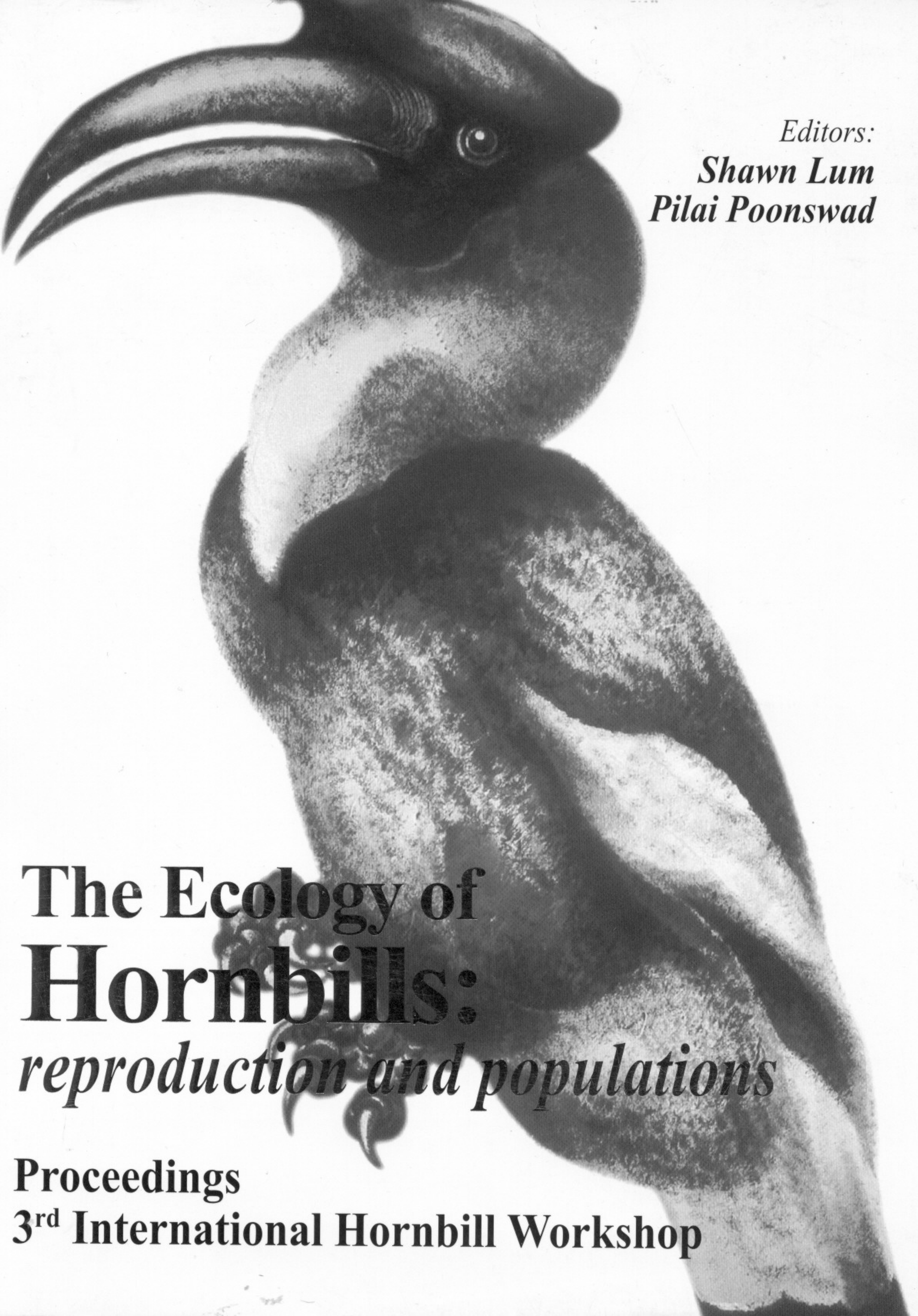

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The Ecology of Hornbills:

reproduction and populations

Proceedings

3rd International Hornbill Workshop

Proceedings

The Third International Hornbill Workshop

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PREFACE

Hornbills invite superlatives. Whether they are described as "majestic", "fascinating", "ecologically important", or more technically as "keystone species", hornbills (family Bucerotidae) are recognized for their unmistakable, eye-catching looks, their intriguing life histories, or for the prominent ecological roles that they play. Therefore it may seem surprising that the first time hornbill researchers gathered to share their research findings was not until 1992, at the 1st International Asian Hornbill Workshop held in Bangkok, Thailand. The focus for initial Workshop was to understand the distribution and status of Asian hornbill species. It was felt at the time that such fundamental information was of primary importance in understanding and conserving hornbills. The inaugural Asian Hornbill Workshop and its associated technical workshop conducted at Khao Yai National Park, was deemed to have been enough of a success to warrant a second gathering, which also took place in Bangkok, in 1996. The 2nd International Asian Hornbill Workshop, like its predecessor, focused on Asian hornbill species, but this time the emphasis was on the ecology and conservation of these species.

The 3rd International Hornbill Workshop, as the name suggests, was not as geographically specific as its two forerunners, and featured for the first time participants who specialized in the study of African as well as Asian hornbill species. The broad objectives of the 3rd International Hornbill Workshop, held in Phuket, Thailand in 2001, were to bring together researchers from all parts of the world to share their research experiences and their expertise, to provide a forum for discussing the conservation of hornbills and their habitats, and to serve as a platform from which to identify various "need" areas in hornbill research and conservation.

Over 155 participants from 17 countries took part in the 3rd International Hornbill Workshop (a summary table of participating countries from the 1st to the 3rd Hornbill Workshops is appended at the back of these Proceedings; see Appendix I). Presentations ranged from topics as diverse as the captive breeding of hornbills to long-term studies of hornbill nesting patterns, from surveys of hornbills in various countries, to the feeding ecology of hornbills and other species that share similar food resources with them, and a bit of everything else that currently occupies the hornbill research community. What emerged from the Workshop was both encouraging and worrying.

The Workshop featured posters and presentations not only from senior researchers who pioneered the study of hornbill biology and systematics, but graduate students and others poised to lead the field in years to come. The enthusiasm and passion for hornbill ecology and conservation displayed by Workshop participants was undeniable, and is a reassuring sign for future vigor and creativity in hornbill research. Moreover, there was a balanced representation of participants from traditional centers of ecological and taxonomic study in North America, Europe, and Japan – as well as those from countries in Asia and Africa where hornbills occur. A number of leading hornbill research groups appear to be based at local universities and research institutes in Asia and Africa. This healthy mix of local and foreign-based researchers is certainly a good omen for vitality in hornbill studies in the years ahead. Finally, all Workshop participants, whatever their particular area of research, were also deeply concerned with the conservation of hornbills and their habitats. Discussions both formal and informal often centered on how best to raise awareness for the plight of these magnificent birds and the need to conserve the ecosystems of which they are a part.

The 3rd International Hornbill Workshop also highlighted how much more remains to be done to understand the status, the life histories, and the conservation of Asian and African hornbills. For example, although certain geographic regions appeared to be well represented at the Workshop, there were some critical areas that seem to be in need of more careful study. While there were reports on hornbills in countries and regions such as India, Sri Lanka, Thailand, a few Philippine islands, and parts of Borneo and Sumatra, sizeable sections where hornbills occur were not covered by Workshop presenters. Examples included vast portions of Indonesia, New Guinea, the Philippines, and other countries in Southeast Asia. Alan Kemp notes in his paper in these Proceedings that in Africa, the least attention has been paid thus far to hornbill species inhabiting the lowland tropical rainforests of West Africa. These gaps in geographic coverage at the Workshop may of course be due to the fact that researchers based in these regions were not among the Workshop participants, but this lack of information may nonetheless be a cause for concern.

Given the susceptibility of large animals to habitat disturbance, hornbills might be expected to be among the animals particularly vulnerable to habitat loss and disturbance. As forest hornbills are dependent on the presence of large trees with suitably large potential nesting cavities, forest loss and fragmentation has a doubly large impact on hornbills. Not surprisingly, there were reports at the 3rd International Hornbill Workshop on the critical status of hornbill species from a few study sites. However, aside from a detailed exposition on two rare Philippine hornbill species by Eberhard Curio (see Part I), no other updates on the state of locally and globally endangered hornbill species were presented at the Workshop. Although the 1st International Asian Hornbill Workshop was devoted to generating baseline data on the distribution and status of hornbill species, follow-up studies and close monitoring of threatened hornbill species appear to be limited. More detailed and current information was needed on the status and ecology of threatened hornbill species, in the opinion of Workshop participants.

A few areas of research, such as the population genetics of hornbills, were still in their fledgling stages at the 3rd International Hornbill Workshop. It is a matter of time before new methods and techniques enter the mainstream of hornbill study, but perhaps the challenge facing researchers will be to transfer these methodologies to colleagues in countries lacking the financial resources to carry out such studies. This highlights a more general issue, that of enabling and empowering hornbill researchers everywhere.

It was evident from the presentations that a few countries had very active research groups, both locally based and from institutions outside the area of study. Thailand and South Africa, for example, have vibrant long-term wildlife research programs, which includes hornbill studies. Hornbill research is gaining momentum in India, among other places, and there have been intensive hornbill studies carried out in parts of Indonesia, such as in Sulawesi by Margaret Kinnaird and Tim O'Brien. Many countries, unfortunately, lack the resources, experience and technical expertise to adequately carry out work on hornbills. The first two International Asian Hornbill Workshops attempted to address this with post-conference technical workshops. Skills taught included observing and recording hornbill feeding behavior and radiotelemetry techniques for home-range monitoring, including hornbill trapping, tagging and tracking. However, the gulf between the larger research groups and those of some countries is still considerable. As in many other areas of scientific research, the lack of technical, financial, and manpower resources remains an impediment to expanding hornbill research and conservation efforts. Needless to say, this remains a key issue, one that begs for a solution.

The participants of the 3rd International Hornbill Workshop left Thailand in anticipation of future collaborations, more information on hornbills, and with a greater commitment to reach out to the public and policy makers for the need to conserve vital hornbill habitat in the years ahead. The organizers and participants hoped that the 4th International Hornbill Workshop would represent another step forward in the status of hornbill research and protection.

The Proceedings of the 3rd International Hornbill Workshop are divided into four sections, with papers in each group following a general theme. These are: Part I, Breeding Biology; Part II, Food and Feeding Ecology; Part III, Hornbill Surveys, and Part IV, Hornbill Conservation. The Editors have commented briefly on the papers at the introduction to each of the four sections. The manuscripts have been edited to the best of our abilities but were not submitted for peer-review.

These Proceedings represent most, but not all, of the presentations of the 3rd International Hornbill Workshop. However, all participants are listed at the back of this volume for those interested in a more complete picture of the Workshop (see Appendix 2) A number of the papers presented at the Workshop were published by Birdlife Conservation International in 2004. A handful of papers could not be included in the Proceedings because they were published elsewhere or were not complete at the time this volume went to press. References to the papers that were based on presentations delivered at the 3rd International Hornbill Workshop but were published outside of these Proceedings are listed at the back of this book as well (see Appendix 3).

We wish to thank all of the participants of the 3rd International Hornbill Workshop for a week of inspired sharing, for their continued camaraderie, and for their commitment to the greater understanding and conservation of hornbills. We also thank all of those who so generously gave of their time to assist us at the 3rd International Hornbill Workshop. They include His Excellency A. Senanarong, Mr. S. Osathanugrah, Ms. D. Armstrong, Dr. W. Arthayukti, Mr. B. Bencharongkul, Dr. P. Bandisak, Mr. L. Bunnag, Ms. R. Chantian, Dr. P. Chatikavanij, Ms. Chong Pik Wah, Dr. P. Damrongphol, M.L. T. Devakul, Mr. S. Hayeemuida, Dr. P. Inprakhon, Ms. T. Lelanuta, Ms. B. Kanchanasaka, Mr. N. Kongpien, Ms. Ng Bee Choo, Dr. W. Noonpakdee, Mr. T. Nooyim, Ms. M. Nualcharoen, Dr. P. Ratanakorn, Mr. M. Read, Mr. P. Round, Ms. S. Senma, Ms. W. Simaroj, Dr. S. Sophasan, Mr. M. Strange, Mr. S. Sunprasit, Ms. S. Thong-Aree, Ms. Tai Ping Ling, Mr. U. Treesucon, Dr. P. Vasaputi, Mr. A. Vidhidharm, staff of Thailand Hornbill Project, staff of Rajaphat Institute Phuket, Faculty of Science, Mahidol University, Royal Forest Department and Bird Conservation Society of Thailand. No superlatives can do justice to the respect we have for our colleagues, nor can they adequately describe their dedication and vision.

Shawn Lum
Pilai Poonswad

PART I: BREEDING BIOLOGY

PART I: INTRODUCTION

Hornbills are well-known, at least among those with an interest in wildlife, for their unique nesting behavior. The tendency for the female hornbill to be sealed inside her nesting cavity by a mud wall has gone beyond the realm of biology and into the realm of general knowledge. Given the widespread fascination with this aspect of hornbill natural history, one might think that the breeding biology of hornbills would be a vastly oversaturated corner of avian ecology.

The papers presented at the 3rd International Hornbill Workshop focusing on the breeding biology of hornbills were thoroughly conducted and broad in scope, but they confirmed that the field is far from reaching saturation point. Six presentations from the Workshop are included in this section of the Proceedings, three based on studies conducted in the wild, and another three that deal with the captive breeding of hornbills.

Curio presents work detailing what is known about two endangered Philippine hornbill species, the endangered Visayan Tarictic Hornbill (*Penelopides panini panini*) and the even more critically endangered Writhed-billed Hornbill (*Aceros waldeni*). He considers the dietary requirements of these two species, as well as any potential competition between them and also competition between the hornbill species with fruit bats. The situation is a complex one, as might be expected. Given the endangered status of these two species, such detailed work on understanding their breeding biology and niche overlap is essential. Perhaps similar in-depth work needs to be conducted on other threatened species, in the Philippines and elsewhere.

In ecology, there is no substitute for the long-term study. Conclusions based on a summer or two of fieldwork may not be reliable, as the time involved may not have been sufficient to detect longer-term changes. Mudappa has done the Herculean task of following the dynamics of nesting in the Malabar Grey Hornbill (*Ocyceros griseus*) over an eight year period in the Anamalai Rainforest. Possible competition for nest sites with the larger Great Hornbill was also considered. With the diminution of forests that hornbills are dependent upon, and the fact that potential nest sites are likely to be in the largest trees, studies of the kind reported here by Mudappa are critical if we are to better understand – and possibly even aid – hornbill nesting and breeding biology.

In some circles, a correlation is sometimes made between the degree of technological sophistication and the quality of research being conducted. Somewhere along this shift in values, do we stand to lose some valuable insights obtained through basic but thorough observation? Thiensongrusamee *et al.* demonstrate the value of careful field study in their note on characteristics of the nests of Helmeted Hornbill (*Rhinoplax vigil*). Deceptively "simple" work such as theirs can complement both field and captive based hornbill breeding biology work.

Wilkinson, in his paper on the role of zoos in supporting hornbill conservation and research, highlights the active roles that zoos perform both in the *ex-situ* conservation of hornbills, to their considerable support of hornbill field studies. That zoos form a bridge between field and captive based conservation has long been known, but the extent of the support that zoos have given to hornbill research and conservation may not have been as widely realized. It is hoped that Wilkinson's paper might help address this knowledge gap.

Successful *ex-situ* hornbill conservation is based, not surprisingly, on the ability to get the animals to produce offspring. Different approaches may be taken to encourage and to facilitate the captive breeding of hornbills, and this section features two of them. Bárcena *et al.* report on their novel attempt to assist in the pairing and breeding of Writhed Hornbills (*Aceros leucocephalus*) at the Malaga Zoo, which they call the "dynamic of group" method. While Bárcena *et al.* focused upon the social and behavioral characteristics of the hornbills to achieve successful breeding, Khin *et al.* experimented with the birds' physical environment; factors such as perch siting, next box design and feeding. Better breeding success in captive hornbill populations in the future may be attributable to the kinds of work documented in this section.

While those knowledgeable in wildlife trivia might have a fixation on the birds' nesting behavior, this section details both the tremendous breadth as well as the vast and as-yet unexplored realms of hornbill breeding biology. These selections will give the reader a good sampling of the state of hornbill breeding biology work and may point a way forward for the achievement of stable – or even increased?~~-~~ hornbill populations in the future.

Eight years monitoring of Malabar Grey Hornbill *Ocyceros griseus* nest cavity use and dynamics in the Anamalai rainforest, India

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Abstact Nest cavities used by Malabar Grey Hornbills (*Ocyceros griseus*) were monitored from 1993 in Karian Shola and some rainforest fragments in the Anamalais, Western Ghats, India. Forty six nests were monitored during the breeding season (February-May) for a period of two to eight years. The rates of nest cavity use and turnover were estimated, and causes of nest abandonment identified. New nesting trees were discovered every year. An average of 4.9% of these nests became defunct annually. The causes of abandonment were enlargement or closure of the cavity entrance, colonization by bees, fire, and treefall. Despite the loss of many large trees and high disturbance levels in the forest fragments, Malabar Grey Hornbills have been using the same nest cavities successfully for many years. Nests that were abandoned due to predation during nesting were reused in the following years. Inter-specific competition or nest usurpation by the larger Great Hornbill does not pose a threat to breeding Malabar Grey Hornbills as these two species have distinct nesting habitat requirements. However, further monitoring of nest cavity formation and availability will throw more light on the dynamics of hornbill populations.

INTRODUCTION

Animal populations are influenced by the availability of resources, particularly foraging, resting, and nesting sites. Under natural conditions, resource availability governs their life-history strategies, home-ranges, social-organization, fecundity, and mortality. However, in recent times, human populations and activities have been shown to affect wild populations. The Western Ghats, a biodiversity hotspot (Myers *et al*. 2000), has undergone drastic human-induced changes such as the development of plantations, industries, and hydroelectric projects, resulting in the loss of about 40% of natural forest cover over the last seven decades (Menon and Bawa 1997).

Wildlife and natural habitats, however, receive some protection within wildlife sanctuaries and national parks. In these protected areas, where the direct influence of man is considerably limited, natural processes affect the dynamics of wildlife communities and populations. Under conditions of annual environmental variability, factors influencing wild populations can be identified through long-term monitoring of resource availability, use, and turnover rate. Populations in small, island-like protected areas, as well as rare, endemic species may be especially susceptible to environmental vagaries (Karr 1982). Thus it becomes important to regularly assess the conservation status of these species and plan their management.

One such endemic of the Western Ghats is the Malabar Grey Hornbill (*Ocyceros griseus*). It is a large forest bird, specialized to feeding on fruits and nesting in cavities of large trees (Mudappa and Kannan 1997; Mudappa 2000). Being secondary cavity nesters, they are dependent on the availability of suitable tree cavities. This is especially important as they have relatively long incubation and nestling periods of about three months, when the female and the chick(s) stay incarcerated in the cavity, while the male provides them with food. Hornbills are also known for their nest-site fidelity (Kemp 1978). Dynamics of loss and formation of suitable cavities is therefore a critical factor for Malabar Grey Hornbill populations.

During this study I aimed to (1) identify causes of nest abandonment, and (2) estimate the rates of nest-cavity use and turnover over eight years. The implications of nest recruitment and abandonment for hornbill populations and conservation are discussed.

METHODOLOGY

Study area

Nests of the Malabar Grey Hornbill were discovered and tagged every year between 1993 and 2000 in the Anamalai Hills of the southern Western Ghats, India (Table 1). The study site was in Top Slip in the rainforest of Karian Shola National Park (10˚ 28.56′N and 76˚49.99′E). About 5 km² is located within the Indira Gandhi Wildlife Sanctuary in Tamil Nadu State, which spreads over an area of 987 km² (76˚44′ – 77˚48′E and 10˚12′–10˚54′N), and this patch of forest extends into the Parambikulam Wildlife Sanctuary in Kerala State. The rainforests are found in small natural patches along the ridges and valleys, usually contiguous with dry deciduous and bamboo forests. In some areas, they also occur as fragments surrounded by a mosaic of man-made habitats such as plantations. The Malabar Grey Hornbill is restricted to moist forest habitats. The seasonality can be classified into three periods–dry (February-May), south–west monsoon (June-September), and north–east monsoon (October-January).

Table 1. Distribution of Malabar Grey Hornbill nests monitored in the Anamalai Hills,Western Ghats

No.	Site	Area (ha)	Number of nests
1	Karian Shola	c. 1000	38
2	Bit Shola	< 50	4
3	Manamboli	200	1
4	Anaikundi	200	1
5	Stanmore	10	1
6	Puthuthottam	65	1

Nest monitoring

The breeding season commences by the third week of February in this region, and the chicks fledge around May, just before the onset of south-west monsoon (Mudappa 2000). Nests were discovered and monitored during the breeding season each year. All the nests were visited and their nesting status recorded around the first week of April. New nests discovered were also tagged.

The status of each nest-cavity was recorded as:

(i) ACTIVE- If nesting was in progress, the entrance of the nest-cavity sealed, and/or the midden had a fresh deposition of seeds, fruits, and other food items,
(ii) INACTIVE—If no nesting had commenced and there was no sign of fresh defecation in the midden, and
(iii) DEFUNCT—when the tree itself had become unusable, and the nest had been abandoned for more than 3 successive years.

RESULTS

Nest monitoring

A total of forty six nests were monitored for one to eight years depending on the year of discovery (Fig. 1). In 1993, 18 nests were discovered. All nests discovered in the following years are referred to as "new" nests. New nests were discovered every year thereafter with the greatest number of new nests in 1994 and 1999 (Fig. 1). A steady decline in the reuse of nests was observed, from 77% to 37%, with an average of 63% (±13.6%) of the nests being reused every year. The lowest reuse rate was in the year 2000 (Table 2).

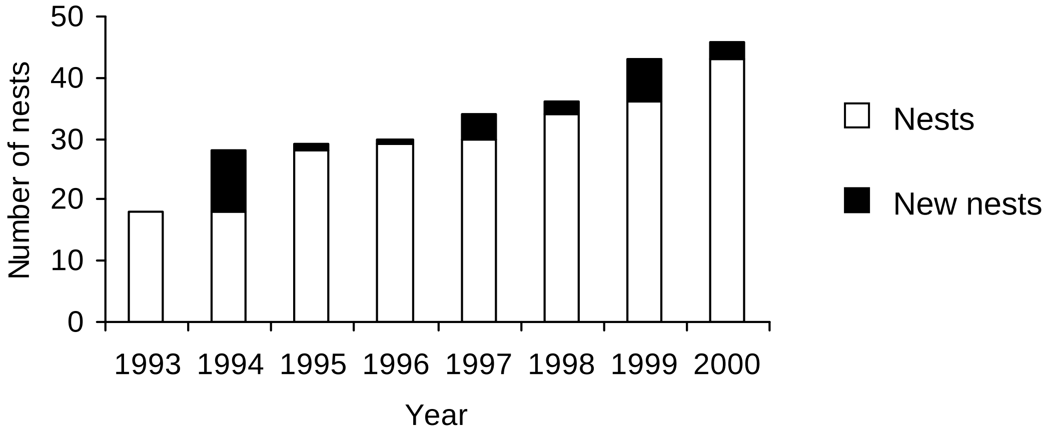

Figure 1. Number of Malabar Grey Hornbill nests monitored in Anamalai Hills.

Table 2. Rates of use and loss of Malabar Grey Hornbill nest sites

Status	Annual rates						
	1993-94	1994-95	1995-96	1996-97	1997-98	1998-99	1999-00
Active (%)	77.80	74.07	70.37	66.67	60.00	58.06	37.14
Inactive (%)	16.67	22.22	25.93	29.63	36.67	41.94	48.57
Defunct (%)	5.56	3.70	3.70	3.70	3.33	0.00	14.29
Number of nests (N)	18	27	27	27	30	31	35

Thirteen nest-trees have become defunct since their discovery. This has been due to (i) tree fall (1 nest), (ii) wildfire (1), (iii) enlargement of cavity entrance (2), (iv) complete closure of the cavity due to growth of woody tissue (6), (v) nest occupation by a colony of bees during the non-breeding season (1), and (vi) predation (2). On average, 4.9% of nests become defunct annually, the highest being in 2000, when a majority of the older nests were abandoned (Table 2).

In five cases, nesting was resumed in the same cavities after having been abandoned for 2–5 years. This included cases where the nesting pair had been disturbed due to (i) probable death of a parent bird, (ii) cavity entrance enlargement or shrinkage, and (iii) possible predation at the nest (claw marks were seen on the bole leading up to the cavity). In two cases, different cavities in the same nest tree had been used. One nest near the forest edge was abandoned mid-way during the breeding season of 1996 due to a wildfire and remained unoccupied thereafter. About 32% of the nests were inactive every year (Table 2).

On average, two-thirds of the nests were active every year (63%). Only three of the 18 nests monitored for eight years, including the year of discovery, were occupied every year. Two of the 10 nests monitored for six years were occupied in all years (Table 3). On average, the annual recruitment (discovery) of new nests is 4.0. Some of the nest-cavities of Malabar Grey Hornbill were occupied by other species, such as the Common Giant Flying Squirrel (*Petaurista phillipensis*), Bengal monitor (*Varanus bengalensis*) and the Malabar Spiny Dormouse (*Platacanthomys lasiurus*) during the non-breeding season.

Table 3. Number of years of reuse of nests by the Malabar Grey Hornbill

Number of years monitored	Number of nests monitored	Number of years the nests were active							
		8	7	6	5	4	3	2	1
8	18	3	4	3	1	1	2	3	1
7	10		2	2	0	3	0	1	2
6	1			0	0	0	0	1	0
5	1				0	0	0	0	1
4	4					2	0	0	2
3	2						1	0	1
2	7							3	4

DISCUSSION

Nest monitoring

Nest abandonment and turnover in cavity-nesting birds can be caused by both natural and anthropogenic forces. If recruitment of new nests does not compensate for the loss of active nest sites, declines in breeding populations may occur. An estimate of the breeding population density may be obtained by mapping the number of active nests (24) observed within an area of about 5 km² of Karian Shola National Park. This is, however, only the minimum nesting density of 4.8 nests per km² (9.6 pairs/km²), and the actual nesting density is likely to be over twice as high since the area was not completely surveyed. Line transect density was estimated to be about 51 hornbills/km² (Raman and Mudappa, unpubl. ms.). This may be one of the highest reported hornbill nesting densities thus far, apart from the 10.4 nests/km² of the Sulawesi Red-knobbed Hornbill (*Aceros cassidix*) reported by Kinnaird and O'Brien (1999). Compare these figures with 0.6 nest/km² for the Great Hornbill (*Buceros bicornis*), 0.3 nest/km² for the Wreathed Hornbill (*Rhyticeros undulatus*), the 0.4 nest/km² of the Brown Hornbill (*Ptilolaemus tickelli*) and the Oriental Pied Hornbill's (*Anthracoceros albirostris*) 0.6 nest/km² reported by Poonswad *et al.* (1987).

In this study, natural forces were observed to be predominantly responsible for the loss of nests. The results of this study suggest that the percentage of new nests required to compensate the annual loss of nests is about 5%. This would imply the importance of the availability of the trees of suitable diameter (60–90 cm, Mudappa and Kannan 1997) in the region of the Malabar Grey Hornbill's distribution. It was observed that most of the rainforest patches were highly disturbed and had very few large trees (Raman and Mudappa, unpubl. data). However, further monitoring of cavity availability, nest initiation and success will throw more light on the dynamics of the Malabar Grey Hornbill population.

Two studies that monitored nest reuse in hornbills were those of Poonswad *et al.* (1987) and Kinnaird and O'Brien (1999). The study in Thailand reported intra- and inter-specific competition to be a major cause of nest abandonment, accounting for 20% of abandoned nests (Poonswad *et al.* 1988). This research team has tried to restore abandoned nest cavities and/or introduce nest-boxes in order to reduce competition. This may not, however, be necessary in the present study site, as (1) competition may not act as a limiting factor as mentioned earlier, due to a distinct choice of nesting sites by the two sympatric species of hornbills, and (2) the densities are high enough to presume that even high rates of nest abandonment does not imply lack of nest cavities, but instead may indicate availability of suitable nesting trees in undisturbed areas like the Karian Shola. The study of the Sulawesi Red-knobbed Hornbill (Kinnaird and O'Brien 1999) reported rates of reuse of nest trees similar to that observed during this study. Where studied, the Malabar Grey Hornbill was sympatric with the Great Hornbill, and these two species were shown to have distinct nesting habitat requirements with little overlap (Mudappa and Kannan 1997). This is probably the reason for the absence of nest usurpation by the larger Great Hornbill, unlike in Thailand where there are two similarly-sized out of four sympatric species (Poonswad *et al.* 1987). Predation usually caused only temporary abandoning of the nests. However, there were two instances of probable predated nests that were not reused in the following years. This complete abandonment of nests after predation may be influenced by the actual suitability of the nest itself.

The extent of human influences on the hornbills and their habitats cannot be ignored. For instance, two of the most threatened nests of the Malabar Grey Hornbill were the ones in the privately owned rainforest fragments of Puthuthottam and Stanmore, where large trees were being felled to establish tea plantations or for fuel wood. The nest tree (*Canarium strictum*) in Stanmore is one among the last few large native trees standing in this patch of forest. This tree has also been girdled and will likely die soon (it was used for nesting even in 2002). In most of the small-sized fragments that are surrounded by human settlements, there is a continuous degradation of the habitats and related loss of important resources such as fruiting food trees and nesting trees of suitable characteristics (Raman and Mudappa, unpubl. ms.). The Malabar Grey Hornbill is among the many endangered species such as the Great Hornbill and the Lion-tailed Macaque (*Macaca silenus*) living precariously in these rainforest patches. The nests along forest edges are also vulnerable to wildfires (usually caused by human settlements in the vicinity) and windfalls. There could be factors other than those listed that are affecting the hornbills in the rainforest fragments around Valparai. The Great Hornbill faces much greater pressure from humans even within protected areas. There is a report of a nest being abandoned from 1996 (for two years) after being disturbed by wildlife photographers. Another nest succumbed to the poaching of chick(s) in 1997 for a private collection/pet trade.

Future research and monitoring

For a more precise and thorough monitoring and management of hornbill populations in the region, several lacunae in our knowledge need to be filled through detailed scientific research. These include:

(i) estimation of availability of suitable nest-cavities
(ii) nest-site fidelity and number of nests used by identified pairs over several years
(iii) population structure and density of both Great and Malabar Grey Hornbills
(iv) restoration and protection of highly degraded rainforest habitats and fragments

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Notes on two species of endangered Philippine hornbills with an emphasis on breeding biology

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Abstract Comparison of various behaviors between two sympatric West Visayan species of hornbills of Panay Island, the Visayan Tarictic Hornbill and the Writhed-billed Hornbill, is presented. Also documented were similarities and differences in the breeding biology and food and feeding ecology of these two species. The need for data for other Philippine hornbill taxa for a wider comparative perspective remains a challenge. Pair density of the endangered Visayan Tarictic Hornbill (*Penelopides panini panini*) is about ten times greater than that of the critically endangered Writhed-billed Hornbill (*Aceros waldeni*). Competition for both food and for nest holes cannot be ruled out for these differences. During the breeding season, the male Visayan Tarictic Hornbill increases the proportion of animal food it provides to the nest inmate. This is likely due to a greater demand for animal protein for chick growth than to a limitation of fruit resources. The average feeding rate, the feeding of one food item in runs, the withholding of food around fledging, and a morning peak in feeding are shared characteristics. Visayan Tarictic Hornbills demonstrate feeding peaks in the morning for certain much sought after fruit, yet not for animal prey. This is regarded as the outcome of competition with other frugivores and the mutual hostility between both species, as that over food and/or nest holes. Feeding rate in the Tarictic Hornbill increases upon hatching while the number of items per visit stays constant. Some behavioral peculiarities of the Tarictic Hornbill, including chorus-calling and looking after injured conspecifics are functionally not yet understood. For other comparisons see Table 1. In a first assessment for the paleotropics conducted at one site, diet overlap between the Tarictic and seven species of frugivorous fruit bats was found to be rather low (0.084-18.9, as measured by Sörensen's similarity index), and is thus comparable to a bird-bat community in the neotropics. As a by-product of the present study, a number of mistakes of the physical description of both species in the literature are corrected. Some Tarictic individuals stain the white portion of their tails with preen-gland oils while others do not.

INTRODUCTION

Whereas the breeding biology of several Asian hornbill species is well documented (Poonswad *et al.* 1987, 1988; Suryadi *et al.* 1994; Poonswad 1995; Mudappa and Kannan 1997; O'Brien 1997; Kinnaird and O'Brien 1999) Philippine hornbills have received scant attention. From both a comparative and a conservation perspective the hornbills of this country, comprising ten taxa (Kemp 1995), were not intensively studied. It is timely that this neglect is changing in recent years. While Diesmos and Pedregosa (1995) and Gonzalez and Dans (1996) carefully charted the conservation situation of the two West Visayan Hornbill species and the Polillo subspecies (Luzon Tarictic Hornbill *Penelopides manillae subnigra*), respectively, Witmer (1993), Kauth *et al.* (1998) and Klop *et al.* (1999, 2000) made contributions to the breeding biology and Curio *et al.* (1996) to some general aspects. Study on these two West Visayan Hornbill species, i.e. the critically endangered Writhed-billed Hornbill (*Aceros waldeni*) and the endangered Visayan Tarictic Hornbill (*Penelopides panini panini*), is of special relevance to help improve the bleak outlook for these species. The same holds true for the critically endangered Sulu Hornbill

(*Anthracoceros montani*), but fieldwork is greatly hampered by the deplorable insurgent situation on the Sulu islands.

The present paper collates the work of the Philippine Endemic Species Conservation Project (PESCP) on Panay Island, and, by comparing these two Visayan Hornbill species, tries to give some new insights while focusing on the breeding biology. Before doing so a brief overview on their conservation status is given as well as a revised description of their appearance to correct some long standing but erroneous descriptions of the color pattern. The paper closes with a brief comparative look at the problem of competition over food between the Visayan Tarictic Hornbill during breeding and fruit bats (Pteropodidae).

Conservation status

Several hornbills are among the most seriously threatened bird species in the Philippines. While three species, including the Sulu Hornbill (*Anthracoceros montani*), Panay Wrinkled Hornbill (*Aceros waldeni*) and Panay Tarictic Hornbill (*Penelopides panini*) were previously classified "critically endangered" (Collar *et al*. 1994), the Visayan Tarictic Hornbill has now been put in the "endangered" category (Collar *et al.* 1999) without explicitly stated reasons. Unfortunately, the Ticao Tarictic Hornbill (*P.* [*panini*] *ticaensis*) must be regarded as functionally or definitely extinct (Curio 1994), as Ticao Island is virtually denuded. This is true for Masbate Island as well so that the future of *panini* race there is looking bleak. The other Visayan species, the Writhed-billed Hornbill, is in a most precarious state. Its global population may not exceed 30-100 pairs, most of which are confined to Panay Island. On Negros Island, the species must be functionally extinct due to too few birds surviving (Klop *et al.* 2000; Collar *et al.* 1999). Because of large-scale forest loss, on neighbouring Guimaras Island both Writhed-billed and Visayan Tarictic Hornbills must have been extirpated. For unknown reasons, Kennedy *et al.* (2000) claimed Guimaras Island as an area of occurrence. Apart from these two species, five more Philippine hornbill taxa are critically endangered (Sulu Hornbill), near-threatened or vulnerable (Collar *et al*., 1999).

The two Visayan hornbills have been used as the focus of a multi-faceted, integrated conservation programme by PESCP since 1995. *In situ* measures comprise anti-hunting campaigns, alternative livelihood and nest-incentive schemes, as well as lobbying at many political levels for protected areas on Panay Island. *Ex situ* measures focus on the rehabilitation and release of birds (Curio 2000, 2001)

Appearance

Visayan Tarictic Hornbill

Different authors (Kemp 1995; Kennedy *et al*. 2000) have given different accounts on the Visayan Tarictic Hornbill appearance. This controversy can be settled as follows. While all authors describe nominate *P. panini panini* with a rufous tail, Kennedy *et al*. (2000) almost correctly observe that it can vary from buff white to rufous, with a terminal black band throughout. The variation of tail coloration is independent of sex and age. Captive birds on Panay of fledgling age through seven years (male) have either a (buff) white or an ochre to rufous tail. The same variation holds for Negros birds, including wild ones. Taking both islands together, there were three white tails among six wild birds and 10 among 19 in captivity. The idea of a color polymorphism can be dismissed since in a half-year-old captive male the brown feathers of its juvenile plumage were being replaced by a white tail. But white is by no means a progressive tail colour since a seven-year-old male had a buff tail. The replacement of white by rufous comes about by preening with same-colored oils of the uropygial gland (see also Kemp 1995: *Aceros corrugatus*, *A. waldeni*).

