-ending quest for food. The structure and behaviour of most animals are affected by the nature of food required and the way in which it is obtained (McFarland 1981).

There are many birds feeding on a mixed diet with more or less marked preference for certain kind of food (Dorst 1974). In frugivorous vertebrates having fixed ranges or year-round territories, the diet may change from more preferred fruit species to less prefered ones when the former becames scarce. Birds with high energetic demands per unit body mass supplement their frugivory with hunting animal preys (Leighton and Leighton 1983).

Asian Hornbills are generally frugivorous, but they become omnivorous, particularly in the breeding season. Proportions of animal food in the diet may vary by species and perhaps by season (Poonswad *et al*. 1986).

In this chapter results of investigations on food and feeding are presented with an emphasis on 1) types of food and their nature, 2) diet composition and consumption, 3) food similarity and preference, and 4) feeding biology of four sympatric hornbill species during the breeding seasons at Khao Yai National Park.

METHODS

Field records and food samples

Approximately 125 food species of fruit and animals were collected and recorded on regular visits to nests from January 1982 through December 1985. Food samples were also collected at fruit trees and roost sites.

Breeding season (January to June)

Observations at nests were carried out from 14 January to 28 June at 2 to 10 day intervals. Food items and the amounts of food which males and nest helpers brought to broods were recorded at one hour intervals from 6:00 -17:00.

Food items were identified using binoculars (8x30), spotting scopes (x20 and x40) and/or photographs taken with 400, 500, and 800 mm telephoto lenses, depending on the distance from the observation blind to the nest. Regurgitated seeds and dropped food, as well as faeces, were collected to ascertain the identification of food items. Food plant specimens for the identification were prepared if a fruit food tree was found. Plant samples were then sent to the Forest Herbarium, Royal Forest Department, for further identification. Efforts were made to identify the food items at least to family.

Feeding frequency and food consumption: Observations were made from the first until the last meals at nests at every other week. Frequency and total amount of food brought per hour by males were recorded. The wet weight of each food item was assessed based on the average wet weight of the same food item which was obtained when males dropped it while feeding or was collected elsewhere later. For animal food, fresh specimens of the animal used for weighing may not always be the same species as those actually eaten by hornbills, but they were in the same groups and similar in size and were obtained within the study site (this presumption was necessary because of the difficulty of collecting and identifying the species in this tropical environment). There was no attempt to study how many kinds of plant species produced fruit food during the breeding season, but duration of various fruit species brought to broods were recorded.

Foraging methods

Direct and indirect observations were made to investigate foraging methods used by hornbills, such as cracking, probing, hawking, plucking, snatching, etc.

Cracking tree bark: The bird inserts its bill in the cracked bark of either a living or dead branch.

Probing: The bird puts its bill into a tree cavity and searches.

Hawking: The bird takes a prey in the air.

Plucking: The bird uses its bill to pluck food, usually fruits without much effort from a perch.

Snatching: The bird picks up food such as a fruit or an insect on leaf with speed.

Types of food brought by males can be an indicator of foraging method. For example, fish may have been caught by snatching

Duration of fruiting

To determine the duration of fruiting in the breeding and non-breeding seasons, direct observations were made occasionally along trails in combination with the recording of fruits brought by males and helpers. Seeds regurgitated by females and/or broods under nest trees were checked and identified. Regurgitated seeds under the roost in the non-breeding season were also checked and identified.

Non-breeding season (July-December)

Observations on hornbill's food were made while hiking along trails (about 80 km) in search of feeding and roosting flocks, as well as of roost sitesing, of hornbills. When a roosting site was found, the site was visited at intervals of 2 weeks to one month to check regurgitated seeds under the roost. However, in case of the roosting site shared by two species, it was not possible to quantify which seeds were regurgitated by which species.

Foraging niche

In order to determine the foraging niche of four sympatric hornbill species, eight trails totaling in about 40 km and with markings at every 100 m were set (Fig. 6-1). Walking along these trails, foraging niches was investigated once a week from July 8, 1991 until June 30, 1993. Sighted hornbills were identified and recorded with data on the position of the bird on branches, e.g. close to tree trunk, middle or the edge of the branch, and the height of hornbills above the ground.

Data analysis

Food diversity: The diversity of hornbill food is expressed by Shannon-Wiener index which is derived from the following formula: .lsl

$$H_S = - \sum_{i=1}^{s} Pi\log Pi$$

where H is index of diversity, s is number of food items and Pi is proportion of number or weight of a particular food item. When comparing H_S value among the four hornbill species, a high H_S value indicates the hornbill species is a general feeder. If the H_S value is low, it indicates that the species is a selective feeder.

Food preference: Data were presented as numerical abundance, weight and frequency that males and helpers brought to broods. I modified the method of Harrison et al. (1983) by ranking each food item in a hornbill nest separately in terms of number, weight and frequency. These three sub-ranks were then summed up and the summed ranks were rearranged in a single sequence, from lowest (highest rank) to highest values (lowest rank) to produce a final ranking for each food item fed by the male at an individual nest. Each food item then possessed a different rank at an individual nest of each hornbill species.

In order to assess the overall rank of each food item for each hornbill species, the real final ranks of food items from each nest must be scored. The sum of scores from each nest could be obtained from

$$S = \sum_{i=1}^{p} f\,[N - (r_i - 1)],$$

where S is a summed score which a given food item possesses from different nests of a given hornbill species, f is a frequency of the individual rank of a given food item, which occurs at various nests, r is the individual rank of the given food item for each nest, p is the total number of nests of the given hornbill species and N is the total number of food items to be ranked for the given hornbill species. The summed scores of each food item from all nests of a hornbill species were then rearranged, so that highest score means highest rank and vice versa. After each food item was ranked for preference by each hornbill species, these ranks were resummed and rearranged in the same manner as used to obtain the sum of the first sub-ranks. This ranking of food items would give an idea of their relative importance in the diet.

Food similarity: To determine food similarity consumed by four hornbill species, a coefficient of similarity was calculated. The degree of similarity between dietary components for each hornbill species was calculated from Kemp (1976):

$$C = \frac{2W}{a+b}$$

where C is similarity coefficient, W is the sum of all food items in the diet which two species share in common, a is the sum of all food items in the diet of one species, and b is the sum of all food items in the diet of the other species.

RESULTS

Food composition and consumption

Hornbills at Khao Yai are obviously omnivorous during the breeding season. Food brought to the brood was of two major groups, fruit and animals. Fruit was the main food and figs Ficus spp. were the major fruit. Food can therefore be classified as figs non-fig fruit, and animals. These food eaten by four hornbill species was very diverse. They comprised 36 identified fruits (Appendix 6-1), 26 unidentified fruits and at least 9 groups of animal food (Appendix 6-2).

The proportion of figs, non-fig fruit and animals in the diet is presented in Figure 6-2. Wreathed Hornbills showed the highest degree of being frugivory (92.5 % fruit), whereas Brown Hornbills the lowest (58.5 % fruit). Brown Hornbills were most carnivorous (41.5 % animal food) among these four species.

When considering the proportions of figs, non-fig fruit and animal food consumed by Great, Wreathed, Oriental Pied and Brown hornbills it is hypothesized that there were no correlations between the proportion of each food category. The results showed that there were no significant correlation between proportions of figs and non-figs (r_s = 0.118, n = 16, P > o.01; r_s = 0.117, n = 9, P > 0.01; r_s = 0.075, n = 24, P > 0.01; r_s = 0.064, n = 14, P > 0.01, respectively) or between figs and animals (r_s = 0.568, n = 16, P > 0.01; r_s = 0.427, n = 9, P > 0.01; r_s = 0.148, n = 24, P > 0.01; r_s = 0.345, n = 14, P > 0.01, respectively).

Feeding of total food and of fruit food varied significantly according to the size of hornbills. The two larger species, Great and Wreathed hornbills, consumed fruit at higher rate (g/h) than the two smaller species, Oriental Pied and Brown hornbills (Table 6-1). However, the feeding rate of animal food did not vary according to bird size. There were significant differences between the four hornbill species in consumption of animal food, except between Great and Oriental Pied hornbills, and Great and Brown hornbills (Table 6-1). Brown Hornbills fed animal food at the highest rate, whereas Wreathed Hornbills fed at lowest rate.

There were a high positive correlation between the feeding rate (g/h) and the feeding frequency per hour of total food for Great, Wreathed and Brown hornbills (r_s =

0.745, n = 16, P <0.01; r_s = 0.919, n = 9, P < 0.01; r_s = 0.780, n = 14, P < 0.01, respectively). Oriental Pied Hornbills may bring few number of food items or food of lighter weight each time. The feeding rate of Oriental Pied Hornbill was not, therefore, correlated with the feeding frequency (r_s = 0.4181, n = 24, P > 0.05).

It was found that there was no significant correlation between the feeding rate and the length of breeding cycle in any hornbill species (r_s = 0.433, n = 9, n, P > 0.05; r_s = -0.40, n = 4, P > 0.05; r_s = -0.342, n = 12, P > 0.05; r_s = -0.257, n = 6, P > 0.05).

The results clearly showed that broods of the two larger hornbill species ate more fruit than did those of the smaller ones (Table 6-1). Considering the two categories of fruits, fig and non-fig, it was found that broods of the two larger species consumed significantly more fig than those of the two smaller species (Table 6-1), but there was no significant difference in the consumption rate of non-fig fruit by these four hornbill species (Table 6-1).

Nature of fruit food

Fruit eaten by hornbills can be characterized into 2 categoreis, i.e. those having a soft pulp and numerous fine seeds (FNS) (which included all species of Ficus) and those having stone seeds (which included all species of non-fig fruits). Figs (fruit of Ficus spp.) eaten by hornbills were soft when ripe, but not juicy, thus hornbills ate them as one piece and fine seeds were passed in faeces. All figs on which hornbills feed have no stalk. These figs were from *Ficus* trees of strangling type or smooth monotrunk type (e.g. *Ficus albipila*).

Ficus racemosa and *F. hispida* are two species of fig trees which occur in Khao Yai but hornbills did not feed on, although their fruit are soft and fleshy. They are relatively lower trees than those of strangling type and produce relatively large clustered fruit on branches and trunks from February to April. Fruit of these two *Ficus* species has relatively long stalks. Other than these two species of *Ficus* spp. which hornbills did not eat but were fed on by other animals such as squirrels were those that have stalked fruit and those that have husky flesh. The reason why hornbills did not feed on those figs is unknown.

Kinds of non-fig fruits were diverse and they can be grouped into: **Split-husked fruit when ripening (SF):** This type exposes seeds which are usually covered by a waxy or pulpy opaque thin layer. Hornbills swallow the whole seed and later regurgitate the stone seed out. Such fruit are members of families Meliaceae, Myristicaceae, and Connaraceae.

Dry fleshy fruit with a single stone seed (FS): Hornbills swallow the whole fruit of this type and regurgitate the stone seed. Fruits of this type are members of the families Burseraceae, Annonaceae, and Olacaceae, Elaeocarpaceae, and Symplocaceae (Appendix 6-1).

Fleshy and soft/or juicy fruit with a single stone seed (FJ): Hornbills swallow the whole fruit and regurgitate the stone seed. Fruits of this type are members of the families Myrtaceae, Podocarpa ceae, Urticaceae, Elaegnaceae, and Lauraceae. All of these fruits have a pulp which is relatively easily separated from the seed.

No hornbills were observed to feed on the fruit which have thick pericarps that require peeling, such as those of Nephelium. The pulp of such fruits which found in the study site is relatively difficult to separate from the seed, as compared with the previously mentioned non-fig fruits.

Duration of fruit food

Ficus spp. were regularly brought to feed broods by all four species throughout the breeding seasons. Non-fig fruit were abundant during the chick-rearing period (April to May) (Appendix 6-3 and also Chapter 4). The non-fig species which produced fruit for three months or longer are Amoora cucullata, Dysoxylum sp., Chisocheton macrophyllus, Eugenia spp., Horsfieldia glabra, Knema laurina, Polyalthia viridis, and Strombosia spp. These fruits were recorded as eaten by all four species throughout breeding seasons. But some non-fig trees, such as Eugenia, Cinnamomum subavenium , Amoora cucullata, etc., may not produce fruit during the breeding seasons in some years, as shown in Appendix 6-3.

Food diversity and similarity

The diversity of food eaten by hornbills did not vary according to the size of hornbill. Of four hornbill species, Oriental Pied Hornbills fed on the greatest variety of food items (fruit and animals), whereas Wreathed Hornbills fed on the least variety (Table 6-2). The results of calculation of Shannon-Wiener index of diversity in Table 6-2 show the degree of being specialist or generalist in these four hornbill species. Wreathed and Brown hornbills are considered as specialists in taking fruit (Hs = 1.557) and animal (Hs = 1.083), respectively, when compared with the other two species (Table 6-2 and Fig. 6-2). As shown in Appendix 6-2, Great Hornbills were more specialized in hunting large preys than Oriental Pied and Brown hornbills.

Since these four hornbill species live sympatrically, therefore, they were expected to use the same food source, particularly the same fruit food. Food items recorded to be eaten by the hornbills showed relatively high similarities (Appendices 6-1 and 6-2). Of 36 identified species of fruits, 21 species (58.3 %) were eaten by all four species. Only four fruit species were eaten by only one species of hornbills. These were Jasminum sp., Trichosanthes tricuspidata and Slonea sigun eaten by Oriental Pied Hornbills, and Podocarpus polystachya eaten by Brown Hornbills.

It is interesting to note that, besides figs, fruits of trees in the family Meliaceae, which yield high energy, were eaten by all four hornbill species (Table 6-4).

Table 6-3 shows that among the four hornbill species, Great Hornbills consumed similar fruit food species in different breeding seasons (*n*=16), whereas Wreathed Hornbills took different fruit food in different breeding seasoons (*n*=9). Likewise, Brown Hornbills took similar animal food in different breeding seasons (*n*=14) and Wreathed Hornbills consumed different animal food in different breeding seasons.

The degree of food similarity between hornbill species as shown in Table 6-3 indicates that Great, Wreathed and Brown hornbills ate similar fruit food. Brown, Oriental Pied and Wreathed hornbills ate similar animal food.

In the case of Great Hornbills, females of which share feeding duty with males after their emergence, the males and the females brought similar food items to broods (C = 0.83, n =16). In Brown Hornbills a cooperative breeding species, almost exactly the same food items were brought to broods by the breeding male and helpers (C = 0.93, n=14). Hence the breeding male and the helpers were thought to be foraging together.

Food preference

It is very difficult to investigate the food preference of these four hornbill species under natural conditions. However, data collected during the breeding seasons of 1982-1985 revealed variations in feeding of food items. These variations were found within and between the species of hornbills, thus permitting ranking preference (Tables 6-4 and 6-5). Among 13 non-fig fruits, Polyalthia viridis, Strombosia sp., and Horsfieldia glabra were most preferred by all four species. In animal food centipedes and cicadas were most preferred.

Percentages of 10 most preferred non-fig fruits (Table 6-4) to the total food by weight are presented in Figure 6-3. It was apparent that Polyalthia viridis contributed most (26.9 %) in the total food of Wreathed Hornbills by weight. Brown Hornbills had Polyalthia viridis, Strombosia sp., Dysoxylum sp. and Cinnamomum subavenium in similar percentage (9.1 %, 8.3 %, 8.7 %, 9.7 %, respectively) in the total food.

The nutritional values of some fruit food recorded in the breeding season indicated that hornbills did not always select those fruit of high nutritional value (Table 6-6). Rather the data suggested that hornbills would select fruit by availability or abundance, in combination with other characteristics such as the ease of eating or of removing seeds, the attractiveness of the fruit by colour, etc.

Feeding biology

Foraging methods

As fruit is the main food for all four hornbill species, foraging methods other than plucking were observed less frequent. The frequency of other foraging methods seemed to be relate to carnivory.

Foraging methods used by each hornbill species are given in Table 6-7. Plucking was mostly used by all four species in obtaining fruit. The use of this foraging method confirmed that all four hornbill species were mainly fruit eaters. Plucking was exclussively arboreal foraging method and was never seen on the ground during the breeding season, except for one occasion in which a breeding male Oriental Pied Hornbill picked up an empty mussel shell on the river bank. The foraging method used by hornbills on the ground was not observed directly, although such animal food as crabs, fish, filopaludina snail, and elongated millipede, may have been obtained either on the tree, on the ground or from the creek.

Foraging niche

The four hornbill species were observed to forage at different levels above the ground. The two larger species foraged at significantly higher levels than did the two smaller species (Table 6-8). The distribution of foraging level above the ground of these four hornbill species is shown in Figure 6-4. It was noteworthy that Wreathed Hornbills foraged at the highest level and Brown Hornbills at the lowest level. This could be related to the differences in food items between these two species (Fig. 6-2).

Generally, four hornbill species showed no specific preference of parts on a branch for foraging. However, Wreathed and Brown hornbills seemed to use areas more in the middle and at the edge of a branch, respectively (Table 6-9).

Feeding and breeding cycle

Feeding of all four hornbill species peaked at two periods, at an early stage of female imprisonment and after chick hatching.

Great Hornbills: The feeding rate (g/h) (equivalent to consumption rate) was high at week 4 after female were imprisoned and at weeks 13 and 14 of the breeding cycle. Consumption rates of both total food and fruit show a little variation. However, in all food types the feeding rate decreased towards the fledging period. (Fig. 6-5). Great Hornbills fed significantly larger quantity of animal and total food but less fruit after chick hatching than before hatching ($F_{77,117}$= 2.21, $P < 0.01$; $F_{77,118}$= 1.67, $P < 0.01$; $F_{75, 118}$ = 1.8, $P < 0.01$, respectively). Before chick hatching, female Great Hornbills ate animal food as well. Around week 13, females emerged (Chapter 4) therefore, the feeding was for the chick alone.

Wreathed Hornbills: Total feeding rate was high at weeks 2 and 4 after female imprisoning. It was noteworthy that before hatching the young, very few animal food was fed to the incubating females (0.2 g/h); hence the animal food fed after week 8 (which significantly increased) ($F_{34,62}$ = 14.2. $P < 0.01$) was for the chick alone. This should confirm the hatching period of this species at about week 8. In contrast to Great Hornbills, Wreathed Hornbills showed no difference in feeding fruit or total food during, before and after the chick hatching period ($F_{34,62}$ =1.31, $P > 0.05$; $F_{34,62} = 1.34$, $P > 0.05$; respectively).

Oriental Pied Hornbills: Feeding patterns for fruit, animals and total food were rather similar to those in Great Hornbills. Oriental Pied Hornbills also fed significantly larger quantity of fruit, animals and total food after chick hatching than before hatching ($F_{62,143} = 1.5$, $P < 0.05$; $F_{62,143} = 9.38$, $P < 0.001$; $F_{62,143} = 2.66$, $P < 0.001$, respectively). The feeding was also high at week 2 after females were imprisoned. After chicks hatched, the feeding was rather uniform with a peak at week 11 and then began to drop towards the fledging period.

Brown Hornbills: Feeding rates of fruits and total food increased significantly at week 2. After week 3, total food and fruits gradually increased and reached a peak at week 9 and then decreased towards fledging. It was confirmed by statistical tests that there were no significant differences in total and fruit food feeding before and after chick hatching ($F_{45,91} = 1.44$, $P > 0.05$; $F_{45,91} = 1.04$, $P > 0.05$, respectively). But the feeding rate of animal food was significantly higher after chick hatching than before hatching ($F_{45,91} = 1.96$, $P < 0.01$).

There were highly significant differences between the means of feeding rates of fruit, animal and total food for the four hornbill species before and after chick hatching (Table 6-10). Before hatching, there were no significant differences in consumption of fruit either between the two larger species, Great and Wreathed hornbills ($F_{43,75}$ = 1.27, $P > 0.05$), or between the two smaller species, Oriental Pied and Brown hornbills ($F_{143,91}$ = 1.37, $P > 0.05$). Great and Brown hornbills showed no significant differences in feeding of animal food before and after chick hatching. The females of these two species were apparently more carnivorous than those of Wreathed and Oriental Pied hornbills (Fig. 6-5).

Weekly feeding frequency after female imprisonment is shown in Figure 6-6. Only Brown Hornbills took animal food more often than fruit, indicating again that the species is relatively carnivorous. There were highly significant differences among feeding frequencies of total food for the four hornbill species (Kruskal-Wallis test, H = 40.762, df = 3, n = 63, $P < 0.001$) except between the two larger species (Z = 1.387, n_1 = 16, n_2 = 9, $P > 0.05$).

Food of nestling (s)

It is very difficult to assess the amount of food eaten by a nestling because it could not quantify the food of each individual directly. Feeding data for Wreathed Hornbills suggested that the animal food feeding rate after the chick hatching (2.3 g/h) was for the nestling because before chick hatching,the male seldom fed the female with animal food (Fig. 6-5). For Great Hornbills, the amount of food consumed by the nestling, as well as the consumption rate of nestlings, could be determined only after females emerged). The feeding rate, particularly that of fruit food, was very high at week 13. It was observed that the nestlings used food, especially fruit, as plaster material to reseal the nest entrance (see also Chapter 4). The consumption rate of the three food categories by the nestlings is shown in Figure 6-7. The amount of figs and animals consumed were highest in the first week after females emerged but decreased towards fledging, whereas non-fig fruit consumption tended to increase. However, the decrease in fig consumption was not correlated with the increase in non-fig fruit consumption ($r_s = -0.143$, $n = 7$, $P > 0.05$).

Daily feeding rate

During the breeding season breeding males of all four species showed different patterns of activeness at different times as shown in Figure 6-8. Competition seemed to be an important factor causing these four species to be active at different time. Great Hornbills were most active early in the morning, whereas Brown Hornbills were most active during 15:00 to 16:00 hours. However, except for Brown Hornbills, all three species seemed to be very active during 8:00 to 10:00 hours. Otherwise, patterns of feeding frequency by hour were relatively similar in all four species.

Food competitors of hornbills

Although hornbills are recognized as omnivorous birds, fruit was definitely the main food. The study site was inhabited by a number of frugivorous birds and mammals. These animals should compete with hornbills for food resource, especially at *Ficus* trees. Figs ripen synchronously in great abundance and thus attract various kinds of animals. The animals observed to compete with hornbills on fig trees were listed in Appendix 6-4. The most important group of avian competitors were pigeons (family Columbidae) including Mountain Imperial Pigeons *Ducula badia*) and Thick-billed Green Pigeons *Treron curvirostra*. These two species of pigeons feed on figs in large flocks of 5 to 83 birds. Another species which regularly comes in flocks to feed on ripe figs was Hill Mynas *Gracula religiosa*, a flock of which consisted as many as 37 birds. Important mammal competitors are Pig-tailed Macaques *Macaca nemestrina*, White-handed Gibbons *Hylobetes lars*, and Black Giant Squirrels *Ratufa bicolor*. The first species usually shows up in troops and they do not only consume fruits but also destroy the fruit crop by shaking and breaking off branches of fig trees while feeding. The last species was observed regularly feeding on figs almost throughout a day.

Food in the non-breeding season

After the breeding season hornbills travell in flocks varying from family size (3 to 4 individuals) up to large number (e.g. 100+ individuals of Wreathed Hornbills were seen) (see also Chapter 8). Little was known about food eaten by hornbills during the non-breeding season. Fruits which were found under roost sites were recorded (Table 6-11). It seems that during the non-breeding season hornbills feed almost entirely on fruit, except for Brown Hornbills which were seen capturing insects twice or three times (out of 20 observations). Brown Hornbills fed their young with several kinds of insects, but most of the time they fed fruit to the young. The kinds of fruit which were directly observed to be eaten by hornbills, or were found under the roost of single species, in the non-breeding season are presented in Table 6-11.

A flock of 12 Oriental Pied Hornbills was observed feeding on the forest floor, with no fruiting trees nearby: Hence this species would hunt animal prey on the ground even during the non-breeding season.

DISCUSSION

Diet composition and preference

Detials of diet composition and food preference observed in this study differ from those found by Leighton (1986) on seven species of Bornean hornbills. All hornbills at Khao Yai except Brown Hornbills fed on figs, non-fig fruits, and animals in decreasing order of consumption. Brown Hornbills consumed animals most, followed by figs and non-fig fruits. Except for Helmeted Hornbill *Rhinoplax vigil*) which fed mostly on figs followed by animals, Borneon hornbills fed on non-fig fruits, figs, and animals in decreasing order of consumption (Leighton 1986). Leighton (1986) also observed that non-territorial Rhyticeros hornbills did less hunting of animal prey and consumed more lipid-rich, drupaceous fruits of the families Lauraceae and Burseraceae, fruits of which are equivalent to non-fig fruits in this study. This is rather similar to the diet of Wreathed Hornbills in this study, especially the diet in the non-breeding season. But during the breeding season in this study, Wreathed Hornbills consumed a great quantity of fruit of Polyalthia viridis despite the fact that this fruit yielded relatively low energy or low lipid. Thus richness in lipids would be less important in food selection than abundance in availability and/or the other characteristics discussed below.

Bushy-crested Hornbills Anorrhinus galeritus have breeding strategy, similar, to Brown Hornbills (cooperative breeding system), but the composition of the diet is different with non-fig fruits taken most, followed by figs and animals in the former species (Leighton 1986). The differences in diet composition between two species may be due to the differences in the availability and abundance of food types within the area and/or competition with other species which live sympatrically.

Hornbills at Khao Yai also had completely different diet from African hornbills, Bucorvus spp. and Tockus spp. Those hornbills are mainly insectivorous, feeding more on insects than on fruit (Kemp 1976, 1979). This is obviously due to the differences in habitat types. The African hornbills live in savannas where fruit trees may be scarce as compared with the forest habitat of the species studied.

Leighton (1986) stated that hornbills prefer lipid-rich fruits. It is suggested that the preference for such fruits may be limited to the non-breeding season, when hornbills could spend more time in searching more favourite fruits. In the breeding season, breeding males may have to spend minimum time in gathering as much food as possible for females and broods. Moreover, competition pressure should be higher in the breeding season than in the non-breeding season. For these reasons, hornbills would feed on less favoured, but most abundant fruits in the breeding season.

It is hypothesized that hornbills' preference on fruits is chiefly determined by abundance of the food fruits. Sorensen (1981) and Foster (1990) have shown that birds become less concerned with the quality of food when a large quantity of the food is available, and they also become less selective. Indeed birds may not be able to distinguish pulp composition of nutrition richness. *Ficus* is obviously the most important dietary component in the hornbills' diet, particularly in the breeding season. Among the non-fig fruits, *Polyalthia viridis* was the most common. My observations in this study strongly indicate that all four hornbill species fed on fruit which were abundant, regardless of nutritional value.

Ficus trees usually produce a large quantity of fruit and they ripen synchronously (Janzen 1979, Leighton and Leighton 1983). This make a *Ficus* tree provide a large patch at one time as compared with trees of the family Meliaceae, the fruit of which are lipid-rich but a few ripen each day (Leighton and Leighton 1983). *Polyalthia* trees also produce as many as 100 fruits on a branch (Corner 1952). Abundance and easiness in obtaining are probably the reasons why the fruit of figs and *Polyalthia* were favoured over others. Leighton and Leighton (1983) stated also that figs were less preferred by Bornean hornbills and in particular White-crowned *Berenicornis comatus* and Bushy-crested hornbills usually neglected figs. They turn to figs when other preferred fruits are less abundant. Brown Hornbills in this study also depended more on non-fig fruits than on figs. However, it was not known whether this was due to its own preference or to competition with other hornbill species.

The characteristics which attract animals to fruit may be its colour and size, as well as the characters of fruiting, (e.g. in clusters, singly, etc.). Fruit which change colour when they ripen and come out in clusters will attract animals to visit (Stiles 1989). The colour of fruit which seems to attract animals who serve as seed dispersers (or swallowers, Foster 1991) is red or black. Both *ficus* and *Polyalthia* seem to posses all of these preripening flags by changing the colour from green, yellow, and orange and to dark purple or black (pers. obs., Corner 1952). The size of fruit may not be so important in the case of hornbills because they posses a large bill which can handle quite a wide range of fruit sizes.

Fruits of *Strombosia* and *Canarium* (the non-fig species and the less preferred than *Polyalthia*,) change the colour from green to black and ripen synchronously. *Canarium* usually has fruits ripen in the non-breeding season and produced bunches of fruit, whereas *Strombosia* produced a single fruit on each stalk. Although these trees produced an abundance of fruit (pers. obs.), they are less common than *Polyalthia* in the forest of Khao Yai (pers. obs.).

The other characteristics which make *Ficus* the fruit favoured by the four hornbill species at Khao Yai are the fact that the entire fruit is digestible. Figs eaten by hornbills were soft with fine seeds. All the non-fig fruits contain of digestible and indigestible parts (mostly seeds), which takes up space in the stomach and consequently results in only partial profit (Leighton 1982, Leighton and Leighton 1983, Stiles 1989). Besides, fruits having the pulp which is easily separated from the seed, such as *Polyalthia* and *Strombosia*, will be favoured over those which the removal of the pulp from the seed is difficult (Stiles 1989, pers. obs.). *Nephelium*, is an example of the latter and neglected by hornbills at Khao Yai. Leighton (1982) reported that Bornean hornbills eat *Nephelium*. It is possible that *Nephelium* sp. found at Khao Yai has different characteristics from the one which occurrs in Borneo.

Corner (1952) mentioned that in some species of Nephelium in Malaysia the pulp is easily separated from the seed when matured.

The split-husked fruit included Horsfieldia, Amoora, Dysoxylum, and Chisocheton. The first genus produced fruit in clusters on branches with non-distinct colour changes from green to yellow and the fruit opened to expose orange pulp. Horsfieldia species produced fruit more abundantly than did species of other genera. All of these genera, besides ripening in small number of fruits each day, they also produce no preripening signs until few fruits ripen then split to expose the seed, which is covered with a thin layer of bright or contrasting coloured pulp and may attract hornbills.

Foraging niche

Niches of the four hornbill species were clearly separated vertically but not horizontally. The height at which a species forage affects the diet of the species (Dorst 1974) or vice versa. Wreathed Hornbills, which forage in the highest niche, were the most frugivorous species because most fruits were obtained from the canopy. Brown Hornbills forage in the lowest niche and mostly carnivorous. It is not known whether niche selection is affected by feeding strategy or feeding strategy is modified by niche selection. Niche selections may be affected by competition. Hornbills may forage in different places, feed on different proportions of food (McFarland 1981) to avoid competition. These competing hornbill species, however, did not arrange themselves in positions on a branch according to their size as has been discovered in fruit pigeons of the genera Ptilinopus and Ducula in New Guinea (Diamond 1973). It may be due to the hornbills are not entirely frugivorous, as in contrast to those fruit pigeons. Then how can the hornbills avoid interaction, besides arranging themselves vertically in the forest? They were possibly avoiding competition by being active at different times. However, this hypothesis needs further study.

The diversity of food eaten by Oriental Pied Hornbills indicates that vertical niches provide different habitats as food resources, especially for animal food. As Oriental Pied Hornbills forage from the ground up into the canopy, which is correlated with greatest variety of their food.

Food consumption

All four species showed peaks of feeding rates or consumption rate during the egg incubation period (Fig. 6-5). Females would need a high energy intake while incubating eggs. However, it is more likely that females needed physical preparations for starvation that may occur after chick hatching. In the case of Wreathed Hornbills fruit fed to females before and after chick hatching were not different. Hence female Wreathed Hornbills were starved after chick hatched. All food fed by the male after chick hatching, particularly animal food, was exclusively for the chick. This was also the case in Brown Hornbills, and females may have starved after chicks hatched. Since the food fed by males and nest helpers was perhaps seemed to be only for chicks (see also Chapter 4).

Table 6-1 Comparison of consumption rates of fruit food, fig, non-fig, animal and total food of four hornbill species statistical tests for significance. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbi BH = Brown Hornbill.

Food type	Consumption rate by hornbill species (g/day)				Kruskal-Wallis Test Corrected for ties			Mann-Whitney U-test Significant level		
	GH	WH	PH	BH	H	n	P(df=3)	Z	n_1, n_2	*P<0.05,**P<0.0
Fruit										
Range	135.2-360.2	126.0-545.3	61.8-237.6	39.9-227.6	36.09	63	<0.001	4.459	16, 24	GH & PH**
Mean	262.6	318.6	138.1	107.5				4.427	16, 14	GH & BH**
SD	66.8	138.6	50.2	44.8				3.537	9, 24	WH & PH**
N	16	9	24	14				3.622	9, 14	WH & BH**
Fig										
Range	42.9-239.0	62.6-410.0	5.2-139.2	0.6-121.5	35.46	63	<0.001	4.597	16, 24	GH & PH**
Mean	170.1	174.4	57.5	44.4				4.178	16, 14	GH & BH**
SD	58.8	106.4	30.9	33.5				3.739	9, 24	WH & PH**
N	16	9	24	14				3.559	9, 14	WH & BH**
Non-fig										
Range	31.6-149.7	22.6-231.0	27.6-236.1	23.1-106.1	9.13	63	>0.01	Not Significant		
Mean	92.5	144.2	82.7	63.2						
SD	31.6	81.3	44.3	24.0						
N	16	9	24	14						
Animal										
Range	0.0-80.0	0.0-46.2	4.2-71.2	13.2-160.0	12.29	63	<0.01	2.066	16, 9	GH & WH*
Mean	42.7	18.7	36.8	63.5				2.324	9, 24	WH & PH*
SD	25.4	16.9	18.5	39.2				3.055	9, 14	WH & BH **
N	16	9	24	14				2.285	24, 14	PH & BH *
Total food										
Range	152.3-423.4	126.0-587.2	66.0-323.5	67.9-336.0	22.55	63	<0.001	3.934	16, 24	GH & PH**
Mean	305.3	337.3	176.9	171.0				3.388	16, 14	GH & BH**

Table 6-2 Food diversity recorded as eaten by four hornbill species during the breeding seasons (1982-1985). H_S = Shannon - Wiener index calculated separately (see text).

Hornbill species	No. fruit species	H_S (fruit)	No. animal species	H_S (animal)	Total food species	H_S (total food)
Great Hornbill	37	1.70	44	2.20	81	1.95
Wreathed Hornbill	30	1.56	20	1.50	50	1.53
Oriental Pied Hornbill	49	1.89	56	2.0	10~~8~~5	1.94
Brown Hornbill	41	1.90	41	1.08	82	1.50

Table 6-3 Degree of similarity (*C* value) of fruit and animal food consumed by four hornbill species at Khao Yai during the breeding seasons from 1982 to 1985. Underlined figures indicate similarity of individual hornbill species by year. Figures in bracket indicate average *C* values for fruit and animal food. (See text for calculation).