The recognition of intra-individual variation of tail coloration is especially significant when comparing nominated *panini* with race *ticaensis* from the East Visayan Ticao Island, described to have a white tail (Kemp 1995). Since the description rests on only two specimens, one cannot rule out the white tail to have been freshly molted and not yet stained by preening. The high proportion (ca. 50%) of *panini* with a white tail suggests that part of the population has never achieved staining their tail with preen-gland oils. The strongest evidence came from two females on Negros that I followed from yearling age through three years in captivity; one is still alive in the Bacolod City Biodiversity Conservation Center and produced the first chick born in captivity at five years old (Ledesma, pers. comm.). Both females maintain a white tail throughout. Comparable evidence from the wild is lacking.

Given the possible equivalence in tail coloration in *panini* and *ticaensis*, minor differences do still remain. These concern the gloss of the upper parts and the rufous of the belly in *panini* versus the buff underparts in *ticaensis*. Incidentally, in *panini*, only the belly, not the whole underside (Kemp 1995), is rufous.

Yet another distinction in coloration between the two subspecies may disappear. The light (pink?) color of the malar skin patch of male *ticaensis* is also present, not absent (Kemp 1995, Plate 14), in *panini* where it is pure white (pers. obs.). The malar patch in female *panini* is white, not blue as shown in Kemp (1995, Plate 14). The color of this patch in female *ticaensis* has not been noted. Kennedy *et al.* (2000) describe this white malar patch in *panini* as a chin patch, thus overlooking the fact that the chin is jet black. The white malar patch of *panini* may occasionally have a bluish tinge as does the circumorbital white skin. This is true for both wild and captive birds.

The basic color of the bill in *panini* is a washed brown with a reddish tinge which is largely present in the male, as correctly depicted in Kennedy *et al.* (2000). The coral red appearing on the bills of both *panini* and *ticaensis* (Kemp 1995) is likely incorrect at least for the former. As the examination of museum skins shows that the red of hornbill bills tends to fade into a brownish grey (pers. obs.), the true bill color of *ticaensis* may never come to light.

With the exception of four captives, the foregoing account on the coloration of *panini* has been documented by color photography (author's archive).

Visayan Writhed-billed Hornbill

While plumage colors have been correctly illustrated by all illustrators, the naked facial skin is still in error. In spite of the first correct description by Curio *et al.* (1996), Kennedy *et al.* (2000) describe the skin of the male as coral red while it is actually saffron, contrasting with the red bill. The picture illustration in Kemp (1995, Plate 10) with an orange yellow gular pouch is close to reality, but is mistaken by a flesh-colored eyering. Similarly, the female's naked skin is not coral red (Kennedy *et al.,* 2000) or dark blue (eyering) and contrasting with the red bill and yellow gular pouch (Kemp 1995). Rather, it is white with a bluish tinge in certain places (Curio *et al.* 1996). The color of the iris undergoes complex changes during maturation. These will be described elsewhere.

Breeding biology

While the processes underlying pair formation are still largely unknown, there is now some solid evidence on aspects of reproduction. Breeding occurs in monogamous pairs, communal breeding as in Sulawesi Tarictic Hornbill (*Penelopides exarhatus*) (O'Brien 1997) has not been observed so far. The following observations were based upon studies of two broods of Tarictics and three of Writhed-billed Hornbills, all on Panay Island. It appears that the male Writhed-billed Hornbill uses its nest hole repeatedly (Kauth *et al.* 1998).

Nest hole

The Writhed-billed Hornbill appears to use holes higher above ground than do Tarictic Hornbills (Table 1). The highest hole was in a strong, oblique limb. Among 24 Tarictic Hornbill nests only three were found in dead trees. The 24 nest trees comprised at least ten species, including *Shorea polysperma* and *Bischhofia javanica.* The orientation of the nest hole entrance of Tarictic Hornbills was randomly distributed in all directions (Klop *et al.* 2000).

Competition over nest holes is suggested by the immediate takeover from a White-bellied Woodpecker (*Dryocopus javensis*) nest hole following the evacuation by a pair of Blue-crowned Racquet-tailed Parrots (*Prioniturus discurus*) (Klop *et al.* 2000). Further, this woodpecker that produces suitable holes is rare for unknown reasons. Moreover, there are skirmishes between both hornbill species at the start of the breeding season.

Pair density

Tarictic Hornbill density on Panay Island is about ten times higher than that of the Writhed-billed Hornbill (Table 1). This difference may be due to a combination of factors, among which are a scarcity of large nest holes, higher hunting pressures and nest robbery. These may have a greater impact on the larger species. Despite being territorial, Tarictic Hornbill pairs exhibit mutual attraction since nearest-neighbor distances are shorter than if the distribution of pairs was random.

Pair density was used to assess population sizes of both hornbills on Panay Island (Klop *et al.* 2000). This is justifiable if one assumes that there are no floaters, and this seems to be the case. In three breeding seasons (1998-2000), I sighted a single female Tarictic Hornbill only twice and no female Writhed-billed Hornbill was sighted at all in March.

Timing of breeding

The breeding season of Writhed-billed Hornbill commences in early March judging from when females disappear from fruiting trees. Tarictic Hornbills seem to start about four weeks later (Table 1). This pattern was also reinforced by the fledging of a Tarictic Hornbill brood on 23 June and a Writhed-billed Hornbill brood on 17 May (Klop *et al.* 1999; Kauth *et al.* 1998). The incubation period of the related Sulawesi Tarictic Hornbill takes 16-19 days (O'Brien 1997). Given that the nestling period of the Visayan Tarictic Hornbill is considered shorter (Table 1), the difference in the start of breeding appears to be conservative. The nestling period of the slightly smaller Luzon Tarictic Hornbill (*P. manillae*) and Sulawesi Tarictic Hornbill is perhaps somewhat longer (62 days: Kemp 1995; 55-68 days).

Brood size

The data of brood size at fledging or shortly before is documented from a nest robbery of the Writhed-billed Hornbill in S Pandan. Although Luzon Tarictic Hornbills are known to lay 3-5 eggs in captivity, and three in the wild for the Visayan Tarictic Hornbill (Kemp 1995), broods fledged no more than two chicks (Table 1). This was also the case for two Sulawesi Tarictic Hornbill broods (O'Brien 1997), and a clutch of two eggs documented by Kemp (1995).

Only three broods of Writhed-billed Hornbills permitted us to infer brood size at fledging or shortly before (Table 1). A brood of three is remarkably large compared with that of the Red-knobbed Hornbill, *Aceros cassidix* of Sulawesi, which invariably fledges only one chick although three eggs are laid (Kinnaird and O'Brien 1999). The difference is exacerbated, given the very similar diet composition of both species (see below). The female Writhed-billed Hornbill of one brood emerged after the first chick had fledged, but before the other two followed suit days later (Kauth *et al*. 1998). The female then brought ca. 5% of the food to the young, indicating that the male can care for them virtually alone. This again is in stark contrast to the Red-knobbed Hornbill where the female breaks free 28 days prior to fledging and helps in feeding the chick (Kinnaird and O'Brien 1999). It is unknown whether a widowed female *Aceros* can raise chicks alone.

Feeding rate

In the Writhed-billed Hornbill, feeding by the male occurs ranging from 1-66 items of usually one food species or more rarely three (Kauth *et al.* 1998). Similarly, the Tarictic Hornbill male delivers up to 57 fruits in one visit, usually of one species. Smaller fruits can be given as full beak loads, not only one at a time as in the Sulawesi Tarictic Hornbill (O'Brien 1997). Animal prey, however, is usually delivered singly (Klop *et al.* 1999). The mean number of food items per family member per day is rather similar in both Panay hornbills (Table 1), though two male Writhed-billed Hornbills differed considerably (Fig. 1, right panel)

Similar to the Red-knobbed Hornbill (Kinnaird and O'Brien 1999), Writhed-billed Hornbills feed nearly 98% fruit to their family, the remainder being invertebrates. One difference from other *Aceros* species (Kemp 1995) was that there was no vertebrate prey in the nestling diet. This is different from the nestling diet of the syntopic Tarictic Hornbill, which consists of nearly 14% animal food (including small vertebrates), delivered by the males (Fig. 1, left panel). This greater proportion of animal diet is also seen in non-breeding captives. On seeing a live or dead prey animal they indulge in a veritable feeding "frenzy" in which group members try to snatch the prey away from the one that has seized it first.

In both species, as few as three fruit species form the staple diet, i.e. about 60% of the food sought. In the best studied Tarictic Hornbill brood, the number of all species together is much larger (48, see below) (see also Kinnaird and O'Brien 1999). In both species figs (*Ficus* spp.) of at least eight species constitute the dominant food (Table 1). This bias is only exceeded by the Red-knobbed Hornbill (Kinnaird and O'Brien 1999).

Table 1. Comparison of some reproductive and other characteristics of the two West Visayan hornbills. d = day

Characteristic	*Aceros waldeni*	*Penelopides panini panini*	Source; comment
Nest height (m)	17[1], 17[1], 12[2], 20[2]	11.2 (1.9 - 16, n = 22)[1]	
Pair density (km^{-2})	0.2 - 0.3[1]	~ 3[1]	
Start of breeding	< 5 Mar[1], 6 Mar[1]	(Mar?) ≤ April[3]	
Brood size at fledging	3[2], 3[2], 3[5]	2[3], 2[4]	
Nestling period	42 d[2], ≤ 60 d[2]	54 d[3], 55 - 58 d[1]	[1,3] 55 - 68 d in *P. exarhatus* (O`Brien 1997)
		[2] Assuming incubation period = 29 d[4]	
Feeding rate (Items/nestling/d)	32[1], 57[1]	69[3]	
Withholding food during fledging	+[2]	+[1,3]	
Diurnal rhythm of feeding rate	Morning & afternoon peaks of any food (1 brood)[2]	morning peak only: fruits no peak: animals (1 brood)[3]	
Food = 100 %			
Fruits: proportion	97 %[2]	83 %[3]	
Fruits: 3 most common species	61 %[2]	60 %[3]	
Fruits: proportion figs	33 %[2]	≥ 23 (< 28) %[3]	
Animals: proportion	2 %[2]	14%[3]	
Flight, long distance	Above canopy	± under canopy	pers. obs.
Flight: silence of ♂ near nest	+[2]	+[3]	
Mutual interspecific aggression of *A. w.* vs *P. p. p.*	+[2]	+[2]	*P. exarhatus* chasing only *A. cassidix*[4]
Group chorus	-	+	pers. obs.; also *P. manillae*[4]
Looking after disabled	-	+	

[1] Klop *et al.*2000

[2] Kauth *et al.* 1998

[3] Klop *et al*. 1999

[4] Kemp 1995

[5] Curio 2000

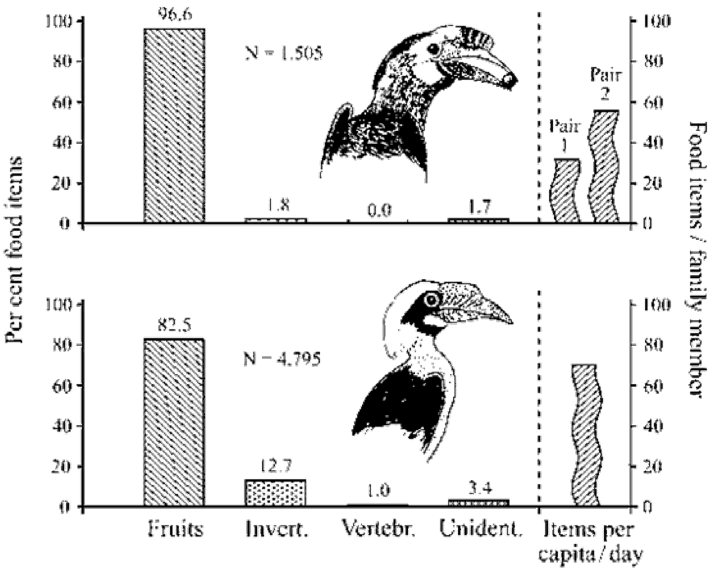

Figure 1. Left panel: Diet composition of *Aceros waldeni* (top) and *Penelopides panini panini* at the nest with broods of 3 (pair 1), 2 (pair 2) and 2 (*Penelopides*). N = number food items recorded during nestling period. Right panel: Food items/ family member/ day. After data in Kauth *et al.* (1998) and Klop *et al.* (1999) for *A. w.* and *P. p. p.*, respectively.

In the Tarictic Hornbill, the feeding rate was found to characteristically change through the breeding cycle. While there are two data sets, one for each pair, covering the pre-hatching period, there is one large data set comprising 5031 food items for one of the two pairs, in Sibaliw, stretching across the entire nesting cycle (Fig. 2). Whereas the Hamtang male delivered somewhat more animal food at the expense of fruits, the reverse occurred in the Sibaliw male though the differences are not significant. Looking at the latter male across the breeding cycle reveals an increase of animal food after hatching, at the expense of fruits.

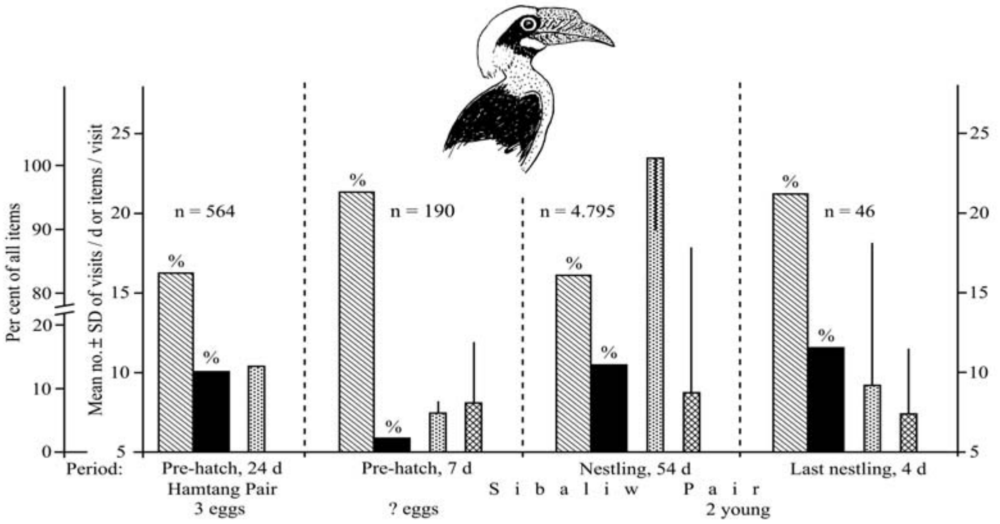

Figure 2. Tarictic diet composition and feeding rate (no. visits/ day or no. items/ visit = dotted and crossed columns, respectively; figures = no. of visits, n = total no. of food items). Hatched column = % fruit, black column = animal prey. Differences from 100% = unidentified items. After data in Klop *et al.* (1999).

The true upsurge in food delivery reflecting the increase in family size is revealed by the absolute numbers of visits per day. This increases from a low pre-hatch rate of five to almost 24 visits per day, a fivefold increase (see also Kauth *et al.* 1998: *A. waldeni*), although the number of items per visit does not noticeably change. After the first chick fledged the remaining one receives about the same amount of the food per day as did the female before the hatching period. Breaking down the daily total amount delivered by the male reveals, however, that the remaining nestling received less than half the number of food items (11.5/day) fed to the female on duty (27.1/day). This could be interpreted as the withholding of food to hasten fledging. This was also observed in the Sibaliw pair of Writhed-billed Hornbills, whereby the male made three nest visits without any food when there were two young just short of fledging remaining in the nest (Kauth *et al.* 1998). Withholding food prior to fledging is apparently a guise in tricking the young to leave the nest (see also Tsuji 1996: *Buceros bicornis*; Kinnaird and O'Brien 1999: *A. cassidix*). In the Writhed-billed Hornbill, the feeding rate also increased after hatching, but the composition of the food delivered did not obviously change. However, sample sizes were too small (Kauth *et al.* 1998) to make a firm conclusion.

Feeding the family undergoes a typical diurnal pattern in both Visayan hornbills. In the Writhed-billed Hornbill, there is pronounced modality with peaks of the feeding rate in the early morning from 0600 to 0700 hrs and a lower one in the early afternoon from 1400 to 1500 hrs (Kauth *et al.* 1998). The massive amount of data collected from one Tarictic Hornbill brood allows us to break down the feeding cycle into fruit and animal food patterns (Fig. 3). There is one pronounced, statistically significant peak for delivery of fruits in early morning, while the daytime distribution of animal prey exhibits a uniform pattern across the day (perhaps there is an increase in the morning hours due to the warming up of poikilothermic prey). The early morning fruit peak may well be due to lipid-rich fruits (*Myristica philippensis*, *M. glomerata* and *Chisocheton cumingiana*) dehiscing overnight (Klop *et al.* 1999). These are harvested by the Tarictic Hornbill during the morning significantly more often than during the rest of the day, and may become quickly depleted. The pattern of depletion may render these fruits a limited resource that is sought after as soon as it becomes available. Remarkably, any diurnal variation of food delivery in the Red-knobbed Hornbill was negligible (Kinnaird and O'Brien 1999).

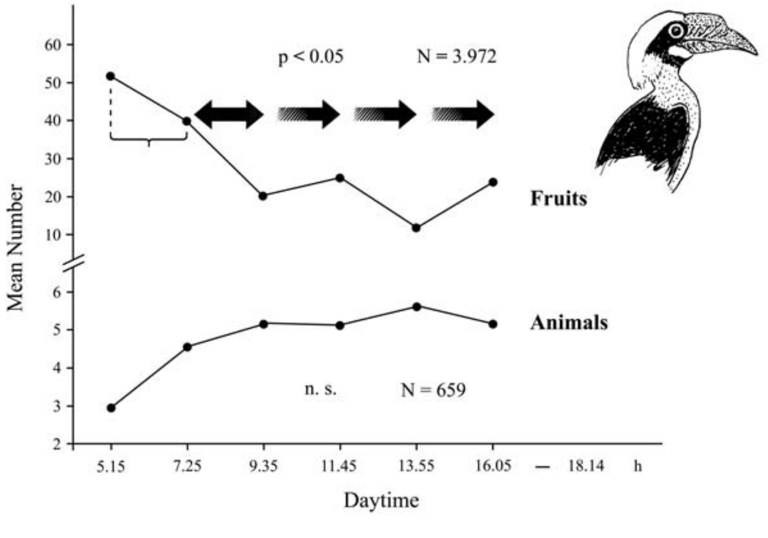

Figure 3. Daytime distribution of fruits and animal prey during the nestling period of a Tarictic brood. N= number of items. Friedman repeated-measures ANOVA; fruits $F_{F5,\,110} = 11.86$. After data in Klop *et al.* (2000).

Flight behavior

There is a distinct difference in flight habits between these two Visayan hornbills. While the Writhed-billed Hornbills move above the canopy the Tarictic Hornbills usually fly under and often in the lowest storey. During flight, both utter contact calls, and the swishing noise of their wings is audible. In contrast, when nesting, males of both species become silent while moving around in the vicinity of their active nest, including the wing noises (Kemp 1995: other species). Rabor (1977) noted that Tarictic Hornbills become silent and motionless when they notice an “intruder” approaching.

Interspecific hostility

A Writhed-billed Hornbill male was seen to chase Tarictic Hornbills that passed by its nest tree during incubation. When there are more than two Tarictic Hornbills, however, they do chase the Writhed-billed Hornbill. These skirmishes took place during the breeding period and are likely an expression of territoriality. Similarly, the Sulawesi Tarictic Hornbill was observed to chase the sympatric Red-knobbed Hornbill only (Kemp 1995). Since chasing was elicited by hornbills in each case, and not other frugivores, it is likely to result from competition over nest holes. This supports the view (see above) that nest holes are a limited resource. Also among four sympatric Thai hornbills there are both intra- and interspecific competition over nest holes as well as with non-avian intruders (Poonswad *et al*. 1988; Tsuji 1996).

Are fruits really an unlimited resource? They may not be. In spite of the tens of thousands of figs on a single tree, hornbills and fruit pigeons (e.g. *Ptilinopus occipitalis*) seem to favor some fruit over others (pers. obs.). These two hornbill species did not feed simultaneously on the same fig tree, yet up to five Writhed-billed Hornbills did (pers. obs.). Likewise, up to 25 of them fed on an *Aglaia* sp. without apparent hostility (Curio *et al*. 1996), but not for Tarictic Hornbills, as they may have no interest in fruits with such large seed sizes. Local Sulud-Bukidnon in Hamtang ascertained the mutual hostility between these two hornbill species when they are feeding on fig-laden trees.

Glimpses at social behavior

Outside the breeding season, small flocks of Writhed-billed Hornbills and the larger ones of Tarictic Hornbills roam the forest. While the former rarely calls, the Tarictics Hornbills frequently do. However, they are silent when being approached, possibly due to intense hunting, or call while flying away. Writhed-billed Hornbills appear to form large flocks only at fruiting trees (Curio 1996). This renders them vulnerable to hunting. One hunter boasted to have shot 40 individuals in one tree on one day (Curio 1998).

A peculiar behavior makes Tarictic Hornbills even more vulnerable to hunting. When a member of the group is shot down the others rally towards the screaming or otherwise conspicuous victim, thereby becoming easy targets for the hunter. In this way, whole groups could be wiped out. This social coherence of Tarictic Hornbills compromises their otherwise more vigilant and wary antipredator behavior towards humans.

Tarictic Hornbills are highly vocal, so that the flocks can easily be located. There is also vocal communication among flocks. Our captive birds often exchanged their one and two-syllable communicating calls with wild ones that were passing by or were attracted by the calls of the captives. While such single (“bleating”) calls are also uttered by Writhed-billed Hornbills, there is a unique, conspicuous chorus-calling among Tarictic Hornbills. Typically five to six birds suddenly start to call by uttering all variety of calls, including single syllable bell-like and “ziks” calls, three-syllable calls (“wa hä hä”) and others, including normal communicating calls. Callers are spread across a canopy area of 1-2 ha, which is wider than usual. A loud chorus was heard during September mornings between 0622 and 0742 hrs, and faded off after that 9 to about 42 minutes later. A chorus gradually merges into the normal monotonous communicating and at a much lower rate. The function(s) of chorus calling remain enigmatic at present.

Food competition with fruit bats?

The question whether hornbills and other avian frugivores overlap in diet with fruit bats (Pteropodidae) has not been tackled previously. It is of potential importance for an evaluation of food as a limiting factor for frugivores. There are 12 fruit bat species on Panay Island, nine of which are fruit-eaters (Luft 1998). Among them, seven sympatrically occur in the study area at Sibaliw and their diet is compared with that of the Tarictic Hornbill in the breeding season when competition may be most intense. The data set on the plant exploitation permits a comparison of fruit categories broken down to the species level. It does not allow a finer-scale analysis that takes into account the relative proportion of plant species in the diet.

The seven fruit-bat species (*Ptenochirus jagori*, *Cynopterus brachyotis*, *Rousettus amplexicaudatus*, *Haplonycteris fischeri*, *Harpyionycteris whiteheadi*, *Pteropus hypomelanus* and *P. pumilus*) consume the fruits of 47 woody plant species. Sampling was done in the same area as was done for the Tarictic Hornbill food, i.e. Sibaliw. Among the bats there is a broad overlap in diet (Luft 1998), so they can be treated here as one group. The Tarictic Hornbill utilizes 48 species of fruits (Klop *et al.* 1999). To assess the overlap in diet, Sörensen’s index of community similarity was used,

$$I_S = 2c / (T + F)$$

where c is number of species in common between both groups of consumers, T is number of species consumed by the Tarictic Hornbill, and F is the number of species consumed by fruit bats. The value of c ranges from 4 to 9, assuming that the maximal five species identified merely at the generic level are the same species in both samples. Accordingly, it turns out that I_S values range from 0.084 to 0.189, or at most about 19% of a complete overlap in diet ($I_S = 1$).

To refine the analysis, a closer look at the four shared plant species may be rewarding. They comprise two palms (*Areca catechu*, *Pinanga insignis*) and two figs (*Ficus botryocarpa*, *F. pseudopalma*). Both the two palms and the two figs are eaten by the two most common fruit bats (*P. jagori*, *C. brachyotis*). Therefore, there is potential for competition between the two species. However, this result is tempered by the fact that *P. jagori* utilizes 30 fruit species in total and *C. brachyotis* 22 species, to which the flowers of six and four species, respectively, must be added, in addition to leaves (*P. jagori*) (Luft 1998). It is currently known that seven tree species are exploited for leaves, five of these exclusively so. Furthermore, *P. jagori* consumes the flowers of six species, three of which offer this food source only and are thus not fruit food sources (Luft, pers. comm.). Since

Tarictic Hornbills feed neither on leaf nor flower, the overlap in diet is even smaller than indicated by I_S value.

While the proportion of the plants shared by the two bat species and the Tarictic Hornbill in the bat diet is not known, the Tarictic Hornbill diet offers some clues. *Pinanga insignis* makes up 20.1% of the latter species' diet, and *A. catechu* negligibly little. This was found only as debris under the nest, but has never been seen being delivered. The two figs are among at least eight others that make up 22.7% of the nestling diet (Klop *et al.* 1999). In conclusion, there is considerable "dilution" of the shared food species by the fact that the bats consume many other food sources beyond those shared with the two hornbills. Furthermore, there is a corresponding reduction in the proportion of the shared figs being smaller than 22.7% of the total Tarictic Hornbill diet. Both facts suggest that the actual overlap in diet is less than that indicated by I_S. However, additional detailed study is needed to confirm this.

DISCUSSION

The scanty data on two more closely studied broods from each of the two sympatric Panay hornbills permit few conclusions. There are similarities and differences, both of which are poorly understood historically and functionally. The much lower density of Writhed-billed Hornbills could be due to a limiting food resource, a shortage of large nest holes and/or greater hunting pressure.

Competition over nest holes is not reflected by the timing of breeding as it is on Sulawesi Island (Kinnaird and O'Brien 1999; see also Poonswad *et al.* 1988; Tsuji 1996). The earlier breeder would have a competitive edge, but Tarictic Hornbills, the smaller species, start breeding several weeks after Writhed-billed Hornbills (Table 1). Hence the timing of breeding is likely due to other factors.

The mutual hostility of both species, at least in the strongly overlapping breeding seasons (see Table 1), could be due to competition for food and/or nest holes. While both species utilize figs to a large extent (Table 1), a further assessment of diet overlap is difficult due to 35.7% of Writhed-billed Hornbill food remaining unknown at present (Kauth *et al.* 1998). Yet this species alone utilizes *Pterocarpus* (Leguminosae; 23.2% of diet), thus mitigating any competition for food.

The great abundance of at least ten fig species in one area (Sibaliw) and their enormous crop sizes are not sufficiently compelling evidence for minimal competition over figs. Both hornbill species and syntopic fruit pigeons may actually choose to consume certain figs from amongst enormous available crops. Red-knobbed Hornbills select fruits according to color (ripeness) and prefer larger over smaller ones (Suryadi *et al.* 1994). The distinct differences in the consumption of animal food (Table 1), that parallel the corresponding differences in the two sympatric Sulawesi Hornbill species (*P. exarhatus*, *A. cassidix*) (O'Brien 1997; Kinnaird and O'Brien 1999), is not likely due to the Tarictic Hornbill's greater hunting ability, but rather because the Writhed-billed Hornbill diet consists almost exclusively of fruit. This food consumption difference may be due in part to differences in respective foraging niches.

The notion that *Aceros* species prefer lipid-rich fruits while Tarictic Hornbills prefer sugary and water-rich fruits has not yet been strongly supported. A palm and a nutmeg (*Myristica glomerata*), typical lipid-rich *waldeni* food, both make up to 37% of the *P. panini* food (Klop *et al.* 1999), thus leading to potential competition over food.

While many aspects of feeding are similar among these two Visayan hornbills (e.g. feeding rate, providing one kind of fruit in runs, withholding food at fledging), there seems to be a difference. Tarictic Hornbills exhibit an early morning peak for fruit feeding but not for animal prey (Fig. 3), while Writhed-billed Hornbills show two peaks of food delivery. The drop of the food peak in the morning is possibly influenced by the rapid depletion of fruit that apparently dehisce overnight. This possibility cannot be ruled out for the morning peak of the Writhed-billed Hornbill but cannot functionally explain their afternoon peak of food delivery.

Upon hatching, a Tarictic Hornbill male increases both its visits per day and the animal prey delivered, yet not the number of items per visit (Fig. 2). It is reasonable to assume that an increasing amount of animal protein is necessary for the young, and may cause stress and strain on the male (see O'Brien 1997). In the Writhed-billed Hornbill, two males differed markedly in the rate of food delivery (Fig. 1). It still remains unknown whether this was offset by the quality of delivered food.

Behavioral differences

Tarictic Hornbills tend to associate more and gather in larger flocks than those of the Writhed-billed Hornbill. Like other *Aceros* species, Writhed-billed Hornbills may form large aggregations at a fruiting tree, although this may be dependent upon fruit crop availability. In relation to the marked social behavior of Tarictic Hornbills, there may be two peculiar behaviors that have never before been described. One is a unique chorus-calling while the flock is dispersing, the other is an apparent altruistic attempt to look after a wounded or killed member. Both of these behaviors are as little understood as are other behaviors associated with their social life.

Food competition with fruit bats

Besides diurnal avian frugivores and macaques, fruit bats and civets (see Corlett 1998) may comprise a nocturnal guild of frugivores in this area. By virtue of their species number and densities, fruit bats are potential food competitors for all avian frugivores. In a first approximation, the overlap in fruit diet between Tarictic Hornbills and seven species of frugivorous fruit bats was assessed. Being carried out at the same site, this comparison is the first of its kind in the paleotropics.

The diet overlap, measured by Sörensen's similarity index, is between 8.4 and 19% of what it could maximally be. Due to insufficient data, the analysis leaves out the proportion of each food item in the diet. A more careful look at the four plant species shared by both competitive groups, i.e. hornbills and fruit bats, reveals that for each case, there are alternative food sources which the two guilds differentially consume such that a lower index value appears more realistic. The consumption of leaves (at least five species) and flowers (at least three species) by fruit bats of plants whose fruits are not consumed, would actually reduce the degree of food competition suggested by Sörensen's index. This supports concepts of a "bat syndrome" and a "bird syndrome" of fruit characters. These character suites can only be functionally understood if the guilds involved exploit different food plants (see also Corlett 1998; Gorchov *et al.* 1995).

In a thorough study, Gorchov *et al.* (1995) found that the diets of fruit-eating birds and bats (Microchiroptera) at a site in the neotropics overlap very little (Morisita index $C < 0.05$ for 29 birds species and 31 bat species, $0 < C < 1$). The few shared fruits were morphologically similar to "bird fruits" suggesting that bats may be choosing these rather than the other way round. The minimal overlap resembles the one found here in the paleotropics and is perhaps not coincidental.

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Zoos supporting hornbill conservation and research

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Abstact Zoos may support hornbill conservation and research both *ex-situ* and *in-situ*. *Ex-situ* breeding programs for endangered hornbills aim to secure viable self-supporting zoo populations and provide the opportunity for husbandry research and studies of breeding biology. An important role is also played in working with related but less endangered species of hornbills to develop knowledge and husbandry skills that may assist the more threatened hornbills. Zoo staff and university students may contribute to these studies. Zoo hornbills can act as ambassadors, for through them information on conservation and threats to wild hornbills and their habitats can be brought to the visitors' attention. Collection planning should address the threats to wild hornbill populations, and zoos can help stem the trade in wild birds by refusing to purchase these birds through the trade. Additionally, the killing of wild hornbills for feathers for ceremonial purposes may be avoided by provision of moulted feathers from zoo hornbills. Direct support of conservation activities may be through agreements with governments, conservation organisations or university research teams to support *in-situ* field research, habitat protection, and wildlife rescue centers and conservation breeding programs. Such schemes range from adoption of island habitats to adoption of individual hornbill families and their nests. Support offered by zoos may be either financial or technical and includes both the seconding of zoo staff and providing opportunities for personal development of local staff members. Exchange visits and exchange of information may be of benefit to both parties. Educational activities and local community involvement may also benefit from zoo support.

INTRODUCTION

Hornbills occur throughout sub-saharan Africa, India and Southeast Asia through to New Guinea. Over 50 species are recognized of which nine are currently considered threatened (Kemp 1995; BirdLife International 2000). Whereas more than half of the African species occur in woodland savanna, with the remainder in tropical forest, in Asia all but one species are restricted to forest. That all nine threatened hornbills are South-east Asian reflects the major threats of deforestation, habitat modification and the vulnerability of island species with restricted ranges. Furthermore, ten of the additional twelve hornbill species listed as near-threatened are Asian.

Seven of the nine threatened hornbills are endemic to small islands, of which five are from the Philippines (Kemp 2001). Because of this and the support by zoos of the Philippines Hornbills Conservation Program many of the following examples are taken from hornbill conservation projects in the Philippines. On top of habitat loss, unsustainable hunting for the live bird trade and for food can severely endanger fragmented and isolated hornbill populations. Hornbills in the Philippines are considered a delicacy and eaten as finger food (*pulutan*) at drinking parties. Furthermore, unregulated illegal commercial hunting poses a particular problem for hornbills on small islands such as Basilan and

Polillo (Gonzales 1998). When hornbills congregate together to feed on fruiting trees they can be in particular danger from hunters. The breeding population of the critically endangered Visayan Writhed-billed Hornbills (*Aceros waldeni*) on Panay has been estimated as 25-30 pairs so the news that 40 hornbills, including Visayan Writhed-billed Hornbills, had been shot by hunters at a single fruiting tree in November 1997 is especially alarming. These birds were shot on one day and probably included more than a quarter of the population of north-west Panay (Kemp 2001; Lastimosa *et al*., in press).

The two other near-threatened species are the Yellow-casqued Wattled Hornbill (*Ceratogymna elata*) and the Brown-cheeked Hornbill (*C. cylindricus*) from West and Central Africa. The West African nominate race of the Brown-cheeked Hornbill, which may prove to be a distinct species, is uncommon and declining, and from its restricted and fragmented range may be expected to be threatened (Kemp 1995, 2001). Both of these are large forest-dwelling hornbills primarily affected by habitat degradation and fragmentation.

In Nigeria hornbills are also traded as fetish birds in the local markets (Nikolaus 2001) and additionally endangered by hunting for food. Ground Hornbills are also hunted for food or pets in some parts of their range. I have personal recollections of one offered for sale by a roadside vendor in Nigeria. This was purchased and released in a nearby game reserve. Hundreds of other hornbills cannot be so lucky and the local trade in hornbills for food or pets in either Africa or Asia should not be exacerbated by the additional pressures of the international bird trade.

HORNBILLS IN ZOOS

Hornbills make superb zoo exhibits. They are active, often colorful and noisy, and show interesting nesting and social behaviors. They are also extremely popular zoo exhibits with considerable numbers in captivity. Only a relatively small number of the world’s zoos report their holdings to the International Species Information System (ISIS) and many hornbills, at least of the smaller species, are maintained unreported in private collections, so the actual numbers of captive birds will be much larger than indicated by ISIS figures.

Taking only the five most popular genera, the ISIS abstracts (as at 31 December 2000) list over 1,100 birds with totals of 204 *Buceros*, 227 *Aceros,* 179 *Bycanistes*, 304 *Tockus* and 250 *Bucorvus*. A survey of hornbills in European zoos in 1996 indicated that there were 828 hornbills including 114 *Buceros*, 178 *Aceros*, 130 *Bycanistes*, 154 *Tockus* and 114 *Bucorvus* in the reporting collections (Brouwer *et al.*1997).

The most popular species, with over 100 individuals of each recorded on ISIS, were the Great Hornbill (*Buceros bicornis*), Northern Ground Hornbill (*Bucorvus abyssinicus*), Southern Ground Hornbill (*B. leadbeateri*), Trumpeter Hornbill (*Bycanistes bucinator*), and African Red-billed Hornbill (*Tockus erythrorhynchus*).

BREEDING FOR CONSERVATION

Hornbills’ nesting strategy of sealing themselves into tree nest holes whilst protecting them from most predators is ineffective against human predation, and nesting females and chicks are particularly at risk. The larger Asian hornbills in particular are threatened because of both habitat destruction and hunting. This may also now apply, at least locally, to some of the forest-inhabiting African hornbills, although the majority of the smaller and medium sized savanna dwellers appear to not currently be at risk. Where hunting is used to supply the wild bird trade then zoos can make a great impact by refusing to buy wild caught stock and supporting national and international trade embargoes on these birds.

A report, in the *Avicultural Magazine*, of the ICBP/IUCN/CBSG workshop on Asian Hornbills held in 1991 in Singapore suggested that conservation through aviculture seems hopeless since there are few pairs in zoos or private collections and, in any case, zoos cannot or are not willing to devote sufficient space for them to breed (Anon. 1998). This challenging statement shocked me into reviewing the current situation through an analysis of reports in the *International Zoo Yearbooks* of hornbills bred in zoos between 1980 to 1989 (Wilkinson 1992). This showed that although reasonable numbers of *Tockus* (mainly Red-billed Hornbills) were being bred, very few of the larger and conservationally-sensitive Asian hornbills were successfully reproducing.

Reviewing the more recent breeding reports for the period 1990 and 1996 as published in the *International Zoo Yearbooks* the situation has shown some improvement with 14-19 species of hornbill reported as rearing chicks in any single year compared to 6-14 species over the previous decade. The more recent period included more reports on successful reproduction of *Aceros* with a greater number of Wrinkled Hornbills (*Aceros corrugatus*) bred and hatchings of Sulawesi Red-knobbed Hornbill (*A. cassidix*), Papuan Wreathed Hornbill (*Aceros plicatus*), and Writhed Hornbills (*A. leucocephalus*) also recorded. However the number of Great Hornbills and Rhinoceros Hornbills (*B. rhinoceros*) bred remained very low.

Regional Collection Plans have been developed by the American Zoo and Aquarium Association (AZA) *Coraciiformes* Taxon Advisory Group (TAG) and by the European Association of Zoos and Aquaria (EAZA) Hornbill TAG. The AZA plan includes a Species Survival Plan (SSP), the highest level management program, for Great Hornbills which are near-threatened and are also one of the most popular exhibit species. Lower level AZA programs are established or pending for thirteen other species including the near-threatened Rhinoceros Hornbill and Wrinkled Hornbill. Tarictic Hornbills (*Penelopides* spp.) are also included within the plan as models for their threatened relatives (Sheppard, in press a).

The EAZA Hornbill TAG Regional Collection Plan includes EEPs (European Endangered species Programme) for Great Hornbills and for Wrinkled Hornbills. The EEP for Wrinkled Hornbills was initiated when these were listed as vulnerable. Further research, rather than improved conservation action, has revised their status to near-threatened but these remain an important species for captive management if only as a model for other threatened *Aceros* species. An EEP for Writhed Hornbills is pending. Eight European Studbook (ESB) programs include two near-threatened species, namely Rhinoceros Hornbill and Malay Black Hornbill (*Anthracoceros malayanus*) and a model program for Tarictic Hornbills (Brouwer 2000a).

AMBASSADORS AND EDUCATORS

Whilst efforts must continue to be made to improve captive husbandry zoos can contribute to conservation by using these birds as ambassadors to educate their visitors and solicit financial and political support for their conservation in the wild (Worth and Sheppard 1999).

Posters such as two spectacular ones produced by and available from the Wildlife Conservation Society (WCS) illustrating Asian Hornbills are most effective in exciting the zoo visitors' curiosity and illustrating the diversity of hornbills. Equally important, the proceeds from the sales of these posters go directly into conservation projects. The work of WCS hornbill researchers Timothy O'Brien, Margaret Kinnaird and their colleagues is well known.

Interpretation signs can also be simple but effective. One we use at Chester Zoo and aimed at our younger visitors asks simply "Why are Asian hornbills in danger of extinction in the wild?" giving the clues that they occur in tropical rain forests and on islands thus reinforcing the message that these habitats need our protection.

RESEARCH ON CAPTIVE HORNBILLS

The bibliography of Alan Kemp's (1992) monograph on hornbills includes, on my count, *ca* 57 references to research and observations on captive hornbills.

Studies of nesting biology is one area where co-operation between zoo biologists and field researchers can be mutually beneficial with insights from nesting behavior in the wild leading to improved captive production that may benefit the species (Worth and Sheppard 1998).

Captive research can assist in elucidating aspects of hornbill biology especially with regard to their nesting behavior that may be more difficult to study in the wild. Examples include the documentation of the growth rates and development of chicks of the African Grey Hornbill (*T. nasutus*) (Mace 1992). Husbandry research on endangered hornbill species or their close relatives may be especially valuable for *ex-situ* breeding for conservation programs including those currently under way in the Philippines for Visayan Tarictic Hornbills (*Penelopides panini panini*) and Visayan Writhed-billed Hornbills (*Aceros waldeni*).

Recent examples of such research, which to be of value must be published and made widely available, include papers on the breeding biology of Wrinkled Hornbills (Siglers and Myers 1992; Wilkinson *et al.* 1996) and the Writhed Hornbill (*Aceros leucocephalus*) (Myers 2000).

Writhed Hornbills are endemic to the Philippines, occurring on the islands of Mindanao, Camiguin Sur and Dinagat. This species was listed as endangered in the Philippine Red Data Book (Wildlife Conservation Society of the Philippines 1997) and in Birds to Watch 2 (Collar *et al.* 1994). It has been reassessed to near-threatened in the 2000 IUCN Red List (IUCN 2000) and Threatened Birds of the World (BirdLife 2000) on the basis of recent observations suggesting they remain fairly common on Mindanao (Collar *et al.* 1999). Information on the breeding in the zoos of the Writhed Hornbills may be important for the captive breeding program based in the Philippines of its close relative the Visayan Writhed-billed Hornbill.

Previously considered to be conspecific with the Writhed Hornbill (Du Pont 1971; Dickinson *et al.* 1991), recent studies have illustrated that *waldeni* is a distinctive species in which the female has a combination of yellow and azure blue facial skin (Curio *et al.* 1996). An estimated 60-100 breeding pairs remain on Panay with probably fewer on Negros (Klop *et al.* 2000).

Similarly, husbandry research on Tarictic Hornbills *Penelopides* in zoos may assist in the breeding for conservation for endangered species including those for the Visayan Tarictic Hornbill on Negros and Panay. Success has already been shown in breeding this species at the breeding and rescue center on Negros indicating that traffic of information and skills will be a two way process.

For the smaller *Tockus* hornbills and some other African species including the Trumpeter Hornbill zoo breeding seems relatively straightforward (Wilkinson 1992 and 1995; Wilkinson and Merry 1991). However for other species, especially the larger Asian hornbills, captive breeding is rarely achieved and research on developing better husbandry techniques is essential. One of the most popular zoo hornbills is the Great Hornbill, yet if zoos are to continue working with these magnificent birds then many more need to be bred. The Great Hornbill EEP breeding program was initiated in 1991 but by December 1998 only eleven chicks had been hatched, of which three failed to survive, and a total of 28 adult birds lost (Brouwer 2000b).

In terms of better husbandry then the production of management guidelines, e.g. the very useful Great Hornbill Management and Husbandry Guidelines (Galama 1996), is an important step forward, but this needs to be translated into improved breeding success and decreased mortality of the remaining captive Great Hornbills.

Unanswered questions revealed in the preparation of Husbandry Guidelines themselves can stimulate research especially when these relate to the reasons why birds are failing to reproduce in captivity. The use of cameras in nests of both wild and captive hornbills is also revealing aspects of hornbill behavior that were previously inaccessible. In particular in our first season of using these cameras at Chester we discovered that our breeding female Great Hornbill, although laying eggs, was not effectively brooding these. This has led to discussion of, amongst other possibilities, improvements to nest box design.

Research has been conducted to determine predictors of reproductive condition and pair compatibility in Great Hornbills. One example is the work conducted across 19 American zoos examining behavioral and environmental correlates of reproductive success. This suggested that those pairs which breed successfully respond less to people and spend more time in close proximity to each other (Sheppard, in press b). Another is a study that has been initiated through Denver Zoo to assess the reproductive condition in reproductively active and non-reproductively active Great Hornbills by the use of fecal steroid metabolite assays.

A study to clarify the systematic identity of Tarictic Hornbills in European zoos using mtDNA analysis is being directly supported by Frankfurt Zoo. This study by Stephan Huebner, of the University of Frankfurt, is of particular interest in that the Frankfurt collection includes birds that resemble Polillo Tarictic Hornbills (*Penelopides manillae subnigra*). A male Tarictic at Chester Zoo, and possibly wild caught, closely resembles *Penelopides affinis samarensis*. However, as always, caution must be taken as the complete history and origins of captive birds are rarely known and the majority if not all of the Tarictic Hornbills presently in captivity in European zoos are considered likely to be of hybrid origin (Bolton 2000).

Other taxonomic studies utilizing mtDNA techniques and feathers collected from captive hornbills include that of Woodruff and Srikwan (1998) using feathers from birds at San Diego Zoo. George Amato of the Wildlife Conservation Society/Bronx Zoo has also conducted mtDNA studies on Great Hornbills and Rhinoceros Hornbills with the aim to investigate whether this reveals any consistent genetic differences between different populations of each species.

Zoo hornbills also make excellent subjects for undergraduate behavioral research projects. A recent example of this was the comparative study of the behavior of pairs of Rhinoceros Hornbills and Wrinkled Hornbills at Paignton Zoo, Chester Zoo and Paultons Park. This study for example suggested that interactions between hornbills held in adjacent aviaries may hinder successful reproduction and that nesting attempts of some pairs appear to be terminated by the failure of the female to seal the nest entrance completely (Harris 2000). These studies, whilst themselves often incomplete, can stimulate further research as well as the students' interest in hornbill biology.

SUPPORT OF FIELD RESEARCH

Frankfurt Zoological Society has funded important field research in the Philippines on two threatened hornbills: the endangered Visayan Tarictic Hornbill and the critically endangered Visayan Writhed-billed Hornbill. The team involved has recently published some of this work in the journal *Bird Conservation International* indicating only 750-1000 breeding pairs of Visayan Tarictic Hornbills and perhaps less than 75 breeding pairs of Visayan Writhed-billed Hornbill remain on Panay (Klop *et al*. 2000).

Many zoos, zoo organizations and bird parks have funded field surveys in the Philippines. An investigation of the distribution and ecology of the Luzon Tarictic Hornbill on the Polillo Islands received support from Vogelpark Avifauna, Alphen a/d Rijn, Netherlands, and the German-based Zoological Society for the Conservation of Species and Populations (Gonzalez and Dans 1996). This survey estimated up to 1000 Polillo Tarictics Hornbill on Polillo Island and fewer than 50 individuals remaining on Patungan Island. On both islands the main threats to these hornbills were the loss of lowland dipterocarp forest and unsustainable hunting.

Chester Zoo helped fund the Oxford University-University of the Philippines Los Baños "Polillo 1999" expedition, which although not specifically aimed at hornbills, included observations on these as well as other birds, reptiles and amphibians on the Polillo Islands.

Supporting local university students can also be an option. In 1992, Chester Zoo assisted Siobhan Cleaver, an undergraduate at the Manchester Metropolitan University, through the award of a Veterinary and Zoological Studentship, to conduct field research on the Sumba Hornbill (*A. everetti*).

Alexis Cahill's PhD studies of the ecology of two sympatric hornbills on Sulawesi, where she investigated habitat use by Red-knobbed Hornbills (*A. cassidix*) and Sulawesi Tarictic Hornbills (*P. exharatus*) also received some financial support from Chester Zoo.

SUPPORT OF FIELD CONSERVATION

Zoos can support field conservation programs through direct funding of field surveys and wardening programs. The Polillo islands, which lie off southern Luzon in the Philippines, are home to the Polillo Tarictic Hornbill. This distinctive race of the Luzon Tarictic now has its main stronghold on Polillo Island. Although extending into adjacent disturbed forest to feed it is dependent on the small watershed forest to the north of Polillo town. Many zoos including Denver Zoo, Columbus Zoo, Bristol Zoo, Melbourne Zoo and Vogelpark Avifauna have supported surveys of the endemic fauna on Polillo Island and elsewhere in the Philippines.

Chester Zoo now funds the salaries of the warden and eight assistant wardens on Polillo Island as well as supporting costs for their assistance by staff from the University of the Philippines Los Baños. The wardens' roles include preventing hunting in the now protected watershed area, and this has community support of the mayor and townspeople. At a recent local festival the Polillo "Taliktic" was featured both as a person in a hornbill costume and depicted on T-shirts.

A Philippine Hornbills poster was produced by William Oliver in his *Only in the Philippines* series and 3,000 distributed to many government and local non-governmental organisation offices and villages on Panay and Negros. This poster which illustrated the Visayan Writhed-billed Hornbill, Visayan Tarictic Hornbill and Sulu Hornbill (*Anthracoceros montani*) was produced in three languages, Tagalog, Cebuano and English, with funding from Vogelpark Avifauna, and from Birds International Inc. Additionally, 500 copies of a flyer based on this poster and with text in Ilonngo were produced and distributed on Panay by the Ruhr University hornbill research team supported by Frankfurt Zoological Society. A revised poster illustrating endemic Philippine Hornbills is under production with funds donated by Chester Zoo.

The Thailand Hornbill Project, developed by Professor Pilai Poonswad, offers an opportunity to support both local community-based conservation and scientific research. Local villagers who previously earned extra money by selling hornbill chicks taken from their nests instead are now paid to protect these nests and gather scientific data for field researchers. The hornbill nest adoption program is an excellent means for zoos to link direct field support with their zoo birds. This scheme encourages individuals or institutions to adopt individual nests and rewards them with details of the history of the adopted nest for the year of their adoption. Nests available for adoption are those of Great Hornbills, Rhinoceros Hornbills, Helmeted Hornbills (*Rhinoplax vigil*), Wreathed Hornbills (*A. undulatus*), White-crowned Hornbills (*Berenicornis comatus*) and Bushy-crested Hornbills (*Anorrhinus galeritus*).

Information on the adopted hornbills including a photograph of their nesting tree can be presented to the zoo's visitors illustrating the links between zoos and field conservation. Zoos and zoo organisations in the USA already having funded this nest adoption project include Audubon Park Zoo, Wildlife Conservation Park- Bronx Zoo, Saint Louis Zoo, Denver Zoological Gardens, Toledo Zoo, the Kansas City and Birmingham Zoo Chapters of the American Association of Zookeepers, Sacramento Zoo and Woodland Park Zoo. Perhaps adoption schemes could, in the future, be developed with live web-cams of hornbill nests that could be presented to visitors at zoos directly supporting conservation and research?

Hornbills may be hunted for feathers or casques for ceremonial purposes or especially in West and Central Africa for the fetish market. In Southern Africa parts of the Southern Ground Hornbill are used in local medicine as a tonic and to produce sagacity (Kemp 2001). In Borneo, the large black and white tail-feathers of Rhinoceros Hornbills are worn by local people as part of their traditional ceremonial costume. Christine Sheppard, of the Bronx Zoo, has developed a scheme to encourage zoos, especially in the USA, to collect molted tail feathers of both Rhinoceros Hornbill and Great Hornbill. These feathers are collected at New York to be then shipped with CITES papers to Malaysia and Indonesia.

BREEDING AND RESCUE CENTERS

Construction of hornbill aviaries at the Negros Forests and Ecological Foundation Inc Biodiversity Conservation Center (NFEFI-BCC), Bacolod City, Negros and at the Mar-it Wildlife Conservation Park, Lambunao, Iloilo, on Panay has been greatly assisted by financial donations from zoos including Dresden Zoo, Germany, Melbourne Zoo, Australia, Vogelpark Avifauna, Netherlands, Chester Zoo, England and the German Zookeepers Association (Bundesverband der Zootierpfeger e. V). These funds have been marshalled by William Oliver, who manages the *Fauna and Flora International* Philippines Biodiversity Conservation Programs, and by Roland Wirth and the Zoological Society for the Conservation of Species and Populations (ZSCSP).

TRAINING AND STAFF EXCHANGES

Training opportunities of staff from hornbill range countries have been enabled through zoo sponsorship. Examples include the sponsorship of staff from the Mar-it Wildlife Conservation Park and NFEFI Biodiversity Conservation Center by the Jersey Wildlife Preservation Trust (now the Durrell Wildlife Conservation Trust) to attend their specialist course on Conservation and Captive Management of Threatened Species at Jersey Zoo. Additional support was given from other European zoos enabling these staff to gain husbandry experience by visiting their collections. Reciprocal visits of both curatorial and keeping staff from host zoos have benefited both parties and hornbill conservation. In early 2001, two keepers from Chester Zoo spent a month working in two of the breeding and rescue centers in the Philippines.

CONFERENCES AND PUBLICATIONS

El Retiro Bird Park, Malaga, hosted the 2nd International Hornbill Workshop in 1997 and sponsored the attendance of three important field researchers. Additionally the El Retiro Bird Park donated the registration fees of all workshop delegates and the proceeds from T-shirt sales to the EAZA Hornbill Taxon Advisory Group for the funding of future *in-situ* conservation projects for hornbills. This, the 3rd International Hornbill Workshop Phuket, Thailand 2001 received some funding from the Bronx Zoo, New York, the Puget Sound Chapter of the American Association of Zoo Keepers and the AZA *Coraciiformes* TAG.

The dissemination of information and networking of hornbill enthusiasts including researchers and zoo personnel is also important for effective hornbill conservation. The production of *World Hornbill News* has been facilitated by either funding or institutional support from Aalborg Zoo, Denmark, Zooparc de Beauval, France, Burger's Zoo, Netherlands, and the National Foundation for Research in Zoological Gardens, Netherlands.

Although not specifically directed to hornbill conservation, the sponsorship of species accounts in *Threatened Birds of the World* (BirdLife International 2000) for the Sulu Hornbill (*Anthracoceros montanii*) (Berlin Zoo), Visayan Tarictic Hornbill (EAZA Hornbill Taxon Advisory Group) and Visayan Wrinkled Hornbill (Chester Zoo) has assisted in the publication and dissemination of these accounts world-wide.

The hornbill bibliography produced by Dennis Vrettos, formerly of Gatwick Zoo and now working at Birdland, Bourton-on-the-Water, which he made freely available to hornbill enthusiasts and researchers, has been invaluable to many as a very useful compendium of published information.

CURRENT AND FUTURE PROJECTS

A memorandum of agreement (MOA) between the Department of Environment and Natural Resources (DENR) of the Republic of the Philippines, Vogelpark Avifauna and the North of England Zoological Society, Chester Zoo, has now been drafted in support of the Philippine Hornbills Conservation Program. Future priorities for this program include surveys of Luzon Rufous Hornbill (*B. hydrocorax hydrocorax*) and the Luzon Tarictic Hornbill (*P. manillae manilllae*) and to determine whether the presumed extinct Panay Tarictic Hornbill (*P. panini ticaensis*) may survive on neighbouring islets. Additionally, there is a need for the establishment of more effective protected areas for the critically endangered hornbills on Negros and Panay.

In addition to the Philippine Hornbill Conservation Programe and the Thai Hornbill Family Adoption Project which deserve our support, there may be other opportunities to assist hornbill conservation and research programs elsewhere. Christian Boix-Hinzen, for example, is currently developing a conservation plan for hornbills in Namibia that involves community work with local schools and funding is sought for research on Southern Ground Hornbills in South Africa. By the time this paper is presented these projects may be fully supported but with increasing pressure on hornbills in the wild similar opportunities for zoos to support field conservation and research will certainly be presented.

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The constitution of a new successful breeding pair of Writhed Hornbill (*Aceros leucocephalus*) at the Ornithological Park El Retiro (Málaga, Spain), using a dynamic of group

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Abstract In March 2000 at the Ornithological Park El Retiro, after two consecutive years without breeding success of the Writhed Hornbills (*Aceros leucocephalus*) obtained from Audubon Park Zoo and San Diego Zoo, we measured some biometrical and blood parameters of breeding pairs as part of a research project carried out by the Universities of Málaga and Extremadura. We designed an experiment called "dynamic of group" to study the possibility of the establishment of new pairs. After eight days a first new pair was formed and was established. Thirteen days later another pair was formed, and which eventually did not breed, possibly because the female had been hand-reared by humans. Few hours after the pairings were established, courtship behaviour was observed. The first copulation was seen on April 30, 2000. On May 2 plastering materials were accumulated and was the last day that the female was seen outside the nest. The nest entrance was closed on May 26. The female laid two eggs and after thirty days of incubation two chicks hatched at two- to three-day intervals. After 117 days of confinement the female emerged from the nest with the two chicks. The failure of the second new pair may have been because the female has been hand-reared. This should be an important consideration for breeding some endangered species in captivity.

INTRODUCTION

The Writhed Hornbill (*Aceros leucocephalus*) is one of the smallest species of the genus *Aceros*, with a body length of 68-70 cm and is endemic to the evergreen tropical forests of the Philippine island of Mindanao. It is also found on the smaller and nearby islands of Caminguin, Dinagat and Siargo (Fig. 1). This species has been reported to be most common in primary forests below 1000 m (Rand and Rabor 1960; Kemp 1995).

The Writhed has been classified as endangered by Collar *et al.* (1994) due to hunting and trapping pressures for the wild bird trade (Kemp 2001) and continued loss of habitat, especially on the smaller islands. The breeding habits of this species are almost unknown in the wild, although a sealed nest was once recorded in March (Dickinson *et al*. 1991).

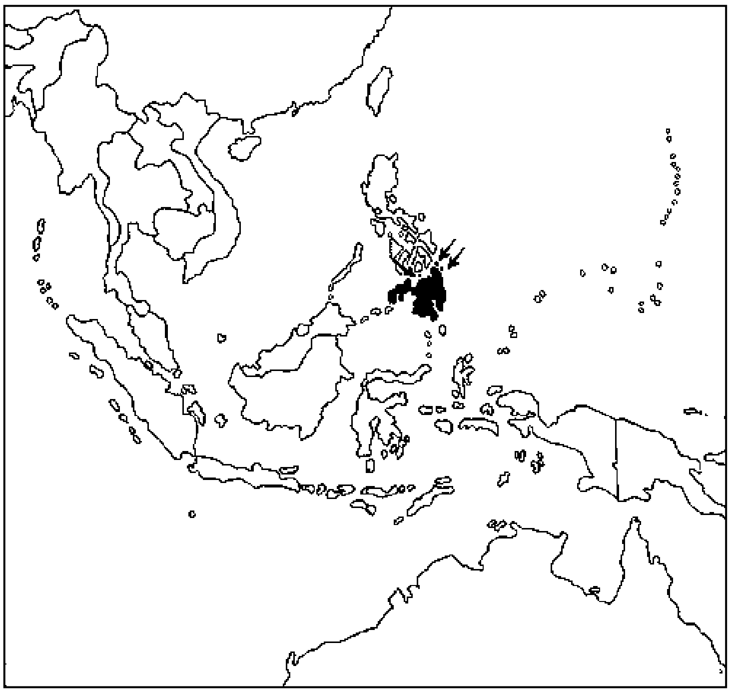

Figure 1. Distribution of the Writhed Hornbill (modified from Kemp 1995).

In 1996, the Writhed Hornbill was selected by the European Endangered Species Program (EEP) Hornbill Taxon Advisory Group for EEP management in Europe. In support of that effort, six individuals of the species were acquired by the Ornithological Park El Retiro, Málaga, Spain from the United States, four from the Audubon Park and Zoological Garden in New Orleans, and two from the San Diego Zoo, to establish a captive stock in Europe.

Until 1996, successful breeding in captivity for this species had only been reported from the Miami Metrozoo, from 1988 through 1990. The breeding female from the Miami Metrozoo was loaned to the Audobon Zoo and successfully reproduced there in 1993 and 1995. All offspring of the pair at Audubon Park Zoo fledged in the 1993 and 1995 breeding seasons were exported to the Ornithological Park El Retiro in 1996 (Myers 2000).

In 1997, the pair at the Audubon Park bred successfully again. The same year one chick was also successfully reared by a new breeding pair formed at the Ornithological Park El Retrio. Consequently, in 1997, the pairs at the Audubon Park and El Retiro Park were the only two successful breeding pairs in captivity world-wide. During the years 1998 and 1999 there were no successful breeding of this species at El Retiro, although an additional pair was formed.

METHODOLOGY

In the year 2000 there were seven specimens of Writhed Hornbill at the Ornithological Park El Retiro, which represented 1/3 of the world captive population. The research project began in El Retiro, carried out by the University of Málaga and the University of

Extremadura, and financed by the Spanish Government and the European Union, which included the improvement of the breeding in captivity of endangered bird species, such as the Writhed Hornbill.

In the beginning of March 2000, before the breeding season of the species, we measured some biometrical features of the individuals of Writhed Hornbill and collected blood samples for analysis of blood parameters. The biometrical features analyzed were the wing length, measuring both the eighth primary (P_8) and the maximum wing cord to the nearest millimetre, the body mass, using a Pesola 5,000 g spring balance to the nearest 50 g, and the total head length, using a dial reading vernier calliper.

A blood sample (1–2 ml) was collected from the brachial vein of each specimen using 2 ml syringes and 22 G needles and was carefully transferred to a collecting tube from which small samples were removed immediately for hematocrit value determination, in heparinized capillary tubes. All tubes were kept at 4ºC in cool containers until they were centrifuged within 6 hours after the sample was drawn. In the laboratory, microcapillary tubes were centrifuged at 6,500 rpm for 15 minutes, and the hematocrit value was determined directly on a microhematocrit reader. Plasma was obtained by centrifugation (6,500 rpm, 15 minutes) and stored at -20°C until the analysis was performed.

For each sample, twelve parameters including uric acid, urea, total proteins, glucose, chloresterol, triglycerides, alanine aminotransferase (ALT), aspartate aminotransferase (AST), lactate dehydrogenase (LDH), alkaline phosphatase (AP), calcium, and phosphorus were analyzed with an autoanalyzer (Falcor 300, Menarini diagnostics) with the reagents recommended by Menagent (Menarini diagnostics). Ions Na, K and Cl were assayed with a Spotlyte Na/K/Cl analyzer (Menarini diagnostics). Means and ranges were calculated for each parameter investigated.

In March 2000, after some years without breeding success, an attempt to facilitate pairing of Writhed Hornbills was made. On March 30, 2000, we set up an experiment called "dynamic of group" to study the possibility of pairing establishment. This experiment was performed by keeping the pair which successfully bred in 1997 in an aviary, and in April we kept the other five individuals (two females and three males) together in another aviary under the continuous observation of a keeper. This experiment was designed to allow the females to select other males to breed.

The aviary where the first new pair was established was of 8 x 4 x 3 m of which 1.5 x 4 m was covered. The vegetation consisted of *Ficus* sp. and was to resemble their natural habitat as much as possible. The nest was installed in the aviary prior to the establishment of the pair. The nest was a wooden barrel measuring 42 cm in diameter and 78 cm in height. It was installed at 1.5 m above the ground and placed on the side of the aviary opposite the staff access door. The aperture measured 10 x 18 cm and was located approximately 27.5 cm from the base of the barrel. A door measuring 15 x 20 cm was situated in the back of the barrel to permit the checking of the eggs or the chicks while the female was imprisoned. We filled the bottom of the barrel with a mixture of peat and sand up to 10 cm to the aperture. We put plastering material, which consisted of a mixture of manure, water, sand and straw, inside the aviary.

RESULTS

The range and average values of the biometrical parameters measured are shown in Table 1 and those of the blood parameters in Table 2.

Table 1. Biometrical parameter values obtained for males, females and two immature Writhed Hornbill. Weight values are in grams and length values are in millimetres

Parameter		Male	Female	Immature
Weight (g)				
	Range	1,200-1,340	820-960	640-750
	Average	1,282.5	890.0	695.0
	n	4	2	2
P_8 length (mm)				
	Range	241-232	187-190	No measurement
	Average	236.5	188.5	-
	n	2	2	-
Wing length (mm)				
	Right	350	No measurement	No measurement
	Left	344	-	-
	n	1	-	-
Head length (mm)		No measurement	No measurement	123
	n	-	-	1

Table 2. Blood parameter values obtained for males, females and an immature Writhed Hornbill. ALT: alanine aminotransferase, AST: aspartate aminotransferase, LDH: lactate dehydrogenase, AP: alkaline phosphatase

	Male			Female			Immature
	Range	Average	n	Range	Average	n	
Hematocrit (%)	42-48	44.6	3	42-45	43.5	-	2
Eric acid (mg/ dl)	6.6-7.4	7.03	3	7.4-8.4	7.9	-	2
Chloresterol (mg/dl)	109-130	119.5	-	-	187	1	171
Triglyceride (mg/dl)	81-211	146	2	-	75	1	181
Urea (mg/dl)	4-6	5	3	5-8	6,5	2	4
Glucose (mg/dl)	285-340	317	3	-	266	1	304
ALT (IU/l)	-	69.9	1	-	55.8	1	-
AST (IU/l)	-	254.3	1	-	240.1	1	419
AP (IU/l)	-	85	1	-	57	1	336
Total Proteins (mg/dl)	3.02-3.3	3.13	3	3.19-3.83	3.51	2	3.05
Ca (mg/dl)	7.3-8.69	7.995	2	-	8.17	1	9.46
P (mg/dl)	3.2-3.7	3.45	2	-	1.2	1	3.3
LDH (IU/l)	-	-	-	-	980.1	-	-
Na (mmol/l)	151.1-155.5	153.3	2	-	155.3	1	-
K (mmol/l)	3.5-4.07	3.785	2	-	2.7	1	-
Ca (mmol/l)	-	113	1	-	116.4	1	-

Eight days after the beginning of the dynamic of group, a new pair was formed, which was immediately established in the same aviary where the male was before the dynamic commenced. Thirteen days later another pair was formed. Then, the unpaired male was removed and put in a separate aviary while the new pair stayed in the same aviary where the dynamic was performed. This second new pair did not breed, since the female did not accept the male.

By April 28, and only few hours after the pair was established, courtship behavior, including food offerings from male to female, nest inspection by the pair, head preening, vocalizations, and chasing flights were observed. The first copulation was seen on April 30, 2000. By May, plastering materials were accumulated on the sides of the nest entrance. This was the last day that the female was seen outside of the barrel. The male was observed participating in the plastering process.

The nest entrance sealing was complete on May 26 and only a small elliptical opening was left for the male to feed the female. The female laid two eggs and after approximately thirty days of incubation two chicks hatched within a two to three day interval. After a total of 117 days of confinement, the female emerged from the barrel and the two chicks followed her on the same day. The chicks were successfully reared by their two parents. In March 2001, we measured the biometrical and blood parameters of a chick (Tables 1 and 2).

The pair which bred in 1997 also tried to breed in this breeding season. On May 23 the female went into the nest and accumulated plastering materials at the entrance of the nest. Although two eggs were laid, and the female stayed inside the barrel for a prolonged time, breeding was not successful.

DISCUSSION

The dynamic of group as that described here is a risky operation, because the newly formed pairs are territorial and may attack and injure other individuals. However, when previously established pairs seem to be incompatible for breeding, it may be worth the risk to try the new pair formation and leaving them in the same aviary, where a well consolidated behaviour in the context of a pair may be modified by the more complex influence of a group of individuals.

The second new pair formed in the dynamic of group was unsuccessful in breeding, possibly because the female has been hand-reared. The female accepted the fruit offered by the male, but showed an aggressive behavior toward the male during the chasing flights. This female showed aggressive behavior to all female researchers, and performed courtship offerings of fruits to a male member of the research team. This highlights the importance of the individuals reared by their parent in the captive stock of endangered species. Except for one adult measured in the spring of 2001, the values obtained for the blood parameters are within the ranges published for other species, none of which are hornbills (Gee *et al.* 1981; Alonso *et al.* 1991; Polo *et al.* 1994; de le Court *et al.* 1995).

All this information could be also of interest for the conservation and captive management of a closely related species, the critically endangered (CR) Visayan Writhed-billed Hornbill (*Aceros waldeni*) (IUCN 1996).

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Breeding Papuan Wreathed Hornbill *Aceros plicatus* at the Jurong BirdPark, Singapore

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Abstact The Jurong BirdPark has successfully bred a number of hornbill species. Here we report our experiences in breeding the Papuan Wreathed Hornbill (*Aceros plicatus*). Experimentation and alterations in feeding, nest box design and perch position, among other factors, led to successful breeding after several failed attempts. Sustained captive breeding of this and other hornbill species could reduce hunting pressure on wild populations.

INTRODUCTION

The Hornbill Exhibit at Jurong BirdPark, Singapore, opened in 1990 and maintains a comprehensive collection of thirteen Asian and four African species. The most recent nesting attempts were Von der Decken's Hornbill (*Tockus deckeni*), the Black Hornbill (*Anthracoceros malayanus*), the Great Hornbill (*Buceros bicornis*) and the Papuan Wreathed Hornbill (*Aceros plicatus*).

This paper examines the problems encountered in breeding the Papuan Wreathed Hornbill in captivity between the years 1992 and 2001 and focuses in particular on feeding practices, nest box design and perch position.

The Papuan Wreathed Hornbill, native to the forests of the Moluccas, New Guinea and the Solomon Islands (Kemp 1995) is listed under CITES Appendix II. Although it is very common in the wild (Hoyo *et al.* 2001), its breeding status in captivity is limited. Only a few zoological gardens (San Diego Zoo, San Diego Wild Animal Park, Philippines Bird International, Garden of Tropical Birds, La Londe France, Ornithological Park El Retiro, Spain, and the Florida Avicultural Breeding and Research Center) have bred them successfully (Priryambada *et al.* 1995; Scheres and Alba 1997). Therefore, the Papuan Wreathed Hornbill was specifically chosen for this study from among nine species bred at the Jurong BirdPark, Singapore in order to address both the lack of published materials available and previous difficulties encountered in breeding this species.

Papuan Wreathed Hornbill and its aviary at the Hornbill Exhibit

On July 26, 1990 two male and two female Papuan Wreathed Hornbills were introduced into an aviary which measured 12.5 m L x 8 m W x 12 m H. The aviary netting used was 3 mm thick knotted into a 1x2 inch pattern which was considered necessary to withstand the hornbills' strong pecking capability.

The aviary was heavily planted with West Indian Cherry (*Muntingia calabura*), Banana (*Musa paradisica*), Macarthur Palm (*Ptychosperma macarthurii*), African Mahogany (*Khaya senegalensis*) and the Common Pulai (*Alstonia angustiloba*). These trees provided food and/or shade. A variety of palms and shrubs were also planted to vary the height and to thereby simulate forest stratification.

A feeding tray was placed on a high pole to stimulate an arboreal feeding habit and a plate was used to prevent contamination. A water sprinkler above the aviary was turned on daily for 5 minutes in the afternoon and for 10 minutes during the breeding season (November-January) to soften the ground and assist the birds in the collection of mud to seal the nest hole. No additional water container was provided.

Rambutan (*Nephelium lappaceum*) and Tembusu (*Fagraea fragrans*) branches were selected for use as perches. The provision of these perches within the aviary takes into account the preferences of the birds. They are very active and like to move around from perch to perch, just as they hop from tree to tree in the wild. The perches were therefore linked and positioned at different heights, both close to the nest box to allow the male to feed the female during the nesting period and near the front of the enclosure to allow visitors a closer view of the birds.

Papaya, banana, honeydew, low-iron pellets, hard-boiled eggs, bread and long beans were given twice a day as a regular diet. Leftover food was cleared in the late afternoon. An additional feeding and food supplement was scheduled in the late afternoon during the breeding season (Table 1).