Fruit food	GH	WH	PH	BH
GH	0.68	0.83	0.75	0.82
WH		0.37	0.69	0.84
PH			0.44	0.70
BH				0.44

Animal food	GH	WH	PH	BH
GH	0.49			
WH	0.68	0.13		
PH	0.74	0.63	0.51	
BH	0.66	0.73	0.75	0.66

Total food	GH	WH	PH	BH
GH	(0.59)	0.75	0.74	0.73
WH		(0.25)	0.66	0.78
PH			(0.48)	0.72
BH				(0.55)

Table 6-4 Rank of 12 important identified non-fig fruits which were observed to be consumed by all four hornbill species during the 1982-1985 breeding seasons at Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill, ND = No data.

Family	Fruit genus/species	Rank of fruit by hornbill sp.				Summed	Fruit	Energy (kcal) per 100 g
		GH	WH	PH	BH	Rank	Rank	fruit wet weight
Annonaceae	_Polyalthia viridis_	2	2	2	2	8	1	90.97
Connaraceae	_Connarus_ sp.	20	11	16	5	52	10	ND
Lauraceae	_Cinnamomum subavenium_	4	24	8	10	46	9	216.0
Meliaceae	_Amoora cucullata_	3	8	6	8	25	5	275.0
	Dysoxylum sp.	5	7	5	7	24	4	250.9
	Chisocheton macrophyllus	9	5	14	17	45	8	323.47
Moraceae	_Artocarpus lakoocha_	18	19	10	24	71	12	98.35
Myristicaceae	_Horsfieldia glabra_	7	4	3	4	18	3	57.6
	Knema laurina	10	16	12	14	52	10	66.92
Myrtaceae	_Eugenia cumini_	8	10	7	6	31	6	87.57
Oleaceae	_Strombosia_ sp.	6	3	4	2	15	2	221.2
Palmaceae	_Livistona speciosa_	12	13	16	9	40	7	199.0

Table 6-5 Ranks of 17 identified animal foods observed to be consumed by four hornbill species during the 1982-1985 breeding seasons at Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Animals	Rank of animal by hornbill species				Summed	Animal
	GH	WH	PH	BH	Rank	Rank
Insect						
Locust	12	10	2	1	33	7
Beetle	11	1	5	11	28	6
Cricket	18	17	21	7	63	15
Wasp's nest	6	17	18	8	69	16
Caterpillar	3	15	5	9	30	8
Cicada	9	8	1	2	18	2
Other arthropods						
Centipede	4	2	7	3	16	1
Millipede	8	3	8	4	23	5
Crab	21	4	8	18	51	11
Reptile						
Snake	4	17	17	22	60	14
Lizard	2	7	6	5	20	3
Aves						
Bird	16	8	23	24	71	17
Bird Chick	7	8	15	19	49	10
Bird's egg	1	10	4	6	21	4
Miscellaneous						
Snail + shell	14	13	11	10	48	9
Earthworm	9	12	13	20	54	12
Rat	4	14	14	24	56	13

Table 6-6 Nutritional values and ranks of some identified fruits which all four hornbill species fed to broods during the breeding seasons from 1982 to 1985 at Khao Yai.

Fruit species	Rank	Nutritional value per 100 g fruit			
		Protein (g)	Fat (g)	Cabohydrate (g)	Ca (mg)
Moraceae					
Ficus sp. (1)	main food	1.66	0.85	9.65	217.4
Ficus sp. (2)	"	1.16	0.75	19.4	94.34
Ficus sp. (3)	"	2.0	1.4	20.5	226.0
Ficus sp. (4)	"	1.2	0.5	39.8	136.5
Ficus sp. (5)	"	2.08	2.6	9.46	930.22
Ficus sp. (6)	"	1.05	0.9	8.67	132.73
Urticaceae					
Artocarpus lakoocha	12	0.86	1.71	19.86	24.44
Myristicaceae					
Horsfieldia glabra	3	1.73	18.59	5.55	26.12
Knema laurina	10	0.95	1.8	11.73	6.98
Myrtaceae					
Eugenia cumini	6	0.91	0.69	19.43	74.04
Podocarpaceae					
Podocarpus polystachya	>20	0.9	0.2	14.6	33.8
Olacaceae					
Strombosia sp.	2	6.63	12.48	20.59	23.1
Annonaceae					
Polyalthia viridis	1	3.66	2.17	14.20	43.7
Burseraceae					
Canarium subulatum	>15	2.94	22.16	2.9	181.0
Lauraceae					
Cinnamomum subavenium	9	2.5	16.5	14.3	56.0
Meliaceae					
Amoora cucullata	5	4.58	24.65	8.85	83.88
Dysoxylum sp.	4	5.75	19.04	14.14	67.24
Chisocheton macrophyllus	8	3.62	28.59	12.92	55.0

Table 6-7 Frequency and percentage of different foraging methods used by four hornbill species observed in the breeding and non-breeding seasons (1982-1985). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Foraging method	Frequency of foraging method used by species								All species	
	GH		WH		PH		BH			
	No. obs	%	No. obs	%	No. obs	%	No. obs	%	No. obs	%
Cracking tree bark	23	11.8	5	1.8	9	4.4	0	0	37	4.4
Probing	7	3.6	0	0	3	1.5	0	0	10	1.2
Hawking	0	0	0	0	12	6.0	21	13.6	33	4.0
Plucking	165	84.6	276	98.2	170	84.6	122	78.7	733	88.1
Snatching	0	0	0	0	7	3.5	12	7.7	19	2.3
Total	195	100	281	100	201	100	155	100	832	100

Table 6-8 Range, mean and S.D. and statistical tests of foraging level above the ground of four hornbill species at Khao Yai.

Hornbill Species	Foraging level above ground			
	Range (m)	Mean (m)	SD	*n*
Great Hornbill	8.0-50.0	26.3	7.99	328
Wreathed Hornbill	10.0-45.0	33.2	9.27	97
Oriental Pied Hornbill	2.0-55.0	21.3	9.72	395
Brown Hornbill	5.0-30.0	16.6	6.49	54

ANOVA Ho: Mean foraging heights of four hornbill species are not different ($F_{3,870} = 67.02$, $P < 0.001$).

Table 6-9 Frequencies of four hornbill species found foraging in different parts of trees. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill

Part on branch	Frequency of birds found				Total
	GH	WH	PH	BH	
	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)
Close to trunk	81 (23.6)	19 (18.6)	123 (26.3)	16 (24.6)	239 (24.4)
Middle	157 (45.8)	55 (53.9)	191 (40.8)	18 (27.7)	421 (43.0)
Edge	105 (30.6)	28 (27.5)	154 (32.9)	31 (47.7)	318 (32.6)
Total	343 (100)	102 (100)	468 (100)	65 (100)	978 (100)

Ho: There is no difference among these four hornbill species in using location in trees. (X^2 = 15.47, df = 6, $P > 0.05$)

Table 6-10 Comparison of range, mean and SD of feeding rates of two different food types and total food before and after chick hatching of four hornbill species the during 1982-1985 breeding seasons at Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Food type	1. Feed rate before hatching (g/h)				2. Feed rate after hatching (g/h)				ANOVA
	GH	WH	PH	BH	GH	WH	PH	BH	
Fruit									
Range	0.0-101.9	0.0-64.6	0.0-23.9	0.7-31.6	0.0-74.1	0.0-105.3	0.9-39.0	0.7-31.9	1) $F_{3,216} = 20.38$,
Mean	22.5	23.3	8.3	9.2	21.9	37.7	11.8	8.3	$P < 0.001$
SD	17.2	19.4	5.4	6.7	12.8	22.2	6.6	5.6	2) $F_{3,414} = 94.93$
n	76	35	63	46	119	63	144	92	$P < 0.001$
Animal									
Range	0.0-14.9	0.0-3.3	0.0-9.1	0.0-13.2	0.0-33.0	0.0-11.6	0.0-56.0	0.0-23.0	1) $F_{3,217} = 6.46$
Mean	1.6	0.2	1.2	2.7	4.6	2.3	4.2	5.9	$P < 0.001$
SD	3.2	0.6	2.2	3.1	4.8	2.2	6.6	4.4	2) $F_{3,414} = 6.32$
n	78	35	62	46	118	63	145	92	$P < 0.001$
Total									
Range	0.0-101.9	0.0-66.4	0.0-26.6	0.7-38.5	0.0-77.7	0.0-108.0	0.1-93.0	1.5-43.6	1) $F_{3,216} = 14.34$
Mean	22.7	23.3	9.7	11.9	26.2	40.0	15.7	13.9	$P < 0.001$
SD	17.6	19.7	6.1	8.1	13.6	22.8	9.9	8.0	2) $F_{3,414} = 64.13$
n	78	35	61	46	119	63	144	92	$P < 0.001$

Table 6-11 Some identified fruits observed as eaten by four hornbill species during non-breeding seasons at Khao Yai.

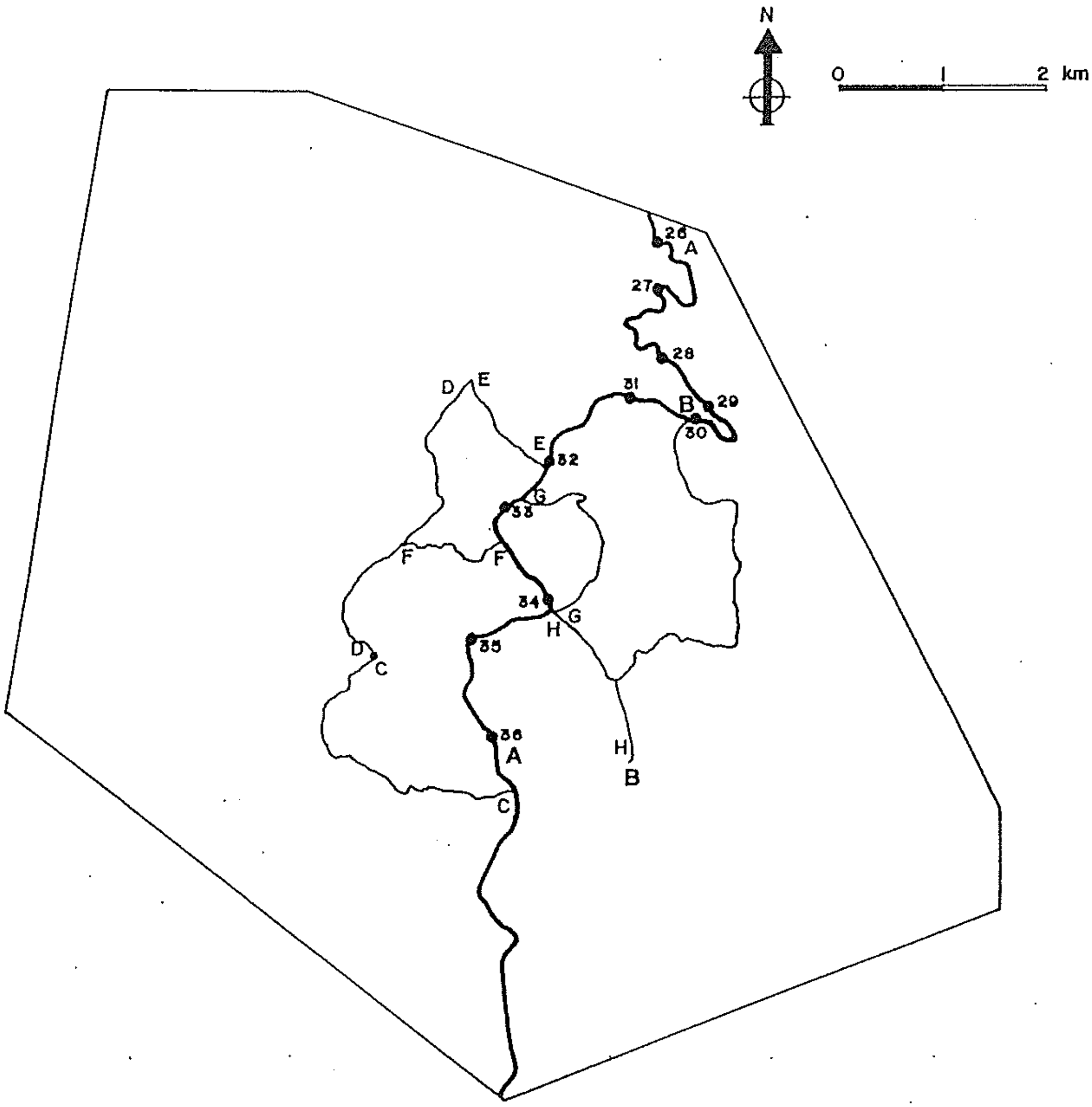
GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill

Identified Fruit Species	Species found on tree				Seed under roost of species				Approx. fruiting period in non-breeding season	Approx. fruiting period in breeding season (Appen.3)	Energy (Kcal.) per 100g fruit wet weight
	GH	WH	PH	BH	GH	WH	PH	BH			
*_Ficus_ spp. (6sp)	x	x	x	x	x	x	x	-	Throughout the year	Throughout	*88.12
Phoebe sp.	x	x	-	-	-	x	-	-	July - September	-	178.0
Nyssa javanica	-	x	-	-	-	x	-	-	August - ?	-	194.8
Strombosia sp.	x	x	-	-	x	x	-	-	May - September	April - May	221.2
Canarium subulatum	x	x	x	-	x	x	x	-	August - December	March - May	222.8
Chisocheton macrophyllus	x	x	x	x	-	x	-	-	May - August	March - June	323.47
Michelia baillonii	-	-	x	-	-	-	-	-	August-October	-	-

* Range 46.98 - 168.1 Kcal

X = 88.12, S.D = 44.44

n = 6



A = 10.0 km
B = 7.3 km
C = 5.3 km
D = 4.6 km
E = 2.8 km
F = 2.6 km.
G = 3.8 km
H = 3.0 km

Fig. 6-1 Map showing the trails used for the study of foraging niche of four sympatric hornbill species at Khao Yai during 1991 to 1993. (see also text).

	Number of nesting pairs	Observation days	Observation hours
GH	16	421	3881
WH	9	240	2161
PH	24	443	4216
BH	14	259	2322

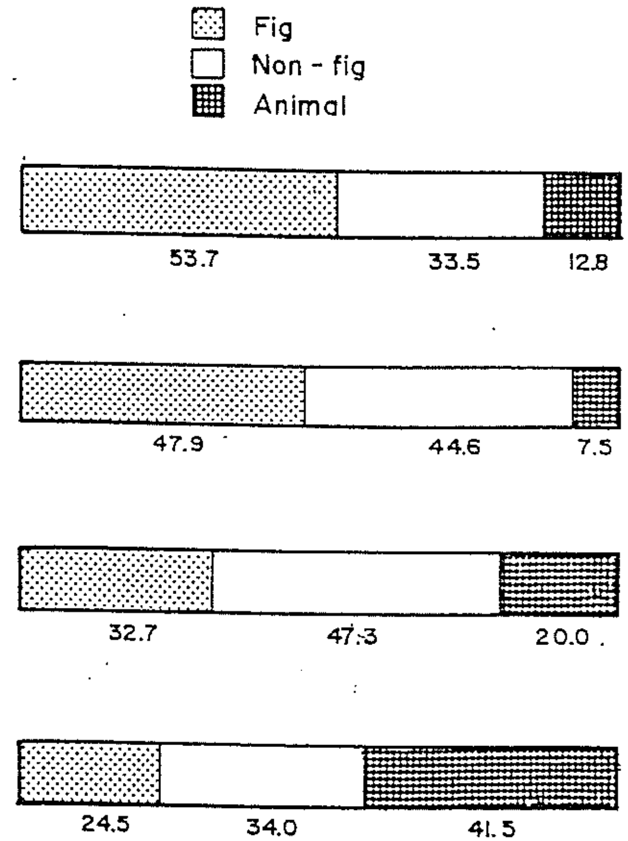
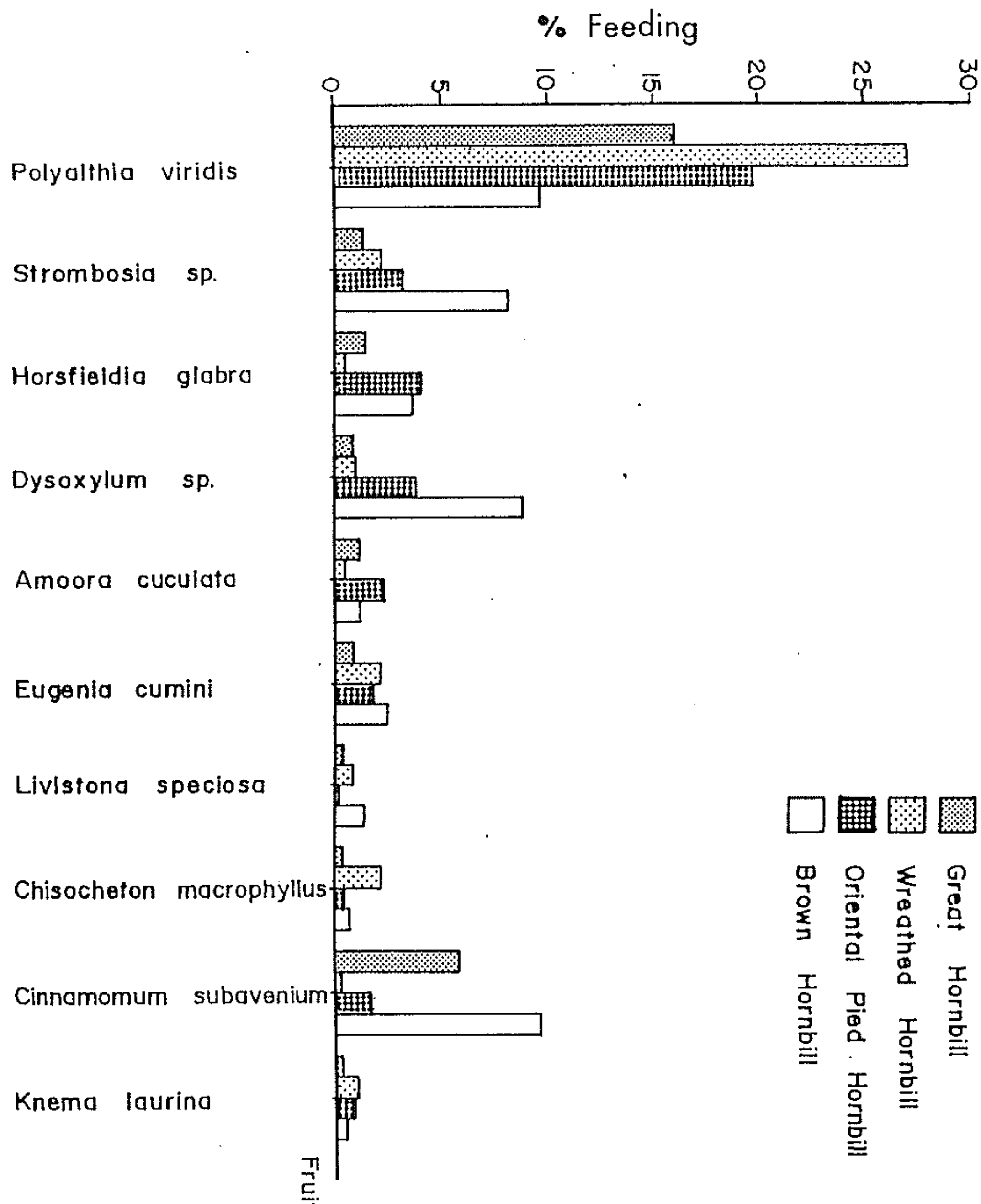


Fig. 6-2 Diet composition of four hornbill species observed during 1982-1985 breeding season at Khao Yai. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.



% Feeding
0
5
10
15
20
25
30
Polyalthia viridis
Strombosia sp.
Horsfieldia glabra
Dysoxylum sp.
Amoora cuculata
Eugenia cumini
Livistona speciosa
Chisocheton macrophyllus
Cinnamomum subavenium
Knema laurina
Fruit
Great Hornbill
Wreathed Hornbill
Oriental Pied . Hornbill
Brown Hornbill

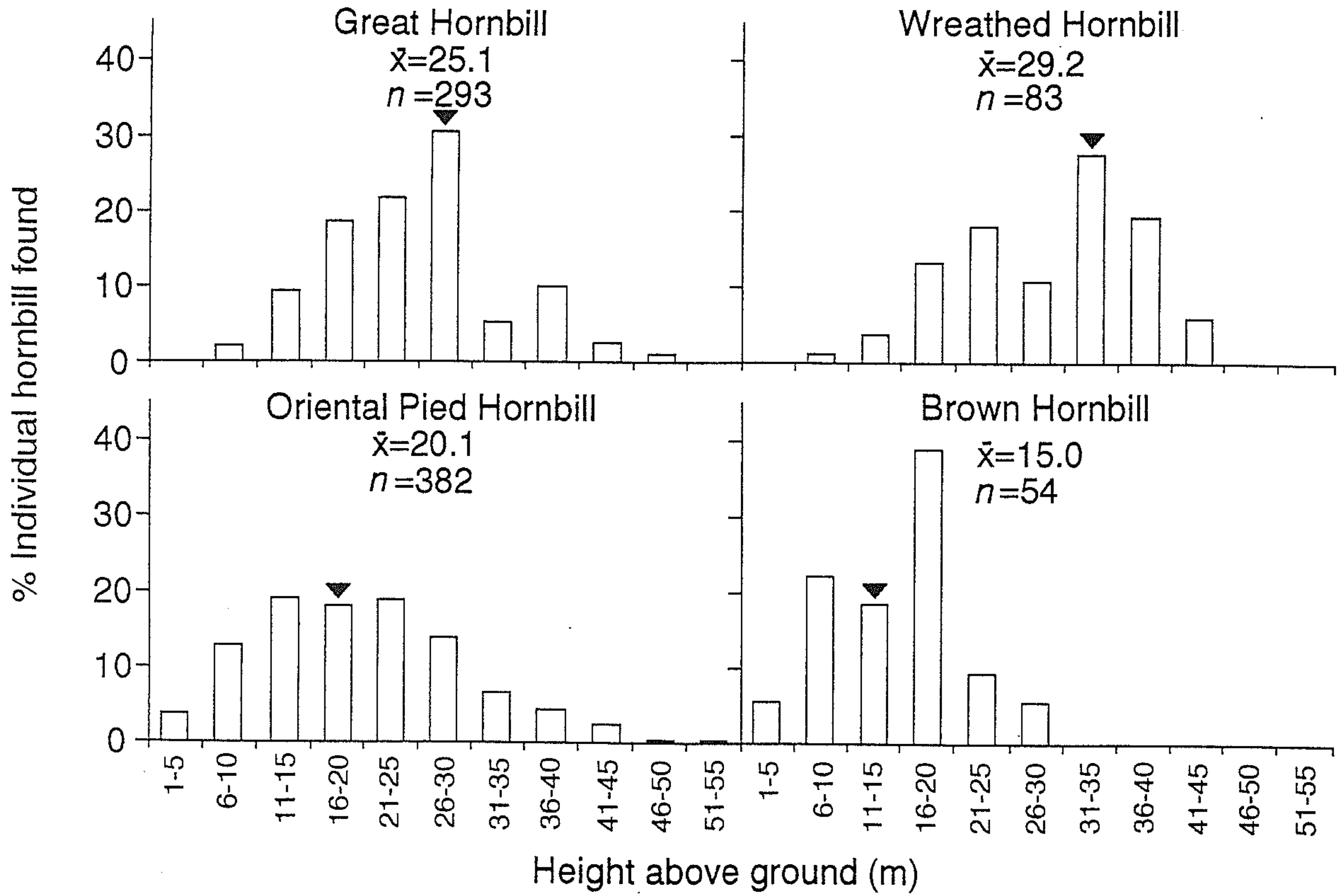


Fig. 6-4 Distribution of foraging niche above the ground of four sympatric hornbill species observed during 1991-1993 at Khao Yai.

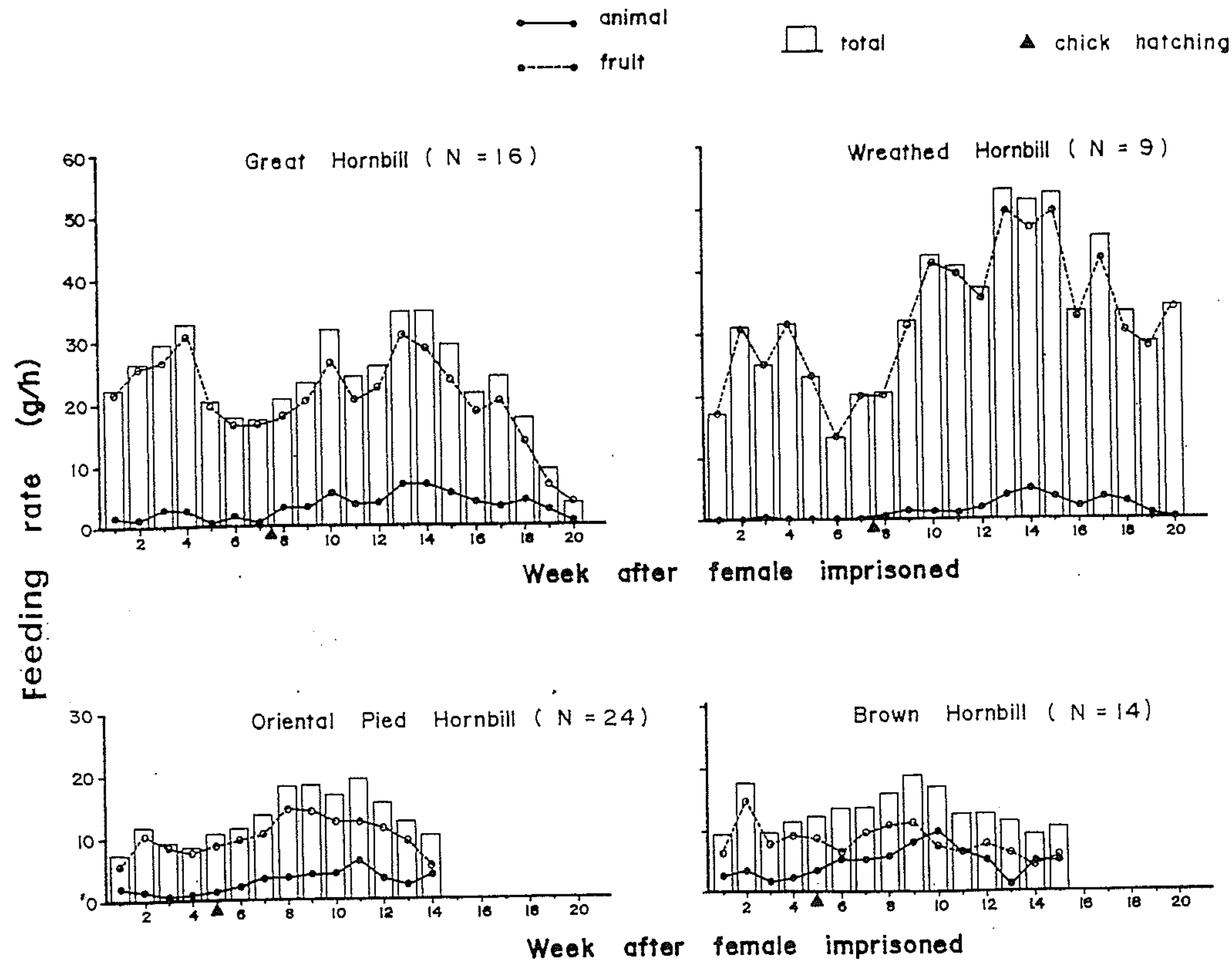


Fig. 6-5 Weekly feeding rate of animals, fruit and total food after

four hornbill species at Khao Yai.

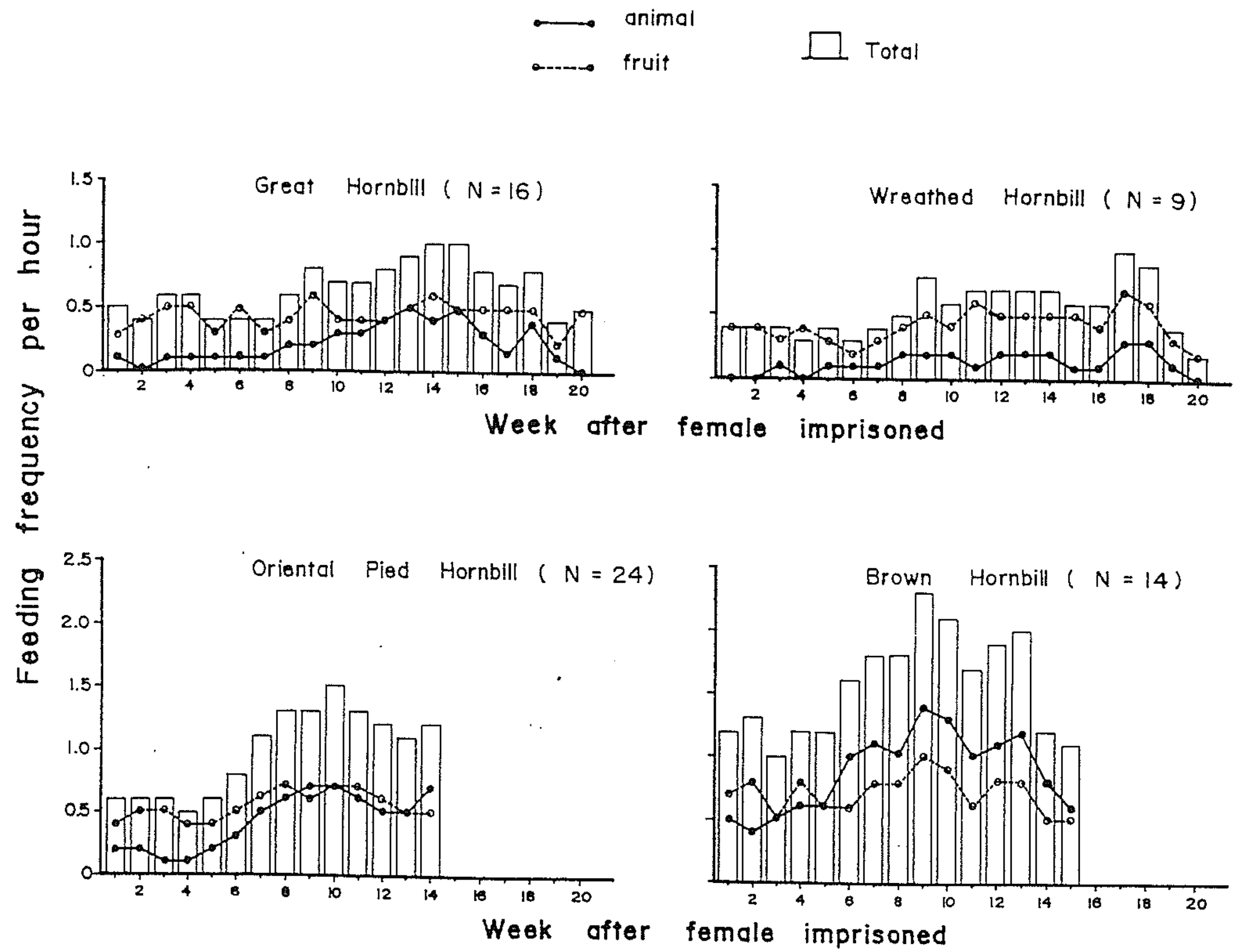


Fig. 6-6 Weekly feeding frequency rate of animal, fruit and total food

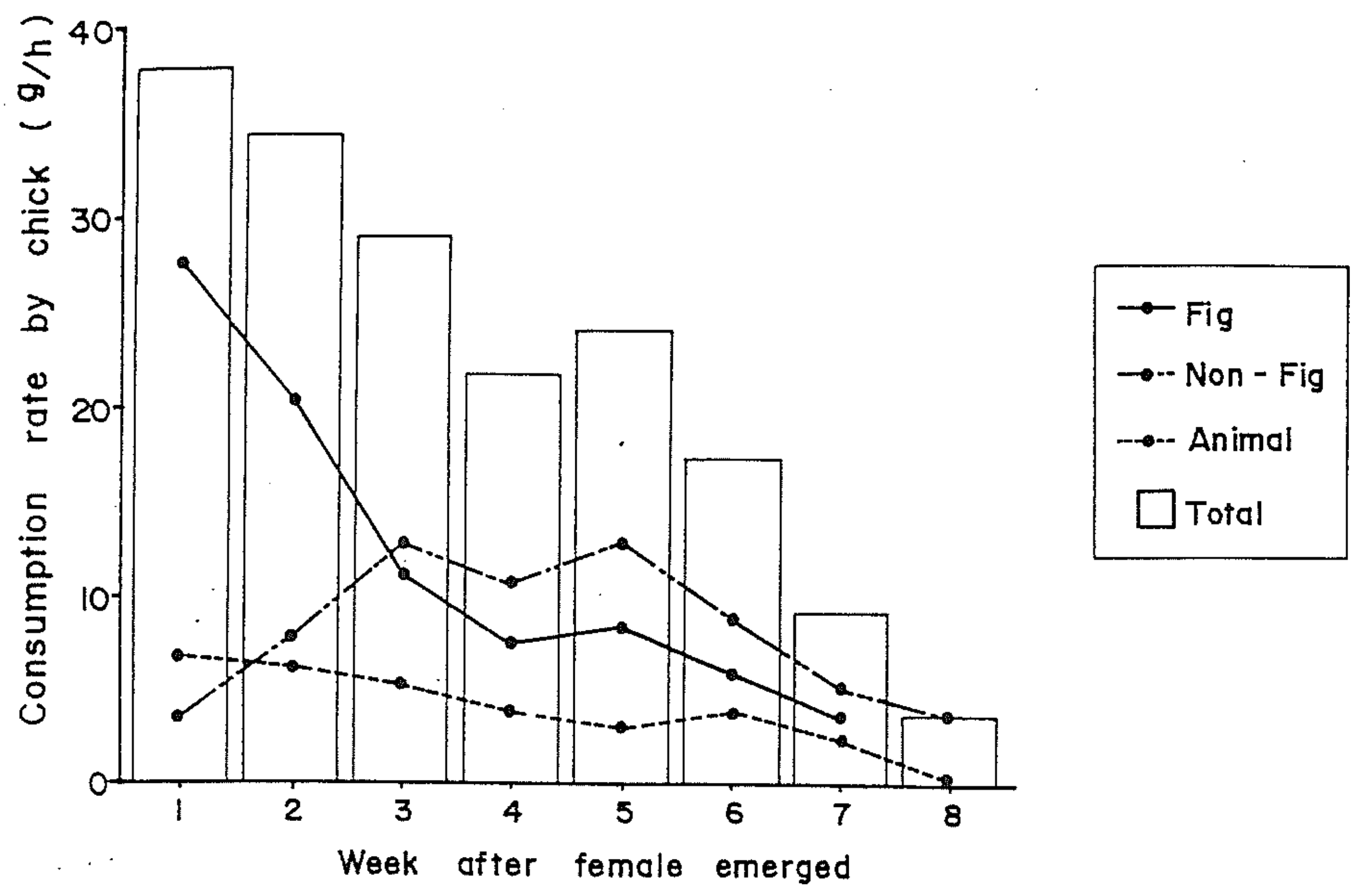


Fig. 6-7 Weekly consumption rate of fig, non-figs, animal and total food by Great Hornbill nestlings after females emerged.

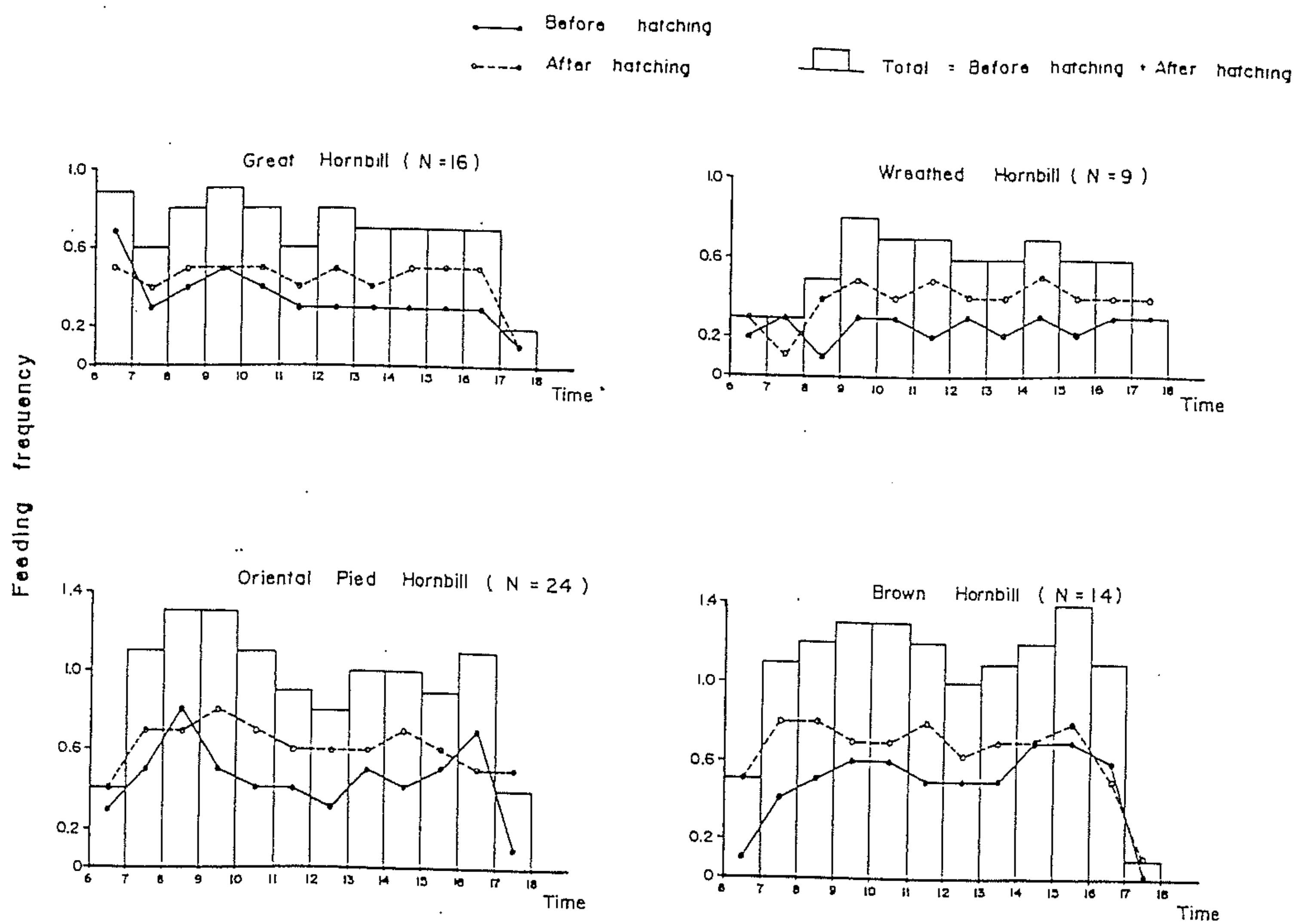


Fig. 6-8 Comparison of feeding frequency between before hatching and after

Appendix 6-1 List of identified fruit eaten by any of four hornbill species at Khao Yai National Park during breeding seasons (1981-1985). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill, FNS = Soft flesh with fine seed, FS = Dry flesh with a stone seed, SF = Split-husked fruit, FJ = Fleshy and juicy.

Fruit species	Characteristic of fruit	Hornbill species feed on			
		GH	WH	PH	BH
Family Moraceae					
Ficus drupacea	FN	/	/	/	/
F. aurantiasia	"	/	/	/	/
F. benjamina	"	/	/	/	/
F. altissima	"	/	/	/	/
Ficus spp.	"	/	/	/	/
Family Urticaceae					
Artocarpus lakoocha	FJ	-	/	/	/
Family Myristicaceae					
Horsfieldia glabra	SF	/	/	/	/
Knema laurina	"	/	/	/	/
Family Myrtaceae					
Eugenia cumini	FJ	/	/	/	/
Eugenia sp. (1)	"	/	-	/	/
Eugenia sp. (2)	"	/	/	/	/
Eugenia sp. (3)	"	-	-	/	/
Eugenia sp. (4)	"	-	/	/	/
Family Connaraceae					
Connarus spp (1)	SF	-	/	/	/
Connarus spp (2)	"	/	/	/	/
Family Piperaceae					
Piper ribesoides	Unknown	/	-	/	/
Family Podocarpaceae					
Podocarpus polystachya	FJ	-	-	-	/
Family Oleaceae					
Jasminum spp.	FS	-	-	-	/
Family Sapindaceae					
Lepisanthes rubiginosa	FJ	/	-	/	-

Appendix 6-1 (cont.)

Fruit species	Characteristic of fruit	Hornbill species feed on GH	WH	PH	BH
Family Symplocaceae					
Symplocos laurina	FS	/	-	/	/
Family Olacaceae					
Strombosia spp.	FS	/	/	/	/
Family Annonaceae					
Polyalthia viridis	SF	/	/	/	/
Uvaria pierrei	"	-	/	/	/
Family Burseraceae					
Canarium subulatum	FS	-	/	/	/
Family Cucurbitaceae					
Trichosanthes tricuspidata		-	-	/	/
Family Elaegnaceae					
Elaegnus latifolius	FJ	/	/	/	/
Family Elaeocarpaceae					
Elaeocarpus grandiflorus	FS	/	/	/	/
Slonea sigun	SF	-	-	/	-
Family Lauraceae					
Cinnamomum subavenium	FJ	/	/	/	/
Litsea cubeba	FS	/	/	/	/
Family Meliaceae					
Amoora cucullata	SF	/	/	/	/
Dysoxylum sp.	SF	/	/	/	/
Chisocheton macrophyllus	SF	/	/	/	/
Aglaia spp. (1)	SF	/	/	/	/
Aglaia spp. (2)	SF	-	-	/	/
Aglaia spp. (3)	SF	/	/	/	/

Appendix 6-2 List of animals observed eaten by any of four hornbill species at Khao Yai during the breeding seasons of 1982-1985. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Hornbill sp. seen feeding on item	Common Name	Scientific Name	Order or family
	MAMMAL		
BH, GH	Insect-eating Bat	Unidentified sp.	Chiroptera
GH	Common tree-Shrew	*Tupaia glis*	Scandentia
GH, PH	Rat	*Rattus* spp.	Muridae
GH	Variable Squirrel	*Callosciurus finlaysoni*	Sciuridae
GH	Flying Squirrel	Unidentified sp.	"
	BIRD		
GH	Barbets	*Megalaima* spp.	Capitonidae
GH	Nightjars	*Caprimulgus* spp.	Caprimulgidae
GH	Greater Racket-tailed Drongo	*Dicrurus paradiseus*	Dicruridae
GH	Collared Scops Owl	*Otus lempiji*	Strigidae
GH,WH,PH,BH	Eggs & Chicks	Unidentified sp.	Pycnonotidae & Columbidae
	REPTILE		
GH, PH	Blind Snake	*Typhlops* spp.	Typhlopidae
GH, BH	Pit Viper	Unidentified spp.	Viperidae
GH, BH	Green Pit viper	*Trimeresurus steinegeri*	"
GH,WH,PH,BH	Lizard	*Acanthosaura* spp.	Agamidae
GH, BH, PH	Flying Lizard	*Draco maculatus*	"
GH, BH, PH	Common Hill Skink	*Sphenomorphus* spp.	Scincidae
GH, PH	Common Flat-tailed Gecko	*Coscymbotus platyurus*	Gekkonidae
GH	Gecko	*Cyrtodactylus* spp.	"
	MOLLUSC		
PH	Filopaludina snail	*Filopaludina* spp.	Viviparidae
GH,WH,PH,BH	Land Snail	*Cyclophorus* spp.	Cyclophoridae
PH	Sea Mussel shell	*Mytilus smaragdinus*	Mytilidae
	INSECT		
BH,PH	Metallic Wood Borer	*Chrysochroa* spp.	Buprestidae
BH,PH		*Lepidiota stigma*	Scarabacidae
BH,PH		*Onitis* spp.	"
BH,PH		*Xylotrupes gidean*	"
GH	Scarab Beetle	Unidentified sp.	"

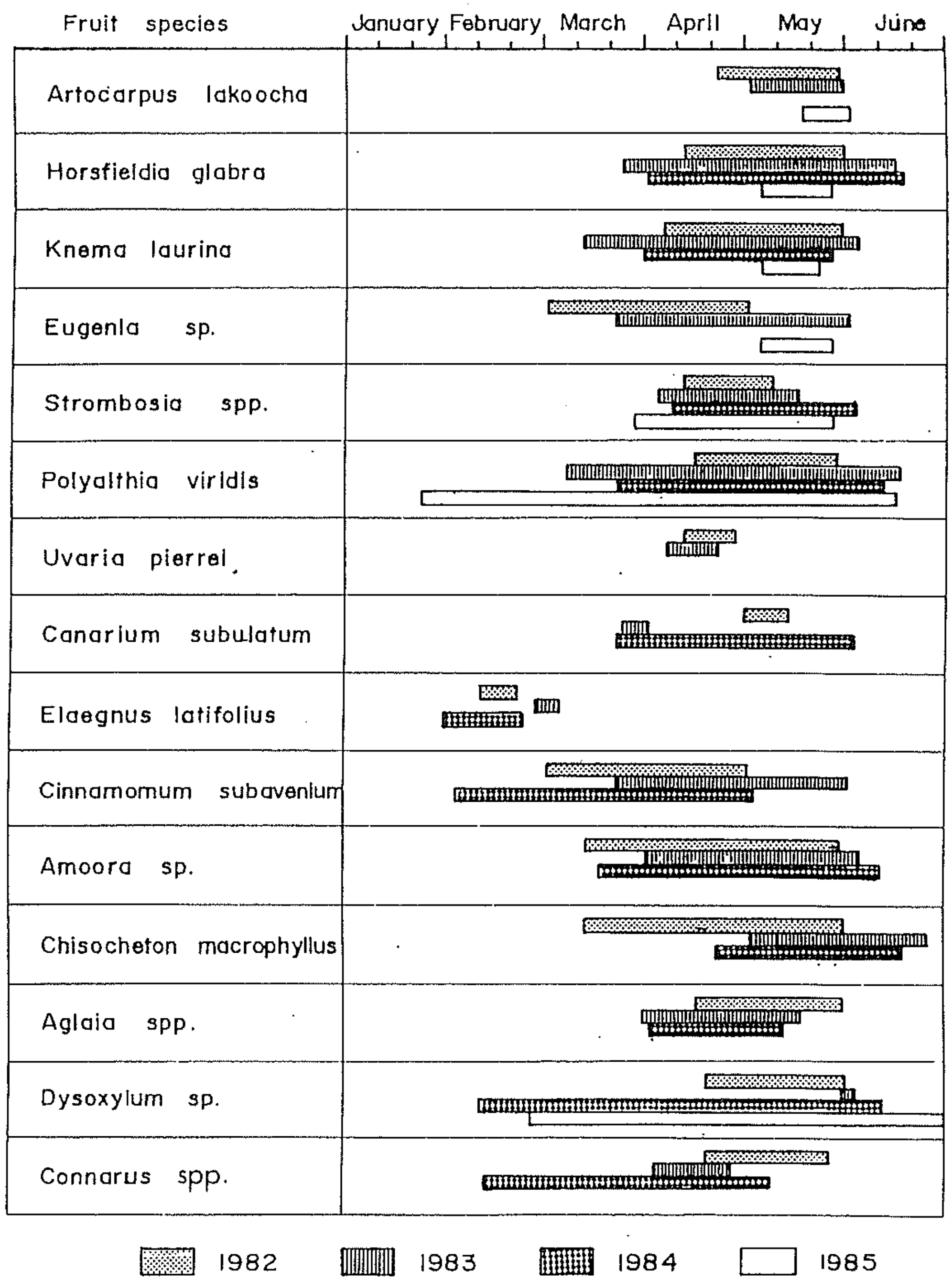
Appendix 6-2 (cont.)

Hornbill sp. seen feeding on item	Common Name	Scientific Name	Order or family
PH	Round Buffalo Dung Beetle	_Copris_ spp. (1)	Scarabacidae
PH	Flat Buffalo Dung Beetle	_Copris_ spp. (2)	"
BH, PH	Long-horned Beetle	_Apriona_ spp.	Cerambycidae
GH,WH,PH,BH	Stag Beetle	Unidentified sp.	Lucanidae
GH,WH,PH,BH		_Acaraius grandis_	Passalidae
PH		_Mouhotia batesi_	Carabidae
GH,WH,PH,BH	Cetonid	Unidentified sp.	Cetonidae
GH,WH,PH,BH	Click Beetle	" "	Elateridae
PH	Assassin Bug	" "	Reduviidae
GH,WH,PH,BH	Green Cicada	" "	Cicadidae
GH,WH,PH,BH	Brown Cicada	" "	"
PH	Ant	" "	Formicidae
GH	Digger Wasp	" "	Scoliidae
BH, PH	Wasp	_Vespa bicolor_	Vespidae
GH,BH,PH	Wasp nest	" "	"
BH, PH	Butterflies	Unidentified sp.	Lepidoptera
BH, PH	Moths	" "	"
BH	Noctuid moth	" "	Noctuidae
WH, BH	Psychid	" "	Psychidae
BH, PH	Stem Borer	" "	Cossidae
PH	Lacewing	" "	Neuroptera
GH,BH,PH	Grasshopper	" "	Orthoptera
GH,WH,PH,BH	Leaf Insect	Unidentified sp.	Lepidoptera
WH,BH, PH	" "	_Pseudophilus tetans_	Tettigoniidae
BH, PH	Long-horned Grass hopper	_Holochlara_ spp.	"
PH	Mantid egg	Unidentified sp.	Orthoptera
GH, BH, PH	Walking stick	" "	Phasmatidae
PH	Tree-Cricket	_Malasumma_ spp.	Gryllidae
GH,BH,PH	Crickets	Unidentified sp.	"
PH	Dragonfly	" "	Odonata
GH,WH,PH,BH	Wild cockroach	_Ergua1a capucina_	Blattidae
GH,WH,PH,BH	Cockroaches	Unidentified sp.	"
GH,WH,PH,BH	Caterpillar	" "	Lepidoptera
	OTHER ARTROPODS		
GH,WH,PH,BH	Crab	Unidentified sp.	Unidentify
GH,WH,PH,BH	Centipede	_Scolopendra_ spp.	Scolopendridae
GH,WH,PH,BH	Elongate Millipede	Unidentified sp.	Julidae
GH,WH,PH,BH	Broad-rounded Millipede	Unidentified sp.	Sphaerotheridae
"	Flat Millipede	" "	Poloydesmidae

Appendix 6-2 (cont.)

Hornbill sp. seen feeding on item	Comon Name	Scientific Name	Order or family
PH	Common Scorpion	" "	Scorpionidae
GH,PH	Giant Scorpion	Heterometrus sp.	"
PH	Spider	Unidentified sp.	Araneida
	MISCELLANEOUS		
GH,BH,PH	Earthworm	Pheretima spp.	
GH,PH	Small green frog	Unidentified sp.	Ranidae
GH, PH	Frogs	" "	"
PH	Fish	" "	Pisces

Appendix 6-3 Duration of Some species of non-fig fruits which were brought to broods by all four hornbill species, when in the fruiting season during the breeding seasons of 1982 to 1985 at Khao Yai.



Appendix 6-4 List of the birds and mammals which were observed to compete with the hornbills' for food sources at Khao Yai during 1982-1985.

Common Name	Scientific Name
Birds	
COLUMBIDAE	
Thick-billed Green Pigeon	*Treron curvirostra*
Wedged-tailed Green Pigeon	*T. sphenura*
Mountain Imperial Pigeon	*Ducula badia*
PSITACIDAE	
Vernal Hanging Parrot	*Loriculus vernalis*
CAPITONIDAE	
Lineated Barbet	*Megaliama lineata*
Green-eared Barbet	*M. faiostricta*
Blue-eared Barbet	*M. australis*
Moustached Barbet	*M. incognita*
Coppersmith Barbet	*M. haemacephala*
PYCNONOTIDAE	
Black-crested Bulbul	*Pycnonotus melanicterus*
Stripe-throated Bulbul	*P. finlaysoni*
Black-headed Bulbul	*P. atriceps*
Swinhoe's White-throated Bulbul	*Criniger pallidus*
Grey-eyed Bulbul	*Hypsipetes propinquus*
ORIOLIDAE	
Black-naped Oriole	*Oriolus chinensis*
IRENIDAE	
Fairy Bluebird	*Irena puella*
STURNIDAE	
Golden-crested Myna	*Ampeliceps coronatus*
Hill Myna	*Gracula religiosa*
Mammals	
Pig-tailed Macaque	*Macaca nemestrina*
White handed Gibbon	*Hylobetes lar*
Pileated Gibbon	*H. pileatus*
Black Giant Squirrel	*Ratufa bicolor*
Variable Squirrel	*Callosciurus finlaysoni*
Common Palm Civet	*Paradoxurus hermaphroditus*
Binturong	*Arctictis binturong*
Bats	Unidentified species

CHAPTER 7

HOME RANGE AND TERRITORY

INTRODUCTION

Although hornbills are large and conspicuous, the determination of their home ranges by visual observation is difficult because they travel long distances and forage in thick foliage in the tops of fruit trees. The large Great and Wreathed hornbills also often fly high above the forest canopy.

There have been previous studies to determine ranges and territories of forest hornbills. Leighton (1982) determined the ranges of seven Bornean hornbills by following habituated birds that could be recognized individually. Tsuji <u>et al</u>. (1987) attempted to determine the range size of the four hornbill species in Khao Yai using radio telemetry and visual observation. This chapter presents findings on home range size and its seasonal changes, in Great, Wreathed and Brown hornbills using radio telemetric equipment, on territory of all four hornbill species which occur in Khao Yai. I also estimate a minimum size of an area to be protected for the conservation of this bird group.

METHODS

Home range study

Hornbills were trapped at nests shortly before fledging time by the use of mist net (mesh size 227 mm, length 12 m, height 4 m, 2 shelves).

Mist nets were hung in front of the nests of target species. Two breeding males of each species were trapped and radio-tagged. Captured birds were harnessed with transmitters (Wildlife Materials Inc., Carbondale, Illinois) on their backs with whip antennas lying along the tails (Tsuji et al. 1987). The radios transmitted at frequencies of 137-138 MHz. The estimated range of a transmitter was 4-7 km and battery life was 3-5 months. The two Wreathed Hornbills were fitted with solar powered transmitters which function for over 36 months. Each tracking unit consisted of a receiver, a double 7-element yagi aerial set horizontally, a null-peak box, and a degree disc.

An attempt to determine the locations of the birds was made each hour between 0700 and 1600 h from two of four fixed stations located on tree platforms. These platforms (TV, MOH, WJP and MYK) were constructed at or near the peaks of hills at altitudes of 850, 860, 890 and 865 m respectively, in tree crowns at heights of 22-35 m above the ground (Fig. 7-1).

Birds were tracked from 31 March to 14 September 1988, 26 March to 28 October 1989, 22 February to 22 August 1990, and 6 July to 8 September 1991. Individuals were tracked from 4 to 18 days during each breeding season and from 5 to 38 days during each non-breeding season (Table 7-1).

The locations of radio-tagged hornbills were obtained by triangulation from two receivers when detected by both at the same time, and were plotted on a 1:50,000 scale grid map. The areas of the ranges of each male hornbill in the breeding and non-breeding seasons were estimated by connecting the outermost location points to form the minimum convex polygons (Schoener 1981). The total range of each male was then estimated by connecting the outermost location points detected in both seasons to circumscribe the areas in the same manner. Thus, all ranges presented in Table 7-1 were the estimated minimum ranges.

The breeding season was defined as the period from final sealing of the female inside the nest hole to the day of chick fledging. The non-breeding season was from the fledging of the chicks to the onset of the next breeding season (see also Chapter 4).

For analysis of daily movement and range it was considered that considered only those days during which at least eight hourly locations were detected during 10 hours of tracking (07:00-16:00 hours). An index of the total daily distance that a bird moved was obtained by adding the distances between sequentially determined positions. The outermost locations were connected to estimate the area of the daily range.

A total of 27 and 13 known nest cavities of Great and

Brown hornbills respectively, in the study site were checked for breeding activity in 1988 and 1989, and 17 known nests of Wreathed Hornbills were checked in 1990.

Nests were located by following lone males as they approached to feed their females or broods, or by inspecting large trees with visible cavities for evidence of use by hornbills(see Chapter 3). Mapping of all active nests of each species was undertaken only in the year when that species was tracked in the breeding season.

Tracking at the nest sites of radio-tagged species was done just after the fledging period using a portable monitoring set until signals were no longer detected. Nests of all radio-tagged hornbills as well as nests of some untagged hornbills were checked for activity at least once a month throughout the non-breeding season.

Territory study

As nest site, food resource and perhaps roost site seemed to be most important basic requirement for hornbills therefore, to determine territory of a hornbill species I made direct observations of hornbills at these three places. Territory is defined here as an area where a hornbills defends. Defensive behaviours include advertising by vocalization, aggression or threat, and fighting (Hinde 1956, Dorst 1974, McFarland 1981).

At nest site: Trees where breeding males of all four hornbill species perched and made vocalization were recorded. Distances, and orientation of perched trees from nest tree were measured. Then farthest positions of such trees were connected to determine minimum size of territory. The observation on territorial behaviours was made at the same time as when food and feeding were observed in 1982-1991 (except 1986, 1987).

At fruiting tree and roost site: Similar observation as at the nest site were made at fruiting trees both in breeding and non-breeding seasons. Time spent at a fruiting trees was ranged from 2-8 hours per day for 1-3 days. At roost site observations were made between 15:00-19:00 hours at each roost site for 2-4 weeks interval in 1981-1985.

RESULTS

Distribution of nests

The nests of all hornbill species breeding in the study area were known. The distribution of active nests of the hornbill species of which males were tracked in the breeding season are shown in Figure 7-2. These include nests of all radio-tagged birds except W 18 (Wreathed Hornbill) which was tagged in 1991 near the end of the breeding season, when it was identified as a new breeding male using a former Wreathed Hornbill nest (W6 in Tsuji et al. 1987, Poonswad et al. 1987). Great Hornbill nests were thus about twice as numerous as those of Wreathed Hornbills and four times as numerous as those of Brown Hornbills within the study site. In 1988, three non-breeding pairs of Great Hornbills and one non-breeding pair of Wreathed Hornbills were sighted in the study area during the breeding season. No non-breeding pairs of Brown Hornbills were observed.

Tracking of hornbills

Generally the birds were detected for fewer days (average = 37.5% of total day tracked) in the non-breeding season than in the breeding season (average = 64.4% of total days tracked). The transmitters on Great and Brown Hornbills ceased functioning within 1-3 months after the chicks fledged. Although tracking Wreathed Hornbills was successful in the non-breeding season (100% in three out of four seasons), they were tracked on only a few days. Birds were tracked from the fledging period until the middle of the non-breeding season, apart from W17 in 1989 which was tracked throughout the non-breeding season. Hence the actual range sizes of each species was probably larger than the estimated minimum range sizes, particulary for the ranges in the non-breeding season presented in Table 7-1.

Daily movements and range

The daily movement was determined adequately for only one male Great Hornbill (G3) during 3 days in 1989 (Fig 7-3). The minimum total distance traveled in one day varied from 3.9 km (8 April) to 14.4 km (16 April) and averaged 7.6 km (n=3). The minimum daily range was 0.7 to 6.1 km^2 (mean = 2.8 km^2, n = 3).

Increase in range size with increase in number of days of detection

Cumulative range sizes increased with the number of days of detection but Figure 7-4 suggests that the detected ranges did not reach their maximum sizes. Furthermore, range sizes increased in a stepwise manner for Great and Brown Hornbills (Fig 7-4) suggesting periodic changes in the areas visited within the total ranges. For Wreathed Hornbill W17, which was detected on 9 days in the non-breeding season of 1989 (Table 7-1), cumulative range sizes could not be determined due to the false directions of detected signals, which prevented proper triangulation. The rest of the data for W17 and W18 was insufficient to estimate cumulative range sizes.

Seasonal changes in range size

The sizes of ranges of all radio-tagged individuals by year and season are presented in Table 7-1 and Figure 7-5.

Great Hornbill.

G3: - This male failed to breed successfully in 1988 and 1989. In 1988, the female emerged from the nest around 7 days after the male was radio tagged (5 days after tracking began). In 1989, the female emerged 22 days after the male was radio tagged (20 days before tracking began). The pair stayed together and remained near the nest site. They showed territorial behaviour by making alarm calls and flew around the nest site. There were insufficient data to show the difference in range size of this male before and after the emergence of the female. Therefore, the range sizes presented in Table 7-1 were the ranges of the unsuccessful breeding male.

G9: Breeding was successful in 1988 and 1989 with one chick fledged each year. The pair with the fledgling stayed near the nest for at least one week. The pair was seen near the nest on 9 October, 20 November and 30 December 1988. The pair gave loud alarm calls and sometimes called in duets and flew around the nest.

One pair of untagged Great Hornbills was seen to inspect their nest cavity on 18 September 1990. This pair also showed territorial behaviour by calling loudly and flying around the nest site.

Wreathed Hornbill. Both males bred successfully with one chick fledging each year following the initial tagging. These two pairs seldom called within their nest sites. (I could not distinguish Wreathed Hornbill's alarm calls from normal calls as I easily could for Great and Brown Hornbills.) When disturbed, the male usually flew away. After a chick had fledged the pair with fledgling stayed around the nest site for up to two weeks and then left the nest site until the next breeding season.

Brown Hornbill. Both males had 2-3 nest helpers and two chicks. These two males did not range far from their nests. The male and helpers showed strong territorial behaviours around the nest site during the breeding season. They screamed and flew around the nest site. They left the nest sites soon after chicks fledged upto 9 days and away from the nest sites. They kept travelling in flocks.

Overlap of home ranges

Figure 7-5 shows the ranges in the breeding and/or the non-breeding seasons over two years for Great Hornbills (G3, G9), over three years for Wreathed Hornbill (W17) and over two years for Brown Hornbills (B12, B13). For each individual of these three species, considerable overlap in ranges was found from the breeding to non-breeding seasons and also from year to year. This was particularly evident for G3, G9 and W17, and suggestive for B12 and B13. The percentages of intra- and interspecific overlap of seasonal ranges between the three species were derived from the following formula, and presented in Table 7-2.

$$\frac{A \cap B}{A} \times 100 = \% \text{ of range of A overlapped by B.}$$

$$\frac{A \cap B}{B} \times 100 = \% \text{ of range of B overlapped by A.}$$

Where A and B are the range sizes of the two species and $A \cap B$ is the area (km^2) overlapped between them.

Intraspecific overlap of ranges was found in all three species to some degree. Only the ranges of Great Hornbills G3 and G9 did not overlap except in the non-breeding season of 1989 (Fig. 7-5a). However, considering the locations of the other Great Hornbill nests in the area (Fig. 7-2a), it is likely that the ranges of different Great Hornbills overlapped seasonally. Similar intraspecific overlapping of ranges probably also occurred for Wreathed (W17, W18; Figs. 7-2b and 7-5b) and Brown Hornbills (B12, B13; Figs. 7-2c and 7-5c). Interspecific overlap occurred among these three species except between the Wreathed and Brown hornbills. however, the locations of nests of Wreathed and Brown hornbills (Fig 7-2), indicate the occurence of overlapped ranges between these two species. Overall, it seems that there was great overlap not only between seasons but also of the total home ranges of different individuals of the same and different species.

Territory

All four hornbill species defended their nest sites. The territory size were similar in all species except for the Great Hornbill as shown in Figure 7-6 A, B, C and D. Ranges, means ± SD in hectare were 0.05-2.09, 0.69 ± 0.58, n=15; 0.05-1.07, 0.05 ± 0.44, n=7; 0.03-0.62, 0.25 ± 0.18, n=10; 0.07-0.32, 0.16 ± 0.08, n=6, for the Great, Wreathed, Oriental Pied, and Brown hornbills, respectively. It was found that only the territories of Great Hornbill were significantly larger than those of Oriental Pied and Brown hornbills (Mann-Whitney U test Z= -2.498, n_1=15, n_2=10, $P < 0.05$; Z= -2.727, n_1=15, n_2=6, $P < 0.01$, respectively).

Great hornbill defended its nest territory by the following behaviours (see also Chapter 4).

Vocalization: a) Advertising call was a single note call *Gok, Gok* ... and sometimes ended with *Gahang, Gahang*. Usually it was uttered when the male arrived within the nest site or territory (Fig. 7-6A) without noticing of any intruder. b) Threatened call or alarm call was a kind of loud and deep roaring calls with two notes *Gawa, Gawa* or *Gahang, Gahang* and these calls became rapid before the bird flew off. This call was uttered when the bird noticed and intruder.

Flying display: To defend territory, Great Hornbill performed flying display around its nest site and made alarm calls until the intruders disappeared.

Plucking branches and cracking tree bark: These were not foraging behaviour but were defensive behaviour. The bird pluck branches vigorously and dropped the same way as did to the barks.

Wreathed Hornbill showed vocalization with two notes *Erg Erk, Erg Erk* but it was difficult to distinguish a normal advertising call from an alarm call (see also Chapter 4). Wreath Hornbills also showed flying display but were not as vigorous and not as insisted as Great Hornbills.

Oriental Pied Hornbill showed vocal and flying displays. Normal advertising call was one distinct note *Gaek, Gaek...* called continuously with soft echo of the same note. For the alarm call it was a long scream of the normal call. Once I saw a breeding male flew to attack a hawk with a loud scream call.

Brown Hornbill showed similar behaviours to Oriental Pied Hornbills. This species demonstrated defensive behaviours not only the breeding male but also nest helpers. The call of Brown Hornbill was also difficult to distinguish between advertising and alarm calls. They always screamed with high pitch of single note and often with chorus of the helpers. When they noticed an intruder, they screamed and flew around but did not insist as long as Great Hornbills.

At food resource

There was only slightly aggressive behaviour (such as raising head feathers observed at fruiting trees made by all four hornbill species but not serious, perhaps to advertise or defend only for its space at that moment. All hornbills except the Brown were observed to feed on the same tree. I once observed the Brown Hornbills came in flock of about 12 individuals to feed on a fruiting fig tree. They showed aggressive behaviour by raising crests toward other birds, causing other birds such as green pigeons Treron sp. flew away.

At a Canarium tree in the non-breeding season Wreathed Hornbill made advertising calls but it was unknown whether these calls were territory advertising or communal calls.

At the roost

I observed mostly at the roost of Wreathed Hornbills. There was fighting for perching space. Great Hornbills were sometimes observed to share roost with Wreathed Hornbills. Hence, there was no territorial defense for the roosting site, except for a family roost of Great Hornbills. The pair of Great Hornbill showed strong defensive calls against other Great Hornbills that came close to thier roosting site. I observed this behaviour for 7 times out of 10 times of two different years at the same roosting site.

DISCUSSION

Range sizes

It is difficult to compare the total ranges of Great, Wreathed and Brown hornbills due to the small sample sizes, varying breeding success, and the different year in which the birds were tracked, but the data indicate some differences among the hornbill species at in Khao Yai.

Interspecific comparisons show that home range size of an animal is often related to body size (Schoener 1968), but the data from my observations do not support such a hypothesis. The Great Hornbill, which is the largest species, did not occupy a larger range than the smaller Wreathed Hornbill. Leighton (1982) studied seven species of hornbills in Borneo, and found that the Helmeted Hornbill Rhinoplax vigil, the largest species, had a relatively small home range. In contrast, the smaller Wreathed Hornbill maintained very large home ranges (Leighton 1986) comparable to those found in the present study. This indicates that there must be other factors affecting the range sizes of hornbills, e.g. food availability and/or food abundance, feeding strategy, breeding strategy, and perhaps territorial behaviour.