Table 1. Feeding schedule of the Papuan Wreathed Hornbill according to phases in its annual cycle at Jurong BirdPark. Meatball = a mixture of hard-boiled egg, bread, minced meat and cooked rice, Kaytee Exact Softbill = Manufactured in U.S., Low-iron Pellet = manufactured in Singapore, Nekton MSA = Manufactured in Germany

Phase	Feeding time	Food item
Regular Feeding (non breeding season)	0830, 1330 hrs	Papaya, Banana, Honeydew, Long Bean, Bread, Hard-boiled Egg and Low-iron Pellet
Courtship Feeding	0830, 1330 hrs	Papaya, Banana, Honeydew, Long Bean, Bread, Hard-boiled Egg and Low-iron Pellet
	1030 hrs	Grape and Cherry
Nest Sealing	0830, 1330 hrs	Papaya, Banana, Honeydew, Long Bean, Bread, Hard-boiled Egg and Low-iron Pellet
	1030 hrs	Macarthur Palm Fruit, Cooked rice, Sweet Potato and Meatball
Egg Incubation	0830, 1330, 1630 hrs	Papaya, Banana, Honeydew, Long Bean, Bread, Hard-boiled Egg, Low-iron Pellet and Macarthur Palm Fruit
Chick Rearing	0830 hrs	Papaya, Banana, Bread, Soft bodied Crickets, White Mealworms and Meatball
	1330 hrs	Hard-boiled Egg, Low-iron Pellet and soaked Kaytee Exact Softbill
	1630 hrs	Papaya, Banana, Macarthur Palm Fruit, Soft bodied Crickets and White Mealworms

RESULTS

The keepers used grapes or cherries to spot signs of courtship and to select from the four Hornbills the best potential mating pair. On December 3, 1990, one pair was seen tossing grapes to each other in a "courtship feeding behavior" and was judged to have bonded. The other unpaired birds were then transferred to an off-exhibit holding area.

On December 15, 1990, a plywood nest box (63 x 63 x 80 cm) with a square entrance hole (25 x 32 cm) was introduced facing westward. Table 2 shows records of breeding attempts in various years and successful breeding in 1997.

Table 2. Breeding record

Year	Female entered Nest box	Chick hatched Confirmed	Female left Nest box	Chicks left Nest box
1992	20 Jan 1992		20 Mar 1992 broken eggshell	
1993	5 Jan 1993		10 Mar 1993 2 infertile eggs	
1994	7 Jan 1994		26 Mar 1994 2 infertile eggs	
1995	01 Jan 1995		15 Mar 1995 2 infertile eggs	
1996-1997	25 Nov 1996	13 Feb 1997 13 Mar 1997	28 Mar 1997	29 Mar1997 3 Apr 1997
2001	29 Jan 2001			

On January 2, 1992, the female was observed collecting mud from the ground but avoided a mixture of mud and earth on the tray provided by the keeper. On January 10, the rejected mixture was added directly into the nest box because no plastering material had been carried inside. On January 20, the female entered the half-sealed nest box. She left the nest box on March 20, 1992, leaving behind broken eggshells.

In June 1992 the nest box entrance hole was redesigned as a diamond shape (50 x 15 cm) in an attempt to narrow the entrance and encourage complete sealing. Black netting was used to screen off the back of the aviary to give more privacy to the nesting female. Further breeding attempts were seen in 1993, 1994 and 1995 with two infertile eggs but again involving an incompletely sealed nest entrance hole. This time, however, the eggs were not broken.

In December 1995, the black netting was removed and the decision was made to introduce more perches. A long horizontal perch was fixed from the nest hole to the tree located closest to the feeding tray. Two additional perches were placed in a location that afforded an improved lookout view for the birds. On November 1, 1996, mating was observed on the new perch in the morning, before feeding time.

The female began sealing the nest entrance on the Nov 3, 1996. She entered the half-sealed nest box on November 25, 1996. The male was seen feeding the female with fruits of Macarthur Palm (Table 3) that had been planted in the aviary. Macarthur Palm fruit was introduced to the diet of the nesting female, while crickets, meatballs and mealworms were not taken during incubation period. Macarthur palm fruit (98–102 fruits), papaya (15-30 pieces), banana (11-13 pieces) and bread (5-11 pieces) were given by the male. The nesting female used the nest hole to void feces an average of two to three times a day. The male frequently used the lookout perch above the aviary door to monitor the surroundings.

Table 3. Some scientific information and nutritional data for the Macarthur Palm

Scientific Name:	*Ptychosperma macarthuri*
Family:	Arecaceae
Origin :	New Guinea
Protein:	1.7%
Fat:	0.56%
Fibre:	23.5%
Iron:	12.7 ppm
Phosphorus:	0.0394%

On January 16, 1997, a soft chirping sound was heard. White-skinned mealworm (30), soft cricket bodies (30), soaked Kaytee Exact Softbill (10 pieces) and meatballs (5) were immediately added to the diet at every feeding. Nekton MSA calcium powder was sprinkled on top. The proud male accepted all the food provided and carried this in his pouch, ranging from 3 to 27 items at a time. He regurgitated and fed from the nest box perch to the female a little at a time. He spent most of the time perching near the nest.

On Febuary 13, 1997, the first chick's head was seen peeping through the hole and on the March 13, 1997, a second chick was confirmed. On March 28, 1997 the female came out of the nest and rested for five days without perfoming any feeding duties. Most of the time was spent preening her feathers and roosting in a shady area in order to regain energy and exercise after her three months of confinement.

The first chick emerged on March 30, 1997 and on April 3, 1997, the second chick emerged from the nest. Both chicks appeared to be female. Subsequently no nesting attempts or aggressive behavior was observed and the whole family (the mating pair and the two young offspring) lived together until 2001.

On January 1, 2001, courtship feeding was again observed. Macarthur Palm fruit and cherries were given. The male carried Macarthur Palm fruit to paste onto the nest entrance and the surrounding area. The female joined in and then went inside the nest and started to seal from the inside with mud, papaya, banana and feces. While the female was inside the nest box the male fed the older female chick. The younger chick ignored the whole process and perched on the lookout perch next to the passageway. Although the nesting female did not show any aggressive behavior towards either of the two young females, she came out from the nest whenever the male fed the older female chick.

Both young females were transferred out of the aviary on January 19, 2001 after it was confirmed that no cooperation in nesting activities had been observed. On January 29, 2001, the female was contentedly sitting inside the nest box (Table 3) and did not leave the box anymore after that. The nest box was still unsealed but plastered with palm fruit at the entrance.

DISCUSSION

1. The correct positioning and location of the perches can support the production of fertile eggs, giving close access to the male when feeding and guarding the nesting female and improving the vantage point for the birds.
2. There was no significant breeding benefit seen from placing netting at the back of the aviary.
3. For a successful breeding result only a true pair should be kept in the aviary. Pair bonding can be identified by introducing grapes or cherries to stimulate courtship feeding.
4. The reason that the male pastes the nest box entrance with Macarthur Palm fruit is unknown. It was observed in the recent nesting season of January 2001.
5. Only partial nest entrance sealing has been observed over six consecutive breeding seasons. It is still unclear whether the birds are sufficiently secure that they feel safe to leave the hole half-open when in captivity. In the wild they seal up the entrance leaving only a narrow vertical slit which prevents predators from entering the nest.
6. Food intake varies depending on the breeding stage. Palm, bread, banana and papaya are selected during the sealing period. Banana, papaya, bread and palm are consumed during incubation phase, and mealworm, crickets, meatballs and Kaytee Exact Softbill are taken during the rearing period.
7. The nesting season is from November to January. Sprinkling or spraying water in the aviary creates artificial rain and simulates the monsoon season. This encourages mud digging activities so that fresh sealing material can be taken from the ground.
8. The collection of nesting materials was not observed with this *Aceros* species unlike the Black Hornbill (*Anthracoceros malayanus*) which had been observed to use a lot of dried leaves to lay a nest floor (Wong and Khin 1998). Therefore pre-nesting material such as a mud and earth mixture should be provided once the breeding season begins.
9. After the female emerged while the chicks were still left inside, the nest box entrance opening was not resealed.
10. No cooperative nesting behavior was observed in this species. As soon as the chicks can feed themselves, they should be transferred out of the aviary so as not to prolong the breeding gap.

CONCLUSION

It is hoped that our findings and experience will contribute to the successful captive breeding of this exotic species worldwide. By increasing the numbers of captive-bred birds available, more exchange programs between institutions can be planned thus helping to reduce trapping pressure in the wild.

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SHORT NOTE

Characteristics of Helmeted Hornbill nests in Thailand

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Abstract Observation on 15 nests of Helmeted Hornbill *Buceros* (*Rhinoplax*) *vigil* revealed that all nests possessed a very distinctive characteristic, i.e. with a knob or stump at the top, bottom or the side of the nest entrance. This protrusion served as a platform for the male to stand on when he fed the brood. We have never observed any males clinging to the nest entrance. It is interesting to note that the majority of the nests were trees in the family Dipterocarpaceae, particularly Ta Khian (*Hopea* spp.) and Kaa-lo (*Shorea faguetiana* Heim.). The diameter at breast height (dbh) of the nest trees ranged from 105-216.6 cm (mean 158.5±40.1 cm, n = 14), while their height ranged from 26-70 m (mean 44.6±10.9 m, n = 15). The nest trees were situated at altitudes ranging from 300-535 m.a.s.l. (mean 389±59.9 m, n = 15). These trees were situated on slopes ranging from 5-60% (mean 30.7+16.6%, n = 14).

INTRODUCTION

Hornbills normally use an existing suitable cavity in a large tree due to their inability to excavate their own nest cavities. Suitable nest availability is an important factor which influences the reproduction of hornbills (Poonswad *et al*. 2000). Most of the hornbill nests are situated in the trunk of trees (Poonswad 1995) with entrances that are elongated or round. For many hornbill species, it is not necessary to have a perch in front of the nest for feeding since the males can cling to the lower edge of the entrance. Although hornbills have limited choices for cavity use, Poonswad (1995) reported some characteristics that may attract certain species. For example, the Great Hornbill *Buceros bicornis* tends to choose a nest with an elongated entrance. The specific characteristics of nest choice may be related to the morphology of certain hornbill species. In our study, we observed and documented characteristics of nests used by Helmeted Hornbills *Buceros* (*Rhinoplax*) *vigil* in an attempt to find determining factors for nest choice in this species.

METHODOLOGY

Study areas

Helmeted Hornbills were studied in Sri Pang-Nga National Park (8°53′-9°20′ N and 98°23′-32′ E) Pang-Nga Province in 1988-1989 and in Budo-Sungai Padi National Park (6°0′-40′ N and 101°30′-55′E), Yala and Narathiwat Provinces in 1994-2000.

All sixteen nests, including three nests of which Helmeted Hornbills obtained following inter-specific competition with other hornbill species, including the Bushy-crested Hornbill (*Anorrhinus galeritus*), Rhinoceros Hornbill (*B. rhinoceros*) and Great Hornbill (*B. bicornis*), possessed a very specific characteristic with a knob or stump on the top, bottom or at the side of the nest entrance (Fig. 1). This protruding structure served as a platform for the male to land and stand on when he fed the brood.

Figure 1. Some examples of characteristics of Helmeted Hornbill nests (a-e)

Nest locating

Lone male Helmeted Hornbills were followed and when they were observed to arrive at a nest the information recorded included nest tree species, diameter at breast height (dbh), tree height, nest height above the ground, altitude at the nest tree, slope at the nest tree and others.

All nests were photographed and sketched except for some broken ones.

RESULTS

Throughout the study sixteen Helmeted Hornbill nests were found. Among these, one nest was found in Sri Pang-Nga National Park, the rest were found distributed on Budo Mountain in Budo-Sungai Padi National Park. Nest tree species and some characteristic parameters of the trees and nests are summarized in Table 1.

Table 1. Nest tree species and characteristic parameters of fourteen Helmeted Hornbill nests in Budo Sungai-Padi National Park

Tree species	dbh (cm)	Tree height (m)	Nest height (m)	Altitude (m)	slope (%)
Family Sterculiaceae					
Scaphium macropodum (N=1)	111.4	43	32	410	25
Family Dipterocarpaceae					
Hopea spp.					
Range	133.8-205.5	26-70	20-45	325-430	10-60
$\overline{X}$	163.9	43	29.5	389.1	35.8
SD	27.0	15.1	9	39.0	19.1
N	6	6	6	6	6
Shorea faguetiana					
Range	105-206.8	33-55	24-34	300-535	5-55
$\overline{X}$	158.5	46.2	30.7	390	26
SD	49.9	9.4	3.9	83.0	18.8
N	5	5	6	6	6
S. curtisii (N = 1)	119.3	50	32	410	25
Family Leguminosae					
Koompassia excelsa (N = 1)	216.6	43	31	340	35

DISCUSSION

The choice of such a special nest characteristic may reflect the morphological suitability of this hornbill species, with its heavy head and long tail. From this finding and the shortage of nest cavities, if one wants to increase the population of Helmeted Hornbill by providing artificial nests, such a characteristic should be the first to be included in the nest design. Another point is that the nests were in trees of the family Dipterocarpaceae, particularly *Shorea faguetiana* and *Hopea* spp. These trees tended to have lower branches broken off. Through these broken wounds, the trunk would be exposed and susceptible to fungi that cause heart and butt rot. This resulted in cavity creation while the stump of a broken branch remained. These trees should be considered as trees of choice for the installation of artificial nests.

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PART II: FOOD AND FEEDING ECOLOGY

PART II: INTRODUCTION

The 3rd International Hornbill Workshop featured a number of papers that did not focus on hornbills, but rather featured other animals (mainly primates) that, like hornbills, were major seed dispersal agents. Perhaps nowhere else in this book is this seeming incongruity as evident as it is in this section, where three of the five papers included deal with non-hornbill study species. However, rather than dismissing the papers as being inappropriate to an International Workshop on hornbills, it might be worthwhile to first ask a few questions concerning hornbill food and feeding ecology. Perhaps when comparisons are made between hornbills and other large frugivores will the inclusion of the non-hornbill papers be better appreciated.

What do hornbill species eat? This question was addressed either directly or indirectly by all of the authors, perhaps most obviously by Plongmai *et al.* in their note on the availability of ripe fruits during different periods of the annual hornbill life cycle. Basic information such as the kind presented by Plongmai *et al.* can not only help us understand the food choice and foraging behavior of hornbills and other animals, but can also help researchers formulate questions ranging from the sharing of food resources between species, to the evolution of dispersal strategies (for the plants) and feeding strategies (for the animals), to the management and restoration of forests to make them better able to support populations of large frugivores.

Who do hornbills share their food with? Ouithavon *et al.* show us, not surprisingly, that hornbills have to share with other hornbills. In their detailed study of the feeding preferences of two sympatric hornbills – the Great Hornbill (*Buceros bicornis*) and the Rufous-necked Hornbill (*Aceros nipalensis*) – they record in great detail who eats what. Whilst there are overlaps in what they eat, the two species are able to coexist despite the possible competition over food resources between them. Introductory ecology teaches us that competition between species is most intense the more similar the various needs of the competitors are – is this the case for the Great Hornbill and the Rufous-necked Hornbill, or do they have means of minimizing direct competition for food?

Hornbills, great consumers of fruit and dispersers of seed though they may be, are not the only major frugivores. Three papers describe the feeding ecology of various primates. Kanwatanakid and Brockelman summarize the characteristics of fruit consumed by the White-Handed Gibbon (*Hylobates lar*). Gibbons, like hornbills, act as general frugivores and as such may to a certain extent compete with them for food. However, Kanwatanakid and Brockelman also examine whether there might be a suite of characters that typify the fruits that contribute most to a White-Handed Gibbon's diet.

Monkeys and apes appear to be important frugivores wherever they occur. African forests support many frugivorous primates; a number of them are featured in papers included in this section. Maruhashi reports on his study of the monkey *Cercocebus albigena* (Grey-cheeked Mangabay), while Yumoto compares the seed dispersal capabilities of two species of great apes, the Eastern Lowland Gorilla (*Gorilla gorilla graueri*) and the Chimpanzee (*Pan troglodytes schweinfurthii*); he also considers the role played by the forest elephant (*Loxodonta africana cyclotis*) in seed dispersal. While some of these very large mammals process fruits well beyond the handling capabilities of hornbills, the approach taken by Yumoto offers insights into the role hornbills play in the greater seed disperser community.

What are the effects of hornbills on the structure, composition, and dynamics of forests? Common sense might suggest that if various frugivores eat and move about differently, they might consequently disperse seeds differently. This in turn could affect the recruitment and regeneration of saplings, and ultimately influence forest structure and dynamics. This is one instance in which intuition might actually be close to reality, as the results of Maruhashi's and Yumoto's suggest (and as reported elsewhere by other studies of seed dispersal). Yumoto also attempts to link contemporary tree distribution patterns in a hyperdiverse rainforest now devoid of most of its large mammals with the activities of presumed seed dispersers in the past, including hornbills.

From the basic data obtained by Plongmai *et al.* to the community ecological work of Yumoto, all of the papers contained in this section are rooted in careful observation and have clear implications for hornbill management and conservation, as well as for the preservation other large frugivores and the plants they depend upon. They also have applications in forest conservation, management, and restoration, as one will notice upon reading through these papers.

A comparative study of the feeding ecology of two sympatric hornbill species (Aves: Bucerotidae) during their breeding season in Huai Kha Khaeng Wildlife Sanctuary, Thailand

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Abstract Food and feeding habits of two sympatric hornbill species (the Great Hornbill, *Buceros bicornis* and the Rufous-necked Hornbill, *Aceros nipalensis*) during their breeding season were studied in Huai Kha Khaeng Wildlife Sanctuary in western Thailand. In 1999, the breeding season began in January and lasted until June. Two nests of Great Hornbill and two nests of Rufous-necked Hornbill were studied. The entire breeding cycle of the Great and the Rufous-necked Hornbill took about 101-118 days and 117-126 days, respectively. Over 15 species of fruits were eaten by the Great Hornbill and 17 species by the Rufous-necked Hornbill. The study also revealed that over 31 animal species were eaten by the Great Hornbill and over 25 species by the Rufous-necked Hornbill. The Great Hornbill consumed more figs than non-fig fruits, such as Lauraceae, Annonaceae, and Myristicaceae. In contrast, the Rufous-necked Hornbill consumed a larger proportion of non-fig fruits. Crabs were the animal food eaten in the largest quantity by both hornbills. The Rufous-necked Hornbill tended to eat insects more than the Great Hornbill. We found that the Great Hornbill had a higher total food quantity, fruit food quantity, and animal food quantity per day than the Rufous-necked Hornbill though these differences were not significant. The Great Hornbill had a significantly greater number of meals per day and more time spent around the nest tree, while the Rufous-necked Hornbill spent a significantly longer time feeding. This research provides important information for management of hornbill food resources and hornbill conservation.

INTRODUCTION

Hornbills are the largest and most conspicuous birds in the world's tropical forests, well-adapted to an arboreal lifestyle. Generally, they are frugivorous but can adapt themselves to an omnivorous diet in the breeding season (Poonswad *et al.* 1986; Kemp 1993).

The remarkable nesting habits of Asian hornbills are such that the female seals herself in a large cavity of a living tree leaving only a narrow opening for her mate to pass food to her and the chicks (Kemp 1995). The unique breeding biology of these birds means that they are dependent on big trees of primary forest (Collias and Collias 1984).

There are 13 hornbill species in Thailand distributed from the lower evergreen forests up to the upper evergreen forests of Northern, Western, Eastern and Southern Thailand (Lekagul and Round 1991). All Thai species are given threatened status because of deforestation and commercial hunting (Vidhidharm *et al.* 1995).

We studied several aspects of food and feeding ecology with an emphasis on types of food, food diversity, food preference and food consumption of two sympatric hornbill species – the Great Hornbill (*Buceros bicornis*) (Fig. 1) and the Rufous-necked Hornbill, (*Aceros nipalensis*) (Fig. 2) – during their breeding season at Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani Province, Western Thailand.

Figure 1. The male of Great Hornbill (*Buceros bicornis*).

Figure 2. The male Rufous-necked Hornbill (*Aceros nipalensis*).

METHODOLOGY

The study area was in hill evergreen forest and dry evergreen forest located at 15˚27´-15˚29´N and 99˚19´- 99˚21´E , with an altitudinal range of 695-1,330 m a.s.l. in Huai Kha Khaeng Wildlife Sanctuary (Fig. 3).

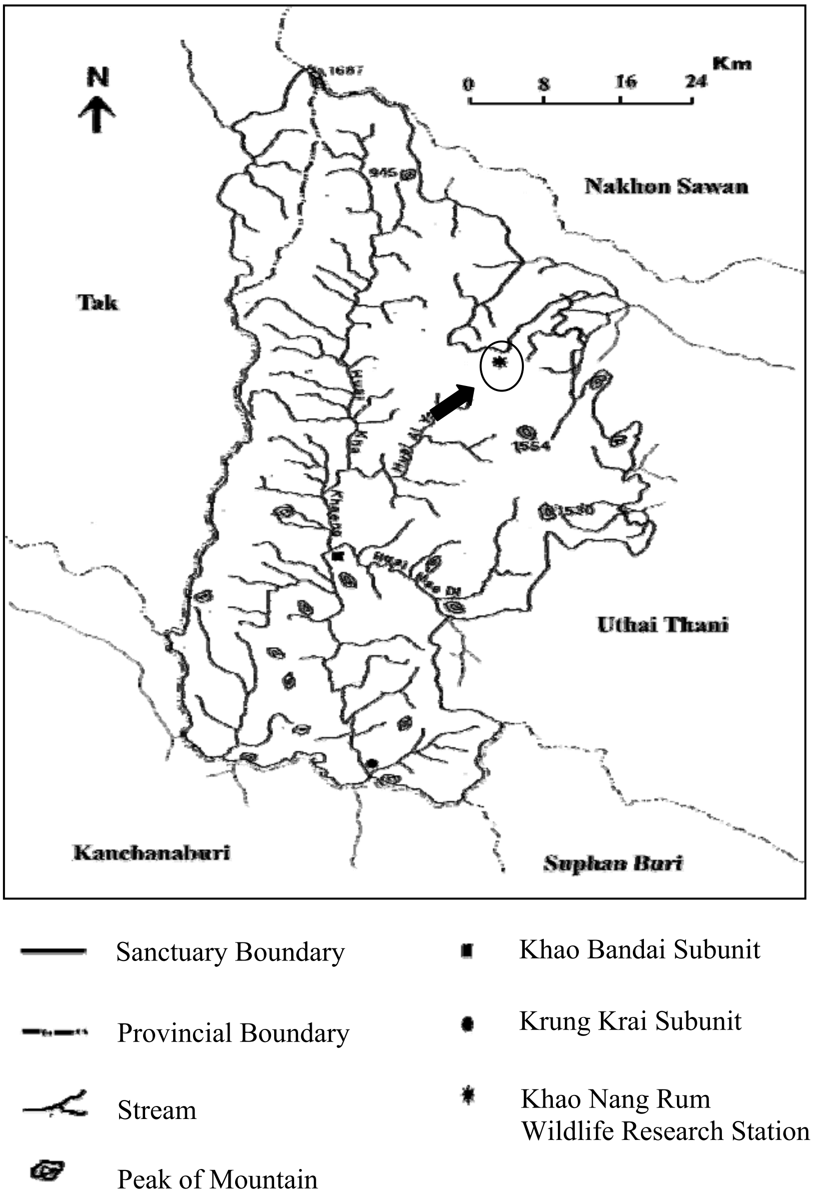

Figure 3. A map of Huai Kha Khaeng Wildlife Sanctuary showing the study area.

Regular observation at the nest trees was carried out from January to June 1999 at 4-7 day intervals. Food items and the amount of food which males brought to broods were recorded at all times from 0700-1700 hrs.

Food items were identified using binoculars or a spotting telescope, depending on the distance from the observation blind to the nest. Regurgitated seeds, dropped food and feces were also collected to help identify some food species. Food samples were collected and prepared for studying characteristics such as weight, length, diameter, sugar content and color. Plant samples were sent to the Forest Herbarium, Royal Forest Department for further identification to at least the family level. We also studied food consumption before and after the chicks hatched to compare feeding at different times of one breeding cycle.

Data Analysis

Food diversity

The diversity of hornbill food was determined by using the Shanon-Wiener index (Ludwig and Reynolds, 1988) which is derived from the following formula:

$$H' = -\sum_{i=1}^{S} (P_i \ln P_i)$$

Where H′ is the index of food diversity, S is the number of food items and P_i is the proportion of weight of a particular food item. When comparing H′ values between the two hornbill species, a high H′ value indicates that the species is a general feeder, if the H′ value is low, it indicates that the species is a selective feeder.

Food similarity

To determine food similarity consumed by the hornbills a formula modified from Mueller-Dombois and Ellenberg (1974) was used:

$$I_s = 2W/(a+b)$$

Where I_s is the similarity coefficient, W is the sum of all food items shared by all species, 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.

Niche overlap

Niche overlap of hornbill food choice was calculated by employing Horn's index of overlap (Krebs 1989) using the following formula:

$$R_o = \frac{\sum (P_{ij} + P_{ik}) \ln (P_{ij} + P_{ik}) - \sum P_{ij} \ln P_{ij} - \sum P_{ik} \ln P_{ik}}{2 \ln 2}$$

Where R_o is the index of overlap of the food consumption of the two hornbill species, P_{ij} is the proportion of a particular food item of one hornbill species j, and P_{ik} is the proportion of the same food item for hornbill species k.

Food preference

Food items brought to the nest were ranked in terms of number, weight and frequency. These ranks were then summed to produce a final ranking for each item, which was separate for each nest of each species. In order to assess the overall rank of each food item for each hornbill species, the following formula (Poonswad *et al.* 1998) was used:

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

Where S is a summed score for a food item from all nests of a given hornbill species, f is the frequency of the rank of a food item, p is the total number of nests of that hornbill species, r is the rank of the food item for each nest and N is the total number of food items to be ranked.

Comparison of food consumption

Differences in parameters of food consumption between the two hornbill species such as total quantity of food eaten per day, quantity of fruit eaten per day, quantity of animals eaten per day, number of meals per day, length of time spent around the nest tree per visit and length of time spent feeding per occasion were tested for statistical significance of $P < 0.01$ by using the non-parametric Mann-Whitney U-test. We used the program SPSS software package version 7.5 for-statistical analyses.

RESULTS

Food type and food diversity

Two nests of Great Hornbill and two nests of Rufous-necked Hornbill were found in study area at altitudes ranging from 870-1,240 m a.s.l.

The food eaten by the two hornbill species was very diverse. Fruit food was classified to 9 families comprising 19 identified and two unidentified fruit species, and samples of 15 fruit species were collected (Appendix 1). Animal food could be classified into at least 8 groups comprised of 34 identified species and 2 unidentified species, with samples of 21 animal species collected from this study area (Appendix 2).

We found that fruits from five of the nine families of fruit food (Moraceae, Myristicaceae, Annonaceae, Meliaceae and Luaraceae) were eaten by both hornbills. Food consumed by the two hornbill species can be classified as figs, non-fig fruits and animals. The Great Hornbill consumed 79.3% fruit food and 20.7% animal food, and the Rufous-necked Hornbill consumed 78.5% fruit food and 21.5 % animal food. With fruit food, we found that the Great Hornbill consumed figs and non-figs in proportions of 57.3% and 42.7 % respectively. This differed from the Rufous-necked hornbill, which consumed 5.2% figs and 94.8% non-figs (Table 1).

Table 1. Food diversity and quantity eaten by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Type of food	GH (H′= 2.27)			RNH (H′= 2.53)		
	No. of species	Quantity consumed		No. of species	Quantity consumed	
		(g/ day)	(%)		(g/ day)	(%)
Figs	5	174.9	45.5	3	11.7	4.1
Non-figs	10	130.3	33.8	14	213.0	74.4
Animal	31	79.9	20.7	25	61.6	21.5
Total	46	385.1	100.0	42	286.3	100.0

The results of the calculation of a Shannon-Wiener index of food diversity (as shown in Tables 1, 2 and 3), illustrate the degree of difference between the two species. The Great Hornbill is considered more of a generalist with respect to animal food (H′ = 2.34) while the Rufous-necked Hornbill is more of a fruit generalist (H′ = 2.00).

Table 2. Fruit food diversity and quantity eaten by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Family	GH (H′= 1.58)			RNH (H′= 2.00)		
	No. of species	Quantity consumed		No. of species	Quantity consumed	
		(g/ day)	(%)		(g / day)	(%)
Annonaceae	1	68.3	22.3	1	74.5	33.2
Lauraceae	2	24.9	8.2	4	83.4	37.1
Myristicaceae	1	14.7	4.8	2	40.5	18.0
Meliaceae	4	16.9	5.6	5	13.5	6.0
Moraceae	5	174.9	57.3	3	11.7	5.2
Myrtaceae	1	5.0	1.6	0	0	0
Burseraceae	1	0.5	0.2	0	0	0
Elaeagnaceae	0	0	0	1	0.8	0.4
Olacaceae	0	0	0	1	0.2	0.1
Total	15	305.2	100.0	17	224.6	100.0

Table 3. Animal food diversity and quantity eaten by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Group	GH (H′= 2.34)		RNH (H′= 2.08)	
	Quantity consumed		Quantity consumed	
	(g/ day)	(%)	(g/ day)	(%)
Birds	1.0	1.3	0.8	1.3
Reptiles	14.2	17.8	2.3	3.7
Amphibians	12.2	15.3	8.0	12.9
Fishes	4.0	5.0	2.0	3.2
Mollusks	2.5	3.1	2.2	3.5
Insects	14.0	17.5	17.3	28.1
Arthropods	31.5	39.4	28.8	46.7
Miscellaneous	0.5	0.6	0.4	0.6
Total	79.9	100.0	61.6	100.0

A Kruskal-Wallis test highlighted significant differences among the amount of each food type consumed (GH: H = 98.71, df = 2, *P*< 0.001; RNH: H = 137.13, df = 2, *P*< 0.001). This clearly shows that the Great Hornbill ate figs much more than any other type of food and that the Rufous-necked ate non-figs much more than any other type of food. Within fruit food, the Kruskal-Wallis test confirmed a significant difference between the quantities of each type of fruit eaten (GH: H = 55.67, df = 6, *P*< 0.001; RNH: H = 71.43, df = 6, *P*< 0.001). This shows that the Great Hornbill preferred to eat fruits of the family Moraceae (figs) more than others while the Rufous-necked preferred to eat fruit from the families Lauraceae, Annonaceae and Myristicaceae (Table 2). With animal food, the Krusal-Wallis test demonstrated the significant difference among the quantities of each group of animal food eaten (GH: H = 56.21, df = 6, *P*< 0.001; RNH: H = 136.31, df = 6, *P*< 0.001). It showed that the Great Hornbill consumed arthropods, reptiles, and insects more than they did other animal groups and that the Rufous-necked preferentially consumed arthropods and insects, although both species consumed arthropods in the largest proportion with regard to animals eaten (Table 3).

Food similarity and niche overlap

Because these two hornbill species live in sympatry, they might be expected to use the same food resources. The types of food eaten by the two hornbills showed high similarities (Tables 4, 5 and 6). We found 11 fruit species from a total of 36 species were eaten by both hornbills. Food similarity and niche overlap of food eaten by the two hornbill species, as shown in Tables 4 and 6, indicate that the two hornbills ate similar food. There was high niche overlap in terms of food eaten, which suggests that the two hornbills are in heavy competition. However, the abundance and diversity of animal food species in this habit was apparently sufficient for both hornbills. With fruit food there was also a rather high niche overlap value but less than that for animal food. These two hornbills species appeared to seek fruit food from different sources, as the Great Hornbill preferred figs but the Rufous-necked Hornbill preferred non-fig fruits such as those of the families Lauraceae, Annonaceae and Myristicaceae.

Table 4. Food similarity and niche overlap of food consumed by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill

	Total food	Fruit food	Animal food
Food similarity (%)	70.5	68.8	71.4
Niche overlap	0.69	0.64	0.90

Table 5. Ranks of fruit food consumed by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Family	Species name	GH		RNH	
		Summed score	rank	Summed score	rank
Moraceae	*Ficus altissima*	28	2	20	5
	Ficus nervosa	15	8	8	16
	Ficus sp.	13	10	-	-
	Ficus spp.	10	14	18	8
	Ficus virens	18	6	-	-
Myrtaceae	*Syzygium cumini*	18	6	-	-
Annonaceae	*Polyalthia simiarum*	29	1	34	1
Lauraceae	*Beilschmiedia gammieana*	27	3	32	2
	Cryptocarya pallens	-	-	17	9
	Litsea hansenii	-	-	17	9
	Unknown	14	9	17	9
Myristicaceae	*Knema laurina*	20	4	29	3
	Knema sp.	-	-	17	9
Meliaceae	*Aglaia cucullata*	13	10	25	4
	Aglaia lawii	12	12	10	14
	Aphanamixis polystachya	-	low rank	-	low rank
	Chisocheton ceramicus	20	4	20	5
	Dysoxylum macrocarpum	-	-	9	15
	Melianoidae	11	13	19	7
Burseraceae	*Canarium subulatum*	8	15	-	-
Olacaceae	*Strombosia* spp.	-	-	8	16
Elaeagnaceae	*Elaeagnus latifolia*	-	-	13	13

Table 6. Ranks of animal food consumed by two hornbill species. GH = Great Hornbill, RNH = Rufous-necked Hornbill, U = Unidentified species, rank undetermined

Group	Kind	GH		RNH	
		Summed score	rank	Summed score	rank
Birds	Chicks	20	21	-	-
	Eggs	27	16	21	10
Reptiles	Snake	38	7	-	-
	Acanthosaura spp.	49	4	19	2
	Draco spp.	19	23	-	-
	Scinicidae	42	6	19	13
	Gecko	24	19	9	19
	Cyclodactylus spp.	32	10	13	17
Amphibians	Ranidae	52	1	32	4
Fishes	Fishes	32	10	14	16
Mollusks	*Cyclophorus* spp.	37	8	30	5
Insects	Cicadidae 1	51	3	38	2
	Cicadidae 2	-	-	35	3
	Gryllidae	17	25	11	18
	Orthoptera 1	20	21	22	8
	Orthoptera 2	U	U	-	-
	Copris spp.	18	24	16	14
	Scarabaeidae 1	30	14	27	6
	Erguala capucina	45	5	20	11
	Vespidae	16	27	-	-
	Other Scarabaeidae	U	U	U	U
	Other insects	U	U	U	U
Non-Insect Arthropods	Crabs	52	1	40	1
	Scolopendra spp.	31	12	26	7
	Julidae	37	8	15	15
	Sphaeotheriidae	26	18	-	-
	Scorpionidae	-	-	9	19
	Arachneidae 1	22	20	-	-
	Arachneidae 2	17	25	-	-
Annelids	Earthworm	U	U	-	-
Miscellaneous	*Pheretima* spp.	30	14	-	-
	Larvae	31	12	22	8
	Caterpillars	27	16	-	-

Food preferences

Data collected during the breeding season in 1999 revealed variations in the food items fed to the broods at different nests, thus permitting ranking of food preferences. The ranks of fruit food and animal food are given in Tables 5 and 6. By ranking the feeding frequency, weight and number, *Polyalthia simiarum* was found to be the most preferred fruit food for both hornbills, but the Great Hornbill seemed to prefer figs overall to non-fig fruits, unlike the Rufous-necked Hornbill. We can assume that the reason for hornbill fruit food selection probably depends on factors such as nutritional value and fruit characteristics, which are different for each species. Of the animal food items, crabs were the most preferred for both hornbills. We found that amphibians and cicadas also had high ranks indicating that the important food resources of both hornbills were found near streams and on the trunks or in the canopies of trees.

It was found that there was a significant difference between fruit food quantity and their ranks (GH: $r = -0.586$, $P < 0.05$; RNH: $r = -0.687$, $P < 0.01$) and also between animal food quantity and their ranks (GH: $r = -0.611$, $P < 0.01$; RNH: $r = -0.521$, $P < 0.05$). This indicates that the ranks of food were clearly correlated to food quantity eaten, but the Rufous-necked had a higher correlation in fruit food consumed while the Great Hornbill had a higher correlation in animal food consumed.

Food consumption during the breeding cycle

The breeding cycle is defined as the period from the imprisonment of the female until the fledging of the last chick. The imprisonment of females started between 30 January and 27 February 1999. The entire breeding cycle of the Great Hornbill and the Rufous-necked Hornbills took about 100-118 days and 116-117 days, respectively. A summary of the breeding cycle is given in Table 7.

Table 7. Summary of breeding cycle of two hornbill species (1999). GH = Great Hornbill, RNH = Rufous-necked Hornbill

Nest No.	No. of chicks	Date of female imprisonment	Date of female emergence	Date of chick fledged		Length of Breeding cycle (days)
				1st chick	2nd chick	
2 (GH)	1	27 Feb.	30 Apr.	6 Jun.	-	100
9 (GH)	1	30 Jan.	1 May	27 May	-	118
3 (RNH)	1	15 Feb.	11 Jun.	11 Jun.	-	117
13 (RNH)	2	20 Feb.	15 Jun.	15 Jun.	25 Jun.	116

After collecting data through the entire breeding period, parameters of food consumption of the two hornbill species were tested by using the Mann-Whitney U-test (Table 8). We found the Great Hornbill had higher food consumption, higher fruit consumption and higher animal food consumption per day than the Rufous-necked Hornbill, though this difference was not significant. The Great Hornbill had a significantly greater number of meals per day ($Z = 1160.0$, $P<0.05$) and spent more time around the nest tree ($Z = 45106.0$, $P< 0.01$) than the Rufous-necked Hornbill, while the Rufous-necked spent a significantly longer time feeding ($Z = 61348.0$, $P< 0.05$).