It seems likely that the home range size in the breeding season is restricted by the location of the nesting site and the need for the male to bring back food to his mate and brood as well as to defend them (Poonswad et al. 1987). The time of breeding, and hence a more restricted home range, may be influenced by food availability, which should vary markedly from season to season. For example, the fruit of Cinnamomum subavenium, one of the hornbills' preferred foods in the breeding season, (Poonswad et al. 1987) failed to produce fruit in the study site in 1987 and 1988 (unpubl. obs.).

Interspecific differences in diet composition are likely to cause differences in range size during the breeding season. Poonswad et al. (1987) showed that during the breeding season the proportion of fruits in the diet of the four sympatric species of hornbills in Khao Yai ranged from 60 to 95%. Wreathed Hornbills were almost entirely frugivorous and rarely hunted for animals, as also found by Leighton and Leighton (1983), whereas Great and Brown hornbills took 86% and 60% fruit respectively.

Hornbills, especially Wreathed Hornbills, also feed primarily on fruit outside the breeding season. Leighton (1986) and Tsuji et al. (1987) observed large nomadic flocks of Wreathed Hornbills gathering at fruiting trees and that individual birds might travel more than 10 km between the feeding sites and their roost, greatly extending their foraging range at this time.

Range sizes in the breeding season of different species of hornbills may also be affected by breeding strategy or the number of brood plus female. The female Great Hornbill emerges a few weeks after the chick hatched (Poonswad *et al.* 1987 and see also Chapter 4), whereas the female Wreathed Hornbill stays with her lone chick throughout the breeding cycle which is slightly longer than that of the Great Hornbill (Poonswad *et al.* 1987). The male Wreathed Hornbill therefore has to provide food for both his mate and the young in nest, forcing him to travel further.

The Brown Hornbill is only about one-quarter the body size of the Great Hornbill but the ranges of the two species in the breeding season at Khao Yai were similar. This finding was slightly different from that of Tsuji *et al.* (1987) who reported that in the breeding season a male Great Hornbill uses a 7.5 km^2 range and a male Brown Hornbill ranged over 3.0 km^2. In this earlier study it was suggested that the smaller range size of the Brown Hornbill resulted from its cooperative nesting behaviour, in which other males help, increasing the efficiency of foraging, even within a small area. The range size of the Brown Hornbill may therefore vary according to the number of chicks raised and number of nest helpers.

The Brown Hornbill in this study used a larger range than that used by Bushy-crested Hornbill *Anorrhinus galeritus* (1.3 km^2) in Borneo (Leighton 1982), though these two species are similar in size and in number of nest helpers. Furthermore, the Great Hornbill's range in this study was much larger (16.9 km^2) than that of Rhinoceros Hornbill *Buceros rhinoceros* (2.3 km^2) in Borneo (Leighton

1982). Although these two species have similar breeding strategies (Kemp 1979, Poonswad et al. 1987), the difference in their range sizes is not in proportion to the difference of their body masses (3.5 and 2.3 kg, respectively). Clearly the differences in range sizes in these cases must be affected by other factors such as food abundance within their habitats.

Range requirments and management

In order for effective management to sustain a viable population of a hornbill, it is essential to estimate the minimum suitable size of protected area based on the knowledge of its population density and home range requirements.

The estimated areas suggested by Medway and Wells (1971) are questionable. In natural situations, multiple overlaps of home ranges normally occur. Thus, besides range size and effective number of a hornbill species, the overlapping ratio and number of probable overlapping ranges must be taken into consideration. I suggest that the minimum area required (A) could be calculated as

$$A = R\,[1 - (O \times N)]\,P \quad \text{km}^2$$

Where R is an average home range size of a species, O is overlapped ratio between two ranges, N is number of probable overlapped ranges and P is the effective population size.

From my data I suggest the minimum area for sustaining a population of the Great Hornbill, the largest species in Khao Yai as followed, is 1,859 km^2

$$A = 16.9 [1 - (0.3 \times 2.6)] \times 500$$

Where R is derived from averaging of total home ranges of G3 and G9 regardless of breeding success (Table 7-1), O is from averaging the overlapped ratio (percentage in Table 7-2), N is from averaging number of probable overlapped nests in Figure 2 and Table 2, P is minimum effective population size of 500 animals suggested by Soule' (1980).

My justification for considering the largest species's range is that the availability of their basic requirements, such as the large size necessary for nest trees, large amount of food, etc., may impose greater constraints if the area is small than for smaller species. Although Wreathed Hornbills tend to occupy larger ranges than Great Hornbills, their strong flocking behaviour (Tsuji et al. 1987, Poonswad et al. 1987) indicates that many individuals have greatly overlapping home ranges. I have considered only intraspecific overlapping of home ranges in this calculation because intraspecific interactions are more intense than interspecific ones in the breeding season (Tsuji et al. 1987).

The calculation suggests that a sufficient area of suitable habitat (1,817 km^2 which is about 84% of the park area) of Khao Yai is available for the long-term survival of the Great Hornbill in Khao Yai.

Territory

The results of observations on Great Hornbills in Khao Yai were rather different from those of Leighton (1986) on Rhinoceros Hornbill, the closest relative of the Great Hornbill. Great Hornbill at Khao Yai did not clearly maintain their territory year-round as Rhinoceros Hornbills did in Borneo, but defended the largest territory around nest site only during the breeding season.

A hornbill usually utilizes the same nest cavity year after year (Poonswad <u>et</u> <u>al</u>. 1987). Such a behaviour may be one of functions of terriorial behaviour known as territory attachment (Howard 1948, Hinde 1956). In my study, territorial behaviour was observed in all four species to some degree. This behaviour may be limited to defending the nest site in the breeding season. Great Hornbill in this study showed intense territorial behaviour, but when G3 failed in breeding, it used larger size of ranges than G9 in the breeding season of both years. This state of affair was completely different from Bornean hornbills which defended food resources rather than nest cavities (Leighton 1986).

Results presented in Chapter 3 and 4 have shown that nest site were in shortage and therefore an important limiting factor for hornbills, whereas food resource was not short. Particularly Great Hornbills defended their nest sites, due to few large trees available (Chapter 3). Competition can be predominant single factor which leads to territory defensive behaviour such as aggression (Brown 1964). Because too much aggression to defend an unshort resource would eventually be harmful. Consequently, a balance must be considered between investment in term of time and energy and reward by acquiring nest site or food source (Brown 1964). It spimds reaspmab;e that hornbills at Khao Yai significantly defended only for their nest site because during the breeding season a breeding male must have invested much efforts and energy in gathering food for his mate and chick/s rather than burden itself to defend sources other than nest site.

Degree of territorial behaviour may also be affected by the diet. Hornbills of genus Rhyticeros are frugivorous and they retain no territory (Leighton 1986). In Wreathed Hornbills, which are also mainly frugivorous, territory advertising calls were heard, but defending behaviour was not vigorous.

In the non-breeding season, Great Hornbills in family were more aggressive than in flock in defending their roost site. This species showed strong nest site defense by staying around it even in the non-breeding season.

Table 7-1. Home range and seasonal range sizes, number of days tracked and detected and number of points located for individual radio-tagged male hornbills. BS = Breeding season; NBS = Non-breeding season; ID = Inadequate data. ( ) indicates range size of unsuccessful breeding male.

Hornbill Species	Nest Code		1988 BS	1988 NBS	1988 Total	1989 BS	1989 NBS	1989 Total	1990 BS	1990 NBS	1990 Total	1991 BS	1991 NBS	1991 Total
		Home range (km^2)	(7.0)	7.9	10.8	(14.6)	6.0	17.9	-	-	-	-	-	-
Great	G3	No. days tracked	18	22	40	6	22	28	-	-	-	-	-	-
Hornbill		No. days detected	15	11	26	6	10	16	-	-	-	-	-	-
		No. points located	37	32	69	36	19	55	-	-	-	-	-	-
		Home range (km^2)	6.0	4.1	9.8	1.4	25.2	28.4	-	-	-	-	-	-
	G9	No. days tracked	18	22	40	4	38	42	-	-	-	-	-	-
		No. days detected	6	4	10	4	15	19	-	-	-	-	-	-
		No. points located	7	6	13	11	32	43	-	-	-	-	-	-
		Home range (km^2)	-	-	-	-	34.9	-	10.0	14.6	24.9	-	30.8	-
Wreathed	W17	No. days tracked	-	-	-	-	29	-	5	5	10	-	5	-
Hornbill		No. days detected	-	-	-	-	9	-	4	5	9	-	5	-
		No. points located	-	-	-	-	6	-	15	12	27	-	9	-
		Home range (km^2)	-	-	-	-	-	-	-	-	-	-	31.6	-
	W18	No. days tracked	-	-	-	-	-	-	-	-	-	-	5	-
		No. days detected	-	-	-	-	-	-	-	-	-	-	5	-
		No. points located	-	-	-	-	-	-	-	-	-	-	11	-
		Home range (km^2)	5.9	ID	ID	-	-	-	-	-	-	-	-	-
Brown	B12	No. days tracked	18	22	40	-	-	-	-	-	-	-	-	-
Hornbill		No. days detected	11	6	-	-	-	-	-	-	-	-	-	-
		No. points located	20	2	-	-	-	-	-	-	-	-	-	-
		Home range (km^2)	4.3	ID	ID	2.7	ID	ID	-	-	-	-	-	-
	B13	No. days tracked	17	22	39	4	21	25	-	-	-	-	-	-
		No. days detected	9	2	11	3	2	5	-	-	-	-	-	-

Table 7-2. Intra and interspecific overlap of home ranges of three hornbill species in different years and seasons. G = Great Hornbill, W = Wreathed Hornbill, B = Brown Hornbill, BS = Breeding season, NBS = Non-breeding season

1st Overlapped species		2nd Overlapped species		Distance between nests of overlapped species (km)	Season found overlapping	Size of overlapped area (km^2)	% overlapped area of s	
Nest code	Range (km^2)	Nest code	Range (km^2)				1st overlapped with 2nd	2nd overla with 1st
Intraspecific overlap								
G3	6.0	G9	25.2	3.9	NBS 1989	2.9	48.3	11.5
W17	30.8	W18	31.6	4.8	NBS 1991	15.2	49.4	48.1
B12	5.9	B13	4.3	1.6	BS 1988	2.9	49.2	67.4
Interspecific overlap								
G3	7.0	B13	4.3	2.0	BS 1988	0.9	12.9	20.9
G9	25.2	W17	34.9	1.8	NBS 1989	19.4	77.0	55.6

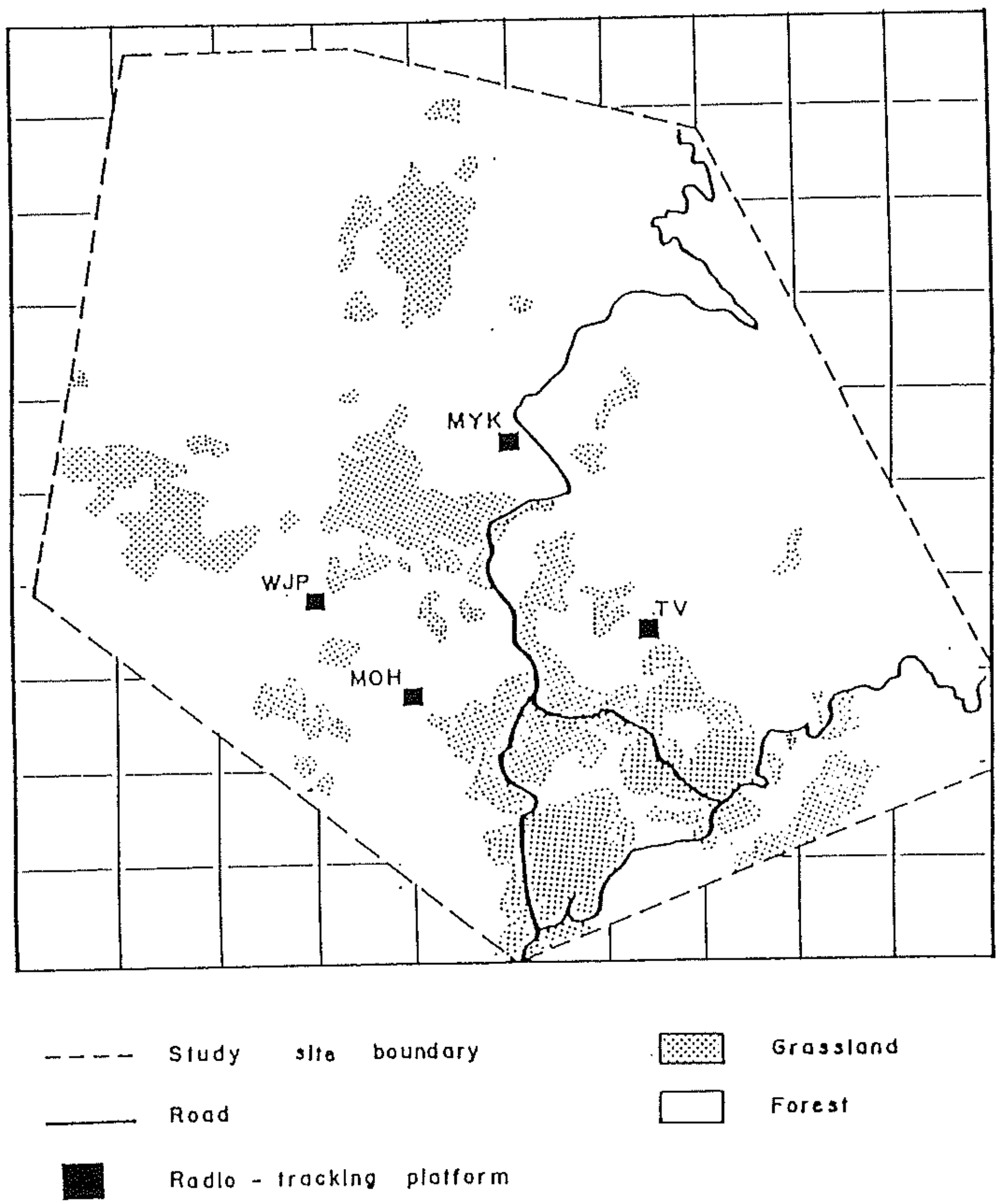


Fig. 7-1 The location of radio-tracking platform in the study site.

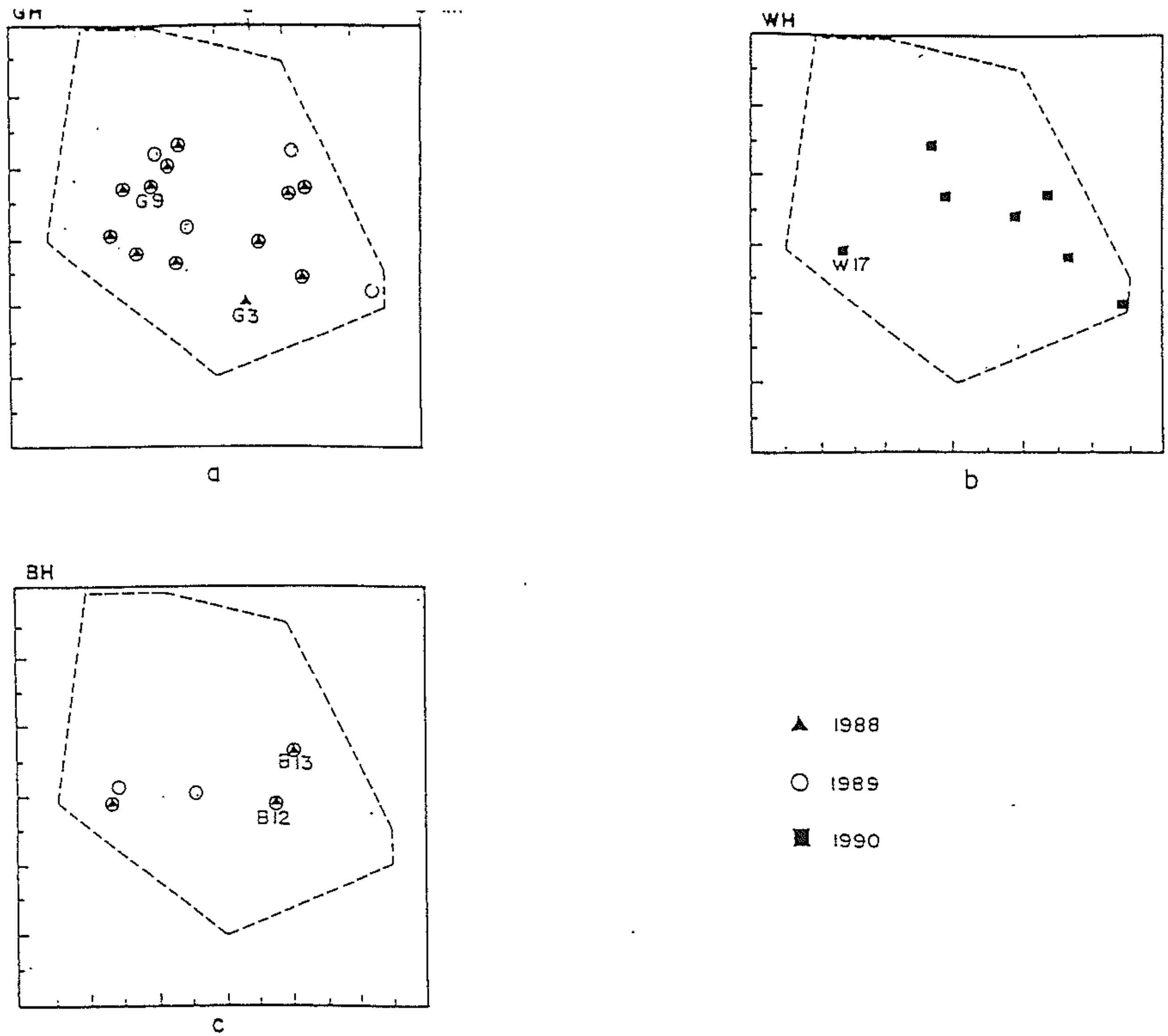


Fig. 7-2 The distribution of nests of Great Hornbills (GH), Wreathed Hornbills (WH) and Brown Hornbills (BH) in the study area in 1988 (▲), 1989 (O) and 1990 (■).

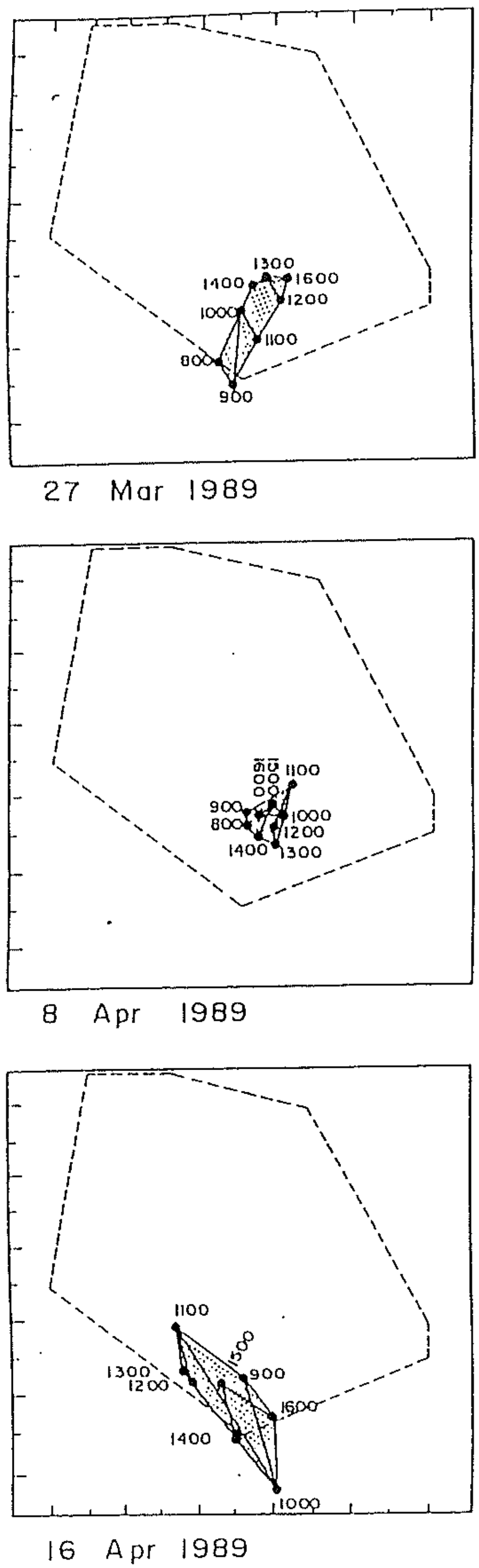


Fig. 7-3 The daily movement and daily range of a male Great Hornbill (G3) on three days in 1989, showing the sequence of tracking locations at 1-h intervals from 0700 to 1600 h. Stippling

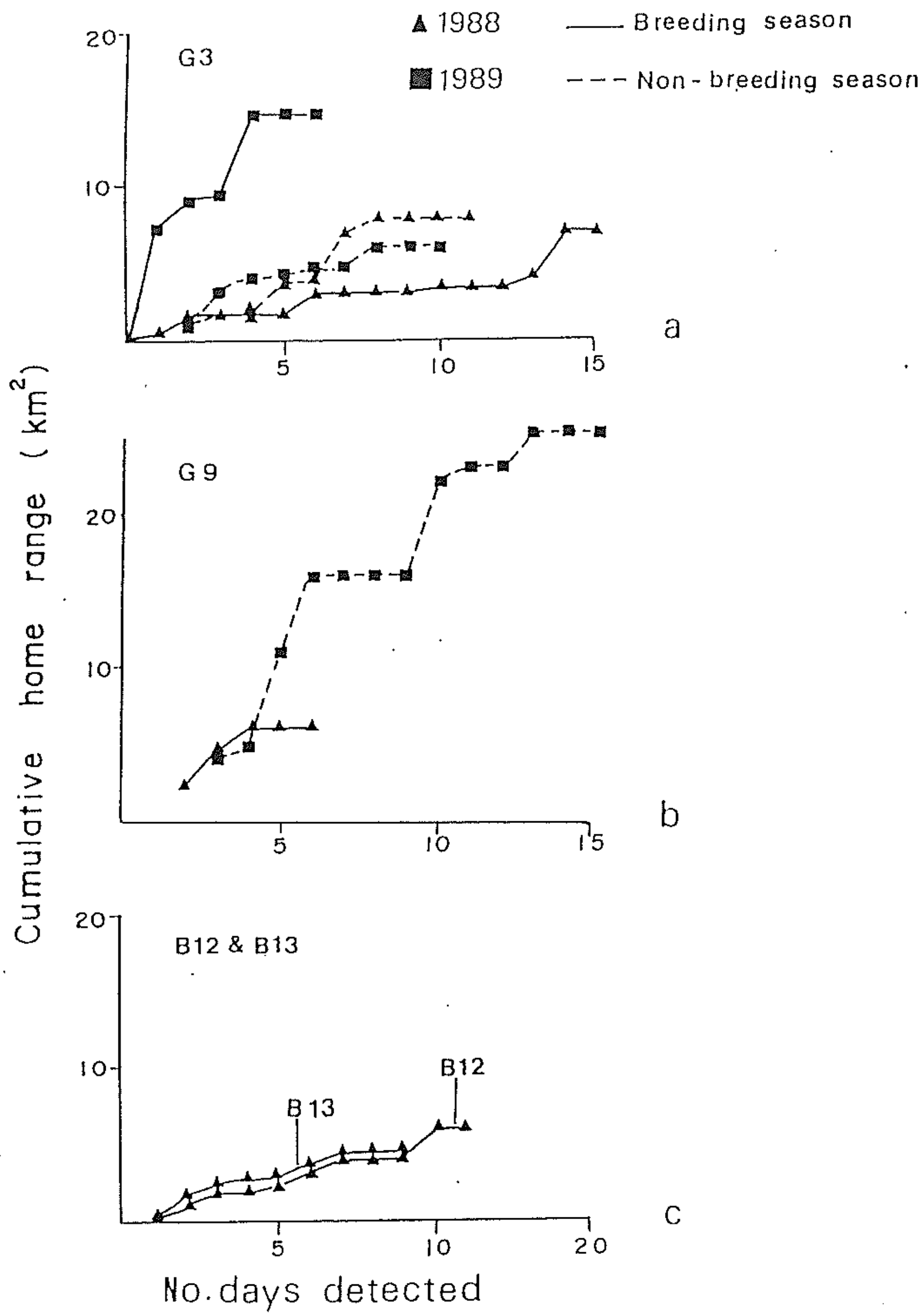


Fig. 7-4. The cumulative range in relation to number of days of radio tracking for (a) Great Hornbill G3, (b) Great Hornbill G9, and (c) Brown Hornbills B12 and B13. Only those ranges based on at least six detectable days are presented. ▲ 1988; ■ 1989; —— breeding season; --- non- breeding season.

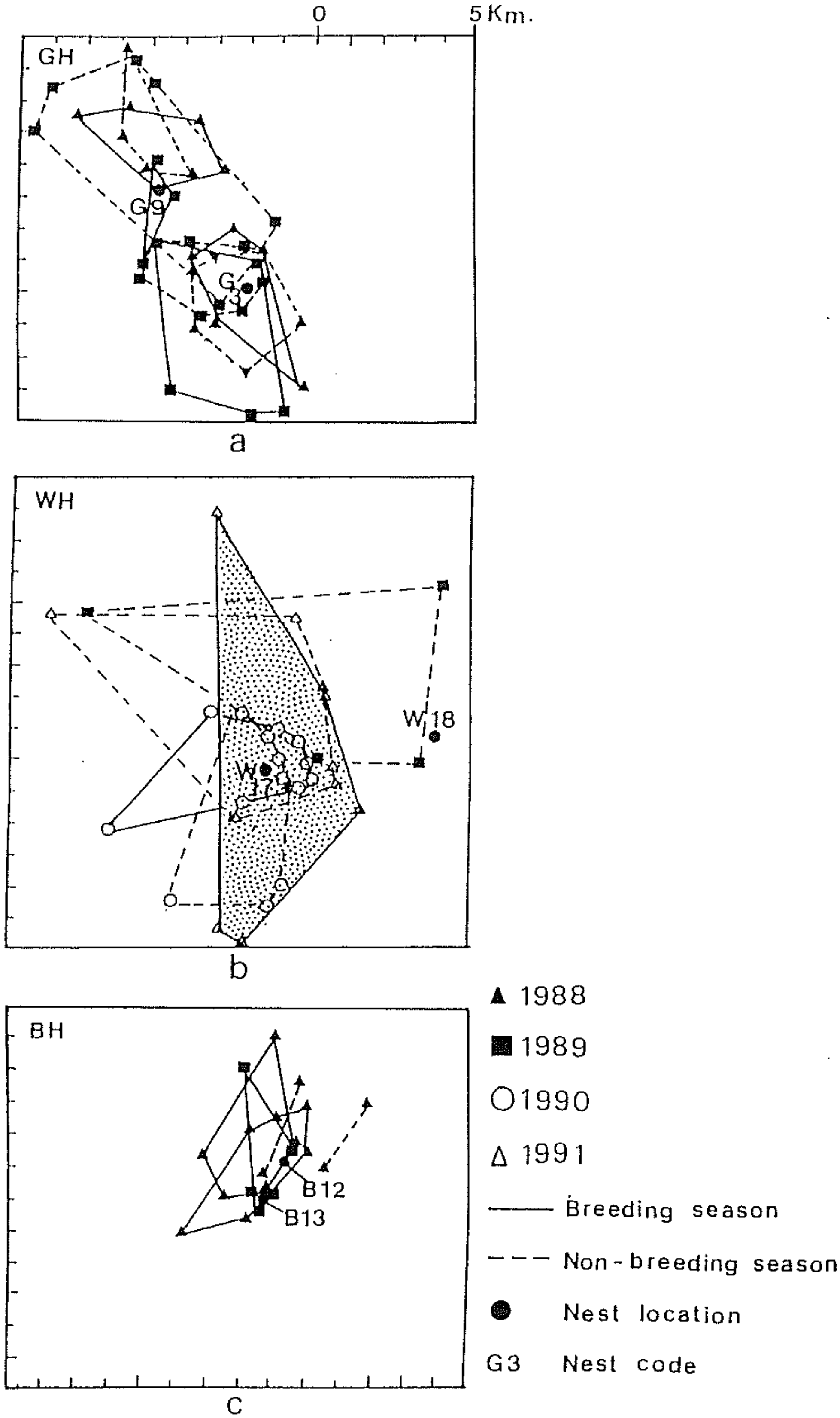


Fig. 7-5. The ranges of (a) Great Hornbills G3 and G9, (b) Wreathed Hornbills W17 and W18, and (c) Brown Hornbills B12 and B13 in the breeding and non-breeding seasons of 1988, 1989, 1990 and 1991. The stippled area indicates the range of

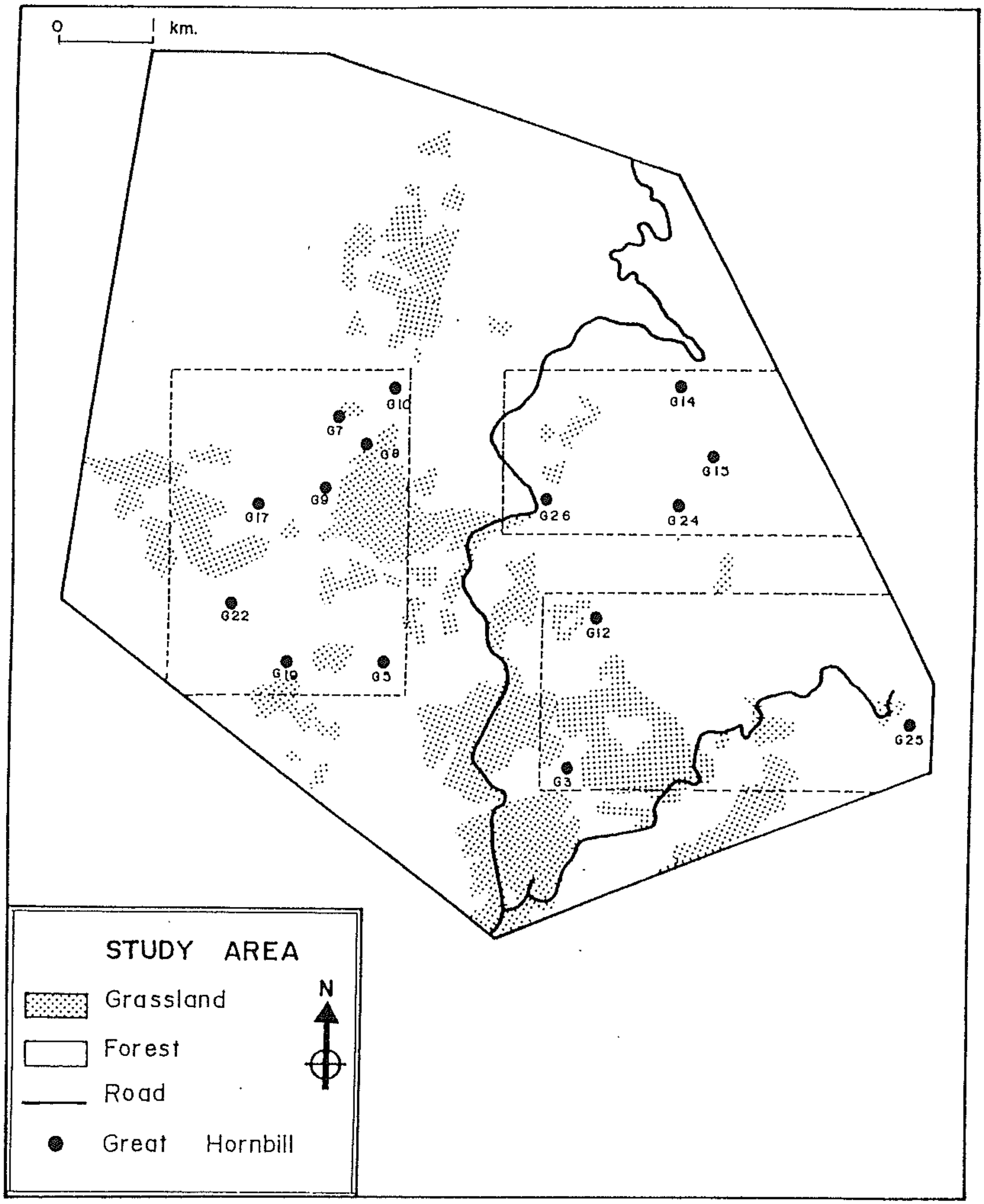


Fig. 7-6A. Nest territories of Great Hornbills at Khao Yai in breeding season of 1991.

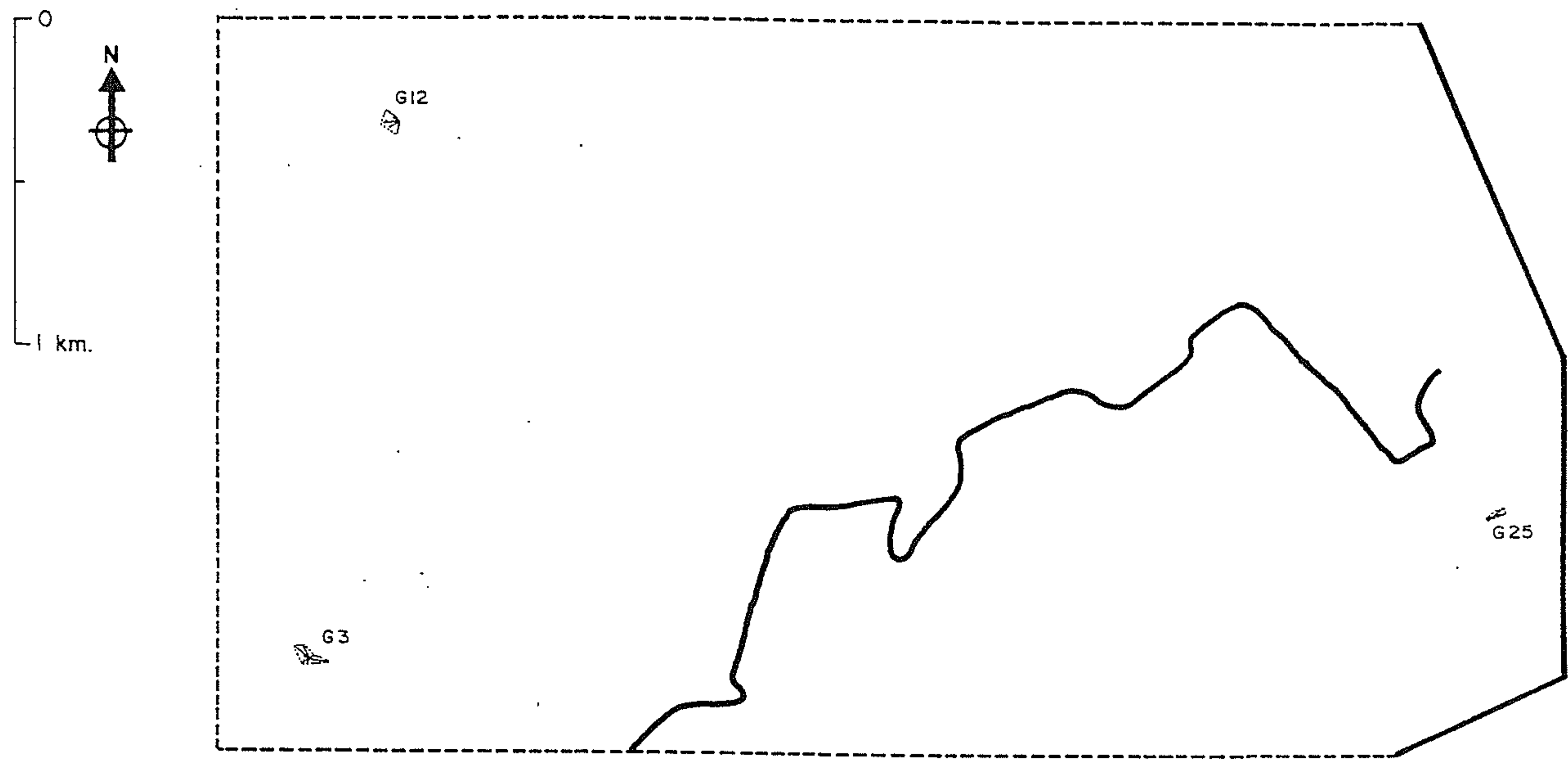


Fig 7-6A. (cont.)

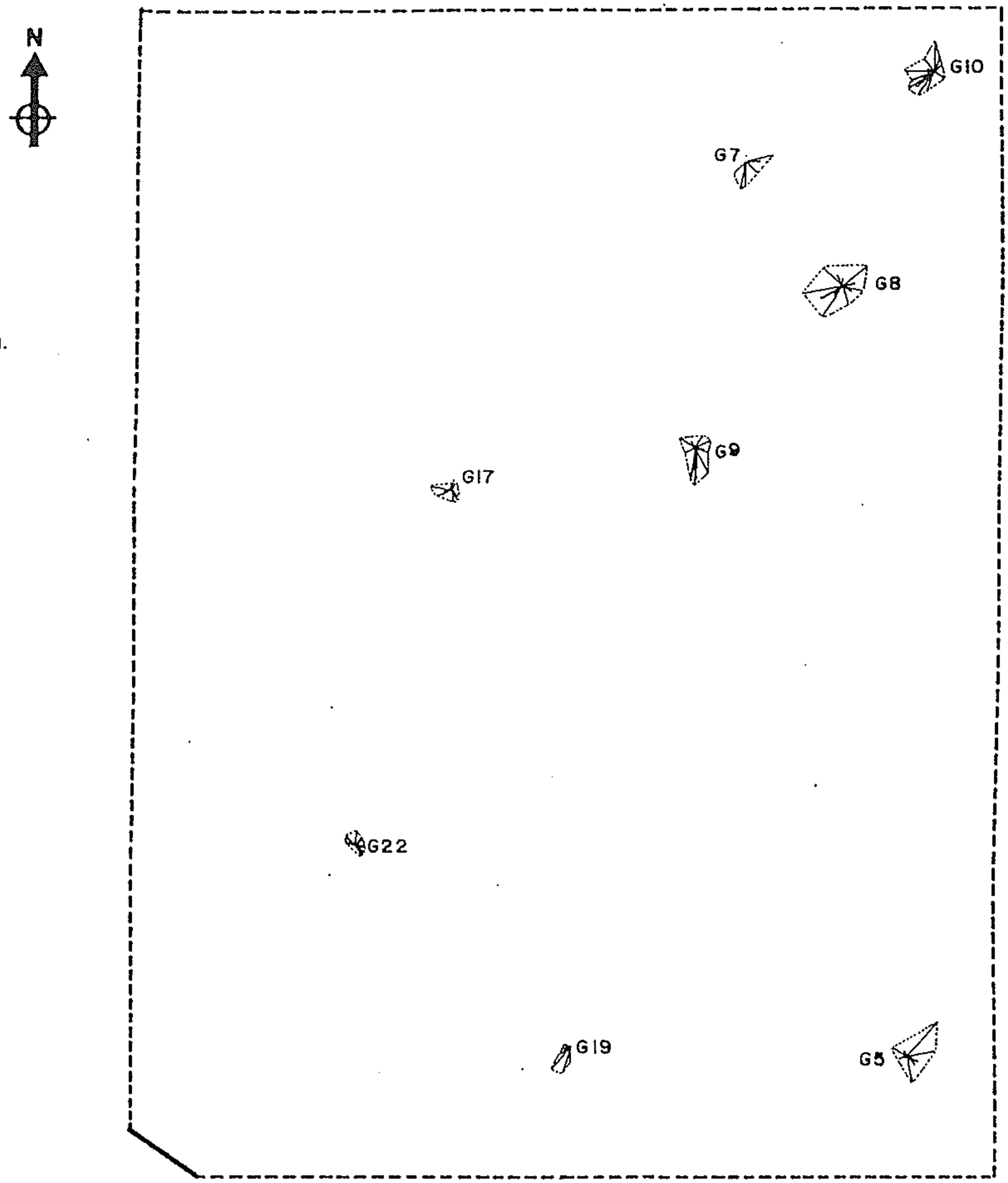


Fig.7-6A. (cont.)

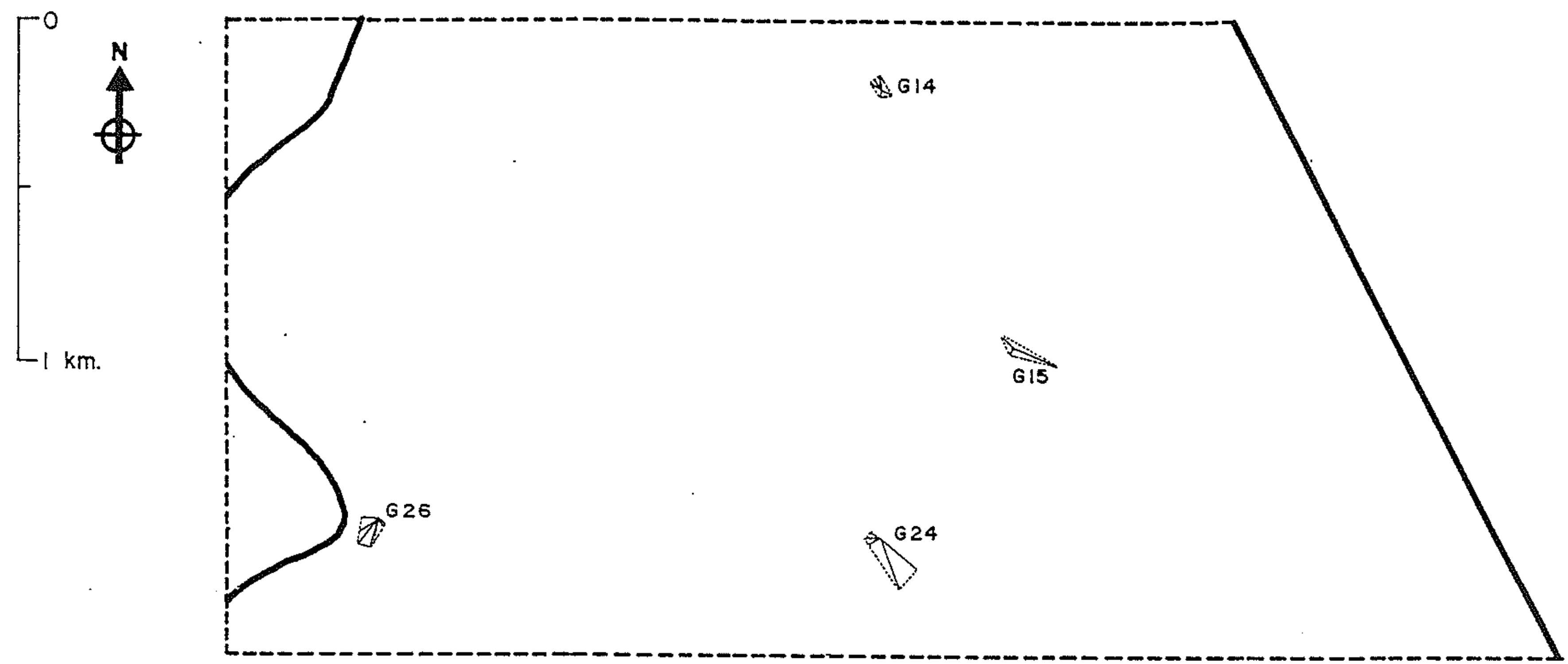


Fig. 7-6A. (cont.)

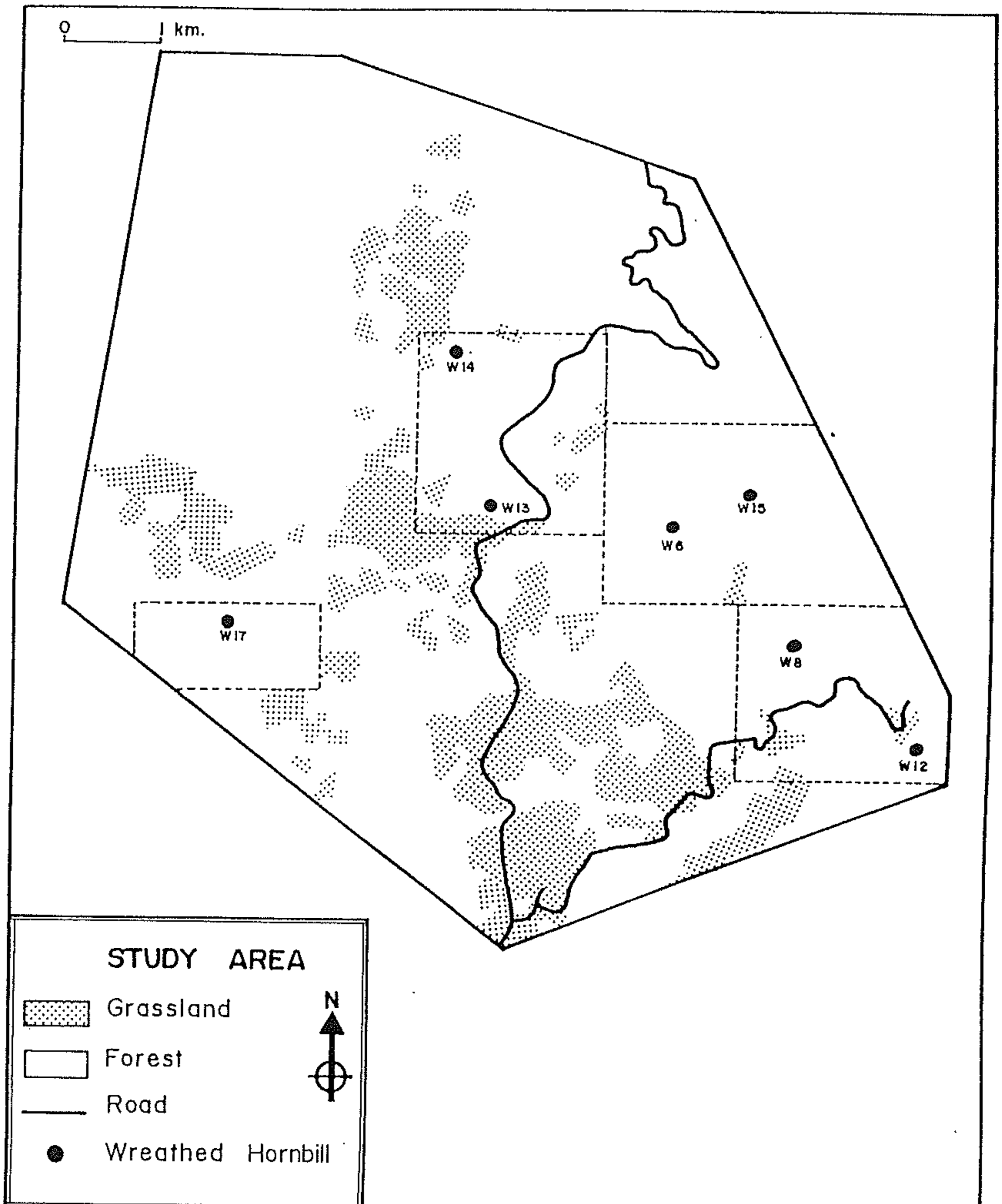


Fig. 7-6B. Nest territories of Wreathed Hornbills at Khao Yai in breeding season of 1991.

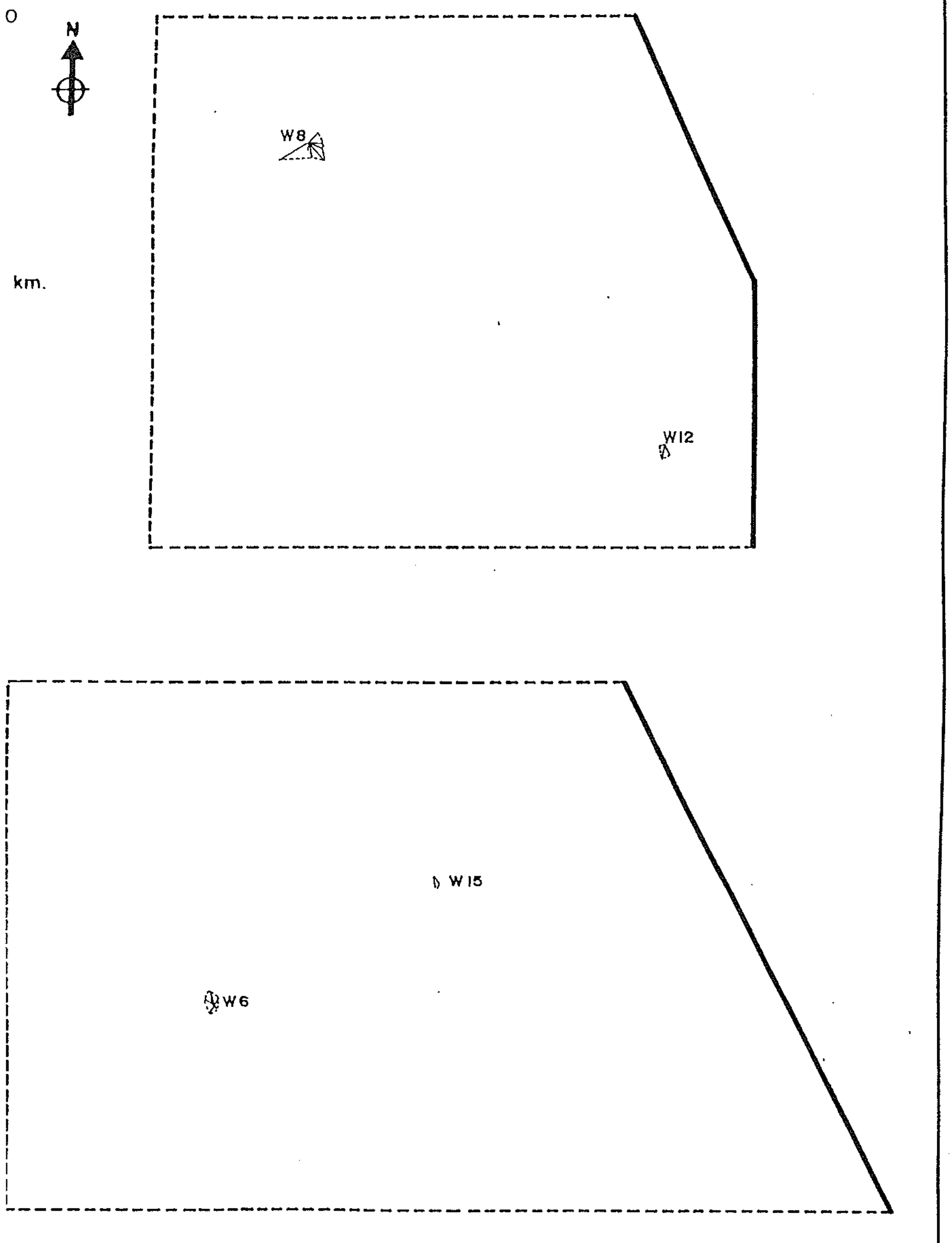


Fig.7-6B. (cont.)

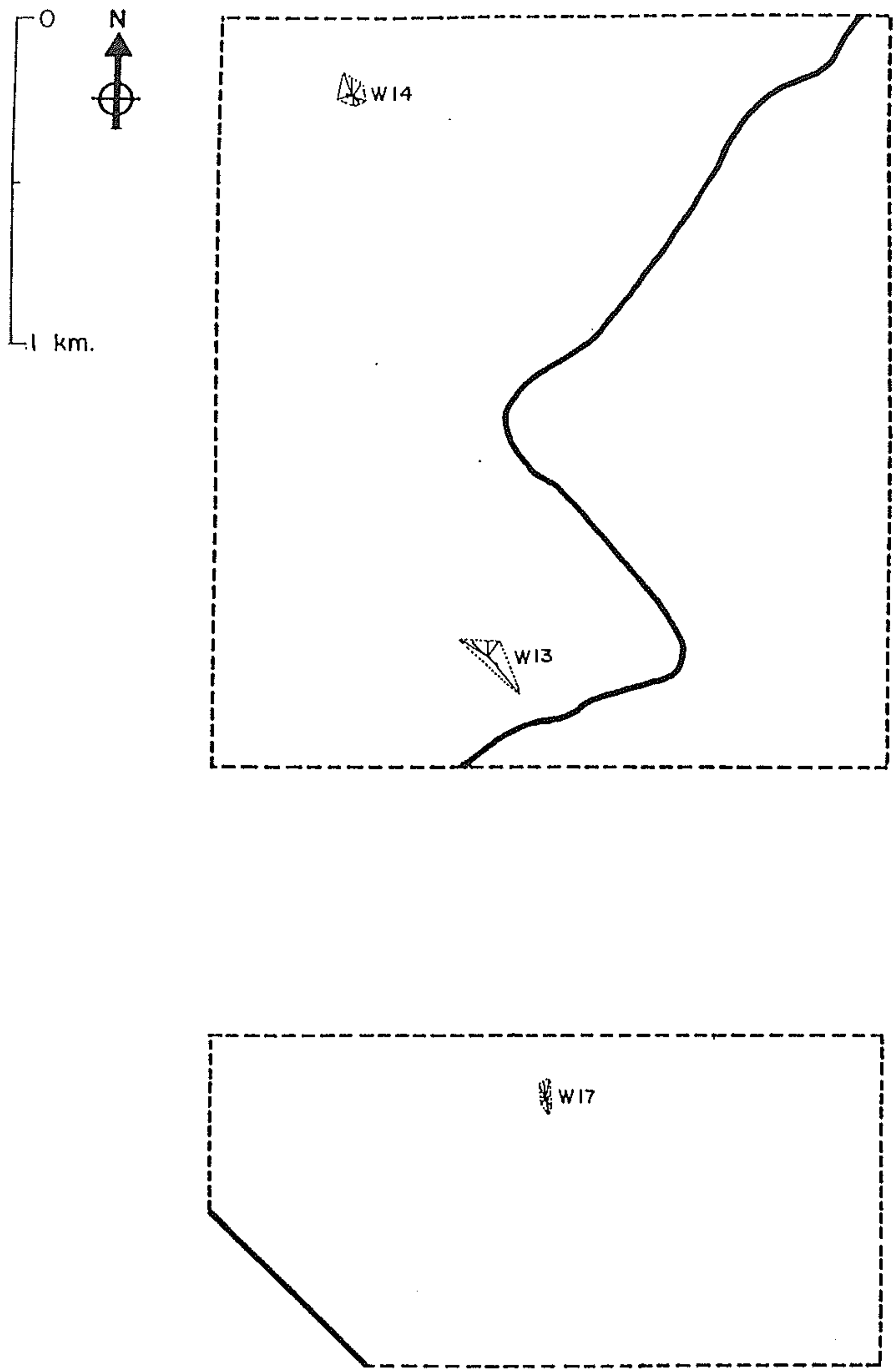


Fig. 7-6B. (cont.)

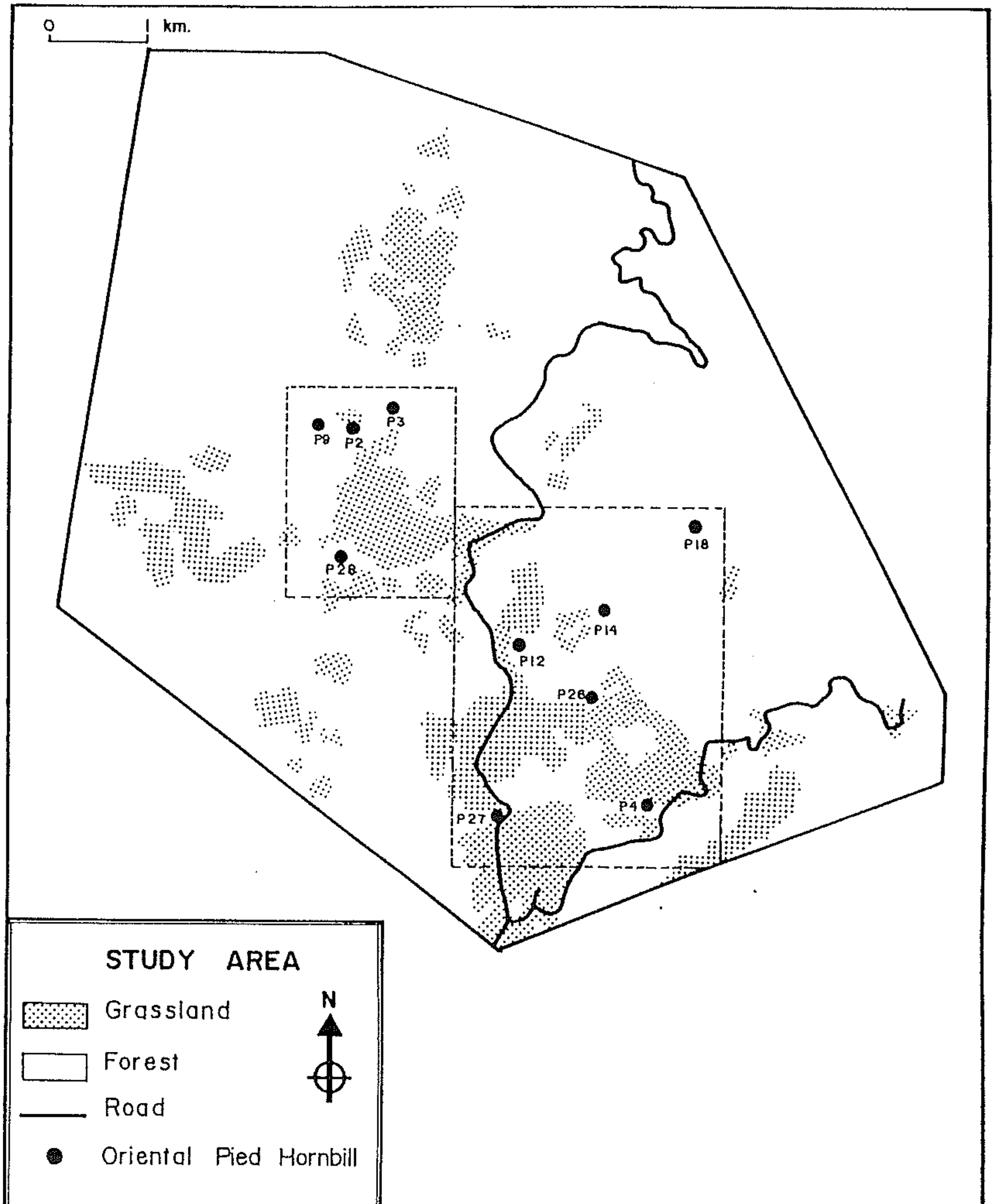


Fig. 7-6C. Nest territories of Oriental Pied Hornbills at Khao Yai in breeding season of 1991.

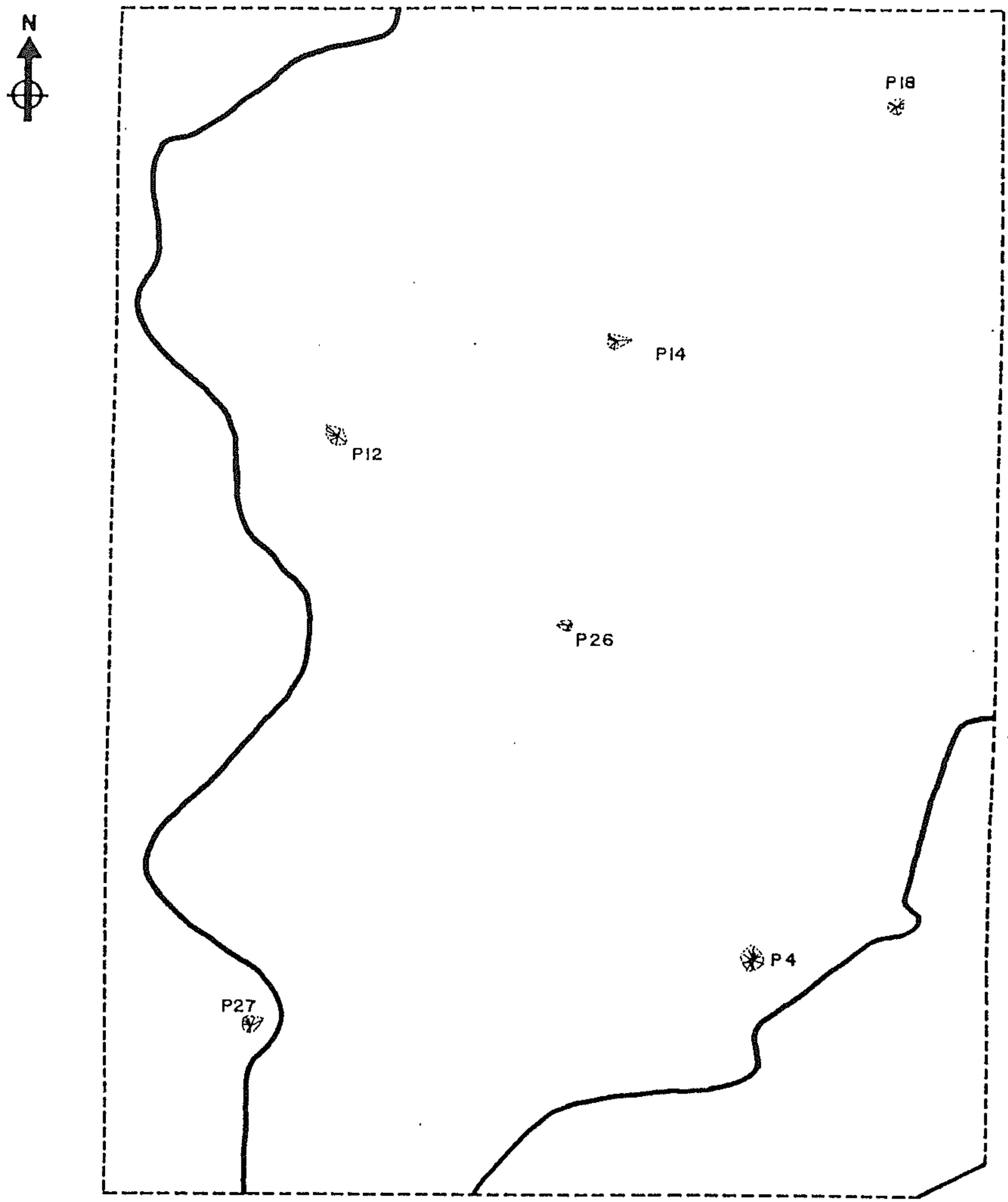


Fig.7-6C. (cont.)

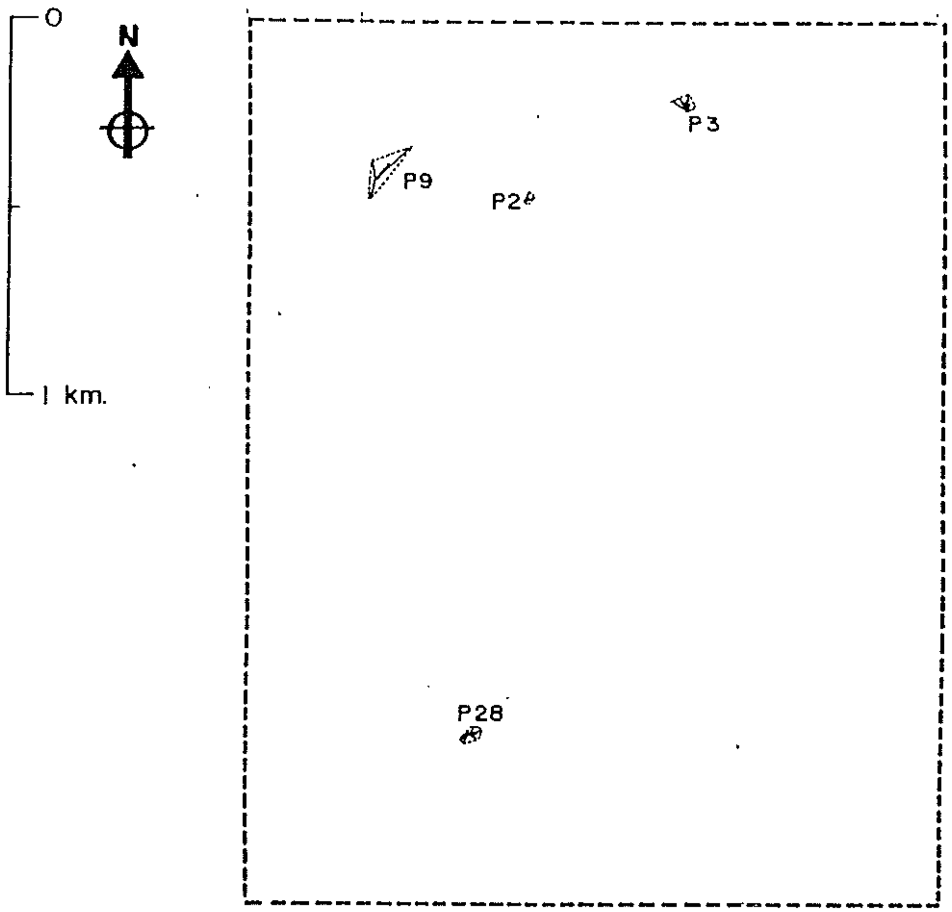


Fig.7-6C. (cont.)

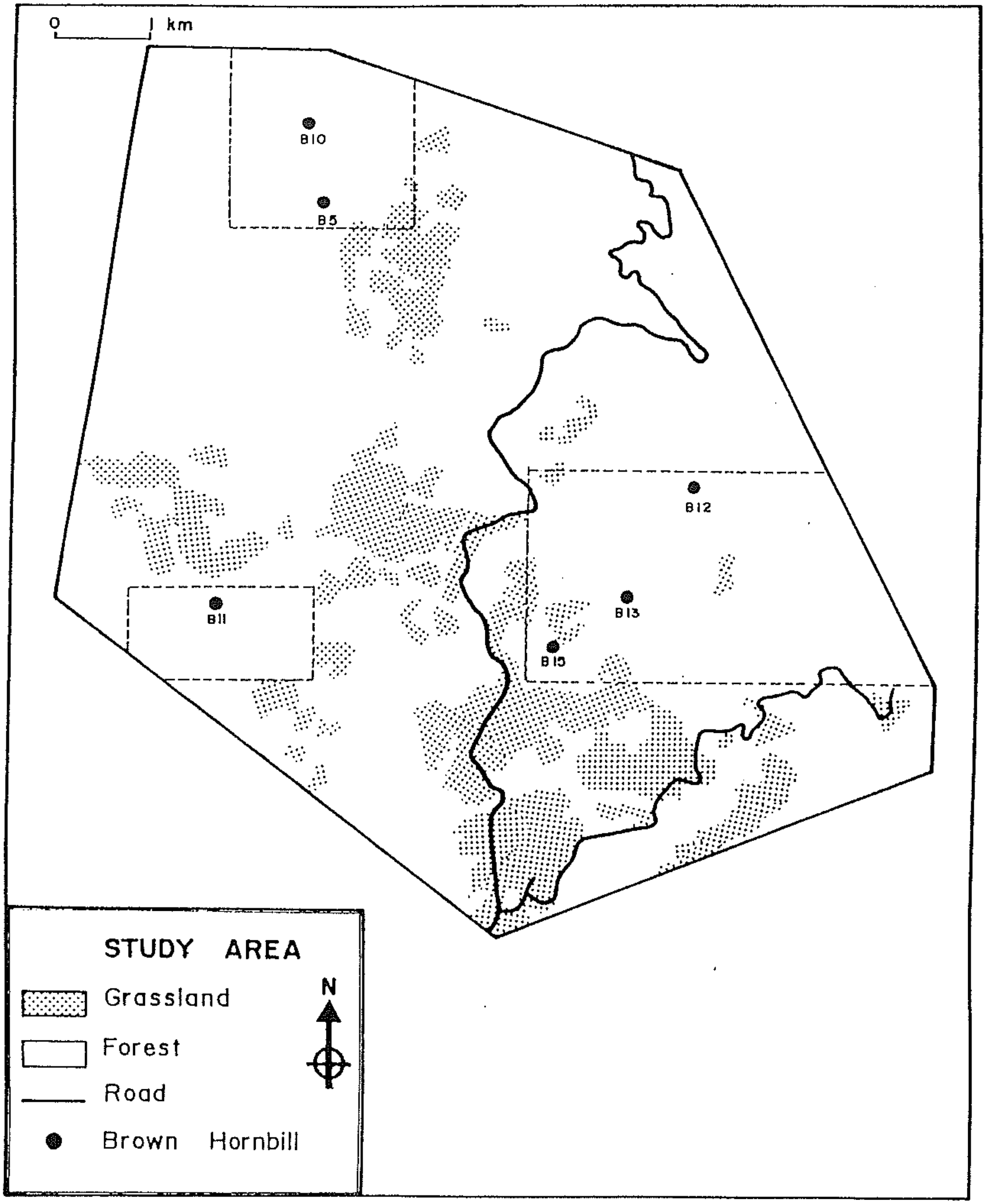


Fig. 7-6D. Nest territories of Brown Hornbills at Khao Yai in breeding season of 1991.