Table 8. Comparison of food consumption rates by two-hornbill species through the breeding period. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Parameter		GH	RNH	Mann-Whitney U-test	
				Z	*P*
Total quantity of food eaten (g/ day)					
	Mean	385.1	286.3	1220.0	0.07
	SD	262.1	173.1		
	N	47	65		
Quantity of fruit eaten (g/ day)					
	Mean	305.2	224.6	1252.0	0.104
	SD	234.7	140.6		
	N	47	65		
Quantity of animal eaten (g/ day)					
	Mean	79.9	61.7	1499.5	0.867
	SD	104.5	76.7		
	N	47	65		
Number of meals/ day					
	Mean	7.2	5.5	1160.0*	0.029
	SD	4.2	2.6		
	N	47	65		
Length of time spent around the nest tree (min/ visit)					
	Mean	12:29	9:23	45106.5**	0.004
	SD	12:48	8:20		
	N	305	341		
Length of time spent feeding (min/ time)					
	Mean	2:14	2:23	61348.0*	0.031
	SD	3:16	2:23		
	N	322	419		

Remark: Difference significant * ($P < 0.05$), ** ($P < 0.01$)

Table 9 compares food consumption between the hornbill species pre- and post-chick hatching. It indicates that the Great Hornbill consumed a significantly higher quantity of fruit per day before chick hatching than the Rufous-necked ($Z = 40.0$, $P< 0.05$). After hatching, the Great Hornbill had a significantly higher total food consumption per day ($Z = 71.5$, $P< 0.001$), number of meals per day ($Z = 609.0$, $P< 0.01$) and length of time spent around the nest tree per visit ($Z = 32628.0$, $P< 0.05$) than the Rufous-necked Hornbill, but the Rufous-necked spent a significantly longer time feeding than the Great ($Z = 43525.5$, $P< 0.01$).

Table 9. Comparison of food consumption rates by two-hornbill species pre- and post-chick hatching. GH = Great Hornbill, RNH = Rufous-necked Hornbill

Parameter	GH	RNH	Mann-Whitney U-test	
			Z	*P*
Pre-hatching				
Total food eaten (g/ day)				
Mean±SD	399.7±265.3	194.3±83.7	77.0	0.957
N	12	13		
Fruit eaten (g/ day)				
Mean± SD	395.9±266.3	189.7±85.0	40.0	0.039
N	12	13		
Animal eaten (g/ day)				
Mean±SD	3.8±9.4	4.6±16.7	72.0	0.563
N	12	13		
Number of meals/ day				
Mean±SD	4.4±1.9	3.8±1.2	67.0	0.539
N	12	13		
Length of time spent around the nest tree (min/ visit)				
Mean±SD	12:38±11:06	10:54±10:17	1044.5	0.156
N	51	49		
Length of time spent feeding (min/ time)				
Mean±SD	3:56±4:55	3:00±2:37	1041.5	0.193
N	49	50		
Post-hatching				
Total food eaten (g/ day)				
Mean±SD	380.1±264.7	309.4±189.4	71.5	0.000
N	35	52		
Fruit eaten (g/ day)				
Mean±SD	274.0±218.4	233.4±150.7	841.0	0.550
N	35	52		
Animal eaten (g/ day)				
Mean±SD	106.0±109.5	76.0±79.3	807.5	0.375
N	35	52		
Number of meals/ day				
Mean±SD	8.1±4.4	5.9±2.7	609.0	0.009
N	35	52		
Length of time spent around the nest tree (min/ visit)				
Mean±SD	12:27±13:08	9:08±7:58	32628.0	0.015
N	254	292		
Length of time spent feeding (min/time)				
Mean± SD	1:55±2:47	2:18±2:20	43525.5	0.003
N	273	369		

DISCUSSION

Diet Composition and Food Consumption

This study found that fruit food in the families Lauraceae, Annonaceae, Myristicaceae, and Meliaceae were consumed by the sympatric hornbills in large quantities. These families comprised 95 % of the fruit diet of the Rufous-necked Hornbill and about 41 % of the fruit diet of the Great Hornbill. We hypothesize that fruit of these families have a high nutritional value that is necessary for hornbills, especially lipids. Snow (1981) stated that most of the tropical fruits eaten by birds are lipid-rich, whereas Temperate Zone fruits eaten by birds have a higher water content and are carbohydrate-rich. The results of this study are similar to those reported by Mudappa (1996) and Leighton (1986), which found that hornbills preferentially ate fruit of the families Lauraceae, Annonaceae and Myristicaceae rather than simply their due to their availability. However, this study differs from the results reported by Poonswad (1993) which found that four hornbill species in Khao Yai National Park fed on fruits which were abundant regardless of nutritional value.

We found that 57.3% of the Great Hornbill's fruit diet consisted of figs (family Moraceae) which was much higher than for the Rufous-necked Hornbill. White (1974) states that some species of tropical fruits such as figs have high carbohydrate and available energy, but low lipid content. Figs collected in the study area had many agaonid wasps inside them. Abrahamson (1989) explains that figs themselves have low protein, but the presence of agaonid wasps through their long co-evolution means that figs are in fact a rich source of protein and calcium. This is in accordance with Poonswad *et al.* (1998) who found that the Great Hornbill consumed figs more than any other fruit. So it is hypothesized that the Great Hornbill needs protein and calcium more than does the Rufous-necked. In addition, we found that figs, which were eaten by hornbills, were from free-standing *Ficus* trees, as well from hemiepiphytes.

This study found that crabs were the most preferred animal food for both hornbills, which is in accordance with Chimchome *et al.* (1998) who studied the breeding biology and ecology of the Rufous-necked Hornbill in the same area. The similarity of animal food from these two studies indicates that this study area has remained stable allowing for a continued supply of rich and diverse animal food species. If we can conserve this habitat and its food resources as at present, the hornbills can also continue flourishing. We believe that crabs were the most preferred food because they live near streams, which are open areas easily accessible to hornbills for hunting. Another possible reason is the nutritional value of crabs, which may have a very high protein and calcium content, but this needs further study.

In the breeding period, we found that the Great Hornbill had higher total food consumption, higher fruit food consumption and higher animal food consumption per day than the Rufous-necked Hornbill. However their total fruit and total animal food consumption over the whole breeding period was less than that of the Rufous-necked Hornbill. This is explained by the Great Hornbill having a shorter breeding period than the Rufous-necked Hornbill. The Great were larger than the Rufous-necked Hornbills, and their chicks had a very high growth rate with a corresponding higher need for protein than the Rufous-necked Hornbill chicks. The Great Hornbill had a significantly higher number of meals per day than the Rufous-necked Hornbill, so their chicks consumed a larger quantity of food and therefore had a very high growth rate. We also found that the Great spent a significantly longer length of time around the nest tree than did the Rufous-necked. From our observations, we suggest that this was not linked to the quantity of food, but rather to their aggressive nest-guarding behavior. We observed them staying around the nest without feeding, sometimes chasing away other animals who trespassed in their nesting territory. Conversely the Rufous-necked Hornbill spent a significantly longer time feeding than the Great Hornbill. This could be explained by the Rufous-necked consuming higher quantities of seed-fruits, which take longer to feed to the chicks because they are given one at a time.

In the post-hatching period, we found that the hornbills clearly increased the amount of animal food and the number of meals, especially the Great Hornbill, in order to obtain the protein necessary for the chicks' development. Because of its higher protein intake and higher growth-rate, the Great Hornbill's chicks could fledge from the nests faster than those of the Rufous-necked. But the length of time spent around the nest tree and the time spent feeding significantly decreased after hatching. We can hypothesize that hornbills need more time seeking food when feeding their chicks and also that most of the feeding in the pre-hatching period was of fruit, which takes longer to eat. Thus, during the post-hatching period, the males left the nest more quickly because of the increasing number of meals needed and the higher proportion of animal food.

We found that in the pre-hatching period, both hornbills had a higher fruit component in their diets than they did post-hatching, which was most evident with the Great Hornbill. This can be explained by the fact that during this period, energy consumption was more important for the female hornbills, which had to molt and replace their feathers before eventually leaving their nests. With Great Hornbills, figs, which are high in protein and calcium as well as energy-rich, were fed by the males to the females in the pre-hatching period to prepare her to leave the nest before her chicks fledged. This is turn allowed the female to assist with feeding the young, thereby aiding in their rapid development.

CONCLUSIONS

Fruits eaten by two the sympatric hornbill species in the families Moraceae (figs), Myristicaceae, Annonaceae, Meliaceae and Lauraceae seem important in the diets of both hornbills, but the Great Hornbill seemed to prefer figs to non-figs fruits, which was opposite to the Rufous-necked Hornbill's preferences.

These two sympatric hornbill species could be expected to use the same food resources and therefore be in competition with each other. Despite almost complete niche overlap in animal food, coexistence may have been made possible because of the abundance and variety of animal food species in this habitat. With fruit food, there was less niche overlap because these two hornbill species seemed to seek fruit food from different sources.

Nutritional values rather than abundance appear to have influenced food preference. Among all ranks of fruit food, *Polyalthia simiarum* was the most preferred fruit species and among all ranks of animal food, crabs were the most preferred by both hornbills.

During the breeding period, the Great Hornbill had higher food consumption per day than the Rufous-necked hornbill because their chicks had a much higher growth-rate than the Rufous-necked chicks. Animal food consumption was increased after the chicks hatched because more protein was necessary for the chicks'growth. Because the female Great Hornbills must leave their nests before the chicks fledge, the males fed them with large numbers of figs, which are high in protein and calcium, to help the females to molt and replace their feathers during the pre-hatching period.

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Some characteristics of food of two sympatric hornbill species (Aves: Bucerotidae) and fruit availability during their breeding season in Huai Kha Khaeng Wildlife Sanctuary, Thailand

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Abstract A study of how food characteristics and ripe fruit abundance influenced the food choice of two sympatric hornbill species, the Great Hornbill (*Buceros bicornis*) and the Rufous-necked Hornbill (*Aceros nipalensis*) during their breeding season was carried out in Huai Kha Khaeng Wildlife Sanctuary, western Thailand from January to July 1999. Both hornbill species consumed fruit with heavy pulp, dark color and large diameter, but avoided fruit with overly large seeds. The Rufous-necked Hornbill also consumed fruit with a high sugar level and fruit species that bore abundant ripe fruits in the study area more so than the Great Hornbill. Both hornbill species ate animal food with heavy body weight, but tended to avoid animals with too long a body length. This observation provides some important information for future management of hornbill food resources, which will be essential for successful hornbill conservation.

INTRODUCTION

Hornbills (Family Bucerotidae) are frugivorous birds in Old World tropical forests which can switch to a more omnivorous diet during the breeding season (Kemp 1995). Their ability, compared with other avian forest frugivores, to open and swallow large ripe fruits, and their regurgitation of the seeds undamaged, makes them ideal dispersers (Kalina 1988; Leighton and Leighton 1983).

Fruits that are usually eaten by birds frequently offer substantial nutritional rewards. The pulp is usually rich in carbohydrate, lipid and/or protein, in addition to water and indigestible fiber (Moermond and Denslow 1985). Highly frugivorous birds have good color vision enabling them to detect ripe fruits and therefore for plants to attract them with visual displays. Not surprisingly, characteristics of fruits dispersed by highly frugivorous birds are large drupes or arilate seeds, dark in color (black, blue, red, green or purple), non-aromatic and lipid or starch-rich (Howe and Westley 1988).

In Thailand, studies of food characteristics have mainly emphasized the nature of fruit food (Poonswad 1993). More study is needed as to what factors influence hornbill food choice. We therefore present our study of some characteristics of hornbill food during the breeding season in Huai Kha Khaeng Wildlife Sanctuary.

METHODOLOGY

Study area

The study was conducted in a hill evergreen forest and dry evergreen forest located between 15°27′- 15°29′N and 99°19′- 99°21′E, with altitudes ranging between 695-1330 m a.s.l. in Huai Kha Khaeng Wildlife Sanctuary, western Thailand (see Ouithavon *et al.* in this volume). Common trees in this area include the genera *Dipterocarpus*, *Lithocarpus*, *Castanopsis*, *Cinnamomum*, *Ficus*, *Syzygium* and *Polyalthia* (Ouithavon, pers. obs.).

Food characteristics

Fruit food samples were collected and prepared for a study of fruit characteristics, including whole fruit weight, pulp weight, fruit length, seed length, fruit diameter, and seed diameter. Sugar content was also measured by pocket refractometer (Belingham and Stanley, BS-R70). Animal food samples were also collected and characteristics including total weight and length were measured. Fruit samples were sent to the Forest Herbarium at the National Park, Wildlife and Plant Conservation Department (former Royal Forest Department) for either confirmation or identification.

Fruit availability

A 3-km trail in the study area was established for fruit tree tagging. These trees were monitored weekly to ascertain the period of ripening fruit trees throughout the breeding season in 1999 and then analyzed in relation to the quantity consumed by hornbills.

RESULTS

Fruit food characteristics

Twenty fruit species were eaten by the two hornbill species during the breeding season in 1999 (Appendix 1). Among these, 15 species were collected and their characteristics are shown in Table 1. Except for four species of *Ficus*, the remaining 11 species had single-seeded fruits.

The analysis for overall correlation between fruit consumption and fruit characteristics shows that the Great Hornbill significantly consumed fruits with heavy pulp and large diameter, while Rufous-necked Hornbills consumed fruits with heavy pulp, large diameter and high sugar content (Tables 1, 2 and 3). The characteristics of single-seeded fruits show no significant correlation with the quantity consumed by both hornbill species (Tables 1, 2 and 3).

Table 1. Characteristics of fruits eaten by Great and Rufous-necked Hornbills during the breeding season in 1999
FW = Fruit weight (g), P = Pulp weight (g), FL = Total length (cm), FDia. (A) = Fruit diameter side A (cm), FDia. (B) = Fruit diameter side B (cm), SL = Seed length (cm), SDia. (A) = Seed diameter side A (cm), SDia. (B) = Seed diameter side B (cm), Sugar = Sugar content (%), Color = Fruit color, Form = Fruit form

No	Fruit species	FW	P	FL	FDia. (A)	FDia. (B)	SL	SDia. (A)	SDia. (B)	Sugar (%)	Color	Form
1	*Aglaia cucullata*	5.96±1.33	1.10±0.30	2.93±0.17	1.88±0.21	1.78±0.18	2.70±0.32	1.82±0.18	1.64±0.18	-	Red	Capsule
2	*Aglaia lawii*	1.79±0.48	0.65±0.26	2.14±0.22	1.32±0.14	1.10±0.12	1.86±0.22	1.09±0.12	0.94±0.11	-	Red	Capsule
3	*Beilschmiedia gammieana*	5.36±1.01	2.58±0.71	2.13±0.20	1.96±0.15	1.94±0.16	1.86±0.13	1.53±0.10	1.55±0.11	10.18±1.07	Black	Drupe
4	*Chisocheton ceramicus*	11.34±2.01	3.04±0.85	1.93±0.32	2.91±0.41	3.15±0.27	1.72±0.16	2.68±0.39	3.10±0.19	-	Yellow	Capsule
5	*Dysoxylum macrocarpum*	8.91±1.19	3.84±0.53	3.30±0.13	2.16±0.33	2.11±0.32	3.02±0.13	1.60±0.34	1.73±0.42	-	Black	Capsule
6	*Ficus altissima*	6.18±1.57	6.18±1.57	3.04±0.41	2.04±0.31	2.05±0.29	-	-	-	9.05±3.02	Dark-red	Syconium
7	*Ficus nervosa*	0.79±0.20	0.79±0.20	1.15±0.09	1.29±0.12	1.15±0.10	-	-	-	7.63±4.07	Red	Syconium
8	*Ficus virens*	1.56±0.22	1.56±0.22	1.04±0.09	1.18±0.10	1.15±0.09	-	-	-	6.68±1.72	Purple	Syconium
9	*Ficus* spp.	1.89±0.47	1.89±0.47	1.65±0.13	1.66±0.13	1.68±0.14	-	-	-	8.23±2.69	Orange-red	Syconium
10	*Knema laurina*	11.42±1.86	6.47±1.53	4.19±0.43	2.46±0.20	2.43±0.19	3.25±0.23	1.70±0.09	1.70±0.10	10.58±2.10	Red	Arillate
11	*Knema* sp.	7.18±2.69	3.44±1.34	2.71±0.43	2.04±0.33	2.08±0.37	2.19±0.37	1.58±0.30	1.57±0.29	10.07±3.33	Red	Drupe
12	Lauraceae 1	7.88±2.32	4.90±1.81	1.84±0.32	2.50±0.24	2.48±0.26	1.55±0.38	1.89±0.28	1.77±0.16	11.77±1.53	Orange	Drupe
13	*Litsea hansenii*	7.29±1.81	5.01±1.05	2.18±0.18	2.44±0.24	2.28±0.39	1.54±0.25	1.41±0.43	1.43±0.45	14.01±3.45	Black	Aggregate
14	*Polyalthia simiarum*	7.52±1.57	3.98±0.98	3.17±0.36	2.05±0.17	2.04±0.17	2.47±0.36	1.45±0.19	1.42±0.15	22.55±5.39	Black-purple	Drupe
15	*Syzygium cumini*	1.25±0.29	0.92±0.28	1.58±0.07	1.12±0.10	1.13±0.12	1.34±0.07	0.72±0.04	0.71±0.05			

We found that both hornbills ate fruits with colors ranging from black, dark purple, dark-red, red, and orange, to yellow. When testing independence by Chi-square test among the three different color tones (categorized into dark purple-black, red-dark red and yellow-orange), we found significant differences among frequencies of fruit color tones consumed by hornbills ($\chi^2 = 439.28$, df = 2, $P < 0.001$). Great Hornbills consumed fruits with a red-dark red tone, while Rufous-necked Hornbills tended to consume fruits that were a dark purple-black (Tables 1 and 2).

Table 2. Daily quantity of fruit food consumed by Great (GH) and Rufous-necked Hornbills (RNH) during breeding season

Fruit species	Daily consumption (g)	
	GH	RNH
Fig		
Ficus altissima	159.0	8.3
F. nervosa	3.2	0.3
F. virens	9.0	-
F. spp.	3.8	3.1
Non-fig fruit		
Aglaia cucullata	2.4	5.2
A. lawii	1.7	0.3
Beilschmiedia gammieana	18.8	49.3
Chisocheton ceramicus	11.3	6.0
Dysoxylum macrocarpum	-	0.7
Knema laurina	15.0	37.3
Knema sp.	-	4.7
Lauraceae 1	6.6	10.2
Litsea hansenii	-	26.3
Polyalthia simiarum	68.4	74.5
Syzygium cumini	5.0	-

Table 3. Spearman's rank test (r) for correlation between fruit characteristics and fruit quantity consumed by Great (GH) and Rufous-necked Hornbill (RNH) (from Tables 1, 2); a. indicates measurements done for single-seeded fruit only, b. indicates fruit with sugar content detectable

Fruit characteristics	Spearman correlation value					
	GH			RNH		
	r	N	*P*	r	N	*P*
Fruit weight (g)	0.503	12	0.095	0.484	13	0.094
Pulp weight (g)	0.776	12	0.003	0.648	13	0.017
Fruit length (cm)	0.406	12	0.191	0.357	13	0.231
Fruit diameter side A (cm)	0.503	12	0.095	0.555	13	0.049
Fruit diameter side B (cm)	0.622	12	0.031	0.462	13	0.112
Seed length[a] (cm)	0.167	8	0.693	-0.115	10	0.751
Seed diameter side A[a] (cm)	0.119	8	0.779	-0.030	10	0.934
Seed diameter side B[a] (cm)	0.214	8	0.610	-0.115	10	0.751
Sugar content[b] (%)	0.604	9	0.085	0.800	9	0.010
Color[b]	0.300	9	0.433	0.516	9	0.155
Color	0.490	12	0.106	0.227	13	0.456

Fruit availability

From weekly monitoring of fruit availability along a 3-km trail through the study area, we tagged 326 trees of 31 species of known hornbill fruit food. The number of trees with ripe fruit began to increase in February and peaked in June (Table 4). *Knema laurina* had the greatest number of ripening fruit trees. The Spearman's rank test between the quantity of fruit consumed by hornbills and the number of ripening fruit trees showed a significant correlation for Rufous-necked Hornbills, but not for the Great Hornbill (Great Hornbill: r = 0.494, *P* = 0.023, N = 21; Rufous-necked Hornbill: r = 0.494, *P* = 0.023, N = 21) (Fig.1).

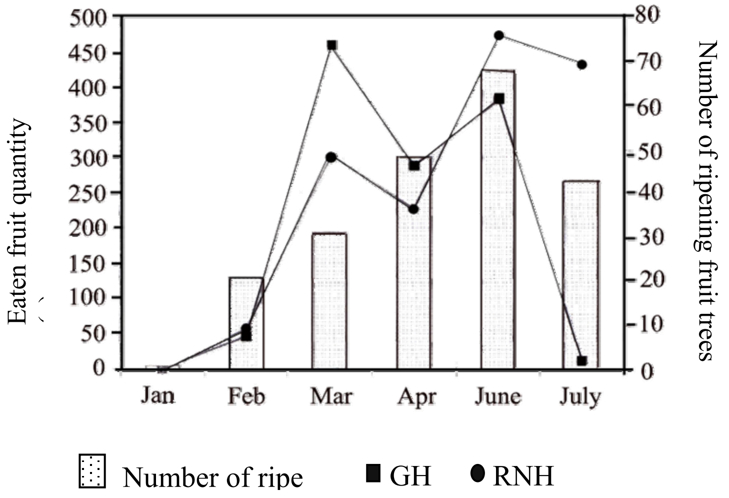

Figure 2. Correlation between fruit quantity eaten and monthly number of ripening fruit trees in the study area in the 1999 breeding season.

Table 4. Monthly number of known fruit food trees ripening during the 1999 breeding season (Jan- June). * indicates species of known food tree

Fruit tree species	No. of trees	No. of ripening trees						Cumulative ripe-fruit trees
		Jan	Feb	Mar	Apr	Jun	Jul	
Annonaceae								
*Polyalthia simiarum**	42	-	-	1	6	14	7	28
Burseraceae								
*Canarium subulatum**	10	-	-	-	-	-	-	0
Elaeagnaceae								
*Elaeagnus latifolia**	4	-	-	-	-	-	-	0
Icacinaceae								
Platea latifolia	2	-	-	-	-	-	-	0
Lauraceae								
*Beilscmiedia gammieana**	13	-	4	4	-	-	-	8
Cinnamomum sp.	7	-	-	-	-	-	-	0
*Cryptocarya pallens**	29	-	-	-	-	1	-	1
Cryptocarya sp.	6	-	-	-	-	-	-	0
Lauraceae 1*	2	-	-	-	-	-	-	0
Lauraceae 2	1	-	-	-	-	-	-	0
Litsea cubeba	1	-	-	-	-	-	-	0
*Litsea hansenii**	6							0
Phoebe paniculata	40							0
Meliaceae								
*Aglaia cucullata**	20	-	1	1	1	1	-	4
*Aglaia lawii**	1	-	1	1	1	1	-	4
Aglaia macrocarpa	12	-	-	-	2	9	5	17
*Chisocheton ceramicus**	3	-	-	2	3	3	3	11
*Dysoxylum macrocarpum**	1	-	-	-	-	-	1	1
Melioidae*	24	1	3	2	-	9	5	20
Moraceae								
Artocarpus lakoocha	1	-	-	-	-	-	-	0
Ficus altissima *	1	-	1	1	1	-	-	3
Ficus nervosa *	2	-	-	1	2	1	1	5
Ficus sp. *	1	-	1	-	-	-	-	1
Ficus spp.*	9	-	1	2	5	3	1	12
Ficus virens *	1	-	-	-	1	-	-	1
Myristicaceae								
*Knema laurina**	34	-	9	16	28	29	10	92
Knema sp.*	25	-	-	-	-	6	14	20
Horsfiedia sp.	1	-	-	-	1	1	-	2
Myrtaceae								
*Syzygium cumini**	20	-	-	-	-	-	-	0
Olacaceae								
Strombosia sp.*	1	-	-	-	-	-	-	0
Palmae								
Livistona speciosa	5	-	-	-	-	-	-	0
Total	326	1	21	31	51	78	47	229
% ripe-fruit trees		0.3	6.4	9.5	15.6	23.9	14.7	

Animal food characteristics

Thirty-six animal species were eaten by the two hornbill species, and we were able to collect samples of 19 species from the study area. Characteristics including body weight and length were recorded (Table 5.) Among all hornbill animal food, snakes were the heaviest (>70 g) and longest (>40 cm) and were only eaten by the Great Hornbill. Crabs, the second heaviest prey, appeared to be the favorite food of both hornbill species. Small animal prey included wild cockroaches, crickets, grasshoppers, and caterpillars, and were not less than 1 g in weight and 2.5 cm long (Table 5).

Animals consumed by the Great Hornbill showed a positive correlation with body weight (Tables 5 and 6). However, Great Hornbill males tended to hunt heavier and longer-bodied prey than the Rufous-necked Hornbill did, though this difference was not significant. Although the Great Hornbill did not always hunt longer-bodied animals, such as snakes, the Rufous-necked Hornbill tended to hunt short-bodied animals, such as cicadas and insects.

Table 5. Characteristics of animal food and daily quantity consumed by Great (GH) and Rufous- necked Hornbills (RNH) during the breeding season

No	Animal species	Characteristics		Daily quantity consumed	
		Body weight (g)	Body length (cm)	GH	RNH
1	Birds' chicks	10.53±7.19	3.62±0.79	0.2	-
2	Lizards	21.60±9.41	9.20±0.73	5.5	1.0
3	Flying lizards	9.95±2.40	7.83±0.76	0.2	-
4	Skinks	16.10±1.55	8.48±0.92	2.4	0.7
5	Snakes	71.66±17.56	42.40±8.38	4.6	-
6	Frogs	29.02±32.98	5.98±2.23	13.0	8.0
7	Crabs	30.05±46.19	5.25±2.01	28.1	26.4
8	Elongate millipedes	12.58±2.23	12.55±4.30	3.2	0.8
9	Broad-rounded millipedes	3.58±2.00	4.44±1.50	0.4	-
10	Snails	17.52±14.84	4.91±0.79	2.6	2.2
11	Cicadas 1	1.61±0.72	3.49±0.68	5.0	3.0
12	Cicadas 2	2.71±0.77	4.86±0.18	-	3.0
13	Other Insects	1.91±1.10	3.87±0.87	5.0	4.6
14	Beetles	1.99±0.76	3.55±0.69	3.9	6.0
15	Wild cockroaches	1.15±0.36	3.29±0.68	0.5	0.1
16	Grasshoppers	2.96±0.98	2.86±1.12	0.1	0.2
17	Leaf-grasshoppers	2.00±0.49	6.64±1.72	-	0.04
18	Caterpillars	1.18±1.07	4.11±1.21	0.1	-
19	Earthworms	1.58±0.42	8.41±0.24	0.2	-

Table 6. Spearman's rank test (r) for correlation between animal food characteristics and quantity consumed by Great (GH) and Rufous-necked Hornbills (RNH) (from Table 5)

Animal prey characteristics	Spearman's correlation value					
	GH			RNH		
	r	N	*P*	r	N	*P*
Body weight (g)	0.531	17	0.0274	0.319	13	0.278
Body length (cm)	0.272	17	0.284	-0.0413	13	0.878

DISCUSSION

The characteristics which attract animals to fruits, besides color and size, could be the way in which the fruit is presented, e.g. in clusters, or singly, with pre-ripening sign (Stiles 1989) as in the case of *Polyalthia viridis* at Khao Yai (Poonswad 1993). This study found that both hornbills tended to choose fruits with high pulp weight and large diameter, but not too large a seed. This result may reflect plant and animal co-evolution, where the hornbill's fruit food must be of a suitable size for carrying. The high pulp weight and large seed of these fruits displayed trade-offs in size and weight with respect to total food mass. The birds tended to neglect the fruits with large diameter seeds because they might have less pulp or may not be able to pass though the narrow nest-hole while feeding or regurgitating the seed out. In addition, we agree with Howe and Westley (1988) regarding the fruit color choice of highly frugivorous birds such as hornbills, in that they prefer black, blue, red or purple tones in the form of drupes or arillate seeds. It would be interesting to study whether color and texture of pulp (such as a shiny pulp) are a reflection of nutritional value.

Fruits eaten by the Great Hornbill were smaller than those eaten by the Rufous-necked Hornbill. This can be explained by the fact that Great Hornbill fruit food comprised a greater proportion of figs, which were generally smaller than other fruits, a finding similar to that of a study at Khao Yai, Thailand by Poonswad *et al.* (1998). Overall, both hornbills tended to choose relatively large fruits more than they did small. High sugar content was not a factor affecting the Great's fruit food choice, but the Rufous-necked ate large quantities of fruit with high sugar content. Great Hornbills may have consumed other kinds of nutrient-rich food which meet their overall energy demand.

This study found that *Polyalthia simiarum* was the most preferred fruit of both hornbills. This differs from the findings of Chimchome *et al.* (1998), who studied the Rufous-necked Hornbill in the same area and found that they consumed *Cryptocarya pallens* in the highest quantity. This could be because differences in the most consumed fruit species would be related to variations in fruit crops between years. *Cryptocarya pallens* may have had a good seed year in 1998, whereas *Polyalthia simiarum* had good fruit set in 1999, when this study was conducted. We can hypothesize that the seed-year interval of each fruit species may differ every year.

Polyalthia simiarum, the non-fig fruit consumed in the greatest quantity by both hornbill species, was relatively abundant and changed color from early to late ripening (yellow, orange, red, red-purple, and dark-purple to black). These two factors may have a great influence on food choice. This is similar to the studies of Poonswad (1993) and Poonswad *et al.* (1998) at Khao Yai. The pre-ripening characteristics might be a cue for hornbills and deserves further study.

However, some fruits eaten by the hornbills had high productivity only after the breeding period, for example, *Litsea hansenii* and *Knema* sp., so we cannot conclude that the hornbills avoided them. In accordance with Poonswad *et al.* (1998) we found that one factor clearly influencing hornbill food choice was the fruiting period, which enabled the hornbills to utilize them. We recommend that additional study of year-round fruit availability including outside the breeding season, should be conducted to find out which fruit tree species are keystone species for hornbills.

The Great Hornbill tended to choose longer-bodied animals such as snakes and lizards more than did the Rufous-necked, but they did not have a high preference rank nor were they eaten in large quantities. The Rufous-necked Hornbill tended to choose heavy and large bodied animals in relatively high quantity, while light and short bodied prey such as insects also had a high preference rank. This suggests that one factor influencing choice of prey was ease of carrying. Crabs and insects were commonly found in the area where there is a stream running through and were presumably easily found by the hornbills, which partly explains their importance in the hornbills’ diet.

These results demonstrate that food choice specialization and fruit availability are key factors for hornbills, which might make them prone to local extinction. We suggest that forest areas need to be large enough to support sufficient fruit resources for year-round availability, so primary forest stands in all protected areas must be declared strictly inviolate within the range of the hornbills. In addition, hornbill fruit food trees should be planted to improve the quality of their foraging habitat in certain areas.

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Appendix 1. Some fruit species eaten by hornbills

Aglaia cucullata

Aglaia lawii

Aglaia macrocarpa

Beilschmiedia gammieana

Chisocheton ceramicus

Dysoxylum macrocarpum

Ficus virens

Knema laurina

Knema sp.

Lauraceae 1

Litsea hansenii

Platea latifolia

Polyalthia simiarum

Fruit/seed sizes of animal-dispersed plants: a comparison between African and Asian Tropical forests

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Abstract Fruit and seed characteristics in tropical forests were studied in two tropical forests, Itebero in Kahuzi-Biega National Park, Republic of Congo, in Africa, and in Lambir Hills National Park, Sarawak, Malaysia, in Asia. Size of fruit/seed was a crucial factor in explaining the tendency as to which animal disperses the seeds of each plant species in Itebero. In Itebero, monkeys (*Cercopithecus* spp.) ate the fruits < 30 mm in length, and dispersed the seeds < 20 mm in length. Forest elephants (*Loxodonta africana cyclotis*) seemed to play a unique role in the seed dispersal of several plants which have quite large fruits (> 100 mm in length) and/or seeds (> 40 mm in length). Two species of great apes, eastern lowland gorillas (*Gorilla gorilla graueri*) and chimpanzees (*Pan troglodytes schweinfurthii*), also dispersed seeds < 35 mm in length. The size limitation of fruits may be attributed to the handling ability of each animal species, and that of seeds may be to its gut diameter. In Lambir, where few large frugivores survive, there were two clusters in the size distribution of fruits and seeds: one could correspond to monkey dispersal, and the other can possibly correspond to hornbill and/or orangutan dispersal.

INTRODUCTION

In tropical forests, 45-90% of tree species show an adaptation for seed dispersal by vertebrates (McKey 1975; Howe and Smallwood 1982; Fleming 1991). Fruit characteristics are coevolved with frugivores (McKey 1975), and some of these characteristics may determine the nature of the seed dispersal agent. Several studies so far have shown that the size of fruits and seeds is the most essential character for dispersal, since larger frugivores can handle larger fruits and swallow larger seeds (Wheelwright 1985; Noma and Yumoto 1997).

Although the interaction between plants and seed dispersers is not usually characterized by strong species-species interactions (Wheelwright and Orians 1982), frugivores can have an evolutionary effect on their food plants as a consequence of fruit choice (Mack 1993). Assuming that fruit characteristics have coevolved with animals, differences in fauna can affect fruit availability and plant species diversity at the community level.

Large frugivores are vulnerable to extinction because of habitat loss and fruit scarcity resulting from forest fragmentation (Terborgh and Winter 1980). Some large fruits may be considered relictual or anachronisms, as their dispersal agents (some of the largest frugivores) have disappeared (Janzen and Martin 1982). This paper aims to show differences in fruit/seed size distribution between two forest communities: Itebero in Kahuzi-Biega National Park, Republic of Congo, and Lambir in Lambir Hills National Park, Sarawak, Malaysia. Although Itebero has suffered from hunting and partial deforestation, its large mammal and bird faunas are still intact. On the other hand, Lambir

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is surrounded by oil palm plantations, and its large mammals and birds have become rare, and in some cases have disappeared.

Study areas

Itebero in Africa

The study site was situated in the Itebero region (1'40"S, 28' 20"E, 600 m - 800 m above sea level), in Kivu district, Republic of Congo. This montane area was protected as part of the Kahuzi-Biega National Park (ca. 6000 km^2). According to rainfall records at the meteorological station in the Kahuzi region (Casimir and Butenandt 1973), a year in the study area can be divided into four seasons: the short dry season, January-March; the long rainy season, March-June; the long dry season, June-September; and the short rainy season, September-December.

The Itebero region is covered with tropical forests, which include primary forests, secondary forest (both recent and older), abandoned cultivated fields, and swamps. Primary stands of trees such as *Gilbertiodendron dewevrei, Staudtia gabonensis, Michelsonia microphylla* and *Cynometra alexandri* are frequently found together with sparse ground vegetation in the primary forest. *Musanga cecropioides* and herbaceous plants belonging to the Zingiberaceae and Marantaceae are found in big gaps in the forest, beside ravines and along rivers. Secondary forests are characterized by *Musanga cecropioides* and *Macaranga spinosa* with a dense cover of herbaceous plants. Several small cultivated fields surrounded by secondary forests were abandoned by local people prior to 1985. Oil palm trees (*Elaeis guineensis*) are frequently found in these areas. Older secondary forests were produced as a result of deforestation by a mineral company in the colonial era with subsequent successional regeneration. *Ficus sur, Uapaca guinensis*, *U. paludosa* and *Celtis brieyi* are commonly found in this type of forest. *Halopegia azurea* is one of the dominant herbaceous plants, and *Uapaca corbisieri* is occasionally found in swamps (Yumoto *et al*. 1994).