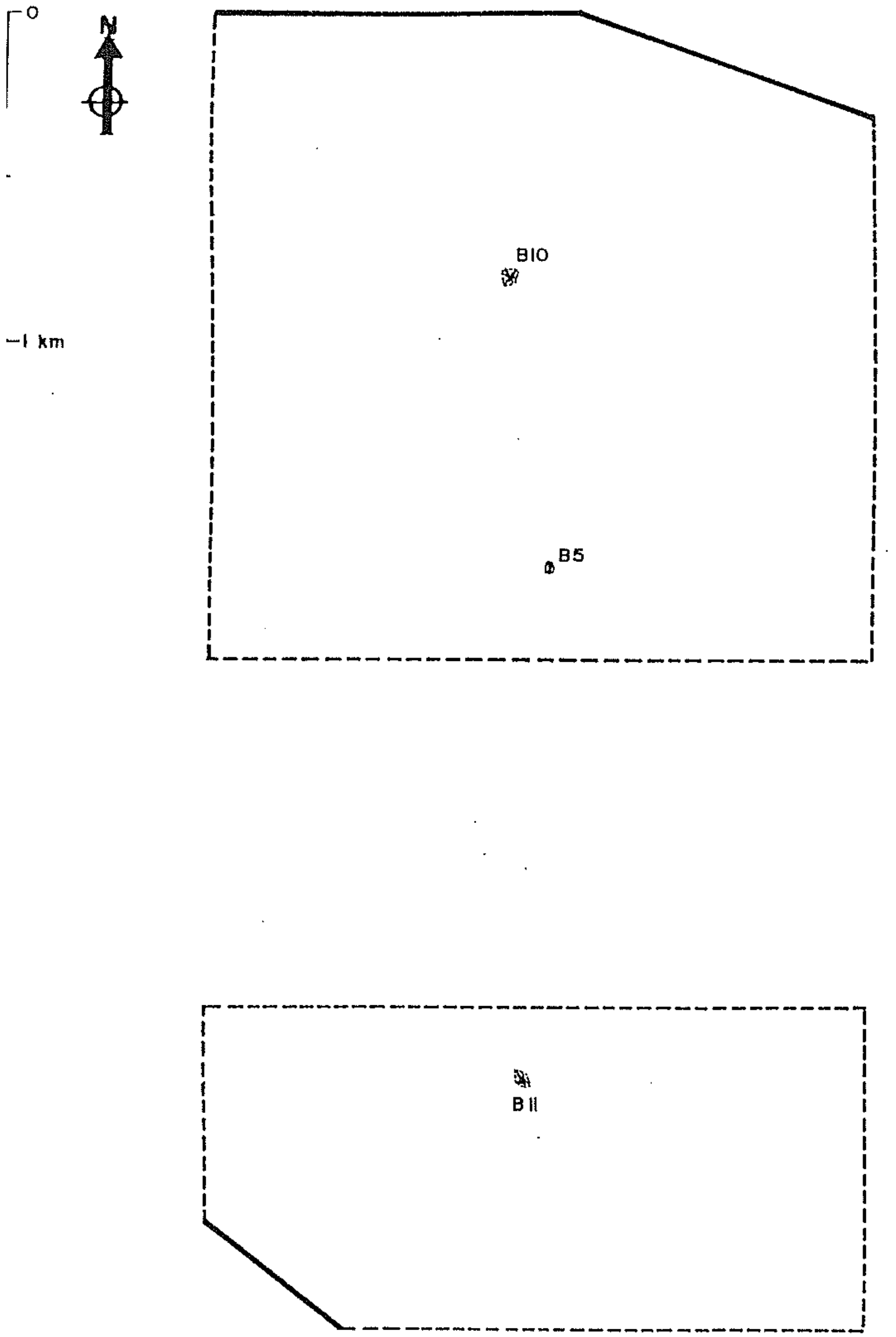


Fig.7-6D. (cont.)

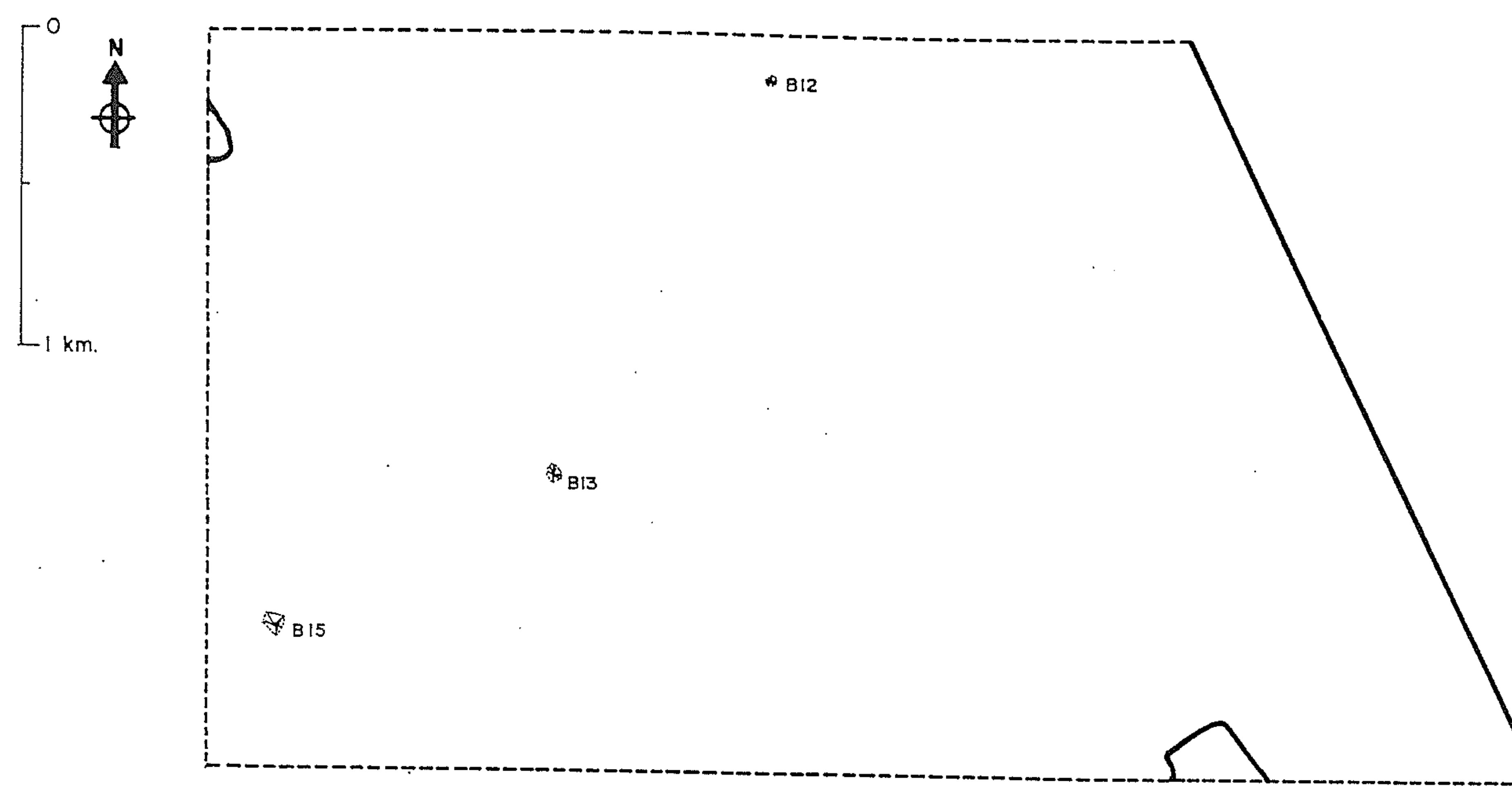


Fig. 7-6D. (cont.)

CHAPTER 8

FLOCKING AND ROOSTING

INTRODUCTION

Many species of birds show flocking behaviour at some stage of their annual life cycle. Flocking in birds is associated with at least two aspects of social behaviour involving attraction between individuals and food resources. Survival of individuals could be improved as a result of their association with other individuals for several reasons, for intance, increasing chances of food capture. When food supply is variable in space and time, flocking fruit-eating birds will have highest potential in finding food patches (Horn 1968, Orians 1971, Leighton 1986). But most flocking birds do not form flock throughout the year and flocks do not necessarily consist of individuals hatched in the same clutch (Orians 1971, McFarland 1981). However, there are species of birds which live permanently in small social groups, e.g. 5-15 individuals, most or all being close kin (McFarland 1981). Some known cases are cooperative breeders (McFarland 1981, Poonswad et al 1986).

Advantages of flocking are related to efficiencies in feeding and predator detection. Obviously, a number of eyes can spot food patch and enemy better than a sigle pair (McFarland 1981). However there must also be disadvantages of flocking, such as rapid exausting of food source and/or easier detected by predators.

This chapter presents my findings on flocking and communal roosting behaviours in the breeding and non-breeding seasons and some characteristics of roosting sites.

METHODS

Study of roosting in the breeding and non-breeding seasons

In the breeding season of 1985, a breeding male of Wreathed(W6) and Brown (B6)hornbills respectively was radio-tagged on 26 April. The roosting sites of these two breeding males were tracked between 20:00 and 23:00 hours at nest sites or from high locations using 3-element yagi antenna. The location of roosts was obtained by triangulation of signals detected from two high locations and plotted on a grid map (scale 1 : 50,000).

Direct observations were also used to locate roosting sites of Wreathed, Great, and Brown hornbills in the non-breeding seasons from 1981 through 1985, by searching out on foot through the study site, and by searching from high clifts where wide area of valleys could be seen. Binoculars (8x30) and spotting scopes (x20) were used to spot feeding and roosting flocks. Once flocks of hornbills were found, they were watched for 4 to 11 weeks per season. Observations from high clifts were made from 05:30 to 07:00 and from 15:00 to 19:00 hours to record their movement between the feeding and the roosting sites. Main roosting site is defined here where there were 100 individuals (or close to 100) or more except for the smaller flocking species as Great and Brown hornbills.

During the non-breeding season of 1984, two female Oriental Pied Hornbills were trapped and radio-tagged at a fruiting fig tree on June 17. Tracking was performed either on foot or from high locations. A flock of Oriental Pied Hornbills that inhabited an area of about 5.0 km^2 around the golf course in the national park area was observed from high vantage points from 4 to 8 days per month between 05:30 to 09:00 and 15:00 to 19:00 hours.

Structure of a flock

The sex and age composition of a flock were analyzed by direct observations and by photographing. This study was done only for Wreathed Hornbills , since the other species the sex and age could not be determined easily in the field. Quick-looked characteristics used to identify the sex of Wreathed Hornbills are the buffy white face and upper breast and the yellow gular pouch in males and the entire black body and wing except for the pure white tail and the blue pouch in females (see also Chapter 1). Age was determined by the number of ridges on the casque. Birds with one to two ridges on the casque were identified as immatures. Besides number of ridges, immature females could be identified with the yellow gular pouch (see also Chapter 1).

Characteristics of roosting sites

Two roosting sites of Great, Wreathed, Oriental Pied, respectively and one roosting site of Brown Hornbills were investigated. At each roosting site, a sample plot of 20 x 80 m was laid with the longer side laid along north-south. Unless the terrain was too difficult to set the sample plot, then the plot laying was slightly shifted from north-south direction to obtian the suitable location. Trees with the diameter at breast height (dbh) greater than 4.5 cm were recorded and the following data were collected:

1. tree species
2. number of trees in the sample plots
3. locations of trees
4. dbh
5. total tree height
6. height at first branch
7. crown cover

No attempt has been made to study the conditions of forest floor except for identifying the plant species found in the sample plot. The data obtained from each plot were then interpreted and drawn the scheme of vertical profile and crown cover of the forest at these roosting sites.

In order to determine the tree species of importance at the roosting sites, the important index value (IVI) was used (Raunkiaer 1934, Whittaker 1970). Thus the data obtained from each sample plot were calculated for:

$$\text{Density} = \frac{\text{No of individuals}}{\text{Unit area}}$$

$$\text{Relative density (RD)} = \frac{\text{Density of a species}}{\text{Sum all species density values}} \times 100$$

$$\text{Frequency percentage} = \frac{\text{No. sample plots a species occurs}}{\text{Total no. sample plots}} \times 100$$

$$\text{Relative (RF) frequency} = \frac{\text{Frequency of a species}}{\text{Sum all species frequency values}} \times 100$$

$$\text{Relative (RDo) dominance} = \frac{\text{Basal area of a species}}{\text{Total area of all species}} \times 100$$

Basal area is calculated from:

$$ba = (1/2 \times d)^2 \times H$$

where *ba* is basal area or stem cover, *d* is dbh and *h* is tree height. Then the value of IVI was calculated from:

$$\text{IVI} = \text{RD} + \text{RF} + \text{RDo}$$

RESULTS

Roosting, feeding and dispersion of the flocks in the non-breeding season

Roosting and feeding sites of Wreathed Hornbills were restricted to valleys at the northwest edge of the study site (Fig. 8-1). Most activities of the hornbills were concentrated in c. 8.0 km^2 of forest, within which there was a major feeding area of c. 2.5 km^2 and a second suspected feeding site of about c. 1.0 km^2. The feeding sites were located by tracking the route of hornbills going back to roost (Fig. 8-2). A large flock (more than 300 individuals) occupied the extreme northwest of the area and the rest of birds at medium density was found in the southeast of the study site (Fig. 8-1).

The maximum numbers of Wreathed Hornbills recorded annually varied from 373 to 1,040 and a total of five communal roosting sites were located from 1981 to 1985. Different combinations of roosting sites were utilized from year to year (Table 8-1, Figs. 8-2 and 8-3). Two main routes were used regularly between the roosting and feeding sites (Fig. 8-2) but it was not known whether or not a route was used by the same flock.

Great Hornbills formed a smaller flock than the Wreathed Hornbills. In 1981, one pair was seen to roost with Wreathed Hornbills at WH I (Fig. 8-1 and Fig. 8-2). In 1983, 67 Great hornbills were observed to share feeding and roosting sites with the Wreathed Hornbills at WH IV (Figs. 8-2 and 8-4). In 1982, 1984 and 1985 their roosting sites were unknown.

In 1985, two roosting sites shared by Great and Wreathed hornbills were found in the valley in the southeast of the study site (Fig. 8-1). At these two sites were about 500 m apart and contained apploximately 200 Wreathed and 30 Great hornbills all together. But from 1988 through 1992, it was found that the Great and Wreathed hornbills used these two sites separately. Thus, the sites were named separately as GH II and WH VI (Fig. 8-1). However, Great

Hornbills did not roost at GH II every year, whereas Wreathed Hornbills roosted at WH VI continuously. Great Hornbills were not seen to roost at GH II in 1990 and 1991. In 1992, the maximum number of the Great Hornbills recorded at this roosting site was 49 individuals. Great Hornbills were also regularly seen in pair or family parties. One pair was observed to use same roosting site (WH I) for five consecutive years from 1981 to 1985, and was joined by a chick in 1983.

In 1988, another roosting site (GH III) of the Great Hornbills was found in a valley by the road in the northeast section of the study site (Fig. 8-1). At this site in 1988, the largest number of Great Hornbills recorded was 157 individuals.

Roosting sites and number of individuals of Oriental Pied Hornbill recorded at the sites are presented in Figure 8-6. In 1981, the biggest flock of up to 133 Oriental Pied Hornbills were recorded to roost in a small forested area in the golf course area at Khao Yai. In 1983, no observation on roosting of this species had been made.

Movement of Oriental Pied Hornbills in the non-breeding seasons appeared to be most erratic. They did not use roosting sites with the same regularity as did Wreathed Hornbills and parties dispersed independantly from the roosts. Members of flocks regularly crossed open areas in a follow-my-leader fashion.

The flock of Oriental Pied Hornbill changed the roosting site from year to year and from time to time within one season (Fig. 8-6), but all roosting sites were at the edge of forest patches (Fig. 8-1). In Oriental Pied Hornbills no regular route to roosting sites or feeding sites was noted, though the roosting site PH II (Fig. 8-6) was used frequently. Flock size became maximum between late July and August, but the birds dispersed and only a small flock remained in the area thereafter (Fig. 8-5). None of the radio-tagged Oriental Pied Hornbills roosted in this area, but radio-tracking confirmed that different flocks sometimes gathered in the same fruiting trees. In 1988, at the site PH IV, there were 115 individuals seen roosting.

Flocks of Brown Hornbill were smallest among these four species. A roosting site (BH I) of this species was found near WH III (Figs. 8-1 and 8-2). The maximum number of their flocks varied from 26 to 54 individuals. There seemed to be two flocks joining to feed and to roost together.

The dispersion of a Brown Hornbill flock seemed to be rather uniform with a tendency to decrease gradually (Fig. 8-7), in contrast to the dispersion of Wreathed Hornbills (Fig. 8-3) which dispersed abruptedly.

Roosting in the breeding season

Roosting of breeding males in the breeding season was known for Wreathed and Brown hornbills. The male Wreathed Hornbill (W6) roosted randomly in at least seven sites in its feeding range (Fig. 8-8a). None of these roosting sites was found near its nest, but at least a site was close to a fruiting fig tree.

The male Brown Hornbill (B6) did not roost far from its nest. It roosted for several nights at a particular roosting sites and only three sites were detected (Fig. 8-8b). Two other flocks of the breeding males and their helpers (about 10 to 12 individuals) were observed roosting at a regular site which was about 0.5 to 1.0 km apart from their nests and passed by my camp each morning enroute to their nests. Hence Brown Hornbills flock all year round, and they formed a bigger flock in the non-breeding season. These two flocks used the same roosting site as in the non-breeding season (Fig. 8-1, see also Chapter 5)

Structure of a flock

I examined sex and age ratios in Wreathed Hornbill flocks totaling in 89 flocks with 960 individuals between 1981 and 1983. Results showed that the sex ratio of male to female was on an average 1 : 1.04 or 48.9 % males to 51.1 % females. The age ratio was on an average 1 : 1.4 or 41.8 % adults to 58.2 % immatures.

Figure 8-9 shows annual variations in sex and age composition during the three- year study. The sex ratio was similar in 1981 and 1982 and the age ratio was similar in 1981 and 1983. The data suggests that the structure of Wreathed Hornbill flock was not stable as to sex and age.

Characteristics of roosting sites

The characteristics of roosting sites of the four hornbill species are summarized in Table 8-2. Profiles of forest structure at roosting sites of Great (GH II & III), Wreathed (WH IV & VI), Oriental Pied (PH II & IV) and Brown (BH I) hornbills are shown in Appendices 8-1a & b, 8-2a & b, 8-3a & b and 8-4, respectively. In general the forest structure was divided into three layers, excluded the forest floor.

Details of the characteristics of these roosting sites are as follows:

Great Hornbills: Roosting site GH II (Appendix 8-1a) was located by a creek. The first layer or top canopy was rather high, 36 to 40 m tall and consisted of a single species of trees, <u>Acrocarpus fraxinifolius</u>.

The second layer, 18 to 28 m tall, was a very dense canopy with some emergent trees, which included <u>Toona ciliata</u>, <u>Eugenia operculata</u>, <u>Aglaia pirifera</u>, <u>Macropanax</u> sp., <u>Nyssa javanica</u>, <u>Drypetes hoaensis</u>, <u>Choerospondias axillaris</u>, and <u>Sapium baccatum</u>. The Great Hornbills were observed to roost in those first and second layers.

The third layer was low, 2.5 to 16 m tall. Trees in this layer which included <u>Amoora cultrata</u>, <u>E. operculata</u>, <u>Pterocymbium javanicum</u>,<u>Glochidion</u> sp., <u>Bichofia javanica</u>, <u>Semecarpus cochinchinensis</u>, <u>Baccaurea ramiflora</u>, <u>Mollotus philippenensis</u>, and <u>Memecylon caeruleum</u> were also dense and mixed with bamboos <u>Neohouzenea mekongensis</u> and palms <u>Livistona speciosa</u>.

The forest floor was dense and covered by Robus molluccanus, particularly by the creek. Other species of plants on the floor were Lasia spinosa, Eupatorium ordoratum, ferns of genus Tectaria sp. and seedlings of Cinnamomum subavenium and E. operculata.

GH III (Appendix 8-1b) was located by the creek with rocky bed. The soil layer was thin. The forest structure was different from GH II in having a lower first layer of 28 to 35 m tall and the trees consisted of strangling figs Ficus benjamina, Sterculia ornata and Tretameles nudiflora

The second layer was rather high, 20 to 25 m tall and consisted of trees of Spondias pinnata, Bombax anceps, E. subumbrans, Terminalia undulata, and T. negrovenulosa, which were scattering between rocks.

The third layer was similar to GH II in height (4 to 15 m tall) and formed by shrubs and medium-sized trees mixed with saplings. The plant species found were Stercospermum neuranthum, Vitex guinata, Wrightia tomentosa, Albisia lebbeckoides, Lagerstroemia dupperiana, etc. Great Hornbills roosted mainly in the third layer and also on bamboos.

The forest floor was covered with scattered seedlings of those trees composing the first and second layers mixed with dense bamboos Thyrsostachys siamensis. Herb species found on the ground were Boesenbergia pandulata, Globba annumensis, and Cyperus sp, etc., together with ferns of genera Selaginella, Adiantum, and Pteris.

Wreathed Hornbills: The first layer of roosting site WH IV (Appendix 8-2a) was not very high as compared with GH II and WH VI (see below), consisting of trees of Parkia sumatrana, Prunus arborea, Schima wallichii Podocarpus imbricartus, and Castanopsis acuminatissima.

The second layer was similar to GH II in height (Table 8-2) and consisted of trees of P. niriifolia, Adinandra intergerrima, Gironniera nervosa, Paranephelium longifoliolatum, Nyssa javanica, Litsea umbrellata, S. wallichii, P. arborea, and C. acuminatissima. Wreathed Hornbills were observed to roost in the second as well as in the first layers.

The third layer consisted of small and medium sized trees which ranged from 4 to 15 m in height. The trees included M. floribunda, Glycosmis pentaphylla, Neolitsea siamensis, W. robusta, Symplocos laurina, Aporusa planchonniana, and bamboos Cephalostachyum pegracile which was found in clumps, particularly along steep slope areas.

The forest floor was covered with bamboos N. mekongensis, seedlings of Pristomeris malayana and Dracaena angustifolia, herbs such as B. plicata, ferns of genera Pseudodrynaria and Pyrrosia eberhadtii, orchids, ect.

At roosting site WH VI (Appendix 8-2b), the first layer was 40 to 55 m tall (Table 8-2) and highest among all roosting sites visited. Trees were A. fraxinifolius, Platymitra siamensis, Artocarpus dadah, and Castonopsis sp. Besides those trees, palms L. speciosa were scattered with a density of 4 trees in 20 x 80 m plot.

The second layer was slightly lower than those of GH II, GH III and WH IV, and the canopy was not as dense as that of nearby GH II. There were a few *E. subumbrans* and *Oxylum indicum* scattering between gaps of the first layer. The hornbills were seen to roost in the first and and second layers.

The third layer was dense and was similar in height to the sites already described (Table 8-2). The trees consisted of shade tolerant species including *M. philppenensis*, *A. cultrata*, *Ulmus lancifolia*, *Exocoecaria oppositifolia*, and *Knema elegans*.

The forest floor was covered with seedlings of hornbill's food plants, such as *C. subavenium*, *K. elegans*, and *L. speciosa*. Herbs of the family Zingiberaceae including *Catimbium speciosum*, and *A. oxymitra* were also found.

Oriental Pied Hornbills: Roosting site PH II (Appendix 8-3a) was a remnant forest of dry evergreen type and located between the grassland and a creek. The first layer was 25 to 28 m tall (Table 8-2) and relatively low as compared with those of Great and Wreathed hornbills.

The second layer, 18 to 24 m tall (Table 8-2), was very close to the first layer and the trees included *Altingia siamensis* and *Dipterocarpus gracilis*, both were found along the creek.

The second layer was very dense. The trees included *S. baccatum*, *A. siamensis*, *Litsea* sp., *T. ciliata*, *N. javanica*, *S. laurina*, *F. benjamina* and *C. axillaris*.

Oriental Pied Hornbills were observed to roost in this layer.

The third layer was similar in height to other sites (2.8 to 16 m tall, Table 8-2), but it was formed by trees of small size and saplings and was very dense, especially along the forest edge. Trees and saplings observed were Gonocaryum lobbianum, Eurya acuminata, K. linifolia, G. nervosa, and E. oppositifolia.

The density of tree (dbh > 4.5 cm) was remarkably high at PH II (Table 8-2).

The forest floor was very dense and was covered with ferns of genera Diplazium and Selaginella, rattans Daemonerops sp., plants of the family Zingiberaceae such as C. speciosum and seedlings.

PH IV (Appendix 8-3b), was also situated in a remnant forest surrounded by grassland. It was found that the first layer was lowest, 16 to 20 m tall (Table 8-2), among the roosting sites studied. Trees found in the first layer included Lithocarpus annumensis, E. operculata, Firmiana colorata, Elacocarpus robustus and Ficus sp.

The second layer was also lowest, 12 to 15 m tall (Table 8-2), among those of the sites studied. The trees found were E. bantamensis, A. cultrata, E. robustus, P. acerifolium, A. intergerrima, C. iners, E. cumini, A. lakoocha and S. luarina. The hornbills were observed to roost in this layer.

Third layer at PH IV was again lowest, 4 to 9 m tall (Table 8-2), among all sites studied, and was very dense, particularly in the areas next to the grassland. The trees found consisted of W. robustus, Linociera microstigma, Sladenia celastrifolia, M. caerulium, E. siamensis, P. paniculata, Clansena wallichii, G. lobbianum, E. acuminata, and P. malayana.

The density of trees was found to be highest among all roosting sites studied (Table 8-2).

The forest floor was rather open with an evidence of being fired and seedlings and rattans were found scattered.

Brown Hornbills: BH I (Appendix 8-4), the only site of Brown Hornbills I discovered, was located in a wet evergreen forest and situated by a creek. The first layer was slightly taller than at WH IV (35 to 40 m tall, Table 8-2), which located not further than 2 km. BH I was on a more gentle slope than WH IV and Trees found in the first layer were Slonea sigun and D. gracilis

The second layer was also relatively taller than at WH IV (Table 8-2) with a dense canopy particularly between the gaps of the first layer. Trees found were S. sigun, P. neriifolia, N. javanica, G. nervosa, and P. arborea. Brown Hornbills were seen to roost in this layer.

The third layer was dense and consisted of small trees similar in height to those of WH IV (Table 8-2). The trees were included Horsfieldia wallichii, Pittosporopsis kerrii, A. perifera, Baccaurea ramiflora, S. luarina and W. robustus.

The forest floor was very dense. The plants found covering the floor were ferns of Cibotium barometz, Cyathea contaminans, Diplazium sp. and Selaginella, seedlings of C. subavenium and Lasianthus spp., and rattans Daemonorops.

DISCUSSION

Flocking and dispersion in the non-breeding season

In hornbills studied the gregariousness and dispersion during the non-breeding season appear to be related to the degree of frugivory of each species. All four species of hornbills gathered in flocks during restricted periods of the year although Brown Hornbills flocked throughout the year. Wreathed Hornbills appear to form largest flocks and are most frugivorous species. These habits were also noted previously by McClure 1970, Leighton 1982, Poonswad et al. 1983, 1986.

At Khao Yai, Wreathed Hornbills gathered in numbers exceeding 200 individuals after breeding, from about July to November. Baker (1927), on the other hand, found that in the western Himalayas Great Hornbills gathered in large flocks when roosting (200+ individuals), but the Wreathed Hornbills never did. The cause which made the Great Hornbills gathered in such a large number was unknown.

The duration spent on feeding and roosting at feeding and roosting sites seemed to be related to flock size. When flocking birds exceeded 700 individuals, they dispersed abruptly. Smaller flooks tended to be more stable and the members stayed longer and departed gradually. Presence of large flocks possibly indicated a limited and/or patchy food supply (Leighton 1986), since such sources could attract large numbers of birds but was soon exhausted. Conversly, small numbers in flocks may suggest that fruiting trees are more evenly distributed during that season. Thus, the annual fluctuation of the maximum number of Wreathed Hornbills at roosting site may determine the size of a food patchy source within an area and vice versa.

Moreover, the area in the northwest of the study site must have provided a large food supply to support so many large birds as Wreathed Hornbills. *Ficus* and *Phoebe* trees seemed to be frequently encountered when hiking through the study site (pers. obs. see also Table 6-11, Chapter 6), suggesting a high density of potential feeding trees although fruiting patterns would affect the immediate availability of food.

The reliance on fruit by Wreathed Hornbills was reflected in its direct travel between roosting and feeding sites (Leighton 1986), which was also confirmed in this study (Fig. 8-2).

Horniblls normally move and roost in family groups. Larger flocks may have been non-breeding members of the population or pairs from the marginal areas which could not support them throughout the year (Leighton 1986). The four hornbill species at Khao Yai were seen most often in flocks of family size ranging from 1 to 5 individuals (unpubl.

data).

Roosting sites of breeding males

Wreathed Hornbill males were most erratic in their choice of roosting sites, whereas Brown Hornbills were least. The difference may be related to changing of fruit food supplies within the feeding range of the former species and is supported by their sometimes roosting close to fruiting food trees.

Structure of a flock

The differences in the sex and age composition of flocks in different years suggest changes of the structure of flocks or changes of flocks roosting in the area. It also may indicate variations of the sex and age ratios of the flocks. On the other hand, the feeding and roosting flocks of the Wreathed Hornbills basically consisted of several small flocks.

Thus, the age ratio in particular is related to annual breeding success. In 1983, the ratio of immatures to adults in Wreathed Hornbills was highest throughout three-years of observations. This was well supported by the average breeding success of this species (Table 4-7 of Chapter 4).

The sex ratio on the other hand, may involve more at genetic level, However, from this study, the fluctuation in the sex ratios may indicate the tendency of the breeding pairs produced more females than males. It may also be possible that motality of males was higher than females, which also affect the sex ratio in a population. Unfortunatlly, there was no study to support this hypothesis. In addition, the Wreathed Hornbills raised only one, rarely two chicks (Chapter 4, pers. obs.). Therefore, it was possible that the population may skew to females.

Characteristics of roosting sites

Characteristics of roosting sites of Asian hornbills has been well invertigated. although data are small, the present study suggested that Wreathed Hornbills prefered to roost in the primary forest in the valley with very steep slope. In contrast, Oriental Pied Hornbills prefer seemed to the forest edge with rather flat terrain and dense vegetation. Great Hornbill may prefered the sparse vegetation on a steep slope as roost and Brown Hornbills roosted in the deep forest with more gentle slope.

It is difficult to explain why the Wreathed and Oriental Pied hornbills use completely different characteristics of roosting site? The differences between the roosting site of these two species may have some relations to foraging niches (Chapter 6) and the ability of flying. Wreathed Hornbill is recognized as one of the strongest fliers among this bird family (McClure 1970), and they move among the high canopy (Leighton 1986). Oriental Pied Hornbills usually prefer open forest and feed on the ground as well (Ali and Riply 1987), and they are not as strong flier as the Wreathed Hornbill (pers. obs.).

Table 8-1 Maximum flock size and the use of roosting site in Wreathed Hornbills in 1981-1985. (See also Fig. 8-2).

* Found roosted with small number (> 20 < 50 individuals).

Year	Maximum no. found	Roosting site				
		WHI	WHII	WHIII	WHIV	WHV
1981	699	x	x			
1982	373		x	x		
1983	700			*	x	
1984	1,040		x	x	*	
1985	474	x				x

Table 8-2 Summary of characteristics of roosting sites of the four sympatric hornbill species studied in a 20 x 80 m sample plot at each site.

Hornbill sp. (Roost site)	Forest type	Range of forest layer height(m)			Av. slope	No. trees per plot (dbh>4.5 cm)	No. tree species in plot	Dominant tree sp.	IVI
		1st	2nd	3rd					
Great Hornbill (GH II)	Wet ever-green	36-40	18-28	2.5-16	13	128	51	*Acrocarpus fraxinifolius*	35.5
								Nyssa javanica	26.0
								Eugenia operculata	22.6
(GH III)	Mixed deci-duous	28-35	20-25	4-15	37	41	21	*Ficus benjamina*	36.6
								Grewia laevigata	34.6
								Terminalia undulata	27.3
Wreathed Hornbill (WH IV)	Hill ever-green mixed bamboo forest	30-35	18-28	4-15	42.5	135	50	*Castanopsis acuminatissima*	21.9
								Schima wallichii	19.7
								Memecylon floribunda	19.1
(WH VI)	Wet ever-green	40-55	18-24	4-15	50.0	125	49	*A. fraxinifolius*	55.3
								Exoecaria oppositfolia	23.5
								Claoxylon indicum	17.8

Table 8-2 (cont.)