Eastern lowland gorillas (*Gorilla gorilla graueri*) and chimpanzees (*Pan troglodytes schweinfurthii*) inhabit this area sympatrically and their population densities in 1987 were 0.27-0.32 head/km^2 and 0.27-0.33 head/km^2, respectively (Yamagiwa *et al*. 1993). Also in this area, forest elephants (*Loxodonta africana cyclotis*) as well as seven species of diurnal monkeys are found: *Cercopithecus mitis, C. ascanius, C. hamlyni, C. mona, Cercocebus albigena* and *Papio anubis*. Eight hornbill species, *Bycanistes subcylindricus*, *B. albotibialis, B. fistulator*, *Ceratogymna atrata, Tropicranus albocristatus*, *T. alboterminatus, T. fasciatus* and *T. hartlaubi* are recorded in this region (Byamana K., pers. comm.).

Lambir in Asia

The study site was in Lambir Hills National Park, Sarawak, Malaysia (4° 20′ N, 113° 50′ E, altitude 150-250 m). Lambir Hills National Park is ca. 70 km^2 in area surrounded by oil palm plantations. Rainfall data collected over 30 years at the Miri Airport, 20 km from the research site, show that monthly rainfall fluctuated greatly up to 800 mm, and that annual rainfall ranges between 2100 and 3300 mm. Though a drier period was observed from January to March in some years, a clear annual rhythm of rainfall is not found and mean monthly rainfall rarely is exceeded by mean monthly evaporation (100 mm).

Lambir Hills National Park is situated on undulating low hills (ca. 60-450 m), and ca. 85% of the area is covered by primary lowland dipterocarp forest. The Dipterocarpaceae thus characterizes the forest, and in particular, *Dryobalanops lanceolata*, *D. aromatica*, *Dipterocarpus* spp. and *Shorea* spp. tend to dominate the forest.

Lowland tropical rainforests in west Malaysia are characterized by a high diversity of tree species (Whitmore 1984) and the phenomenon of supra-annual mass flowering (Ashton *et al*. 1988; Appanah 1993). Several studies conducted during the peak flowering period in 1996 in Lambir Hills National Park, Sarawak, Malaysia, were reported by Momose *et al*. (1998) and Sakai *et al*. (1999 a, b). The reproductive phenology of 576 individual plants representing 305 species in 56 families was monitored for 53 months from 1992-1996. Among 527 effective reproductive events during 43 months, 57% were concentrated in a peak flowering period of 10 months in 1996, and 35% of the species only flowered during that period (Sakai *et al*. 1999b). Fruits were collected after this general flowering period.

Pig-tailed macaques (*Macaca nemestrina*) and Bornean gibbons (*Hylobates muelleri*) both inhabit the forest, but their population densities during the observation period were quite low. The Orangutan (*Pongo pygmaeus*) has long since disappeared from these forests. In addition, sun bears (*Helarctos malayanus*), and three species of hornbills (*Anorrhinus galeritus*, *Berenicornis comatus*, *Anthracoceros malayanus*), all of them are large frugivores known to exist in the forest, but they also were rarely observed.

METHODOLOGY

In this paper, I use “fruits” in an ecological and not an anatomical sense to denote “functional fruits” (Herrera 1987), i.e. packages made up of seeds plus accessory tissues provided as rewards and displayed to animal dispersers, irrespective of their anatomical origin. Also, I use “seeds” including both the seed itself and the seed plus endocarp.

In Itebero in Africa, the survey was conducted intermittently from 1987 to 1990. Gorillas and chimpanzees in this region did not tolerate human presence because of previous high hunting pressure. Poor visibility in the tropical forest also hindered us from observing them. Therefore, data used here were mostly based on feces and field signs collected on the gorillas’ and chimpanzees’ fresh trails. We collected as many fecal samples as possible and washed them in sieves to identify the seeds contained within them. We also collected fecal samples of monkeys and elephants when we encountered their fresh trails.

The fruits whose seeds were found in dung piles of apes, monkeys and elephants were freshly collected from their respective plants. The characteristics of the heaviest fruit samples obtained were measured, because only one sample of fully developed fruit was available for several plants. The size of the fruit and seeds were measured with calipers, and fruit color was recorded for each species. The largest value among three dimensions was used for analysis, because it can be reasonably assumed that the largest value, not the smallest, limits the handling ability and passage through the intestine of animals.

In Lambir in Asia, fruits which showed animal-dispersal syndromes (seeds or seed clusters embedded in pulp in a fruit) were studied. As in Itebero, the characteristics of the heaviest fruit samples obtained were measured, because only one sample of fully developed fruit was available for several plants. Fruit and seed sizes were measured with calipers, and fruit color was recorded for each species. The largest value among three dimensions was used for analysis.

RESULTS AND DISCUSSION

Comparison of fruits as assemblages between Itebero and Lambir

Fruit/ seed size distribution was compared between sites (Fig. 1). Average length of fruits measured at Itebero was 65.1 mm (SD = 79.8, n = 34) and that of Lambir was 47.9 mm (SD = 42.1, n = 64). The largest fruit in Itebero was of *Anonidium mannii* (Annonaceae, 352.8 mm in length), and that in Lambir was of *Artocarpus integer* (Moraceae, 248.3 mm in length). Average length of seeds at Itebero was 22.5 mm (SD = 13.1, n = 34) and that of Lambir was 23.3 mm (SD = 18.2, n = 64). The largest seeds in Itebero were of *Mammea africana* (Guttiferae, 65.7 mm in length), and at Lambir was that of *Eusideroxylon zwageri* (Lauraceae, 108.4 mm in length).

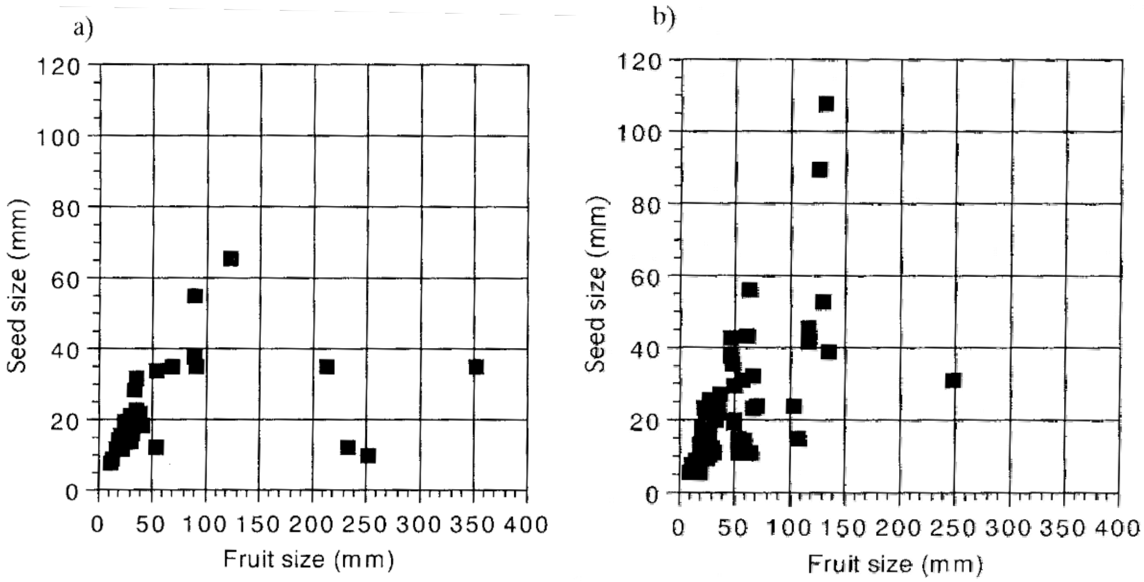

Figure 1. A comparison of fruit size and seed size in a) Itebero in Africa, and in b) Lambir, Asia. Maximum sizes of fruits and seeds from among three dimensions, obtained from the largest specimen for each species, are plotted.

Observed fruit - frugivore relationships in Itebero

Fruit and seed size seemed to be crucial factors determining the dispersal agent for plant species in Itebero (Fig. 2). In Itebero, monkeys (*Cercopithecus* spp.) ate the fruits < 30 mm in length, and dispersed the seeds < 20 mm in length. Forest elephants (*L. africana cyclotis*) seemed to play a unique role in the seed dispersal of several plants which have quite large fruits (> 100 mm in length) and/or seeds (> 40 mm in length). Two species of great apes, eastern lowland gorillas (*G. gorilla graueri*) and chimpanzees (*P. troglodytes schweinfurthii*), also dispersed seeds < 35 mm in length. The size limitation of fruits may be attributed to the handling ability of each animal species, and that of seeds may be to the diameter of its gut.

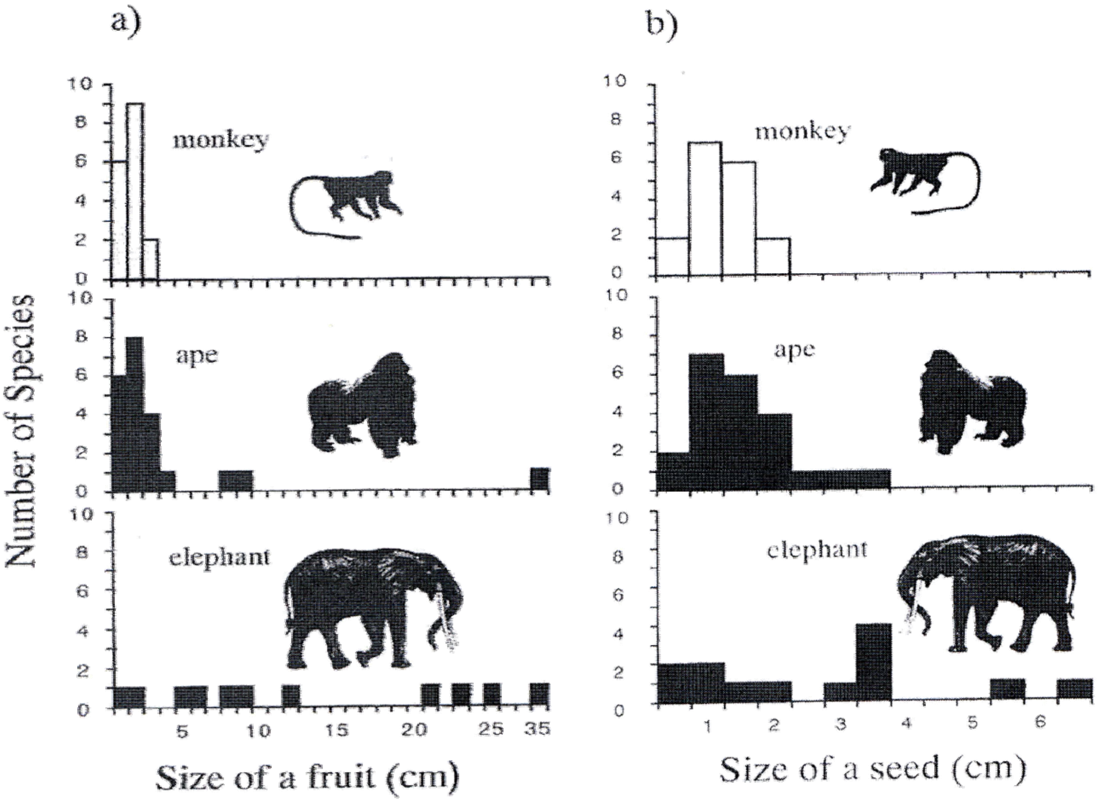

Figure 2. a) Size distribution of fruits that monkeys, apes and elephants ate and b) size distribution of seeds which monkeys, apes and elephants excreted in their feces in Itebero. Maximum size of a fruit and seed among three dimensions obtained in the largest specimen for a species is shown.

Sizes of fruits eaten by gorillas and chimpanzees ranged from the smallest (*Grewia mildbraedii*, 12.1 mm in length) to the largest (*Anonidium mannii*, 352.8 mm in length). The largest seed dispersed by gorillas was that of *Anonidium mannii* (35.5 mm in length), while the largest seed dispersed by chimpanzees was that of *Gambeya lacourtiana* (35.3 mm in length).

The largest seeds excreted by eastern lowland gorillas were those of *Anonidium mannii*. *Antrocaryon nannanii, Autranella congolensis* and *Mammea africana* have larger seeds than *A. mannii*, and their seeds were excreted only by elephants. The seeds of *Klainedoxa gabonensis* and *Treculia africana* were smaller than those of *A. mannii*, but only fragments of the seeds were found in fecal samples of gorillas. Intact seeds were never found, indicating that these were crushed by their teeth. *Omphalocarpum mortehani* also had smaller seeds but the pericarp was 7 mm thick and tough. Although rodents may nibble at the pericarp, only elephants could crack the pericarp and eat the fruit pulp.

Reconstructed fruit-frugivore relationships in Lambir

In Lambir, two clusters in size distribution of fruits were recognized: from 10 mm to 70 mm, and from 100 mm to 140 mm (Fig. 3a). Also, two clusters in size distribution of seeds were recognized: from 5 mm to 25 mm, and 30 mm to 55 mm (Fig. 3b). The smaller cluster in fruit/ seed size included plants of the Annonaceae, Euphorbiaceae, Myrtaceae, and Meliaceae, and the larger cluster included plants of Bombacaceae (*Durio graveolens,* *D. kutejensis, D. griffithii, D. grandiflorus, D. oblonga*) and Anacardiaceae (*Mangifera pajang*). The fruit sizes of *Dacryodes rostrata* and *D. incurvata* (Burseraceae) and *Beilschmiedia turfosa* (Lauraceae) belong to the smaller cluster (46.0 mm, 47.1 mm and 48.0 mm in length, respectively), but their seed sizes belong to the larger cluster (38.3 mm, 43.1 mm, and 36.0 mm in length, respectively). The fruit size of *Eusideroxylon zwageri* (Lauraceae) was 131.6 mm in length which belongs to the larger cluster, but its seed size was 108.4 mm in length and beyond the range of the larger cluster. In contrast, the fruit size of *Artocarpus integer* was larger (248.3 mm in length) than those in the larger cluster, and its seed size (31.2 mm in length) belonged to the larger clusters. Besides these five species, the cluster of fruit size and seed size to which each plant species belonged was quite consistent.

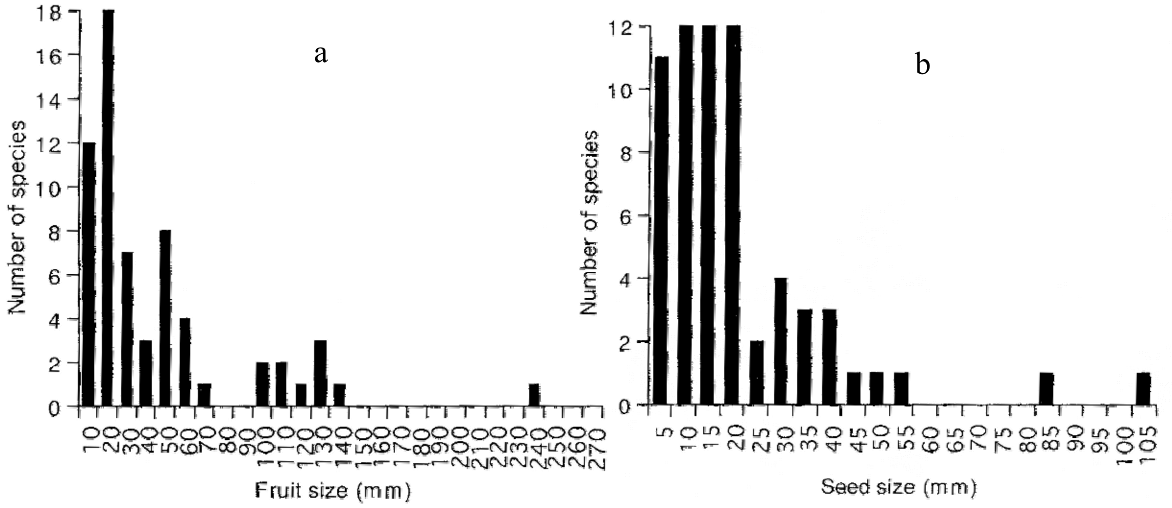

Figure 3. Size distribution of a) fruit and b) seeds obtained in Lambir. Maximum size of a fruit and a seed among three dimensions obtains in the largest specimen for a species is shown.

Very few feces and field signs which suggested feeding traits were obtained because of the scarcity of animals. We could only make assumptions regarding dispersers for each plant species. The cluster of small fruit and seed sizes are likely to correspond to monkey dispersal, and the larger cluster can possibly correspond to hornbill and/or orangutan dispersal.

The most probable consumers and seed dispersers of plants in the smaller fruit/seed size cluster are macaques and birds. No dietary study has been published on the pig-tailed macaque (*Macaca nemestrina*). But studies of the long-tailed macaques (*M. fascicularis*) in Singapore (Corlett and Lucas 1990) and Japanese macaque (*M. fuscata*) in Yakushima Island, Japan (Yumoto *et al.* 1998) proved that the smallest seeds (< 3~5 mm diameter) were regularly swallowed, and that larger seeds were spat out. In Yakushima, brown-eared bulbuls (*Hypsipetes amaurotis*, gape width 13.3 mm) consumed fruits smaller than 13.2 mm diameter, while red-capped green pigeons (*Spenurus formosae*, gape width 12.7 mm) and Japanese macaques (gape width 53.6 mm) consumed the fruits smaller than 16.0 mm diameter (Noma and Yumoto 1997).

There is almost no information on the diet of Bornean gibbons (*Hylobates muelleri*). However, according to the diets and the treatment of seeds by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park (Whitington and Tresucon 1991), Thailand, and gibbons (*Hylobates*) in Sumatra (Ungar 1994) smaller and unprotected fruits are preferred. Ungar (1994) suggested that large fruits which require extensive preparation with the incisors may be less attractive to gibbons, because of their need to keep their hands free for support and locomotion.

Head and body sizes of *Cercopithecus* spp. occurring in Itebero range from 34 cm to 60 cm, and body weights range from 1.8 kg to 10 kg (Kingdon 1997). This study shows that they ate the fruits < 30 mm in length, and dispersed the seeds < 20 mm in length. Pig-tailed macaques (*M. nemestrina*) are ca. 50 cm in head and body size and 4 – 9 kg in body weight, and Bornean gibbons (*H. muelleri*) are ca. 45 cm in head and body size and 5 – 6.4 kg in body weight (Payne *et al.* 1985). The sizes of macaques and gibbons in Lambir are quite comparable to the monkeys in Itebero, and it is not too great a leap to assume that their handling ability and treatment of seeds might be similar.

The sun bear (*Helarctos malayanus*) in Central Kalimantan was reported to have dispersed the seeds of *Canarium pilosum* (18 mm in seed size), *Erycibe maingayi* (17 mm in seed size) and *Ficus consociata* (McConkey and Galetti 1999). These seed sizes would be included in the smaller cluster in Lambir. Sun bears thus can be considered as seed dispersal agents in addition to macaques, gibbons and birds for plants belonging to the small fruit/seed size cluster.

What of the larger fruit/seed size cluster? Galdikas (1982) reported that the seeds of *Dacryodes* sp., *Baccaurea pendula*, *Baccaurea* sp., *Aphanamixis humilis*, *Nephelium* sp. and *Artocarpus* spp., which are genera commonly categorized in the larger fruit/ seed size cluster in this paper, were recovered from feces of orangutans at Tanjung Puting, Central Kalimantan, and that wild orangutans discard the seeds of *Durio oxleyanus* up to 50 m away from the mother tree, meaning that the orangutan can act as a seed dispersal agent for wild durians.

A great number of orangutan remains (pieces of jaw and isolated teeth) have been found from 40,000 to 12,000 year old deposits in the Niah Cave, which is located ca. 60 km away from Lambir (von Koenigswald 1982). Wallace (1896) wrote in his famous book *The Malay Archipelago* that there were plenty of orangutans in lowland forests in Sarawak at that time in 1854. We do not know for how long the orangutan persisted in Lambir, but some plants belonging to the large fruit/seed size cluster may well have been dispersed by them.

There is scant literature available as to which fruits are eaten by the Bornean gibbon and hornbills inhabiting Sarawak. Our study in Khao Yai National Park, Thailand is proving that hornbills are the main seed dispersers for several species of the Burseraceae including *Dacryodes* spp. and of the Lauraceae including *Beilschmiedia* spp. (Kitamura *et al.* 2004). The largest size of fruits which hornbills can handle is 42.2 mm in length (*Elaeagnus latifolia*), and the largest seeds they convey are 35.3 mm in length (*Canarium euphyllum*) at Khao Yai National Park (Kitamura *et al.* 2004). Hornbills discard seeds from their beaks. Therefore although they can only handle fruits as large as monkeys can, they can also carry seeds as large as those that apes are able to.

The distribution of the color of fruits is shown in Table 1. In both sites, yellow was the most frequently occurring color at ca. 27%. The second most frequent color in Lambir was orange, while that in Itebero was brown. In Lambir, black and purple were less frequent than in Itebero, although the difference was not significant because of the small sample size. Several investigations have stated that black and purple are the commonest bird-fruit colors in tropical forests (Wheelwright 1985; Gorchov *et al.* 1995). Kitamura *et* *al*. (2004) mentioned that the commonest color of hornbill-consumed fruits at Khao Yai National, Thailand was black/purple. In Lambir, purple fruits included those of *Dacryodes incurvata* (46.0 mm fruit length, 38.3 mm seed length), *Ixora woodii* (15.3 mm fruit length, 6.6 mm seed length), and *Polyalthia cauliflora* (14.4 mm fruit length, 8.5 mm seed length), and black was possessed by *Vitex vestica* (9.5 mm fruit length, 5.9 mm seed length). *D. incurvata* is presumed to be dispersed by hornbills, and the other three species are in the 10% of smallest fruits and are presumed to be dispersed by smaller birds including bulbuls.

Table 1. Comparison in fruit color between Itebero and Lambir. The number of species is shown in the upper row, and percentages in the lower row for each site.

	Black	Brown	Green	Yellow	Orange	Red	Purple
Itebero	2	4	3	6	3	2	2
%	9.1	18.2	13.6	27.3	13.6	9.1	9.1
Lambir	1	7	8	17	16	10	3
%	1.6	11.3	12.9	27.4	25.9	16.1	4.8

CONCLUSION

Based on the information obtained from Itebero in Africa, it is suggested that the size limitation of fruits may be attributed to the handling ability of each dispersal agent, and that of seeds may be to the diameter of their guts. I applied these findings to data from Lambir, Malaysia, where few large frugivores survive. Two clusters in size distribution of fruits and seed were observed: one may correspond to monkey dispersal, and the other can possibly correspond to hornbill and/or orangutan dispersal. As the large frugivores have nearly been extirpated in Lambir because of forest fragmentation and hunting pressure, several plant species may not be able to maintain their populations or they may suffer from genetic problems in the near future due to severe dispersal limitation.

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Characteristics of fruits consumed by the White-handed Gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand

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Abstract Gibbons act as generalized frugivores in tropical rain forests. They play an important role in the forest ecosystem as seed dispersers. Fruit characteristics also have an important role in explaining coevolution between plants and gibbons. Feeding behavior of White-handed Gibbons (*Hylobates lar*) was studied in Khao Yai National Park, Thailand. The main purpose of this research was to identify the diverse foods in the gibbons' diet and to determine the fruit characteristics that influence the White-handed Gibbon's choice of food. The methods of study included direct observation of gibbon behavior and of the morphology of fruits, leaves and other plant parts. Fecal samples were also collected. Collected fruit was analyzed for nutritional value in the laboratory at the Institute for Nutrition, Mahidol University. The method of handling of fruit by gibbons was also observed in the zoo. Sixty five species from thirty plant families were collected and identified in the diet of one gibbon family. The bulk of their food diet came from trees (72%), but also from climbers (26.6%) and treelets (2.1%). The gibbons fed on 50 species of fruit with *Ficus* as the most frequently consumed fruit. Young leaves, flowers, spadices, and spathes were also observed to be consumed. Gibbons mostly consumed ripe fruit with bright colors (yellow, red, orange and purple), which were soft and juicy. Fruits of small size (less than 10 mm), light weight (less than 10 g) and with a single well-protected seed were consumed more than other fruit by the gibbons. The nutritional value of six consumed types of fruits and leaves did not differ much. Field observations were supported by an experiment in the zoo which revealed that gibbons chose food items of suitable size and weight that could fit in their hands. These results indicated that food characteristics are one of the main factors along with other factors such as food availability and abundance determining the gibbon's choice. However, there are many factors that influence food selection of gibbons which can explain their behavior and the territorial defense hypothesis. Study of fruit characteristics should be carried out in relation to other factors which might be important in food selection. This will explain food selection of white-handed gibbons which in turn is important for gibbon conservation in the future.

INTRODUCTION

The tropical rain forest ecosystem has high species diversity and complex relationships between species. Many plants depend on birds and mammals for dispersal of their seeds. The traits of fruits and their frugivores are the product of diffuse coevolution in which groups of plants interact with group of animals (Fleming 1991). Coevolution between plants and their seed predators may help to explain some events of plant reproductive biology and animal feeding habits (Krebs 1985).

Seed dispersal plays a potentially important role in ecology in maintaining the structure and diversity of the plant community. The relationship between a fruiting plant and its seed dispersers is a dynamic mutualism in which frugivores use fruits for food, and the plants depend on the frugivores to disseminate their seeds (Howe 1986).

Seed dispersal is the transport of seed away from the parent plant. Many species of seed-bearing plant have fruits that attract birds, mammals or ants that will bury, regurgitate or defecate seeds away from the parent plants. Howe and Westley (1988) suggested that the most highly developed modifications for dispersal are those adapted for consumption by fruit-eating birds and mammals which frequently offer substantial nutritional rewards (Howe 1986).

Primates are the single most important group of mammals in many tropical forests. Their dietary habits are extremely varied. Most commonly, they eat fruits and foliage, but many species are specialized and feed on such items as seeds, bamboo gum, nectar or small animal prey (Terborgh 1992).

Gibbons are an example of primates which have mutualistic relationships with fruits. These developed through coevolution, and fruits adapted their morphology and physiology for attracting gibbons. Host selection criteria are one of the first priorities to study and concern the role of color in the attracting dispersal agents (Julliot 1996).

Although many studies have been done on seed dispersal in mammals, information about seed dispersal syndromes for primates is very rare. Gibbons may help maintain species diversity in their home range through beneficial seed dispersal and their role still needs further investigation (Whitington 1990). The main purpose of this research was to identify the diverse foods in the diet of White-handed Gibbons (*Hylobates lar*) and to determine the fruit characteristics that they use to select their food.

The project also sought to address the relationship between fruit availability and selectivity of gibbons in comparison with other studies on fruit choice by birds and other primates. What determines the syndrome and what is the effect of certain morphological characteristics of fruit species on dispersal by gibbons? This study will also provide basic information for gibbon conservation and management.

METHODOLOGY

Study area

Khao Yai National Park lies between 14°05′ and 14°15N′, and 101°05′ and 101°50′E. It consists of a mountainous area which is a part of the Phanom Dongrak range which lies between 250 and 1351 m above sea level (Treesucon 1984).

Mo Singto study site

The research site was located at Mo Singto, Khao Yai National Park. This site is located at 101° 22′ E, 14° 26′ N at an elevation of 730-860 m above sea level (Whitington 1990). The park has a very large area of primary tropical semi-evergreen forest.

Observation and feeding behavior

A group of White-handed Gibbons (*Hylobates lar*) was named “Group A” by Brockelman (1998) and was habituated. The group consists of five individuals, 3 males, 2 females, both adults and juveniles. The group occupied a home range of about 30 ha (Brockelman 1998). Observations of this gibbon group took place from June 1997 to November 1998.

The gibbon diet was studied by observation, and directly through the collection of fecal samples and recording of morphology of fruits, leaves and other plant parts. All five individuals in Group A were observed until September 1997, when the juvenile male disappeared from the group. Observation records included time, date and individual animal for each fecal stool collected for analysis. Each fecal sample was placed in a separate plastic bag and labeled with all the information recorded.

The collection of seeds and fruit twice each month was planned, with each collection taking place over five days. Fruits, leaves, and some kinds of termites observed to be eaten by gibbons were collected for identification and nutritional analysis in the laboratory. Uneaten parts of plant specimens fed upon by gibbons were collected from the ground.

Species identification of food plants via seed examination

Within 24-48 hours of collection, fecal samples were suspended in water and washed through sieves (mesh size of 1.00 mm and 2.00 mm) in order to separate seeds for species identification. Seeds were identified with the aid of reference specimens deposited at the herbarium of the Center for Conservation Biology, Department of Biology, Faculty of Science, Mahidol University (Bangkok, Thailand).

Characteristics of fruit and seed

The adaptive hypothesis predicts particular trends of variation in fruit characters such as overall fruit size, color, structure, seed number, relative yield of pulp and nutrition (Julliot 1996)

The different morphological characters studied were

1. Size and weight of fruits and leaves of wet and dry specimens. Weight was measured using a digital balance. A vernier caliper was used for measuring the length of leaves and fruits. The maximum length of each fruit and was recorded.
2. Kind of pulp: only water content was considered. Two classes were defined as dry pulp and juicy pulp. Arillate fruits were included in the dry or juicy pulp types according to their water content. Thus, various types of arils were not distinguished, because arils can have different aspects and may differ in water content.
3. External color of mature fruit. The colors recorded were yellow, orange, red, purple, green and mixed colors.
4. Seed number and seed size per fruit given as an average value.
5. Seed protection (the hardness of seed test). This morphology can be noted as:
    - (n) no protection (very soft and very easy to break)
    - (+) can be opened with fingernail
    - (++) can be opened with a knife
    - (+++) cannot be opened with a knife.
6. Seed volume

The volume of the seeds of each species was determined by putting the seeds in water and measuring the displacement in volume. Volume per seed was calculated, as well as seed volume per fruit.

Nutritional values of fruits and leaves

Collected fruit was analyzed for carbohydrates, lipids, sugar, energy content and water at the Institute for Nutrition, Mahidol University.

Parts of six plant species were used for nutritional analysis. These species were available in the forest and their fruit was easily collected.

1. *Balakata baccatum* (Roxb.) Esser (Euphorbiaceae) (ripe)
2. *Balakata baccatum* (Roxb.) Esser (Euphorbiaceae) (unripe)
3. *Walsura robusta* Roxb. (Meliaceae)
4. *Diospyros glandulosa* Lace (Ebenaceae)
5. *Choerospondias axillaris* Burt & Hill (Anacardiaceae)
6. *Ficus* sp. (Moraceae)
7. *Polyalthia viridis* Craib (Annonaceae) (mature leaves)
8. *Polyalthia viridis* Craib (Annonaceae) (young leaves)

RESULTS

Food consumption

The plant diet consumed by gibbons included fruits, leaves, flowers, and shoots. In addition they consumed some termites. Overall, sixty five plant species from thirty four families comprising three different life forms were found to make up the gibbons' diet (Fig. 1). Four of the plant families were unidentified.

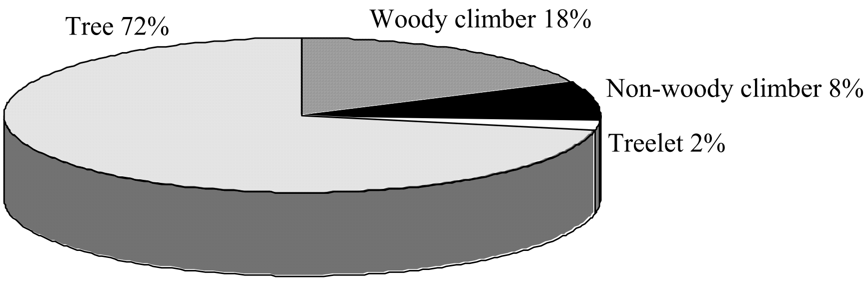

Figure 1. Proportion of life forms of plant species eaten by White-handed Gibbons.

Gibbons of Group A consumed a variety of plant parts, including fruits, leaves, young shoots, flowers, legume pods, and spathes/spadices (Table 1).

Fruit formed the bulk of the plant diet (73.5%; 75% including legume pods), and were from 50 species of plants, including fifteen species of *Ficus*. There were six non-fig species whose fruits were a major part of the gibbons' diet: *Choerospondias axillaris*, *Alphonsea boniana*, *Sandoricum koetjape*, *Gnetum montanum*, *Knema laurina* and *Garcinia xanthochymus*. The list of plant species eaten by the gibbon group is shown in Appendix 1.

Table 1. Percentage of species whose plant parts are eaten by White-handed Gibbons.

Eaten Part	Proportion (%)	Number
fruits (fleshy fruits)	73.5	50
leaf	19.1	13
young shoot	3.0	1
flower	1.5	1
legume	1.5	1
spadix, spathe	1.5	1

Characteristics of consumed fruits

There were many types of fruits eaten by the white-handed gibbons, but most were drupes. Fruits were categorized into four groups, each having varying size, shape and color.

1. *Need peeling:* these fruits were peeled by gibbons to remove the pericarp before eating. Examples include *Gnetum montanum* and *Balakata baccatum.*
2. *Ready to be eaten whole:* Gibbons did not remove the pericarp before consuming this kind of fruit. They ate the fruits whole with seed and flesh. Examples of this fruit type are *Eberhardtia tonkinensis* and *Choerospondias axillaris.*
3. *Seed and pulp easily separated:* These fruits have various seed shapes and juicy pulp. Most fruit of this type are common and were not very large, such as *Polyalthia viridis*, *Elaeagnus latifolia*, *Knema laurina*, and *Walsura robusta.*
4. *Husky fruits:* Some fruit species possessed very hard rinds, which the gibbons had to employ a fair amount of effort to get at the flesh and seeds inside. *Melodionus cambodiensis* and *Garcinia xanthochymus* are the examples.

Gibbons were also observed to feed on young leaves, flowers (*Dipterocarpus gracilis*), and young shoots.

The morphology of plant species eaten by gibbons are categorized in Table 2. The fruit in a gibbon's diet have many varied characteristics such as the pericarp color, seed number, kind of pulp and seed protection.

The colors of fruits consumed by gibbons were compared with the color of hornbill-eaten fruits, and were tested by chi-square analysis. There was no significant difference between the proportion of color choice of fruits consumed by hornbills and those eaten by gibbons ($x^2 = 4.8$, df = 4, $P = 0.05$). Figure 2 shows the parts of the fruits consumed by the gibbons. Gibbons mostly consumed the fruits whole.

Table 2. Number and percentage of fruits eaten by White-handed Gibbons according to fruit characteristics

Characteristics	Number	Proportion (%)
Colors		
yellow-green	3	6.5
yellow	17	37.0
dark blue or purple	13	28.3
orange	6	13.0
red	6	13.0
brown	1	2.2
Size (mm)		
<10	12	27.3
10–20	9	20.5
20–30	11	25.0
30–40	4	9.1
>40	8	18.2
Weight (g)		
<10	30	68.2
10–20	3	6.8
20–30	5	11.4
30–40	3	6.8
>40	3	6.8
Kind of pulp		
dry pulp	9	19.2
Juicy pulp	40	80.9
Seed number		
1	21	44.7
≤10	10	21.3
>10	16	34.0
Seed hardness		
Could be opened with finger nail	15	30.0
Could be opened with knife	25	50.0
Could not be opened with knife	10	20.0

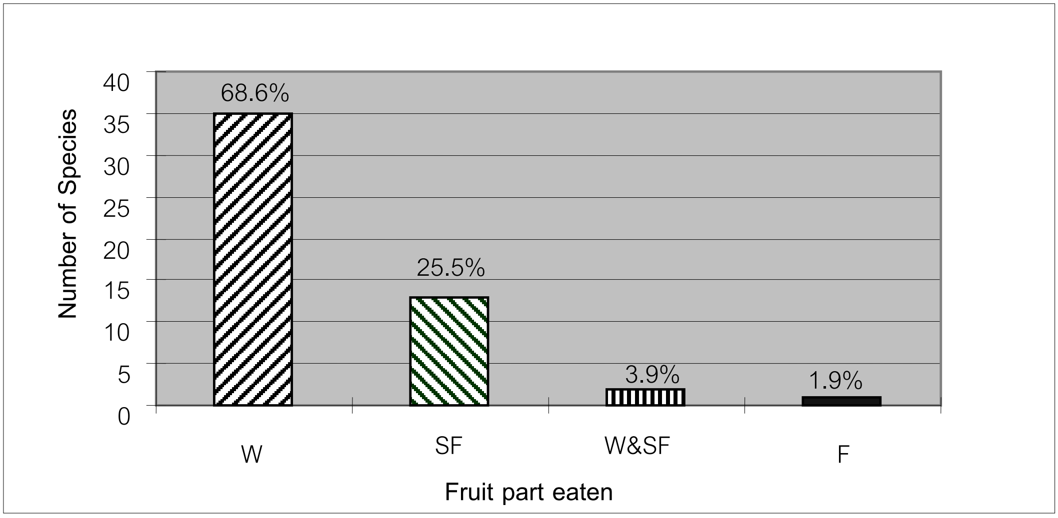

Figure 2. Number of fruit species consumed by gibbons according to parts eaten: W = whole fruit, SF = only seed and flesh were taken only, W&SF = whole fruits eaten but sometimes only seed and flesh were taken, F = only flesh eaten.