Hornbill sp. (Roost site)	Forest type	Range of forest layer height(m)			Av. slope	No. trees per plot (dbh>4.5 cm)	No. tree species in plot	Dominant tree sp.	IVI
		1st	2nd	3rd					
Oriental Pied Hornbill (PH II)	Dry ever-green	25-28	18-24	2.8-16	15.0	188	60	Altingia siamensis Ficus benjamina Camellia oleifera	28.2 19.8 17.0
(PH IV)	Dry ever-green	16-20	12-15	4-9	2.8	201	54	Eugenia claviflora Pterospermum acerifolium Phoebe paniculata	28.0 24.3 20.1
Brown Hornbill (BH I)	Wet ever-green	35-40	25-32	4-18	8.5	118	36	Slonea sigun Dipterocarpus gracilis N. javanica	69.8 41.4 27.2

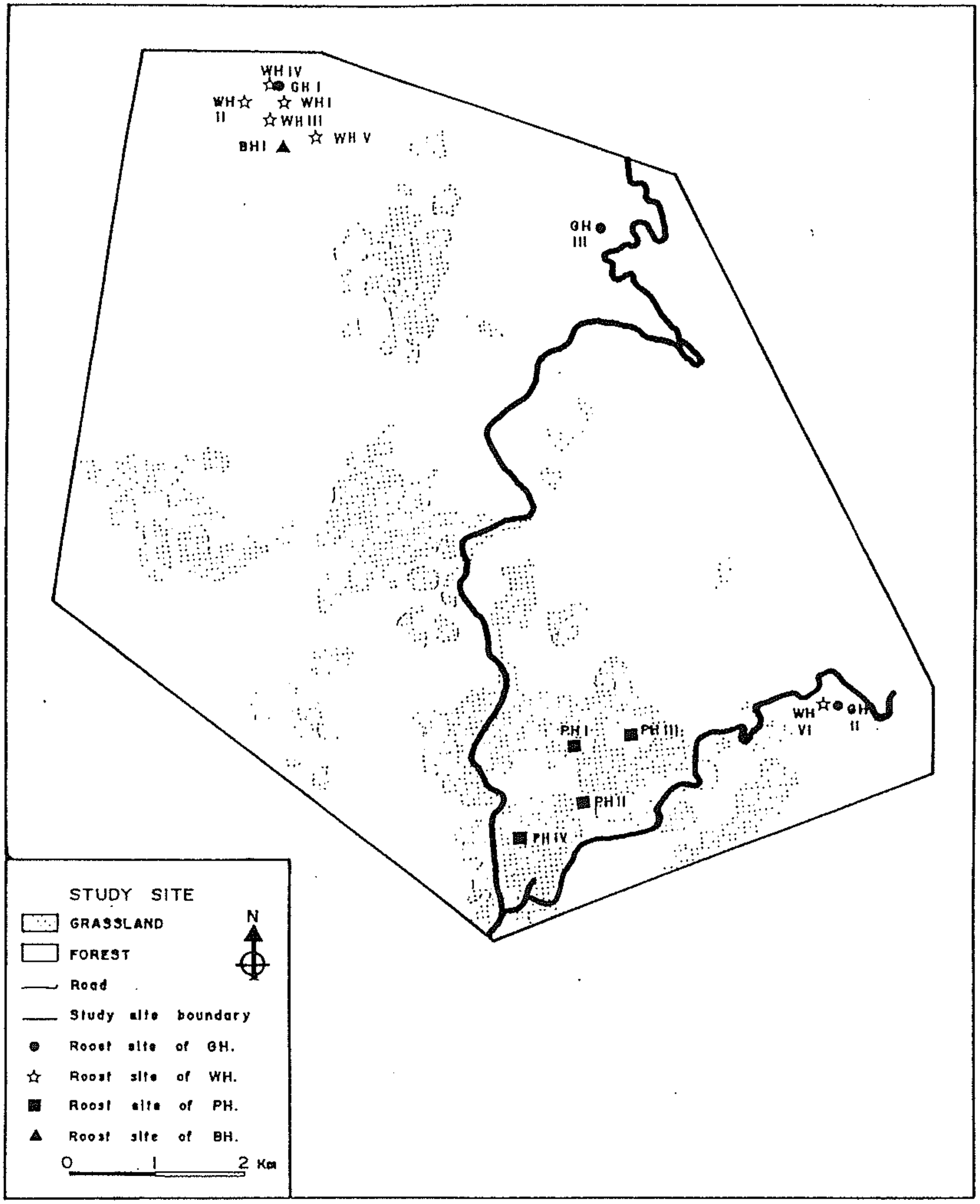


Fig. 8-1 Roosting sites of four hornbill species found in the study site at Khao Yai in the non-breeding seasons of 1981-1985 and 1988.

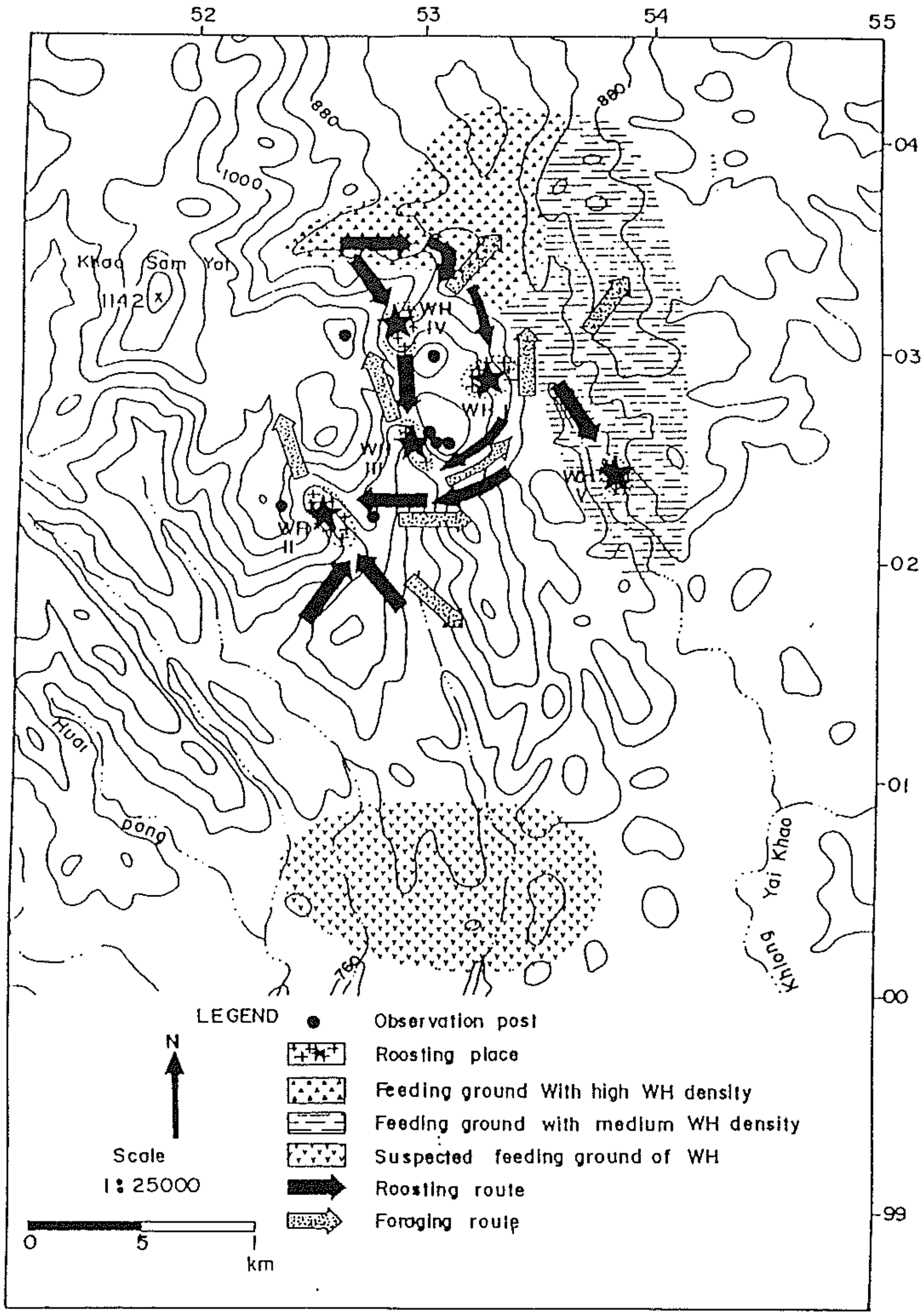


Fig. 8-2 Two major feeding sites and the routes between the feeding and roosting sites of Wreathed Hornbills in the northwest section of the study site at Khao Yai.

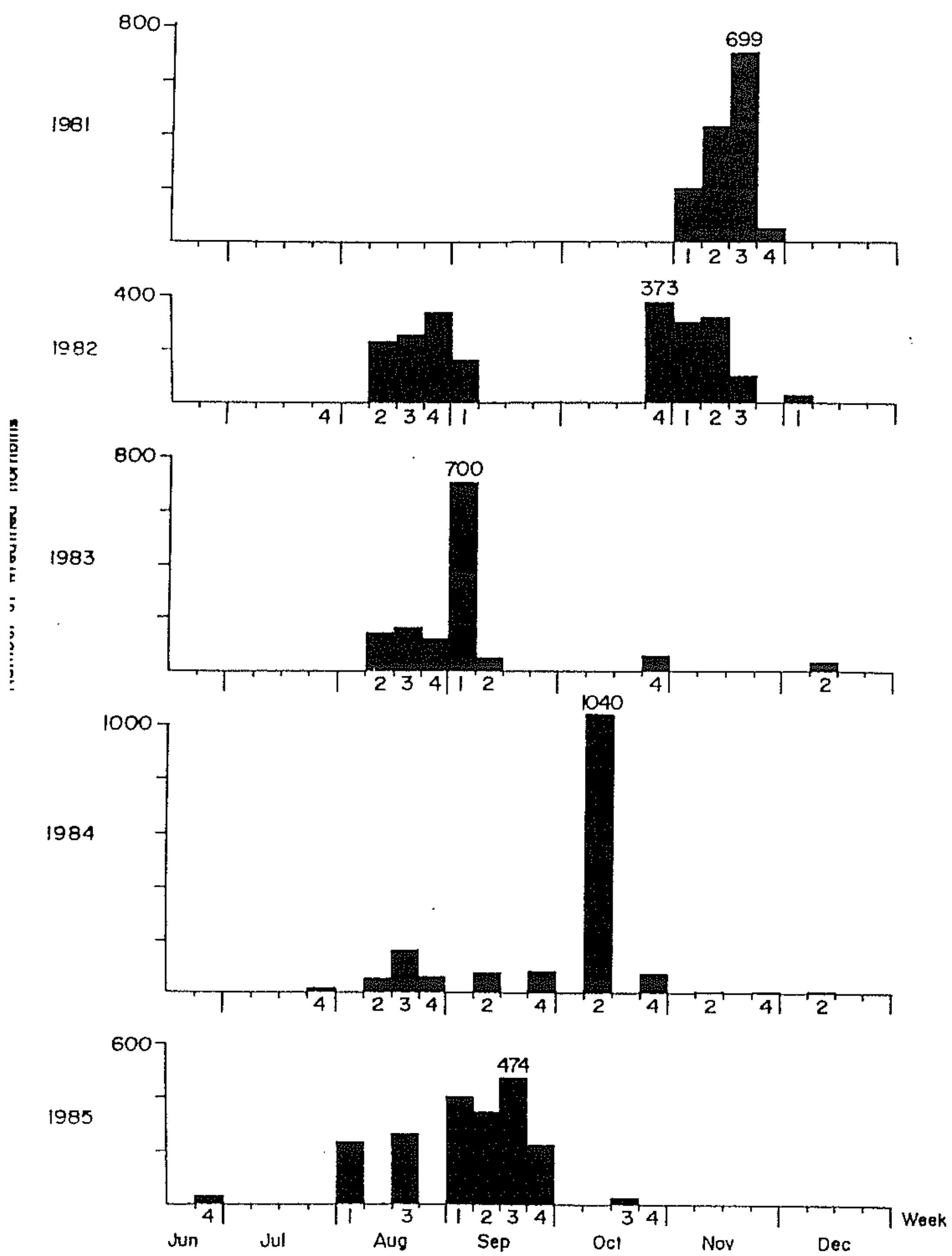


Fig. 8-3 Maximum number of individual Wreathed Hornbill in flocks in the non-breeding seasons observed from 1981 to 1985. The number 1,2,3 and 4 indicates the week that observations were made, otherwise there was no observation.

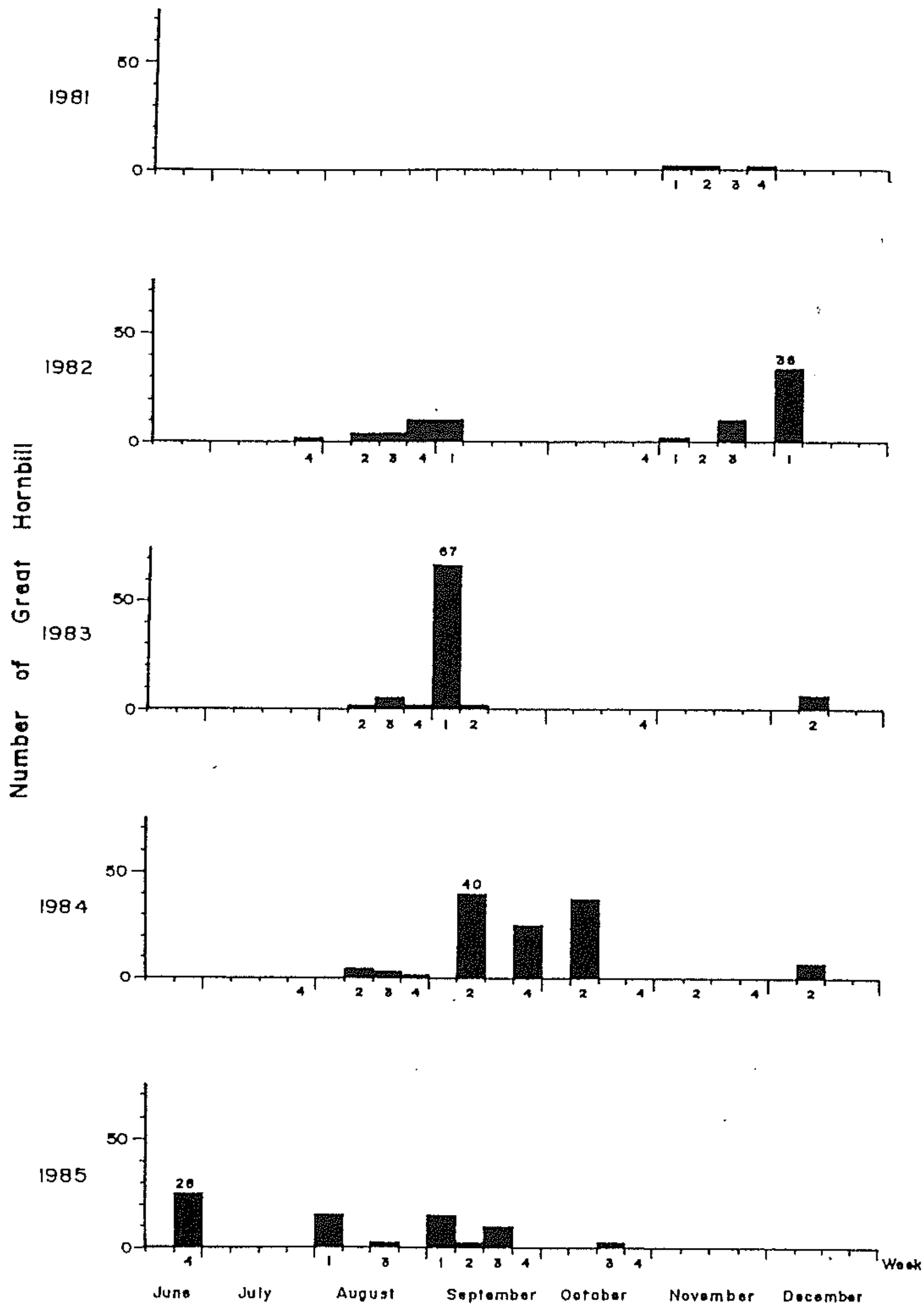


Fig. 8-4 Maximum number of individual Great Hornbill in flocks in the non-breeding seasons observed from 1981 and 1985. The number 1,2,3 and 4 indicates the week that observations were made, otherwise there was no observation.

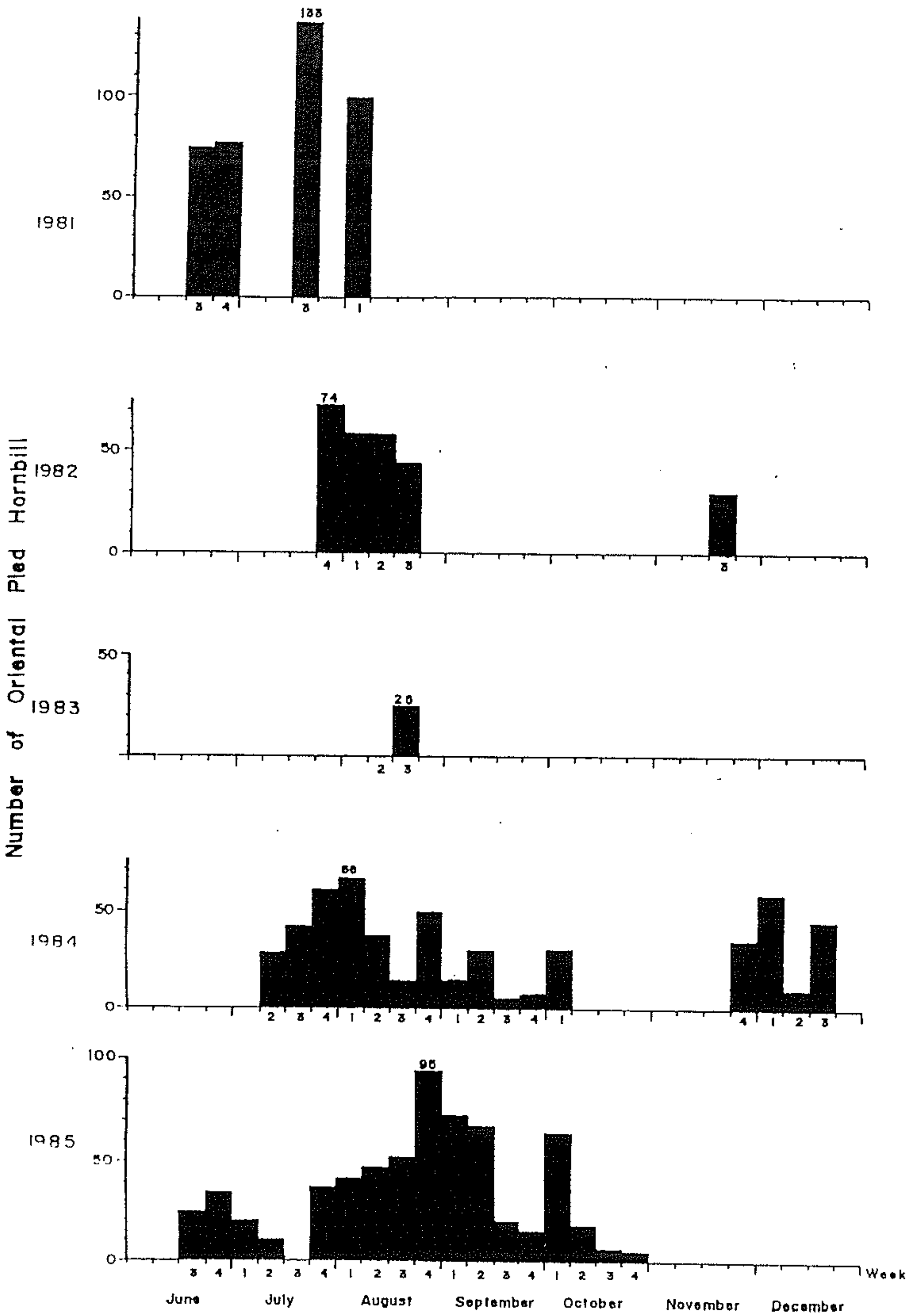


Fig. 8-5 Maximum number of individual Oriental Pied Hornbill in flocks in the non-breeding seasons observed from 1981 to 1985 around Golf Course area within the study site. The number 1,2,3, and 4 indicates the week that observations were made, otherwise

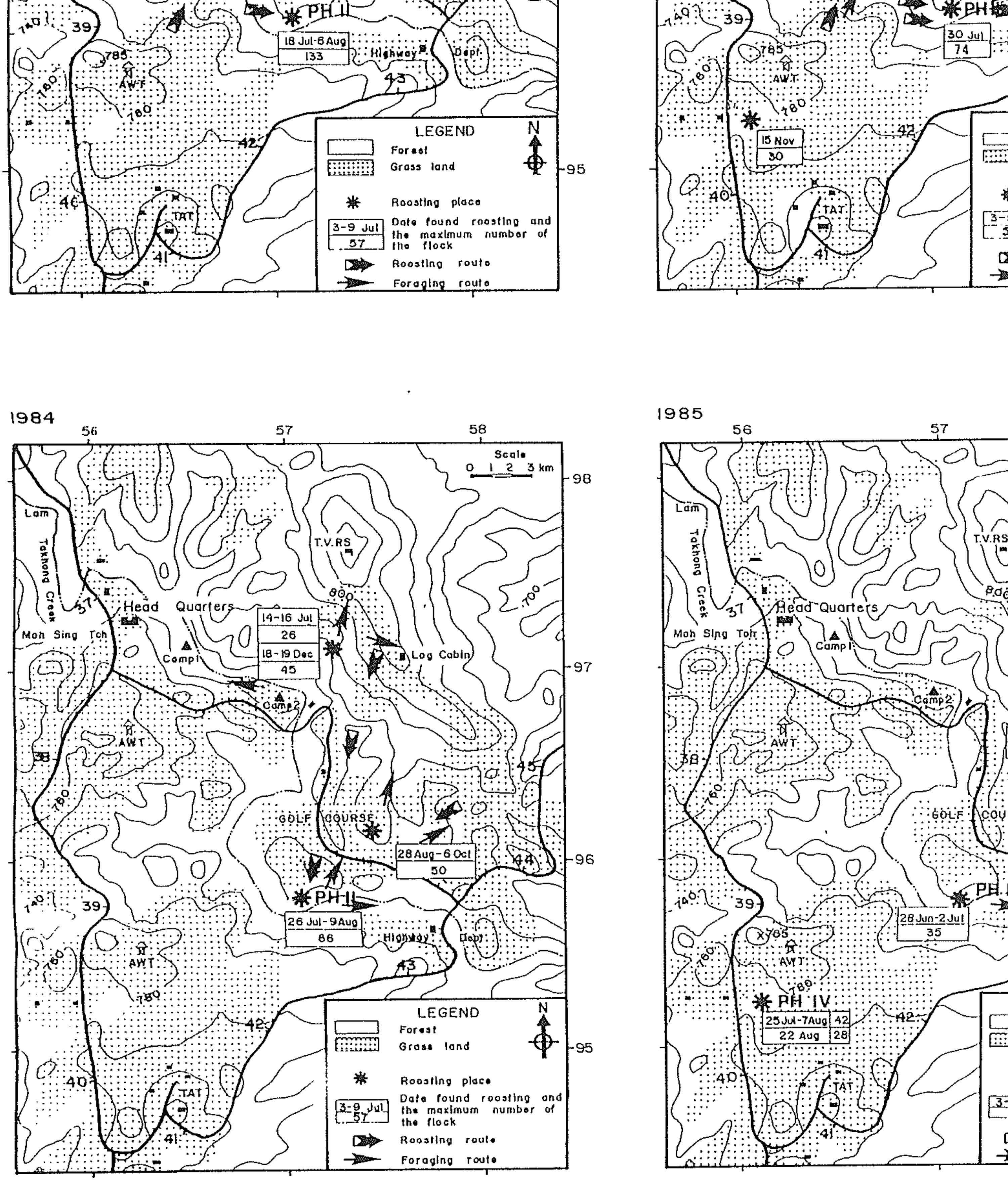


Fig. 8-6 Roosting sites of Oriental Pied Hornbill and the routes they to
in the non-breeding seasons observed from 1981 to 1985. Numb
indicates the maximum number of hornbills recorded to roost at th

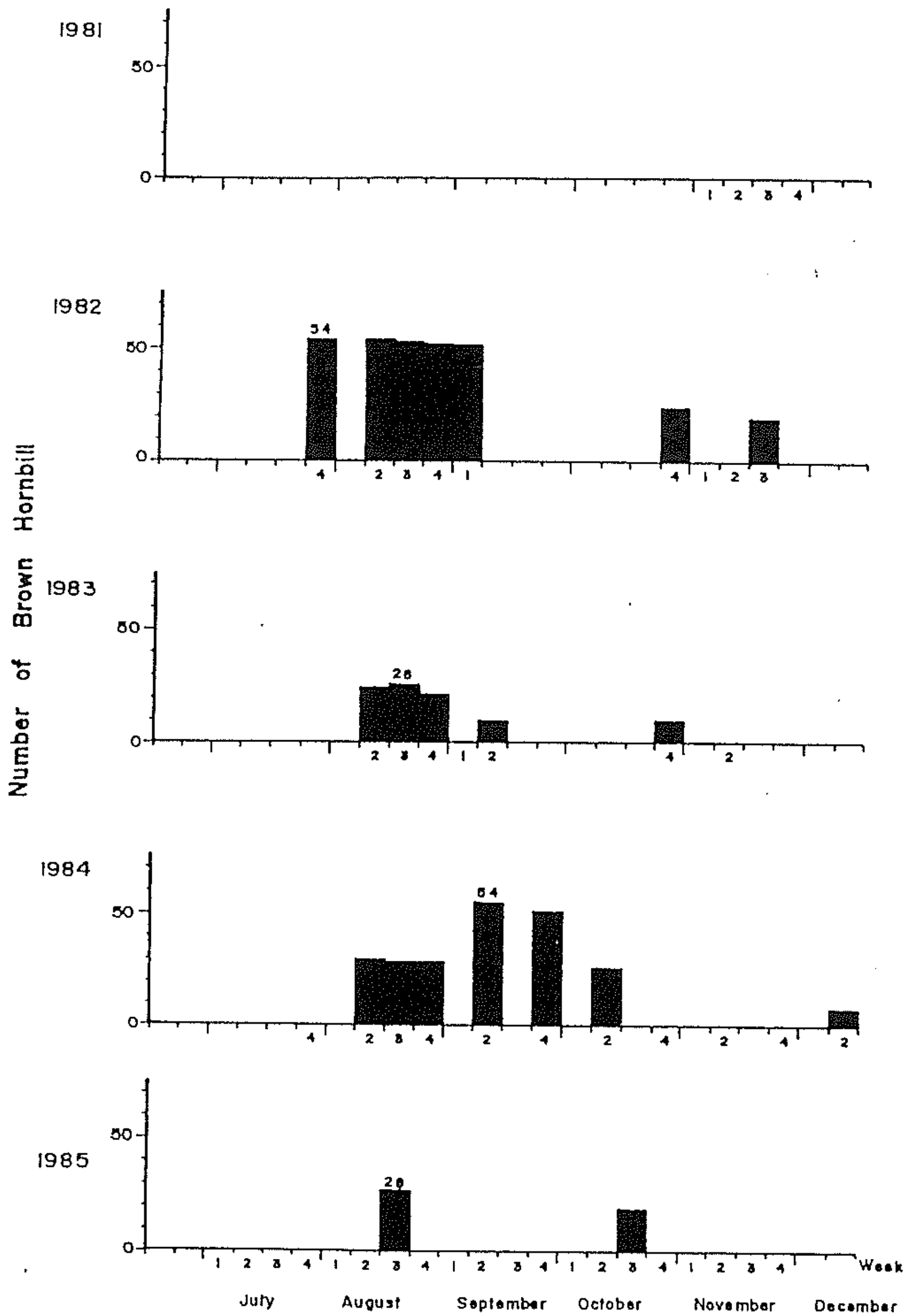


Fig. 8-7 Maximum number of individual Brown Hornbill flocks in the non-breeding seasons observed from 1981 to 1985. The number 1,2,3 and 4 indicates the week that observations were made, otherwise there was no observation.

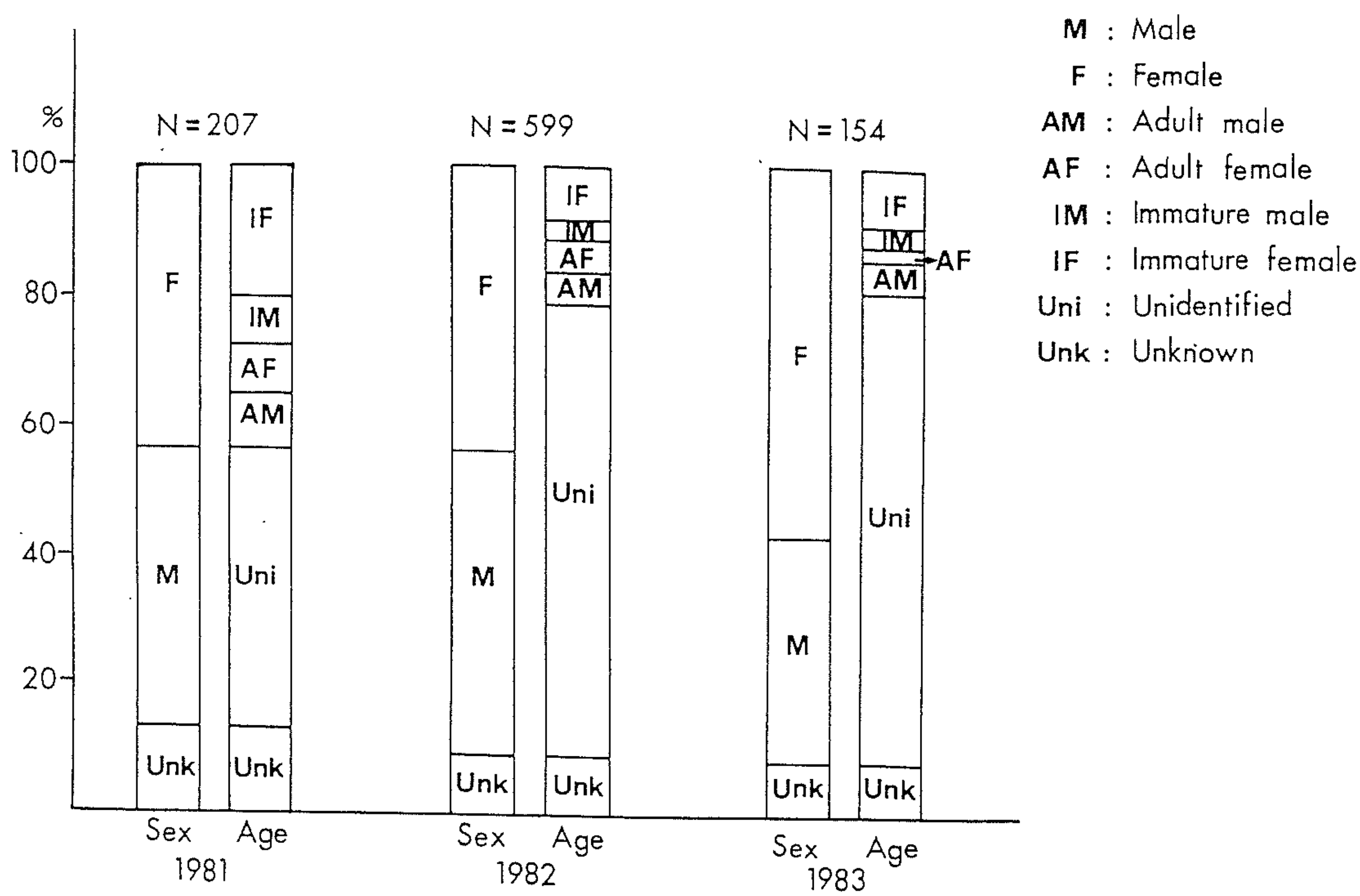
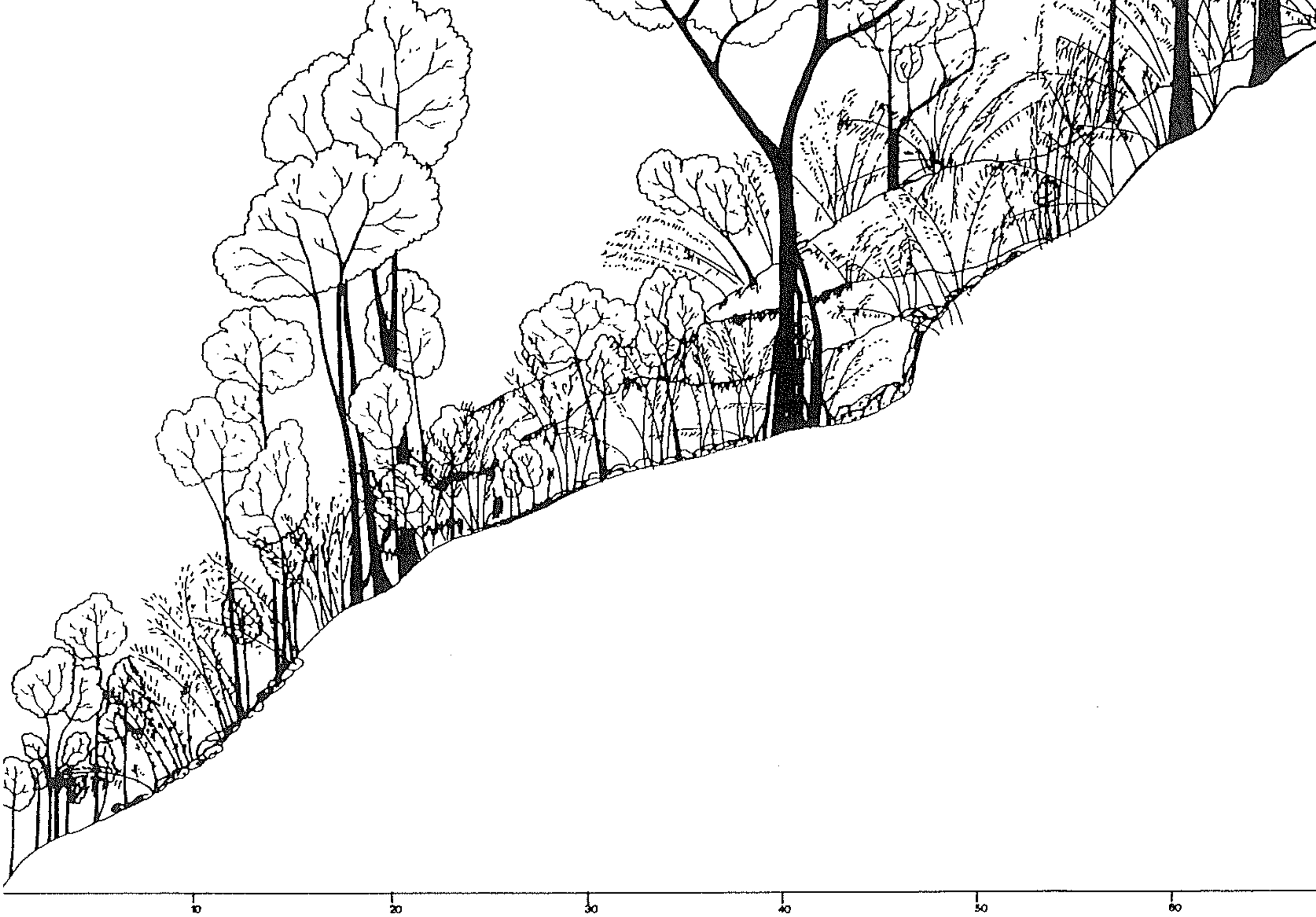


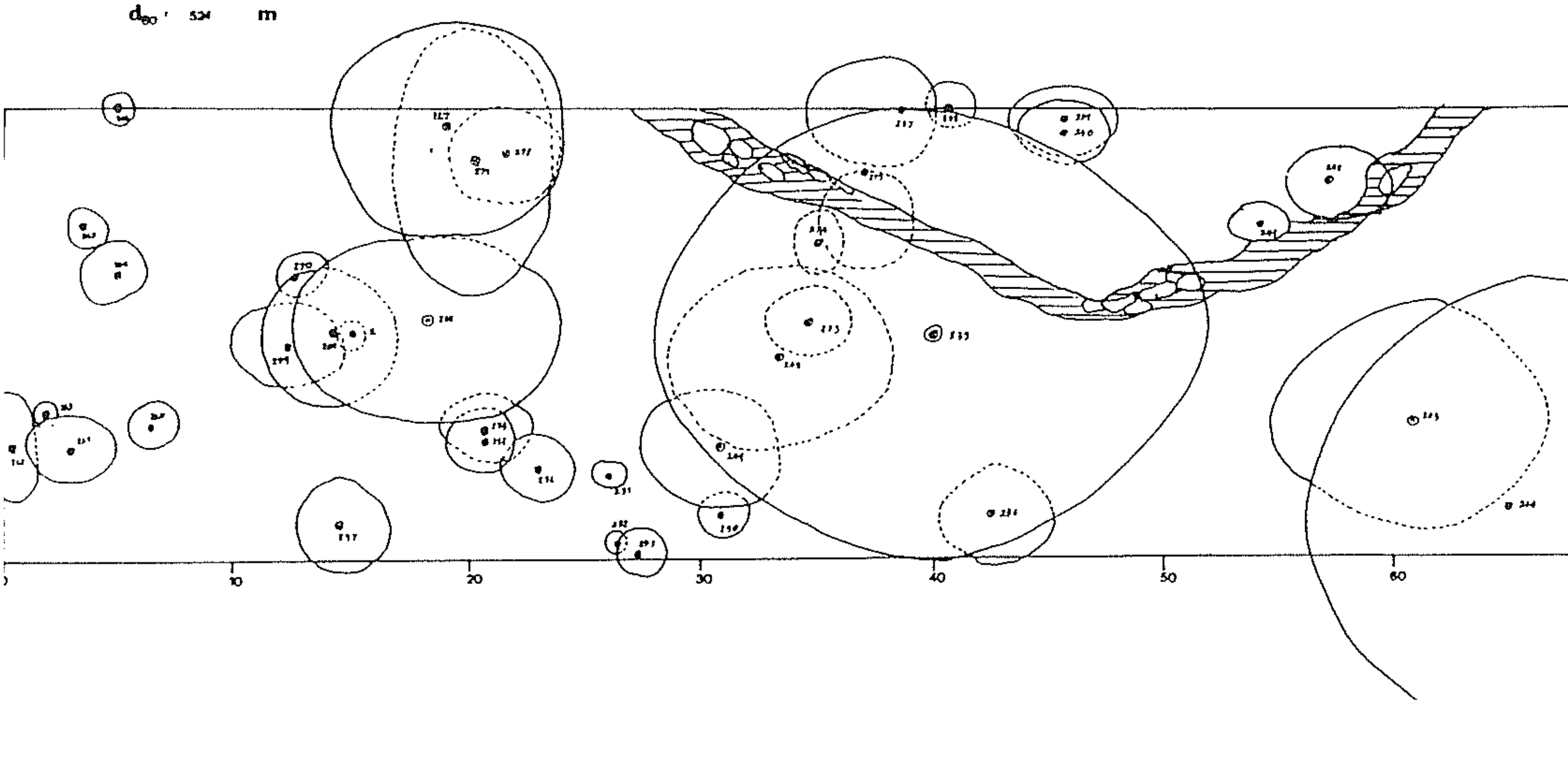
Fig. 8-9 Organization of flocks in Wreathed Hornbills observed between 1981 and 1983 non-breeding seasons.