Two sample groups of eaten fruit were measured for their dry weights and fresh weights of both eaten and uneaten parts. They were:

1) Fruit consumed whole such as *Bridelia tomentosa, Desmos chinensis* and *Toddalia asiatica.*

2) Fruit in which gibbons discarded the exocarp such as *Alphonsea boniana, Salacia macrophylla, Baccaurea ramiflora* and *Knema laurina.*

Fecal examination and characteristic of seeds

Adult females usually produced larger piles of feces than other members of the same group. Seeds of thirty-six species were collected from gibbon feces. Ten species were from unknown plants, which were not found in the fruit and seed collection of the Center for Conservation Biology. Seeds of *Ficus* spp. were most numerous amongst the collected seeds, and most fecal piles contained *Ficus* seeds. Table 3 shows the fruiting phenology for species eaten by gibbons at the Mo Singto study site. The results show there was at least one *Ficus* sp. available every month (Table 3).

Table 4 shows the frequency and percentage of eaten seeds in the feces. Seeds of *Ficus* spp. are found in feces the most followed by *Aidia cochinchinensis.* Gibbons consumed the entire fruits of this species.

Collected seeds from gibbons feces were counted each month (April 1997-July 1998). Gibbons ate fruits from fruiting trees more than they did from climbers during April 1997-December 1997. The result shows that feeding in climbing plants dipped in September (1997) and increased a month later. Between November (1997) to May (1998) gibbons fed on climbers more than on trees, after which they started to feed on fruiting trees again (Fig. 3).

Table 3. Cumulative overlap of fruit season among species eaten by White-handed Gibbons during the study

species		----------1997----------									----------1998----------					
	no. of months in fruit	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
Ficus spp.	15	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Nephelium melliferum	3	▨	▨	▨												
Knema laurina	1	▨														
Aphananthe cuspidata	9	▨	▨	▨	▨	▨	▨	▨	▨	▨						
Aidia cochinchinensis	11	▨	▨	▨	▨	▨	▨	▨					▨	▨	▨	▨
Cleistocalyx operculatus	2		▨	▨												
Diploclisia glaucescens	5		▨	▨	▨	▨	▨									
Gnetum sp.	6		▨	▨	▨	▨	▨	▨								
Unk. 04	2			▨	▨											
Piper sp.	1			▨												
Garcinia xanthochymus	6			▨	▨	▨	▨	▨	▨							
Seed Unk. 01	1				▨											
Bridelia tomentosa	2				▨	▨										
Sandoricum koetjape	1					▨										
Seed Unk.02	1					▨										
Seed Unk. 03	1					▨										
Alphonsea boniana	9					▨	▨	▨	▨			▨	▨	▨	▨	▨
Fissistigma rubiginosum	4					▨	▨	▨	▨							
Choerospondias axillaris	5					▨	▨	▨	▨	▨						
Platea latifolia	1						▨									
Seed Unk. 05	2						▨	▨								
Seed Unk. 04	3						▨	▨	▨							
Neolamarckia cadamba	4						▨	▨	▨	▨						
Toddalia asiatica	9							▨	▨	▨	▨	▨	▨	▨	▨	▨
Seed Unk. 06	1							▨								
Beilschmiedia glauca	1							▨								
Seed Unk. 08	1								▨							
Tetrastigma laotica	2								▨	▨						
Seed Unk. 07	5								▨	▨	▨	▨	▨			
Elaeagnus latifolia	2									▨	▨					
Desmos chinensis	3										▨	▨	▨			
Balakata baccatum	6										▨	▨	▨	▨	▨	▨
Melodionus cambodiensis	2										▨	▨				
Diospyros glandulosa	2										▨	▨				
Polyalthia viridis	5										▨	▨	▨	▨	▨	
Seed Unk. 09	1												▨			
Eberhardtia tonkinensis	1												▨			
Prunus javanicus	2												▨	▨		
Gnetum macrostachyum	3													▨	▨	▨
Walsura robusta	2														▨	▨
Number of fruiting species		5	7	10	9	13	13	14	12	9	9	9	11	8	8	7

Table 4. Affinities of seeds found in the feces of gibbons and their frequencies (number of fecal piles out of 390) (April 1997- July 1998)

Species	Frequency	Percentage
Aidia cochinchinensis	12	10.3
Alphonsea boniana	4	3.4
Aphananthe cuspidata	8	6.9
Alphonsea boniana	5	4.3
Balakata baccatum	4	3.4
Beilschmiedia glauca	2	1.7
Bridelia tomentosa	1	0.9
Choerospondias axillaris	5	4.3
Cleistocalyx operculatus	2	1.7
Desmos chinensis	3	2.6
Diospyros grandulosa	2	1.7
Diploclisia glaucescens	4	3.4
Eberhardtia tonkinensis	1	0.9
Elaeagnus latifolia	4	3.4
Ficus spp.	*	*
Fissistigma rubiginosum	2	1.7
Garcinia xanthochymus	6	5.2
Gnetum sp.	9	7.8
Knema laurina	1	0.9
Melodionus cambodiensis	1	0.9
Neolamarckia cadamba	6	5.2
Nephelium melliferum	2	1.7
Piper sp.	1	0.9
Platea latifolia	2	1.7
Polyalthia viridis	1	0.9
Prunus javanicus	1	0.9
Sandoricum koetjape	3	2.6
Tetrastigma laotica	2	1.7
Toddalia asiatica	3	2.6
Unk 01	1	0.9
Unk 02	1	0.9
Unk 03	1	0.9
Unk 04	1	0.9
Unk 05	1	0.9
Unk 06	1	0.9
Unk 08	4	3.4
Unk 09	6	5.2
Unk 10	1	0.9
Walsura robusta	2	1.7
Total	116	100.0

* *Ficus* seeds were found every time in large quantities in the feces of gibbons.

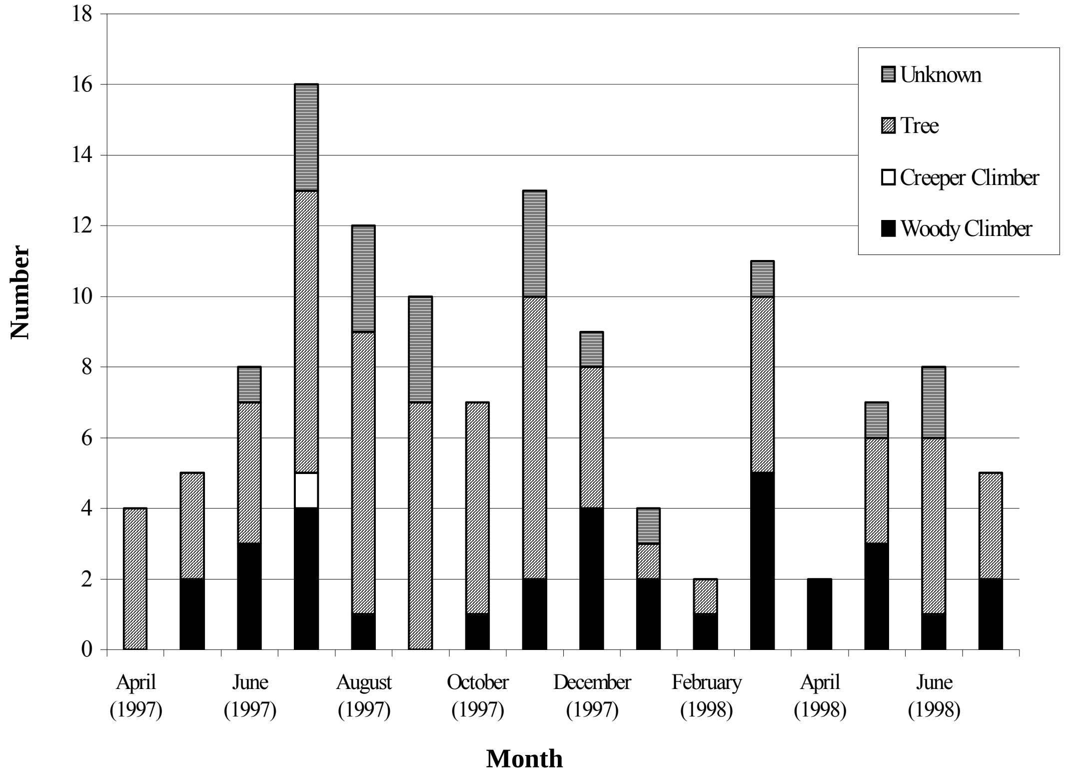

Figure 3. Number of fruiting plant species and their life forms collected in feces of White-handed Gibbons during April 1997-1998.

Table 5 lists the plant species eaten by White-handed Gibbons, with their numbers and volume. The volume of most seeds studied was less than 1.0 cm^3. Some seeds have large sizes, with their seed volume exceeding 2.0 cm^3 such as *Choerospondias axillaris*, *Polyalthia viridis*, *Platea latifolia*, *Sandoricum koetjape* and *Prunus javanicus.*

Nutritional analysis

Eight species were chosen for nutritional analysis, including six species of fruits and leaves. Young and mature leaves of *Polyalthia viridis* were chosen to compare their nutritional value (Table 6). Nutritional quality in the mature leaves was higher than that of the young leaves for all classes.

Table 5. List of plant species eaten by the White-handed Gibbon Group A with seed number and volume

No.	Species	Volume per seed (cc)	Seed Number Average	SD	Seed Volume (per fruit)
1	*Choerospondias axillaris* Burt&Hill	2.300	1.00	None	2.300
2	*Alphonsea boniana* Fin.& Gagnep.	0.400	5.77	None	2.308
3	*Desmos chinensis* Lour.	0.100	1.00	None	0.100
4	*Polyalthia viridis* Craib	2.200	1.00	None	2.200
5	*Fissistigma rubiginosum* Merr.	0.216	1.00	None	0.216
6	*Melodionus cambodiensis* Pierrs ex Spire	0.007	16.33	3.51	0.120
7	*Salacia macrophylla* Bl.	0.011	11.70	1.42	0.123
8	*Diospyros glandulosa* Lace	0.030	13.50	2.26	0.405
9	*Elaeagnus latifolia* L.	0.013	2.25	0.07	0.028
10	*Baccaurea ramiflora* Lour.	0.001	1.00	None	0.001
11	*Bridelia tomentosa* Bl.	0.027	1.00	None	0.027
12	*Balakata baccatum* (Roxb.) Esser	0.425	2.00	None	0.850
13	*Gnetum macrostachyum* Hook.f	0.026	1.00	None	0.026
14	*Gnetum montanum* Markgraf	0.113	1.00	None	0.113
15	*Garcinia xanthochymus* Hook.f.	0.440	5.56	1.30	2.446
16	*Platea latifolia* Bl.	2.000	1.00	None	2.000
17	*Sandoricum koetjape* (Burm.f.) Merr.	2.750	3.85	1.57	10.588
18	*Walsura robusta* Roxb.	0.500	1.00	None	0.500
19	*Diploclisia glaucescens* (Bl.) Diels	0.330	1.00	None	0.330
20	*Knema laurina* Warb.	1.630	1.00	None	1.630
21	*Cleistocalyx operculatus* Merr.& Perry	0.500	1.00	None	0.500
22	*Piper* sp.	0.160	1.00	None	0.160
23	*Prunus javanica* (Teijam.&Binn) Miq.	2.000	1.00	None	2.000
24	*Aidia cochinchinensis* Lour.	*	1.00	None	*
25	*Toddalia asiatica* Lamk.	0.100	4.66	1.07	0.466
26	*Nephelium melliferum* Gagnep.	1.700	1.00	None	1.700
27	*Eberhardtia tonkinensis* H. Lec.	0.700	3.85	1.03	2.695
28	*Aphananthe cuspidata* (Bl.) Planch	0.300	1.00	None	0.300
29	*Tetrastigma laotica*	0.200	3.30	1.26	0.660
30	Unknown 01	0.051	N	N	N
31	Unknown 02	0.250	4.50	0.70	1.125
32	Unknown 03	0.510	1.00	None	0.510
33	Unknown 04	0.970	3.95	1.23	3.832
34	Unknown 05	0.990	N	N	N
35	Unknown 06	0.480	N	N	N
36	Unknown 07	0.25	N	N	N
37	Unknown 08	0.05	N	N	N
38	Unknown 09	0.96	N	N	N
39	Unknown 10	0.962	N	N	N

Table 6. Nutritional quality (per leaf) of mature and young leaves of *Polyalthia viridis*

Nutritional quality (n=60)	Nutritional quality per leaf	
	Mature leaves	Young leave
Energy (kcal)	0.965	0.172
Moisture (g)	0.773	0.392
Protein (N*6.25) (g)	0.078	0.035
Fat (g)	0.017	0.004
Carbohydrate (g)	0.126	0
Dietary fiber (g)	0.382	0.068
Ash (g)	0.022	0.008

DISCUSSION

Some plant species that were chosen by the gibbons at the Mo Singto site are the same species that were found in other research sites, but others are not. This may be explained by the fact that the conditions during this time period were different from what it might have been like during other studies. There was less rainfall and more dry days during this study. This problem may have led to some species not to producing flowers and fruits. This is supported by Glander (1981), who noted that flower and fruiting availability was linked to rainfall, with flowering being a dry season phenomenon and fruiting a wet season phenomenon. *Nephelium melliferum* is a good example of this.

Most food items came from trees (72%) and climbers (27%), which is similar to the proportion of species consumed by hornbills at Khao Yai National Park (Kitamura 2000). The major foods of gibbons are fruits and leaves and the minor foods are flowers, shoots and some small animals. Fruit is expected to be a “high yield” food to compensate for the high cost of traveling. A few mature leaves were consumed by gibbons so mature leaves are expected to be a kind of "low yield" food that requires low cost to harvest (Agetsuma, 1995).

Most of the fruits that were collected and consumed by gibbons in this study consisted of *Ficus* spp. (Moraceae). Observations suggest that figs are a keystone species in Khao Yai National Park, which supports the findings of Bartlett (1999). These keystone resources were consumed the most when other (sometimes more favored) fruits were unavailable.

Fruit preferences of gibbons in this study were based on fruit availability in the forest. The results in Table 1 can be explained when one learns that most chosen fruits came from trees and climbers that were fruiting during feeding time. There were fewer fruiting trees in 1998 so gibbons selected more fruiting climbers. It was likely that food availability influenced food selection by gibbons.

Syndrome: characteristics of plant species consumed

Fruits consumed by gibbons were ripe and juicy, confirming what other researchers have observed. One reason that gibbons chose juicy fruit was that they needed water from the flesh. Food preferences of hornbills are for the ripest fruits with high nutritional value, but these fruits are usually not juicy (Poonswad 1988). The choice of ripe fruit for birds may be guided by softness and color.

Fruits chosen by gibbons were compared with those chosen by the hornbills studied by Poonswad (1994). The results support Glaser *et al.* (1978) who suggested that bright external colors mostly occur in the ripe fruits which have a sweet taste and are juicy for animals. There is not much difference between the syndromes of gibbon and hornbill fruits with respect to color alone. The results are in accordance with the bird-gibbon syndromes noted by Gautier-Hion *et al.* (1985) (Bartlett, 1999). The proportions of colors of fruit consumed by gibbons were similar to those eaten by hornbills (x^2, df =4, P=0.05).

Poonswad (1994) explained that birds did not choose juicy fruit as did gibbons because they were not able to determine the pulp composition and nutritional richness. The hypothesis was that a hornbill's preference for fruits is chiefly determined by the abundance of food items (Sorensen 1981; Foster 1990). Hornbills also have to select fruits they can swallow whole and therefore they are more limited in their choice than are gibbons.

The structure of fruits might influence their selection by gibbons. Gibbons preferentially fed on fruits containing one seed with good protection. Gibbons could consume many types of fruits, but most fruits consumed were drupes that were ready to be eaten whole. One reason that gibbons chose the drupes may be because most drupes contain substantial amounts of flesh.

In this study, white-handed Gibbons primarily consumed ripe fruits with juicy pulp and bright colors (red, orange and yellow); these fruits had generally well-protected seeds. Dark blue fruits were also sometimes chosen by gibbons. Colors, especially yellow, seem to be the primary criterion for the choice of fruit eaten by gibbons. Orange and red fruits are also often consumed, though green fruits were not totally avoided. However, there were many green fruits available in the forest that the gibbons did not select. The observation is similar to the findings of Julliot (1996) but it contrasts with observations of Janson (1983), who considered that Neotropical primates eat principally brown, green, yellow or orange fruit and avoided red fruits.

Gibbons appear to always select fruits that are most readily available in the forest. This supports Fleming (1991), who noted that fruit size is a basic morphological parameter that influences frugivore food choice. In general, mean and maximum fruit size tends to be positively correlated with body size of frugivore. Gibbons may choose a fruit size that is easy to pick up and handle. However, the distribution of size classes of fruit consumed by gibbons was relatively even, indicating a lack of strong size preference. However, they ate more species of small fruits or more by number or weight. This may be because gibbons chose many species of fig with small and well-protected seeds, as there were figs available throughout the entire year. For example, most fruits (except *Ficus* spp.) consumed by gibbons from this study contain one seed. Gibbons chose fruiting trees in the peak of that fruit's abundance and chose fig fruits when other fruit species were rare.

Fruit size is an important factor in attracting consumers. It has been proposed that the evolutionary trend toward larger fruit benefits the plant by limiting its dispersers to a restricted set of specialized animals. Species with large fruit and seed need to be attractive to large animals, as their weight might otherwise be an obstacle to effective seed dispersal. This supposition is different to the gibbon fruit choice observed in this study. Gibbons chose many size classes of fruits, not only the larger ones.

Fruit protection is also an important characteristic as regards seed dispersal because it also limits the number of potential dispersers. Some vertebrates, especially primates, can open fruits with hard and indehiscent pericarps with their teeth~~;~~, so seed size, and not fruit size, limits the number of dispersers that can swallow seeds.

However, McKey (1975) suggested that there is no relationship between fruit nutrition and fruit size that points to evolution favoring specialization by plants for reliable dispersers. Many smaller fruits contain nutritious arils or flesh and are dispersed by a wide variety of opportunistic consumers.

This study may indicate that although gibbons are generalized frugivores, they might be particularly important dispersers for some plant species. Although these plant species cannot be eaten by birds and other frugivores as their fruits may be well-protected, or have large fruits with large seeds, gibbons may have the ability to consume them. For example, *Platea latifolia*, *Elaeagnus latifolia*, *Sandoricum koetjape* and *Garcinia xanthochymus* are large fruits that cannot be swallowed by birds, and they may rely on gibbons to disperse their seeds. Fruits of *Platea latifolia* and *Elaeagnus latifolia* do not have a tough covering, so any animal or bird should be able to eat them, but may not be able to swallow the seeds. Thus, their seeds would be dropped under the trees and not dispersed as far as gibbons can disperse them.

Total seed volume per fruit may influence the types of seeds that gibbons can swallow. They might know when they should stop feeding on fruit of a given seed size. Gibbons can therefore obtain a greater volume of flesh by swallowing small seeds than by swallowing large seeds. They will stop swallowing seeds when they gain a high seed volume or when their stomachs are full. Thus the relative seed volume may be a factor in fruit selection of gibbons as they select fruit species that should provide the most benefit.

Gibbons preferred feeding on whole fruit which is shown in Figure 2. Table 3 shows the weight of fruits eaten by gibbons. The weights of parts of some fruits that were consumed whole show that the quantity of flesh and cover fresh weight and seed fresh weight were not much different from each other. It seems that gibbons consumed a lot of flesh and swallowed medium-sized seeds. Gibbons also consumed many fruits for which they had to remove the rind such as *Walsura robusta* and *Balakata baccatum.*

Gibbons also fed on young leaves, shoots and flowers. Feeding on leaves may be explained by the need for energy or protein. Whitten (1982) noted that Kloss gibbons appeared to differ from other gibbons in that they did not feed on tree leaves. They ate arthropods as a major part of their diet. There is evidence from several studies that secondary plant metabolites may mediate food selection in primates. Thus, gibbons may try to avoid leaves with unusually high levels of secondary compounds.

From this study, it appears that gibbons prefer feeding on young leaves which may be explained by their need for the protein in these leaves. They chose young leaves although protein content in mature leaves is higher than in young leaves. However, by doing so, gibbons may avoid consuming dietary fiber, which is higher in the mature leaves.

Foraging strategies of gibbons

This study showed that gibbons have the ability to find the ripest fruit and most nutritious plant species very efficiently. It seems that they usually move directly to the fruiting target trees. This is supported by Brockelman (unpublished paper) and Carpenter (1967), who found that gibbons habitually use routes of foraging through the branches toward a goal. They also easily find alternative sources of ripe fruit when fruit availability changes in the forest. Moreover, gibbons may sometimes compete for food with neighboring groups. Thus, competition for food among gibbon groups might also be a factor in their food selection.

Although gibbons have experience in finding food, there are also variables that influence their decision to select food. These may also relate to gibbon foraging behavior. Gibbons defended large fruiting trees from neighboring groups. Evidence of food selection can support the resource defense hypothesis for territoriality in primates. It may explain that the reason why gibbons defend their territories and live in small groups is to ensure an adequate resource supply.

Gibbons have a relatively small size so they can reach the top branches of fruiting trees. Moreover, the high energy expenditure of brachiating may limit the distance that single animals can economically travel and thus lead to families inhabiting small defended areas of forest. As a result, gibbons tend to have small group size and travel only within their own territory.

Plant-primate coevolution

This study found that many of the fruits and seeds consumed by gibbons were small, such as figs. Thus, the Moraceae (figs) seems to be important for gibbons in this study. Moreover, *Ficus* species also were observed to have been consumed by a variety of birds and mammals with general diets. Some fruits which have large seeds and high nutritional value were also consumed by many kinds of birds and mammals, such as *Choerospondias axillaris*, *Balakata baccatum* and *Diospyros glandulosa.* Fruits may be adapted for dispersal in many ways based on the type of frugivores (specialized or opportunistic). For example, if seeds are large, the only way to attract frugivorous birds is a coat them with nutritious flesh (Snow 1981).

Gibbons are primates that have special digestive adaptations that allow them to consume immature fruits protected by plant secondary compounds. Thus, this may be the reason that these frugivores can consume foliage as well, because plants use similar substances to protect both their fruits and their leaves (Cipollini 1997). However, gibbons consume only limited foliage from a few species, and the leaves often pass through undigested. It is supported by the finding of leaves of *Polyalthia viridis* in the gibbons' feces.

Evolution of secondary metabolites in fleshy fruits is the result of multifunctional selection. It may be expensive to produce, so it may serve a variety of adaptive purposes (Cipollini 1997). Seed dispersers as such gibbons may have adapted by changing their behavior and physiology for feeding on selected plants. They feed on fruits which contain high nutritional value, and their long guts are adapted for passing through the seeds unharmed by digestion to avoid secondary metabolites.

From the results it can be summarized that many factors influence food choice in gibbons. The consumption of fruit was linked to the seasonal availability of trees of each species in the habitat, but some fruit species were strongly preferred. Gibbons are fairly generalized frugivores but it seems that they have fruit preferences to some extent. Gibbons select fruits with higher production cost; these often display a high rate of germination. These fruits with one seed usually peak in abundance over a short time. Thus, food availability also influences food selection by primates. Fruits are adapted not only for gibbons but also for other large or small vertebrates such as deer, hornbills, monkeys, and elephants. As a result, food plants in the forest always vary in size, shape, color, and taste in order to attract various frugivores. It seems that the coevolution between plants and animals may not be specific, although in general the relationships between plants and animals have evolved together based on natural selection. Animals tend to select the best food for their survival, and plants may thus adapt their physiology and morphology to attract their dispersal agents.

ACKNOWLEDGMENT

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Appendix 1. List of plant species eaten by White-handed Gibbon Group A

No.	Species	Family	Eaten Part	Life from
1	*Choerospondias axillaris* Burt&Hill	Anarcardiaceae	fruit, leaf	Tr
2	*Alphonsea boniana* Fin.& Gagnep.	Annonaceae	fruit	Tr
3	*Desmos chinensis* Lour.	Annonaceae	fruit, leaf	Cl
4	*Polyalthia viridis* Craib	Annonaceae	fruit, leaf	Tr
5	*Fissistigma rubiginosum* Merr.	Annonaceae	fruit	Cl
6	*Melodionus cambodiesis* Pierrs ex Spire	Apocynaceae	fruit	Cl
7	*Philodendron* sp.	Araceae	young shoot	Cl
8	*Rhapidophora* sp.	Araceae	spadix, spathe	Cl
9	*Scindapsus hederaceus* Schott	Araceae	leaf	Cl
10	*Dischidia nummularia* R. Br.	Asclepiadaceae	leaves	Cl
11	*Salacia macrophylla* Bl.	Celastraceae	fruit	Cl
12	*Erycibe elliptilimba* Merr. & Chun	Convolvulaceae	fruit	Cl
13	*Dipterocarpus gracilis* Bl.	Dipterocarpaceae	flower	Tr
14	*Diospyros glandulosa* Lace	Ebenaceae	fruit	Tr
15	*Elaeagnus latifolia* Linn.	Elaeagnaceae	fruit	Tr
16	*Baccaurea ramiflora* Lour.	Euphorbiaceae	fruit	Tr
17	*Bridelia tomentosa* Bl.	Euphorbiaceae	fruit	Tl
18	*Balakata baccatum* (Roxb.) Esser	Euphorbiaceae	fruit	Tr
19	*Beilschmiedia glauca* Lee	Lauraceae	fruit	Tr
20	*Gnetum macrostachyum* Hook.f	Gnetaceae	fruit	Cl
21	*Gnetum montanum* Markgraf	Gnetaceae	fruit	Cl
22	*Garcinia xanthochymus* Hook.f.	Guttiferae	fruit	Tr
23	*Platea latifolia* Bl.	Icacinaceae	fruit	Tr
24	*Cinnamomum subavenium* Miq	Lauraceae	fruit	Tr
25	*Acacia pennata* (Linn.) Wild.	Leguminosae-Mimosoidae	legume	Cl
26	*Sandoricum koetjape* (Burm.f.) Merr.	Meliaceae	fruit	Tr
27	*Walsura robusta* Roxb.	Meliaceae	fruit	Tr
28	*Diploclisia glaucescens* (Bl.) Diels	Menispermaceae	fruit	Cl
29	*Ficus hirsuta* (*Ficus hispida* Linn.f.)	Moraceae	fruit	Tr
30	*Ficus benjamina*	Moraceae	fruit	Tr
31	*Ficus nervosa*	Moraceae	fruit	Tr
32	*Ficus virens*	Moraceae	fruit	Tr
33	*Ficus altissima*	Moraceae	fruit	Tr
34	*Ficus annulata*	Moraceae	fruit	Tr
35	*Ficus* no. 361	Moraceae	fruit	Tr
36	*Ficus* no.373	Moraceae	fruit	Tr

Appendix 1. Cont'd

No.	Species	Family	Eaten Part	Life from
37	*Ficus* no. 379	Moraceae	fruit	Tr
38	*Ficus* sp.07	Moraceae	fruit	Tr
39	*Ficus* sp.09	Moraceae	fruit	Tr
40	*Knema laurina* Warb.	Myristicaceae	fruit	Tr
41	*Syzygium grande* (Wight) Walp. var *grande*	Myrtaceae	fruit	Tr
42	*Cleistocalyx operculatus* Merr.& Perry	Myrtaceae	fruit	Tr
43	*Piper* sp.	Piperaceae	fruit	Cl
44	*Prunus javanica* (Teijam.&Binn) Miq.	Rosaceae	fruit	Tr
45	*Aidia cochinchinensis* Lour.	Rubiaceae	fruit	Tr
46	*Neolamarckia cadamba* (Roxb) Bosser.	Rubiaceae	flower	Tr
47	*Toddalia asiatica* Lamk.	Rutaceae	fruit	Cl
48	*Nephelium melliferum* Gagnep.	Sapindaceae	fruit	Tr
49	*Eberhardtia tonkinensis* H. Lec.	Sapotaceae	fruit	Tr
50	*Gironniera nervosa* Planch.	Ulmaceae	leaf	Tr
51	*Aphananthe cuspidata* (Bl.) Planch	Ulmaceae	fruit	Tr
52	*Tetrastigma laotica*	Vitaceae	leaf,fruit	Cl
53	Unknown 01	Annonaceae	leaf	Tr
54	Unknown 02	Annonaceae	fruit	Tr
55	Unknown 03	Unknown	fruit	Cl
56	Unknown 04	Rubiaceae	fruit	Tr
57	Unknown 05	Unknown	leaf	Tr
58	Unknown 06	Moraceae	leaf	Tr
59	Unknown 07	Unknown	young leaf	Tr
60	Unknown 08	Unknown	leaf	Tr
61	Unknown 09	Araceae	shoot, leaf	Tr
62	Unknown 10	Moraceae	young leaf	Tr

Tr: Tree
Cl: Climber
Tl: Treelet

Seed dispersal pattern of the primate, *Cercocebus albigena* in African tropical forest

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Abstact The biomass of primates occupies a major part of total biomass of all vertebrate seed dispersers in the canopy of the tropical forests. In this paper, the utilization pattern and distribution pattern of food trees visited by *Cercocebus albigena*, a large frugivorous monkey that was studied in the African tropical forest of Nuabale Ndoki National Park, Congo, were analyzed. One habituated group of 14 animals was followed daily during the dry season. During twenty six observation days, *C. albigena* fed on 111 trees which is ca. 1.2% of the total number of living trees over 30 cm dbh occurring in their home range. They fed on 25 plant species. However, the summed percentage of feeding time on the top five species was 76% of the total feeding time. Time spent on feeding in the most top 20 visited food trees was 65% of the total. Thus, the bulk of the energy needs of this group were supplied by 20 food trees and by a few main food species. During this study period it was estimated that the group dispersed 44,321 seeds for four major plant species and that on average they dispersed 3,044 seeds per day per square km. In the case of *Erythrophleum* (Caesalpiniaceae) the monkeys took ca. 2,000 to 4,000 seeds from each of several principal food trees. On the other hand, in the case of a tree known locally as Ndengo, the troop used only one tree, and 3,549 seeds were taken away during seven feeding visits. *C. albigena* used their cheek pouches in processing the fruits and dispersed the seeds from the mouth only a short distance from the mother trees. It was found that there are positive inter-species relationships between *C. albigena* and plants in seed dispersal as well as in the defensive characters of resin and hard fruit coats against their seed predators at mature and immature stages. The distribution pattern of their food plants was not uniform, but rather some high density patches of their food trees were found in its home range. In such areas, positive feedback of recruitment of the monkeys' food species could occur. Primates might change the forest structure because of their large biomass and concentration on a few primary food species.

INTRODUCTION

Primates represent the largest biomass among vertebrate arboreal seed dispersers in tropical forests (Terborgh *et al*. 1988). Primates have a unique suite of adaptations to arboreal life, such as large body size, dextrous hands, a large brain, a large mouth, and differentiated teeth such that they occupy a special niche in tropical ecosystems; one that is presumed to be coevolved between primates and plants (Fleagle 1988; van der Pijl 1982). Gautier-Hion *et al*. (1985) defined a monkey fruit- syndrome as a product of diffuse coevolution; an indehiscent fruit with a sweet edible part together with the large seed and a bright fruit coat. Primates are good seed dispersers (Howe 1980) but at the same time they feed on seeds using their exceptionally large mouths and strong teeth as compared with other arboreal seed dispersers. Some species are specialized in a seed predation niche in New World tropical forest (Kinzey *et al*. 1993).

Primates disperse seeds via two means: (1) they spit seeds from their mouths using their cheek pouches or (2) they swallow the fruits and seeds which are eventually expelled in their feces (Maruhashi 1993). The distribution patterns of seed dispersal by these two means are very different in terms of dispersal distance and numbers and places of seeds dispersed (Yumoto *et al*. 1998). While frugivorous Old World monkeys have cheek pouches, New World monkeys have no cheek pouches. Seed dispersal in feces is found in these two types of primates.

A unique feeding technique of *Cercocebus albigena* in Africa makes it a good seed disperser as well as a seed predator. In this study, I studied how a habituated group used each food tree in its home range and how many seeds were carried away from mother trees. In terms of plant-primate relationships, I observed how these fruits were defended against predation by *C. albigena* at mature and immature stages.

The primate community of the study site consisted of 10 diurnal primate species: two great apes, *Gorilla gorilla gorilla*, *Pan troglodytes troglodytes*; two leaf eaters, *Colobus gureza* and *C. badius*; two mangabeys: *Cercocebus albigena* and *C. galeritus*; and four frugivorous guenons, *Cercopithecus cephus*, *C. nictitans*, *C. pogonias* and *C. neglectus*.

METHODOLOGY

Study area

The study site was located in Nuabale-Ndoki National Park, northern Congo. It took two days' walk across a large swamp 1.5 km in width from Bomassa village on the banks of the Sanga River, on the border between Cameroon, Central Africa, and Congo (Fig. 1), to reach the study site. The vegetation of the study site was classified into four types: (1) swamp forest, (2) swamp grassland (or bai), (3) mixed forest and (4) *Gilbertiodendron* forest on dry land. *Gilbertiodendron* was the dominant species and occupied over 80% of the total basal area of this latter forest type, which was located along riversides.

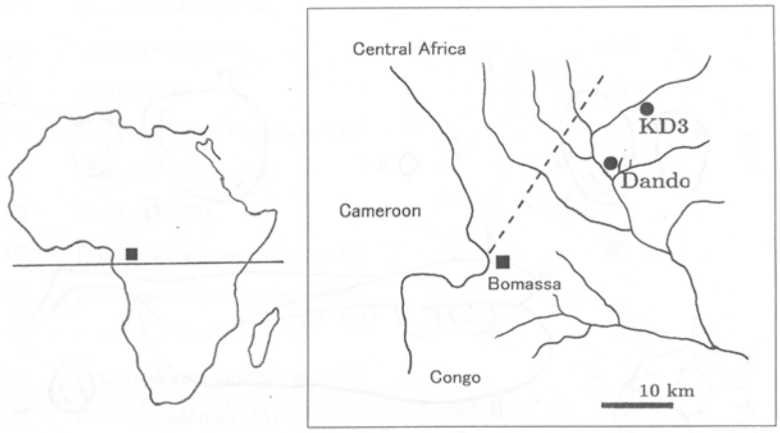

Figure 1. Study site and location of the Dando group of *Cercocebus albigena,* Nuabale-Ndoki National Park, northern Congo. Bomassa is the nearest village from the study site on the bank of Sanga River. KD-3 is another study troop of *C. albigena.*

Observation method and data analysis

Due to known preferred habitats of *C. albigena*, the mixed and *Gilbertiodendron* forest, to estimate the density of trees in the study area, a long transect of 725 m in length and 5 m in width was surveyed in *Gilbertiodendron* forest, and two long quadrats of 975 m and 800 m were surveyed in a mixed forest. All large trees over 30 cm in dbh (diameter at breast height) were recorded.

One group of 14 animals of *Cercocebus albigena* in my study site was habituated, and was named “Dando group”. D-group was observed during the dry season in January and February 1990. This group was followed for 143 hours during 26 days over a 46 day study period.

When the group was observed to feed on a food patch, the spot was tagged. Since the cofeeding group size tended to be small, and in cases when animals fed alone, the arrival and departure time of each monkey could be recorded in several feeding episodes. If some animals moved to a different food patch nearby during the observation period, these feeding events were also recorded. When a cofeeding group or a single monkey fed on a food patch, a feeding bout (FB) was defined as lasting from the first arrival to the last departure of this feeding group on a food tree.

The location of each food patch and the trails were measured using a 25 m measuring tape and a compass. The location data were entered into a computer and inter-FB (feeding bout) distances or moving speeds were calculated. The home range of D-group was divided into 1 ha quadrats (100 m x 100 m) on the map and their land utilization patterns were analyzed.