Distance (m)
80
70
60
50
40
30
20
Altitude d_0 : 750 m
Altitude d_{80} : 760 m
80
70
60
50
40
30
20

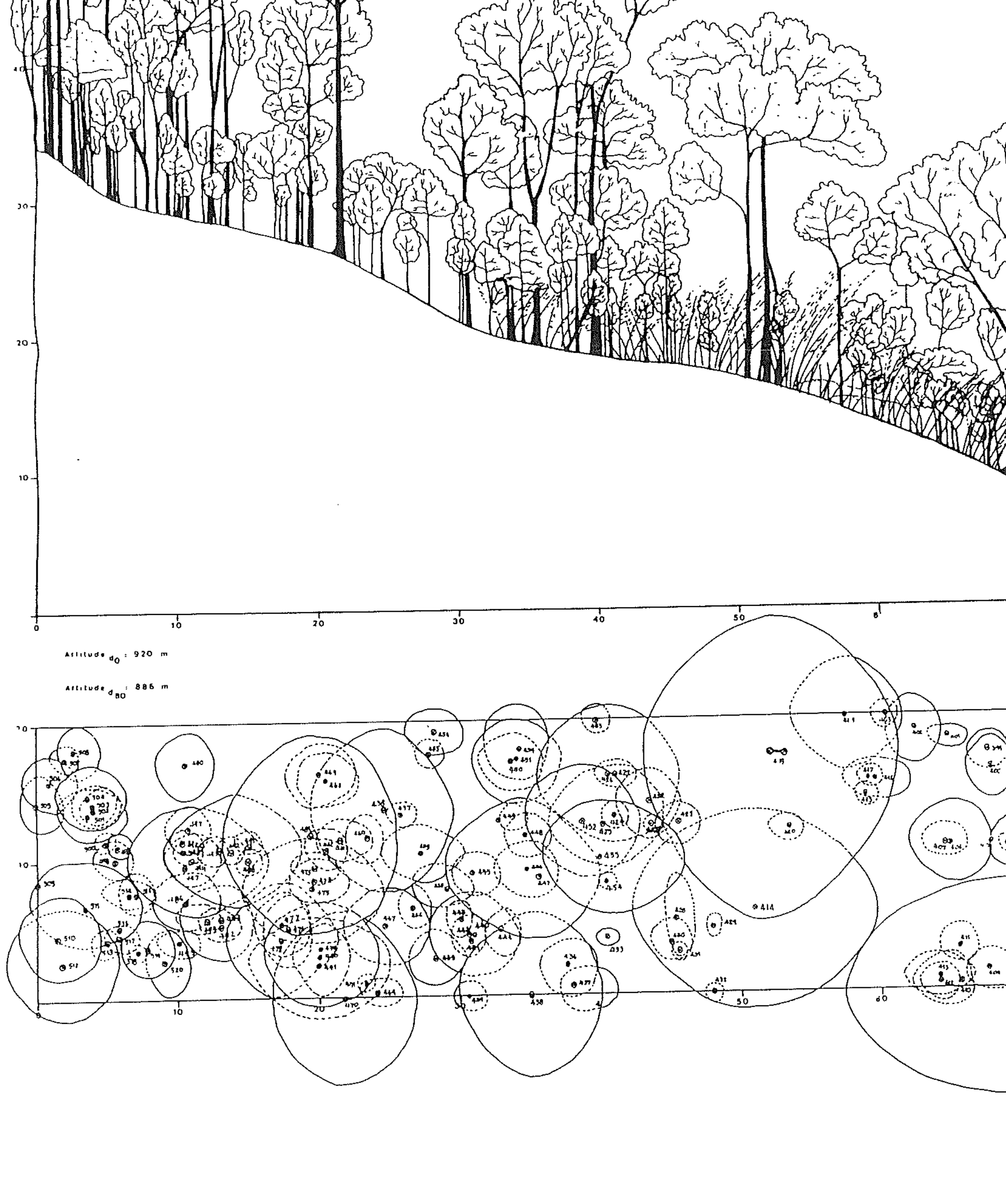


Elevation d_0 : 470 m

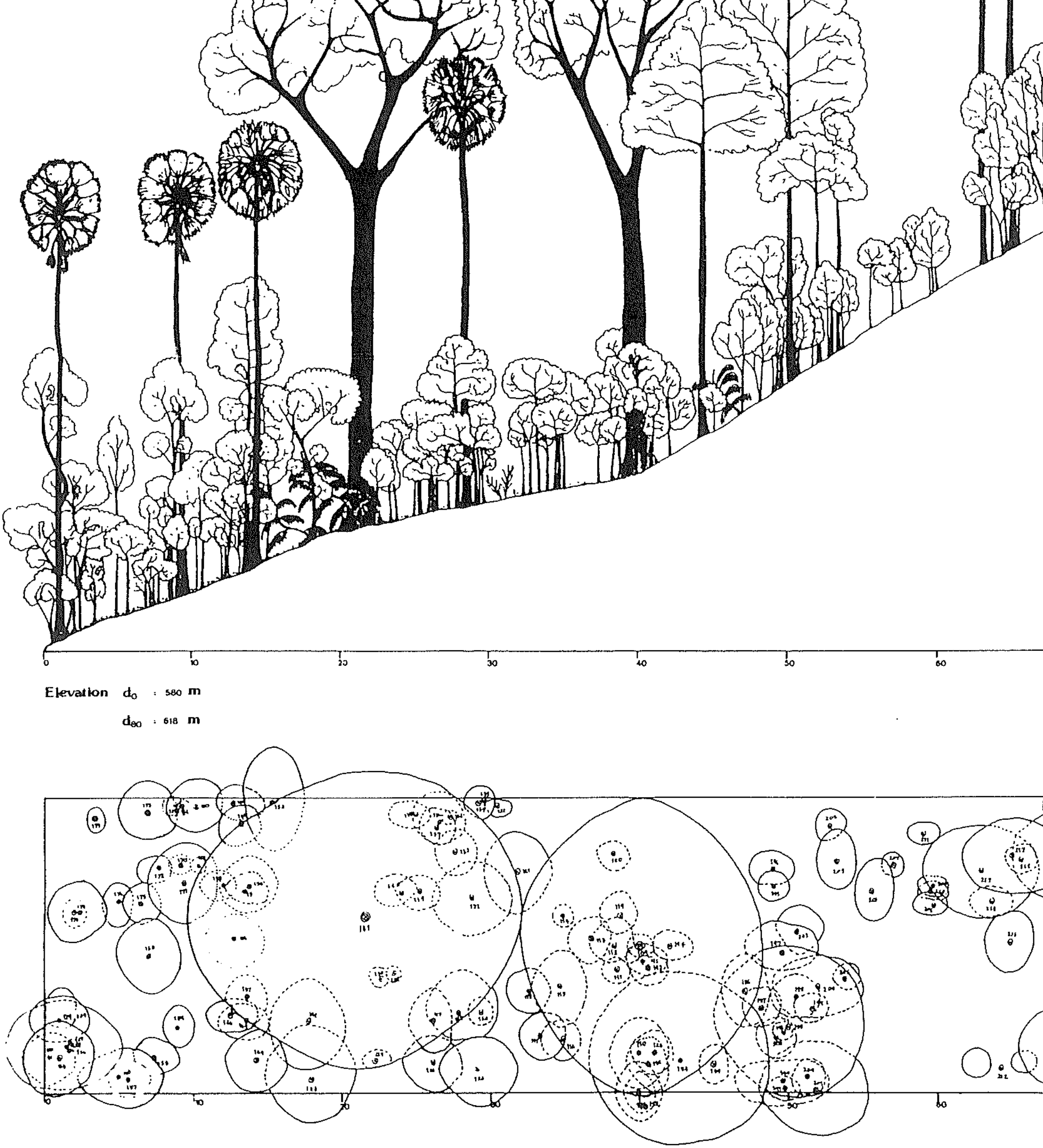
d_{60} : 524 m



Appendix 8-2 Profiles of forest at roosting sites of Wreathed Hornbill, WH IV (a) and WH VI (b).

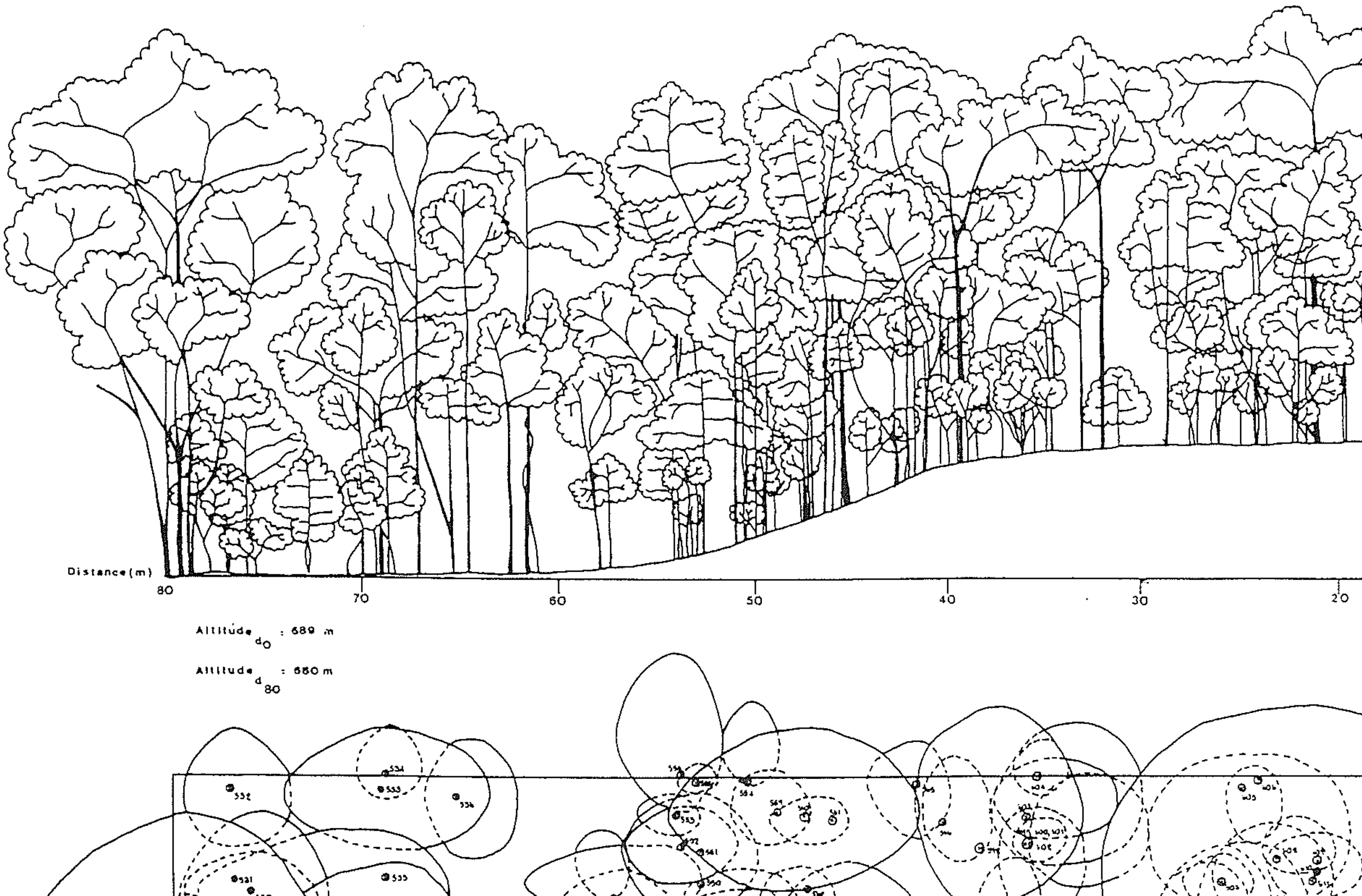


Altitude d_0 : 920 m
Altitude d_{80} : 886 m

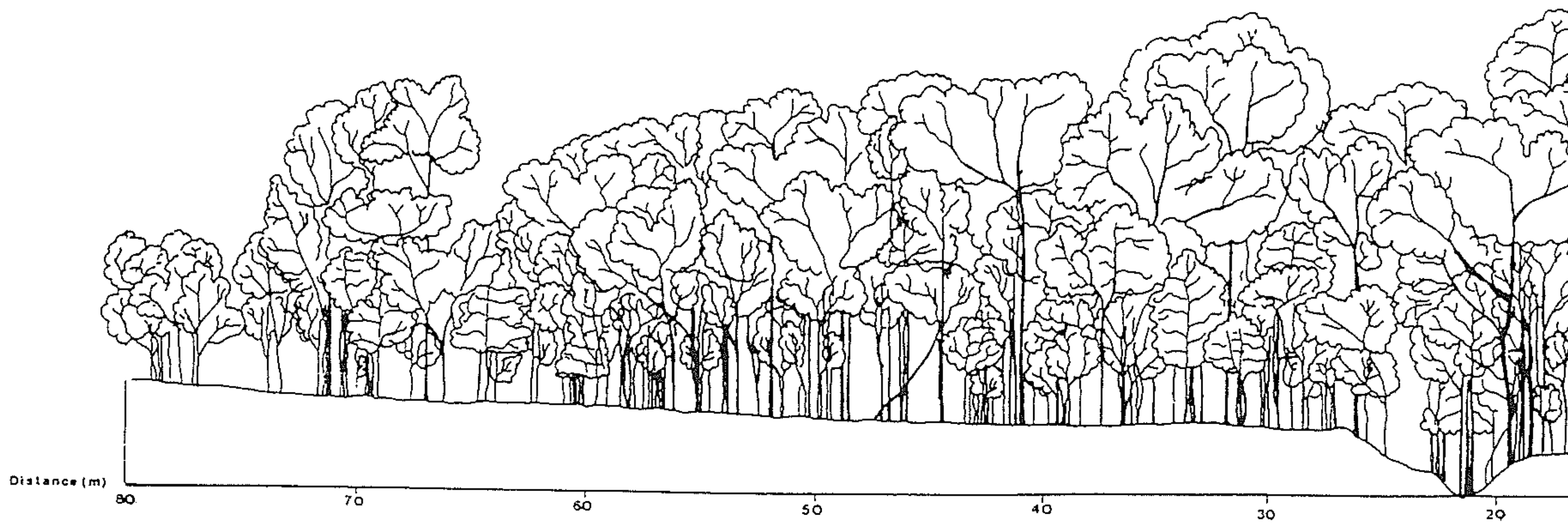

0
10
20
30
40
50
60
Elevation d_0 : 580 m
d_{80} : 618 m

Appendix 8-3 Profiles of forest at roosting sites of Oriental Pied Hornbill, PH II (a) and PH IV (b).

Appendix 8-3 PH II (a)

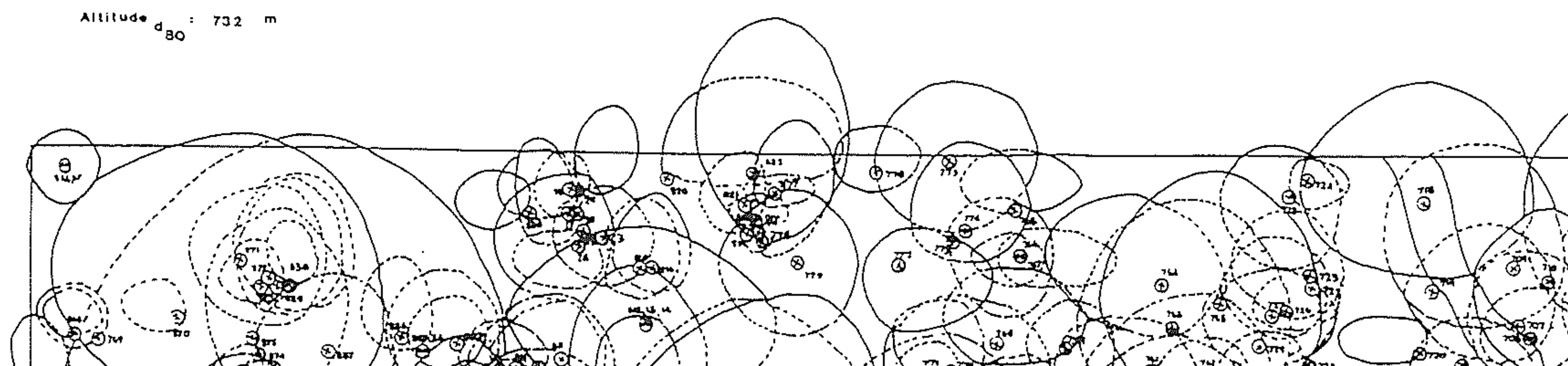


Appendix 8-3 PH IV (b)

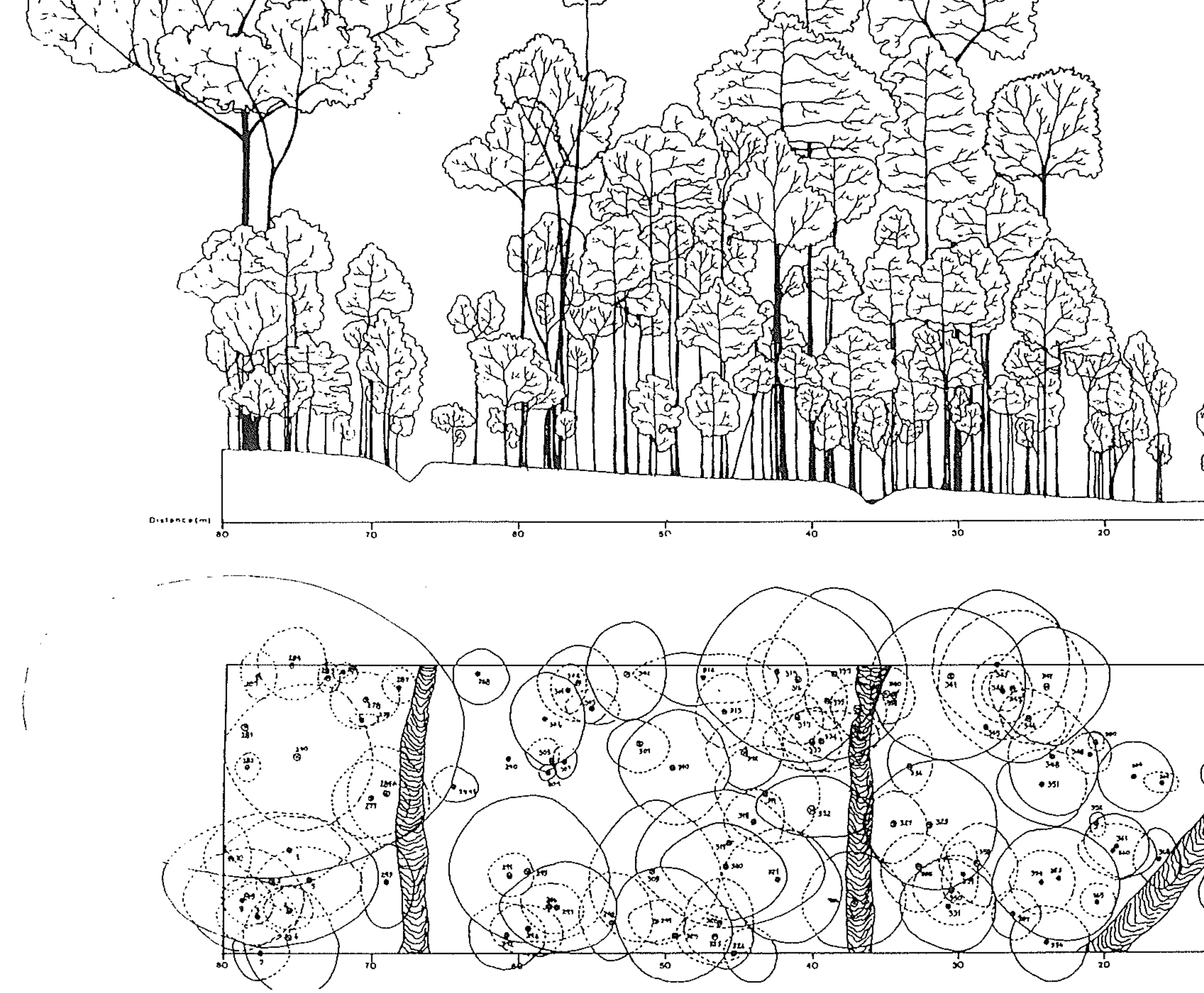


Altitude d_0 : 730 m

Altitude d_{80} : 732 m



Appendix 8-4 Profiles of forest at roosting sites of Brown Hornbill, BH I.


Distance(m)

CHAPTER 9

SUMMARY AND CONCLUSION

SUMMARY

The species of hornbills studied are; Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Rhyticeros undulatus*), Oriental Pied Hornbill (*Anthracoceros albirostris*), and Brown Hornbill (*Ptilolaemus tickelli*). The former two are large species, whereas the latter two are smaller ones. The three former species occur throughout the country, but Brown Hornbills are distributed in the north, and northwest, extending to the central-north in Thailand. The four hornbill species live in evergreen and mixed deciduous forests. The ranges of these four species dwindle due to forest habitat destruction.

Hornbills are well known for their unique nesting habit in such a way that females imprison themselves into natural tree cavities, leaving only a small space to accept the food from male mates. Because of their inability to excavate their own nest cavities, they use available and suitable natural cavities. They are also known as omnivorous birds. The study was conducted in a 70 km^2 area located in the northwest of Khao Yai National Park. The study site consisted of dry and wet evergreen forests and grassland. The altitudes range from 400 to 1,040 m a. s.l. The study was aimed at 1) nest characteristics, 2) breeding biology, 3) food and feeding, 4) home range and territory, and 5) flocking and roostinng

Nests

Nearly all hornbills nested in cavities in the trunks of living trees (78 out of 80 nests). These hornbill species nested in at least 13 different genera of trees, but 60% of the 80 nests found were in two genera, Dipterocarpus (34%) and Eugenia (26%), which comprised only 7% and 3% of all large trees respectively in 302 sample plots. Hornbills tended to prefer cavities high in large emergent trees for nesting, except for Brown Hornbills which preferred nest cavities within or below the main forest canopy (15-25 m high). Most nest sites were between 700 and 800 m.a.s.l (79% of a total of 80 nests). Nests of Brown Hornbill were located at altitudes significantly higher than those of Oriental Pied Hornbills. Hornbill tended to select nest site in forest strata according to their body sizes. Statistical tests showed that the larger species preferred to nest in the middle and top layers, whereas the smaller ones nested in the middle and low layers. These evidences may show avoidance of competition for nest sites between two sizes of hornbills. Hornbills tended to select nest entrances according to their body size. All four hornbill species used oval to elongated nest entrances, with Great Hornbills preferred the most elongated entrances. Hornbills did not select a specific nest entrance orientation. Since the breeding of hornbills entirely depends on the availability of nest cavities, thus, the causes of nest losses were studied. It was found that the most important cause was natural breakage of trees (53.8% of total 26 lost nests).

Breeding

Hornbills breed once a year during dry season. The breeding began in dry month (January and February). The trigger for the onset of breeding is believed to be drought after rainy season. At early stage of the breeding , intra- and interspecific competitions for nest cavity were relatively high (45.5% of 66 nests observed). As a result, 53.3% of competed nests were abandoned. Intraspecific interaction was more vigorous than interspecific one. The larger species, in particular may avoid intraspecific interaction by nesting far from each other. Duration of different phases in the breeding cycle was studied. The entire breeding cycle on average took 122.0 days for Great, 129.3 days for Wreathed, 82.9 days for Oriental Pied, and 92.8 days for Brown hornbills. The diferrences in the lengh of the breeding cycle related to bird size, number of chicks raised and type of parental care.

The ratio of breeding success was highest in Oriental Pied (0.91) and lowest in Wreathed (0.78) hornbills. The number of chick produced was only one in the two larger species, but 1.5 and 2.6 on average in the Oriental Pied and Brown hornbills, respectively.

Three types of parental care were observed in the breeding behaviour of the four hornbill species. Father care type was observed in Wreathed and Oriental Pied hornbills, in which only the breeding males fed females and broods throughout the breeding cycle. Biparental-care was observed in Great Hornbills, in which females emerged after the chick hatched to help the males in feeding the chick. Cooperative care was observed in Brown Hornbills; breeding males having male helpers of various ages that help in feeding and caring female mates and broods.

Cooperative breeding

Cooperative breeding was observed in Brown Hornbill. The breeding males had other males, 1-5 individuals of various ages, as nest helpers. The number of the nest helpers significantly increased in accordance with the progress in the breeding cycle. The roles of helpers were clear in the breeding season and involved feeding, chick raising, and nest territory defence, feeding being most important. It was also found that nests with high number of nest helpers tended to fledge more chicks. These nest helpers were assumed to be offspring or sibling of breeding pairs. With cooperative care type, the breeding pairs could raise 1-3 chicks or 2.6 chicks on average. Of those pairs without helpers (7 pairs), only 3 pairs were successful in breeding with unknown number of chicks.

Food and feeding

Hornbills are known as omnivorous. Food of four hornbill species could be divided into fruits and animals and the former included figs and non-fig. The proportions of different food consumed by hornbills varied from species to species. Great consumed 53.7 % fig, 33.5 % non-fig and 12.8 % animals of total food, Wreathed 48.0 % fig, 44.6 % non-fig and 7.5 % animal, Oriental Pied 32.7 % fig 47.3 non-fig, and 20.0 % and Brown consumed 24.8 % fig, 34 non-fig, and 41.5 % animal. Thus Wreathed Hornbills were most frugivorous, whereas the Brown Hornbills were most carnivorous. The nature of fruits eaten by hornbills were grouped into fruit with freshy pulp and fine seed (figs), split-husked fruit when ripening, dry fleshy with single stone seed, fleshy and soft or juicy fruit with single stone seed.

The four hornbill species consumed relatively similar food. The male and female Great Hornbills while sharing duty in feeding the nestling, and the breeding male Brown Hornbills and nest helpers showed high similarity of food brought to broods (C = 0.83, 0.93, respectively).

Food preference was determined and it was found that hornbills feed more on fruits which are abundant rather than on fruits with high nutritional value. Aside from figs, among the first 13 ranks of non-fig species, Polyalthia viridis, strombosia spp., and Horsfieldia glabra were the most preferred by all four hornbill species. Among animal foods, centipedes and cicadas were most preferred.

The feeding rate of animal food was significantly high after chick hatched in all four hornbill species, thereby confirming the requirement of animal food by chicks. After chick hatching only Oriental Pied Hornbills showed significant increase in feeding fruit, but opositely, Great

Hornbills sifnificantly decreased in feeding fruit.

The four hornbill species live sympatrically, and they may avoid competitive interaction by foraging at different levels above the ground. The two larger species, particularly Wreathed Hornbills, foraged at significantly higher level than the smaller one. They were also active in feeding at different time during the day. Great Hornbills were observed to be active rather early in the morning between 6:00 and 7:00 am, but Brown Hornbills were late in the afternoon between 15:00 and 16:00.

Home range and territory

Ranges of individual males of Great, Wreathed and Brown hornbills were determined by radio telemetry during the breeding and non-breeding seasons. In the breeding season, the range of Great Hornbills was 3.7 km^2, similar to that of Brown Hornbill (4.3 km^2). On the other hand, Wreathed Hornbill occupied the largest home range (10.0 km^2). In the non-breeding season, the range of Wreathed Hornbills (28.0 km^2) was also greater than that of the Great Hornbill (14.7 km^2). Differences in range sizes of different species may be related to differences in diet and parental care strategy. Ranges were found overlapped within and between the species.

The four hornbill species were observed to defend only around nest sites as their territory. However Great Hornbills had a largest territorial area (0.69 ha) on average. This may be due to the large body size, as well as to biparental care, of this species as the chick was left alone in the nest. The territory defensive behaviours included loud call, flying display, plucking branches and cracking of tree bark.

Flocking and roosting

This study showed that Wreathed Hornbills were the most gregarious species in the non-breeding season and gathered into the biggest flocks with a maximum number of 1,040 individuals in 1984. In contrast, Brown Hornbills gathered in smaller flocks with a maximum number of 54 individuals in 1983, althoug this species flocks throughout the year. During the non-breeding season, Wreathed Hornbills seemed to use the same roosting sites more regularly than Great and Oriental Pied hornbills do. In the breeding season, roosting sites of a breeding male Wreathed Hornbill was erratic as compared with a male Brown Hornbill which spent longer time at each roosting site.

Characteristics of roosting sites of the four hornbill species were studied. It was found that Wreathed Hornbills apparently preferred to roost in a primary forest with great slope. In contrast, Oriental Pied Hornbills preferred to roost in low and dense vegetation along the forest edge on flat terrain.

CONCLUSION

The survival of these four sympatric hornbills clearly depends on the condition of the forest habitat, within where vital factors which affect survival and breeding of these birds are available. These factors can be listed in priority as (1) availability of suitable tree cavity for nesting, (2) abundance and diversity of food, (3) presence of competitors for nest cavity and food resources, and (4) presence of predators.

It is no doubt the competition for nesting among these four sympatric hornbill species is intense. In order to reduce the competition, at least partially, they select nest sites at different altitudes or at different height in forest strata within the same geographical area. As consequences, there are ample circumstantial evidences which suggest that the four hornbill species adapt themselves to forage in different niches, feed on different composition of food, and roost in different vegetation types and terrains. Moreover, the three parental care type behaviours may be interpreted as the adaptation of the hornbills to cope with limited resources, such as nest sites, or food source in order to obtain highest potential of the survival of the species that live sympatrically.

These hornbills are an important indicator of the forest condition. They also serve as " key stone species" by their obvious roles as seed dipersers and as predators. For long-term survival of these birds, one must seriously consider to preserve the good intact primary forest of large area, suggesting minimum area of 1,800 km^2, for a viable population.

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