During their feeding bouts under exceptionally good observation conditions, feeding speeds, the number of fruits eaten per minute, were measured for major food species. The estimated number of seeds removed (dispersed) and preyed upon by *Cercocebus albigena* for each tree was calculated by multiplying the total feeding time by the average feeding speed for each food species and the number of seeds inside each fruit.

Diet composition was calculated as the percentage of the total feeding time on each food species over the entire feeding time of all observed feeding animals. The feeding percentages of food species or food trees were arranged in descending rank. To analyze the structure of their feeding behaviors, the summation for some rank classes – for example, the top five – were used. For analyzing changes in diet compositions, the study period was divided into three intervals; I) from 18 January to 4 February, II) from 5 to 13 February and III) from 14 to 26 February.

RESULTS

Dietary composition

D-group used 26 plant species (Table 1 and Fig. 2). Seeds of 12 species were dispersed and seeds of nine species were eaten. They fed also on leaves flowers and shoots of the other species. The top ranking species (*Erythrophleum suaveolens*) occupied 27% of the total feeding time and the second (*Celtis zenkeri*) and third (*Eribroma oblonga*) occupied 20% and 17%, respectively. The top (*E. suaveolens*) and the fifth species (Ndengo) had their seeds dispersed. However, the seeds of the second (*Celtis*), third (*Eribroma*) and fourth species (*Holoptelea grandis*) were preyed upon.

Table1. Food species and feeding percentages used by Dando group, *C. albigena*, in Nuabale Ndoki National park, Congo. Number of trees used and its feeding bouts are shown for all study periods. Feeding percentages for each interval are also listed for each species. For parts eaten, FR means that they fed on its fruits and dispersed the seeds and SE means that they fed on seeds and destroyed them

Ranked	Species	parts eaten	feeding %	n.of trees	n.of FBs	Interval		
						I	II	III
1	*Erythrophloeum suaveolens*	FR	26.8	20	40	29.1	24.1	27.6
2	*Celtis zenkeri*	SE	19.8	38	53	0.9	31.5	27.7
3	*Eribroma oblonga*	SE	16.7	9	18	30.4	-	22
4	*Holoptelea grandis*	SE	8.5	1	9	-	22.7	0.04
5	Ndengo	FR	4.4	1	7	8.1	4.2	0.2
6	*Copaifera mildbraedii*	FR	4.2	4	9	-	2.4	11.6
7	*Ficus* sp.1	FR	3.6	1	4	9.5	0.8	-
8	*Irvingia gabonensis*	SE	3.5	3	8	4.7	5.2	-
9	sp. indet. (legume)	SH	3	3	4	8.7	-	-
10	*Chytrantus atroviolaceus*	FR	2.7	3	14	-	4.9	3.1
11	*Funtumia elastica*	SE	1.1	8	18	1.1	0.9	1.2
12	*Amphimas pterocarpoides*(?)	LF	1.1	1	1	3.1	--	-
13	*Diospyros* sp.1	FR	1	1	1	-	--	3.6
14	insect (inside pith)	IN	0.9	1	1	2.5	--	-
15	*Staudtia kamerunensis*	FR	0.7	2	3	0.3	--	2.2
16	sp. indet.	FR	0.5	2	2	-	1.3	-
17	*Celtis adolfi-friderici*	FR	0.4	3	3	1.3	0.03	-
18	sp. indet. (legume)	SE	0.3	1	1	-	0.8	-
19	*Ficus* sp.2	FR	0.3	1	3	-	0.8	-
20	sp. Indet.	LF	0.2	2	2	-	--	0.7
21	sp. Indet. (legume)	FL	0.1	1	1	0.2	--	-
22	*Dialium* sp.	FR	0.1	1	2	-	0.3	-
23	*Pentaclethra macrophylla*	SE	0	1	1	-	0.1	-
24	*Entandraphragma utile*	SE	0	1	1	0.1	--	-
25	*Diospyros* sp.2	FR	0	1	1	-	0.1	-
26	Annonaceae sp.	SE	0	1	1	-	0.1	-
	Total			111	208			

Parts eaten: LF: leaf, SH: shoot, FL: flower, IN: insect, FR: fruit, SE: seeds. 0.0 % from rank 23 to 26 means that these percentages were less than 0.1 %.

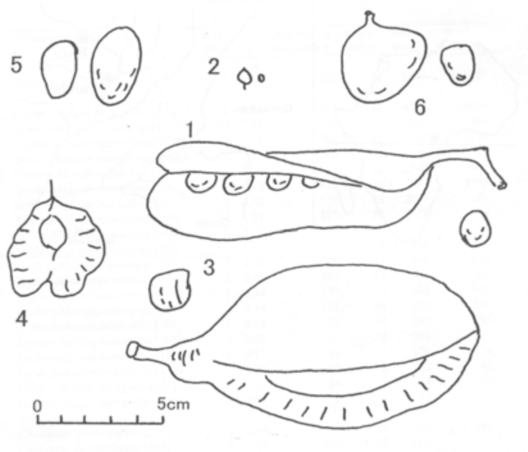

Figure 2. The fruit and seeds of the top six major food species used by the Dando group of *C. albigena*, in Nuabale-Ndoki National Park, Congo. Seed of each species are drawn beside the fruit at the same scale. 1. *Erythrophleum suaveolens*, 2. *Celtis zenkeri*, 3. *Eribroma oblonga*, 4. *Holoptelea grandis*, 5. Ndengo (local name), 6. *Copaifera mildbraedii*.

For 13 of the 26 species fed upon by *C. albigena*, only one individual was visited. For another eight species between two to four trees of each species were used. On the other hand, many individuals of the major food species were fed upon. Twenty *E. suaveolens*, 38 *Celtis zenkeri* and nine *E. oblonga* were utilized by D-group. However, 28 out of the 38 *Celtis* trees and 10 of 20 *Erythrophleum* were visited only once. D-group visited one *Holoptelea grandis* nine times and went seven times to feed on one tree of Ndengo (local name). For these two species, no other trees were found to be visited by the group in the home range.

During the study period, dietary compositions changed rapidly because of the fruiting of the one *Holoptelea* tree, which occupied 8.5% of the group's entire feeding time (Fig. 3). Once this *Holoptelea* bore its wind-dispersed fruit, D-group rushed onto this tree for six consecutive days until all seeds were eaten or dispersed.

The immature fruits of *H. grandis* contain much resin, but once the fruits reach maturity the resin disappears rapidly within a few days. Just after the first dispersal of *H. grandis* fruit was observed, the monkeys dramatically shifted their activity and ate seeds of *Holoptelea*, suddenly stopping their feeding on *Eribroma*. Although they visited several times a day to feed on it, the bulk of the seeds were dispersed by wind.

For other major food sources, Ndengo was observed being eaten in interval I, while *Copaifera* and *Celtis* were used in intervals II and III. *Eribroma* was visited in intervals I and III. *Erythrophleum* was the major food resource from intervals I to III. Many food resources were utilized only in once or a few times for each period.

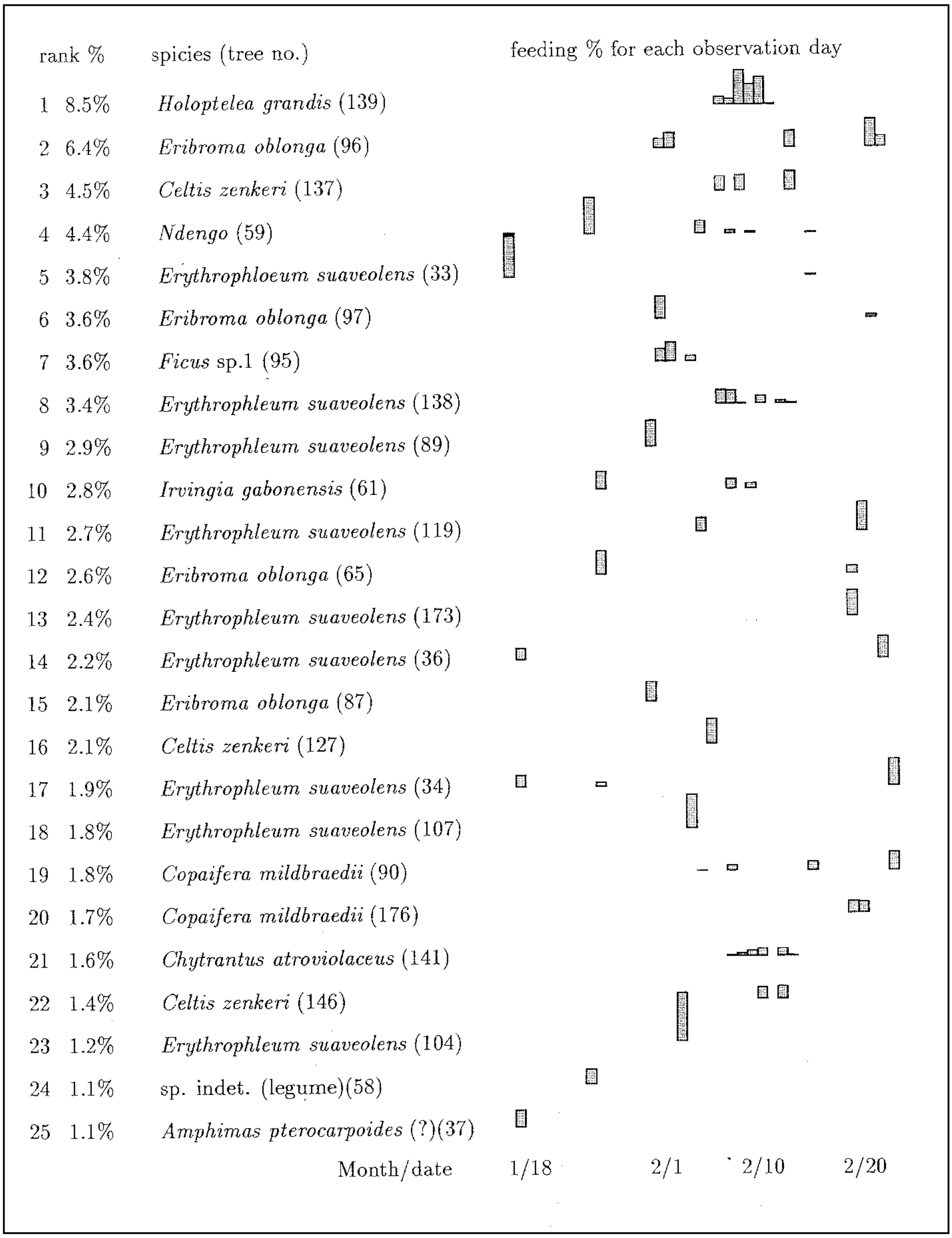

Figure 3. Utilization pattern of each food tree used by the Dando group of *C. albigena*. The food trees are arranged in descending rank in feeding percentage from first to 25th. The individual tree number is showed in parentheses. From 18 January to 26 February, the bars show daily feeding percentages for each food tree.

Structure of feeding behavior

D-group was dependent mainly on a few food trees from a few food species. The total feeding percentage of the top five and the top ten food species were 76 and 93% respectively, from a diet that consisted of 26 species.

During the study period, D-group visited and fed on 110 trees except for one insect feeding bout. These represented an estimated 1.2% of the total number of large trees with dbh over 30 cm occurring in their 56 ha home range. The number of once-visited food trees was 67, while 43 were visited more than once. Of these, D-group visited 19 trees more than three times. The summed feeding percentage of the top five food trees was 28% of the entire feeding time, and those of the top ten and twenty were 44% and 65%, respectively. The group fed 37 times on the top ten food trees.

Moving pattern

The total distance D-group moved over 26 days of observation was 12.3 km with an estimated daily moving distance of 729 m on average. D-group tended to stop their foraging activities at about 4 p.m. even though there was sufficient light for them to move around the forest canopy. The average distance from the last encounter point to the starting point on the following day was 237 m (n = 14).

A total of 208 feeding bouts (FBs) were observed. The average inter-FB distance was 61 m and the average moving speed between FBs was 3.0 m/sec. Their average feeding duration per FB was 22 minutes. One monkey was observed to feed for 32 FBs without any other group members and the average duration of these solitary FBs was 9.3 min. The average duration of cofeeding FBs was 24 minutes, which was much longer than that of the solitary FBs. The group size was 14, and the average cofeeding group size was 5.3 animals.

Within the home range there were some clumped areas of feeding activity (Fig. 4). The home range was divided into two areas: a core area where they passed and fed frequently and a peripheral area where they passed only once or a few times. During 26 observation days, the number of 1-ha quadrats where D-group passed in one or two days was 33 out of the total of 56 quadrats, which accounted for 60% of the entire home range. In five 1-ha quadrats, the group spent more than six days.

When each quadrat was ranked by percentages of feeding in food patches located inside each quadrat, the percentage of the topmost quadrat reached 16% and those of the second and the third were 12 and 11%, respectively. The summed percentage of the top three quadrats was 39% and that of the top ten quadrats was 66%. In these important quadrats, the major food trees and other food trees were also found. Figure 4 showed that D-group moved along a few main routes, since many large gap areas limited their foraging routes to a few frequently visited food trees.

Seed dispersal

Estimated numbers of seeds removed from a tree or dispersed by D-group were calculated for each major food species by using an average feeding speed. As an average feeding speed for Ndengo it took 20 seconds per fruit and for *Copaifera* and *Chytrantus*, it took 25 and 14 seconds per fruit, respectively. Ndengo and *Copaifera* fruit contained a single seed each, while a fruit of *Chytrantus* contained three seeds. For *Erythrophleum* fruit with one seed, it took 15 seconds. For these four species, the monkeys peeled off the fruit husk and stored a mix of edible parts and seeds in their cheek pouches. Dispersal resulted when the monkeys ate the edible parts (arils) and spat out the seeds while either moving or stationary.

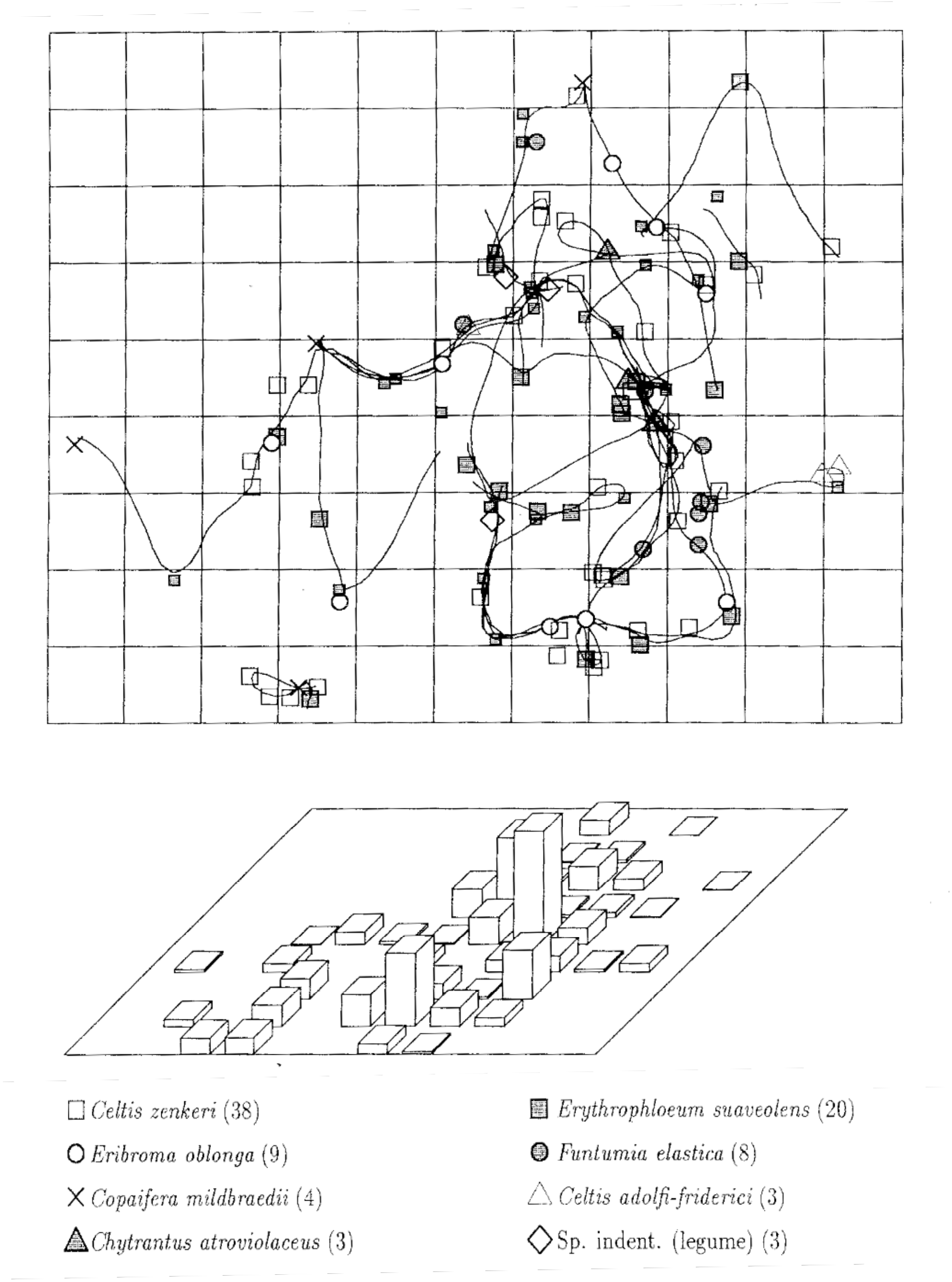

Figure 4. Travel routes and food trees of the Dando group of *C. albigena* during January and February, 1990 in Nuabale-Ndoki National park, Congo. Its home range was divided into 1 ha quadrats. The location of each food tree is shown. Small shaded squares show the locations of other food trees except for the eight food species listed. The number of trees used by D-group for each of the eight species is shown in parentheses. The 3-D figure at bottom shows the utilization pattern of D-group Each shows the total percentage of the food trees located in each 1-ha quadrat irrespective of food species.

The total number of seeds removed from a tree by D-group was highly varied (Table 2 and Fig. 5). Average numbers of seeds per FB also varied from a few dozen to over three thousand. In the most extreme cases, the estimated total number of seeds dispersed from a tree by the monkeys reached 4,128 for *Erythrophleum* (no. 33), 3,549 for Ndengo, 1,834 for *Chytrantus* and 1,154 for *Copaifera*. There were a few trees which were visited only once but from which thousands of seeds were removed, for example, *Erythrophloeum* no. 89 or no. 173. On the other hand, they fed on only a few dozen to a few hundred fruits in some trees.

During 26 days of observation, the total number of seeds of these four species dispersed by the monkeys was estimated at 44,325 seeds; for *Erythrophleum,* 28,824 seeds, for Ndengo, 3,549, for *Chytrantus,* 5,502 and 2,684 for *Copaifera*. It was estimated that *C. albigena* dispersed 79,152 seeds per km^2 during 26 days or 3,044 seeds per day per km^2.

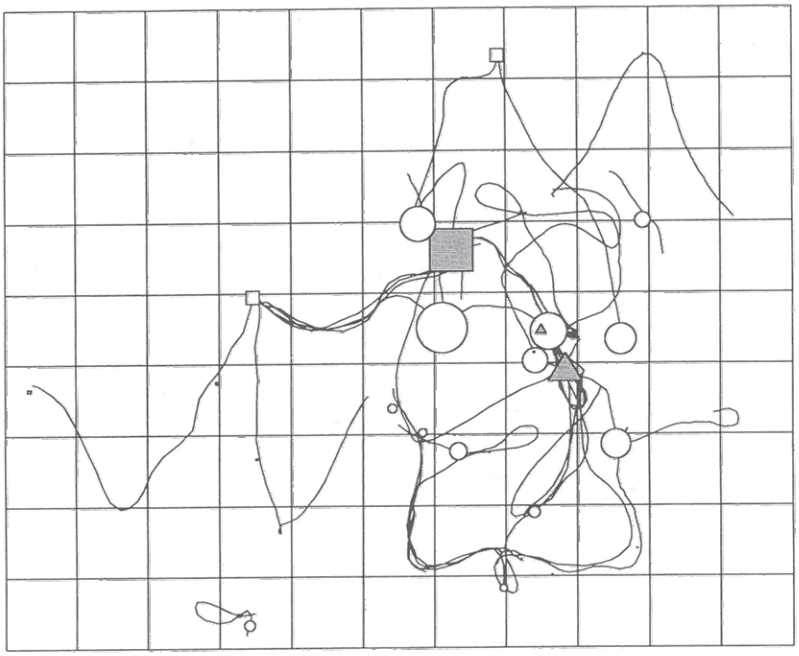

Figure 5. The distribution and number of seeds dispersed for four major food species by the Dando group of *Cercocebus albigena.* The size of the mark reflects the estimated total number of seeds brought out by the group. Open circles show trees of *Erythrophleum suaveolens* and shaded squares, open squares, and shaded triangles show Ndengo (local name), *Copaifera mildbraedii* and *Chytrantus atroviolaceus*, respectively.

Table 2. Estimation of the number of seeds brought out from food trees by Dando group, *C. albigena*, for four major food species in Nuabale Ndoki National park, Congo

Species (tree no.)	n. of FBs	%	total feeding time (min.)	total n. animals	total n. seeds	n. of seeds/FB
Ndengo (59)	7	4.4	1,183	35	3,549	507
Erythrophleum suaveolens (33)	2	3.84	1,032	19	4,128	2,064
Erythrophleum suaveolens (138)	10	3.44	924	36	3,696	369
Erythrophleum suaveolens (89)	1	2.9	780	12	3,120	3,120
Erythrophleum suaveolens (119)	3	2.74	736	25	2,944	981
Erythrophleum suaveolens (173)	1	2.36	635	12	2,540	2,540
Erythrophleum suaveolens (36)	2	2.23	597	19	2,391	1,195
Erythrophleum suaveolens (34)	3	1.92	516	28	2,064	688
Erythrophleum suaveolens (107)	2	1.81	487	13	1,948	974
Erythrophleum suaveolens (104)	1	1.22	326	11	1,307	1,307
Erythrophleum suaveolens (135)	2	0.88	235	9	940	470
Erythrophleum suaveolens (131)	1	0.78	210	7	840	840
Erythrophleum suaveolens (92)	2	0.68	183	10	732	366
Erythrophleum suaveolens (102)	1	0.64	172	10	688	688
Erythrophleum suaveolens (98)	2	0.58	155	10	620	310
Erythrophleum suaveolens (165)	1	0.28	73	9	295	295
Erythrophleum suaveolens (103)	2	0.25	65	10	263	131
Erythrophleum suaveolens (189)	1	0.11	30	1	120	120
Erythrophleum suaveolens (185)	1	0.09	23	3	92	92
Erythrophleum suaveolens (41)	1	0.06	16	2	64	64
Erythrophleum suaveolens (184)	1	0.03	8	1	32	32
Chytrantus atroviolaceus (141)	7	1.59	428	29	5502	786
Chytrantus atroviolaceus (145)	5	0.59	158	12	2031	406
Chytrantus atroviolaceus (151)	2	0.5	135	9	1734	867
Copaifera mildbraedii (90)	5	1.79	481	32	1154	230
Copaifera mildbraedii (176)	2	1.69	453	15	1089	544
Copaifera mildbraedii (170)	1	0.37	100	5	240	240
Copaifera mildbraedii (130)	1	0.31	84	4	201	201

DISCUSSION

Plant and *C. albigena* relationships

C. albigena is an African frugivorous diurnal primate. It is a seed disperser of ripe fruits as well as a seed predator of both immature and mature seeds. Compared with other sympatric frugivorous primates, *C. albigena* has a special niche because of its frequent seed predation. There are some benificial relations between *C. albigena* and plants. Some defensive characteristics of plants against their predation were also observed.

In this study, conducted in the dry season, *C. albigena* most efficiently dispersed the seeds of *Erythrophleum*. The estimated total of 28,824 *Erythrophleum* seeds removed from mother trees accounted for 70% of the total number of seeds of the four food plant species dispersed (Table 2). The characteristics of this fruit were very peculiar. Each seed is covered by a dry and sweet thin aril, which becomes soft and jelly-like after being placed in the monkey's mouth. The monkeys then remove and eat the jelly-like part. Moreover, the fruits open downward and are firmly attached to the branch. While feeding, the monkeys did not knock down these pods. It was observed that there were still many fruits on the tree even after a heavy monkey feeding bout. It may be supposed that *Erythrophleum* has a strong inter-species relationships with the monkeys because of its peculiar fruit structure, which is very different from that of usual monkey fruits.

The fruit of Ndengo is similar to the fruit of Lauraceae, i.e. with a thin fruit skin and an oily edible part. Fruit of *Chytrantus* is a typical monkey fruit, with a juicy and sweet edible exocarp and an inedible endocarp containing three large seeds. The monkeys fed on the immature seeds of *Funtumia.*

Some fruits, such as *Copaifera*, have defensive properties, such as resins or a hard fruit coat to protect against primate predation. Shortly prior to maturation, the fruit produces much resin and becomes difficult even for *C. albigena* to get its thin aril for food. It took much time to tear the husk to get the aril. Also the monkeys salivated a great deal while feeding, probably due to the plentiful resin. The hard husk and plentiful resin might be effective against its premature predation. When *Copaifera* is ripe, the husk becomes thin without any resin and opens spontaneously.

In the case of predation on *Holoptelea*, there is much resin found in the fruit wings during immature stages, but the immature fruit is not hard. The monkeys ate these seeds just after maturation when the resin disappeared.

Eribroma also has a hard and thick husk (1 cm) even when immature, but there is no resin produced. The immature fruit bears soft seeds which are filled with clear liquid. *C. albigena* takes much time to remove the young aril without breaking the seed itself. It appears that this liquid might have some defensive chemicals against predation.

Seed dispersal pattern

Frugivorous Old World monkeys use their cheek pouches to store fruits while foraging. The monkeys usually consume all fruits stored inside the cheek pouches from previous feeding bouts before they reach the next food patch. In the case of the group, the average inter-FB distance was 61 m. This means that seeds stored temporarily inside their cheek pouches were dispersed but a short distance from the mother tree.

It was found that the feeding activity of Dando group depended mostly on about twenty food trees of some major food species. Distribution patterns of the food trees and the utilization pattern of its home range (Figs. 4 and 5) show that there are feeding hotspots, where some important food trees for the D-group had a clumped distribution. The group visited certain key feeding patches even if only one individual of a major food species, such as Ndengo or *Holoptelea*, was present. It is thought that the monkeys enter these key patches and bring with them seeds consumed elsewhere. They then disperse the seeds into these patches at a high density. Thus, a single tree of a major food species can be an important focal point for seed distribution in the tropical forest.

When the total number of seeds from the mother trees located in each 1-ha quadrat are ranked, the top quadrat comprises 18% of all dispersed seeds of four species. The second and the third represented 12% and 9%, respectively. The summed percentages for the top three quadrats were 39% and that of the top ten quadrats reached 81% (Fig. 5).

The feeding behavior of the D-group appeared to accelerate the recruitment of their major food species. This may result in localized patches rich in food species, eventually attracting more monkeys (and hence more seeds) in a long-term positive feedback loop. To confirm this possibility, a comparison could be made of species composition and recruitment between heavily visited feeding places versus peripheral sites.

CONCLUSIONS

1. Utlization pattern of food trees and the distribution pattern of seed dispesal of *C. albigena* were studied in Nuabale-Ndoki National Park, Congo, Africa. The seed dispersal pattern of seeds stored in cheek pouches of *C. albigena* was documented.
2. The monkeys have a special niche in feeding on ripe fruits and dispersing seeds, as well as feeding destructively on seeds at different stages of maturity.
3. Plentiful resin and hard fruit coats of immature fruits may serve as defensive features against predation by *C. albigena*. Such characters were found in *H. grandis*, *C. mildbraedii* and *E. oblonga*.
4. A reciprocal primate-plant relationship was found in *E. suaveolens* (Caesalpiniaceae). Its edible aril was thin and dry. When placed in the monkey’s mouth, it bec~~o~~ame soft and jelly-like and easy for the monkeys to remove and eat. Since the pod is attached firmly to the branches, the monkeys seldom knocked them down while feeding. This pod retention might persuade the monkeys to come back.
5. A group of *C. albigena* depended on a few major food plant species and a few food trees in their home range. They used 1.2% of all large trees found in their home range during this study. They rapidly changed their dietary composition in response to the seasonal change in fruit crops.
6. Feeding activities were concentrated in a few hotspots where many food trees were clumped. This activity pattern accelerates the recruitment of major food species in a positive feedback system.

7. Due to their large biomass and special techniques in feeding on fruits compared to other arboreal vertebrate seed dispersers inhabiting the tropical forest canopy, the primate community might change the forest structure through their seed dispersal capability.

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SHORT NOTE

The availability of ripe fruits in the annual hornbill life cycle

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Abstract The number of fruiting food species attractive to hornbills in Khao Yai National Park was investigated according to the annual hornbill life cycle – early nesting (EN), nesting (NP), late nesting to early flocking (LNF) and flocking periods (FP). The number of fruiting species which ripened during the EN period was 22 identified species, 59 species during NP, 44 species for the LNF, and 37 species in the FP. Numbers of species, duration of ripe fruit period and habit were reported for each category. There were 38 species whose ripe fruit lasted for two months and 29 species whose fruits lasted three months. Eleven species had ripe fruits year-round. The majority of food plants were trees of large size (h > 30 m; 26 species) and medium size (h = 15-30 m; 26 species).

INTRODUCTION

In general, hornbills are considered omnivorous birds but their main diet is ripe fruits of a wide variety, particularly during the breeding season. Animal food appears to be additional food during the chick rearing period (Poonswad *et al.* 1998a; Chimchome *et al.* 1998). Hornbill fruit food includes fig and non-fig fruits. Poonswad *et al.* (1998a) reported that figs are important as the main food of both the Great Hornbill *Buceros bicornis* and the Wreathed Hornbills *Aceros* (*Rhyticeros*) *undulatus*, and constitute more than 50% of the total diet (Poonswad *et al.* 1998a) in the breeding season. Fruit abundance may influence hornbill food choice, particularly during the breeding season. Previous studies in Thailand regarding ripe fruit availability were conducted in the breeding season (Chimchome *et al.* 1998; Poonswad *et al.* 1998a; Poonswad *et al.* 1998b). This paper presents ripe fruit availability in correspondence with the annual hornbill life cycle.

METHODOLOGY

The study was conducted from 1993-2000 in Khao Yai National Park, where four hornbill species are found. Seeds dropped under hornbill nests and roost trees were collected and identified. Identification was also done by searching for mother trees, and in addition phenology was observed. Duration of the fruit ripening period was determined from observation of the seeds dropped under the nest and under roost trees as well as at the fruiting trees.

The annual hornbill life cycle was defined as follows:

Early nesting period (EN) was the period before female imprisonment, normally between December to early January. Nesting period (NP) was the period from female imprisonment until the chick fledged (mid January-end May). Late nesting to early flocking period (LNP) was the period about one week before chicks fledged to the first sighting of hornbills at a roost site (late May-early July). Flocking period (FP) was the continuation of flocking until the flock dispersed (mid July-end October)

RESULTS

There were 84 identified species of hornbill food plants which produced ripe fruits recorded during the study. These were placed into 57 genera from 30 families, which were dominated by fruits in the family Lauraceae (16 species; Table 1). Others that were relatively less commonly found included Moraceae (13 species), Annonaceae (9 species) and Meliaceae (6 species). Among 13 species of Moraceae, 11 species were in genus *Ficus*, the most common genus. *Ficus* spp. were observed to be the most important food for all hornbill species. Furthermore, ripe fruits of *Ficus* spp. were found all year round (Table 2 and Appendix 1). There were 38 fruit species whose ripe fruit lasted for two months and 29 species whose ripe fruit lasted for three months (Table 2).

Table 1. Number of families, genera and species of hornbill food plants observed at Khao Yai National park, 1993-2000

No.	Family	No. genus/ genera	No.
1	Alangiaceae	1	1
2	Anacardiaceae	1	1
3	Annonaceae	6	9
4	Aquifoliaceae	1	1
5	Arecaceae	1	1
6	Burseraceae	1	1
7	Celastraceae	1	1
8	Cornaceae	1	1
9	Elaeagnaceae	1	1
10	Euphorbiaceae	2	2
11	Flacourtiaceae	1	2
12	Gnetaceae	1	1
13	Icacinaceae	1	1
14	Lauraceae	9	16
15	Magnoliaceae	1	1
16	Meliaceae	3	6
17	Memecylaceae	1	1
18	Moraceae	3	13
19	Myristicaceae	2	2
20	Myrtaceae	2	2
21	Oleaceae	1	1
22	Piperaceae	1	1
23	Podocarpaceae	1	1
24	Rosaceae	1	1
25	Rubiaceae	1	1
26	Rutaceae	1	1
27	Sterculiaceae	1	3
28	Symplocaceae	1	1
29	Theaceae	1	1
30	Ulmaceae	1	2
31	Unknown	7	7
	Total	57	84

Table 2. Duration of ripe fruit of hornbill food plants at Khao Yai National Park, 1993- 2000

No.	Family	No. of Months Available							Total
		1	2	3	4	5	6	all year around	species
1	Alangiaceae	-	1	-	-	-	-	-	1
2	Anacardiaceae	-	-	1	-	-	-	-	1
3	Annonaceae	-	4	5	-	-	-	-	9
4	Aquifoliaceae	-	1	-	-	-	-	-	1
5	Arecaceae	-	-	-	-	-	1	-	1
6	Burseraceae	-	-	-	-	1	-	-	1
7	Celastraceae	-	-	1	-	-	-	-	1
8	Cornaceae	-	1	-	-	-	-	-	1
9	Elaeagnaceae	-	-	1	-	-	-	-	1
10	Euphorbiaceae	-	2	-	-	-	-	-	2
11	Flacourtiaceae	-	2	-	-	-	-	-	2
12	Gnetaceae	-	-	1	-	-	-	-	1
13	Icacinaceae	-	1	-	-	-	-	-	1
14	Lauraceae	-	8	6	1	1	-	-	16
15	Magnoliaceae	-	-	-	-	-	1	-	1
16	Meliaceae	-	2	4	-	-	-	-	6
17	Memecylaceae	-	-	1	-	-	-	-	1
18	Moraceae	-	1	1	-	-	-	11	13
19	Myristicaceae	-	2	-	-	-	-	-	2
20	Myrtaceae	1	-	1	-	-	-	-	2
21	Oleaceae	-	-	1	-	-	-	-	1
22	Piperaceae	-	1	-	-	-	-	-	1
23	Podocarpaceae	-	-	1	-	-	-	-	1
24	Rosaceae	-	1	-	-	-	-	-	1
25	Rubiaceae	-	1	-	-	-	-	-	1
26	Rutaceae	-	-	1	-	-	-	-	1
27	Sterculiaceae	-	3	-	-	-	-	-	3
28	Symplocaceae	-	-	1	-	-	-	-	1
29	Theaceae	-	-	1	-	-	-	-	1
30	Ulmaceae	-	-	2	-	-	-	-	2
31	Unknown	-	7	-	-	-	-	-	7
	Total	1	38	29	1	2	2	11	84

Table 3 shows that the majority of hornbill food plants were large and medium sized trees largely from the Lauraceae and Moraceae, whereas shrubs and climbing plants were least utilized. The availability of the food plants which corresponded with the hornbill annual life cycle is shown in Table 4.

As expected, during the nesting period the diversity and availability of ripe fruit was highest (63 species). This availability extended into the early flocking period (47 species; Table 4).

Table 3. Habit of hornbill food plants at Khao Yai National Park, 1993-2000

No	Family	Large tree (>30m)	Medium (15-30m)	Small (<15m)	Shrub	Climber	Unk
1	Alangiaceae	-	1	-	-	-	-
2	Anacardiaceae	-	1	-	-	-	-
3	Annonaceae	2	-	2	-	5	-
4	Aquifoliaceae	-	1	-	-	-	-
5	Arecaceae	-	1	-	-	-	-
6	Burseraceae	1	-	-	-	-	-
7	Celastraceae	-	1	-	-	-	-
8	Cornaceae	1	-	-	-	-	-
9	Elaeagnaceae	-	-	-	-	1	-
10	Euphorbiaceae	-	2	-	-	-	-
11	Flacourtiaceae	-	1	1	-	-	-
12	Gnetaceae	-	-	-	-	1	-
13	Icacinaceae	-	1	-	-	-	-
14	Lauraceae	5	6	5	-	-	-
15	Magnoliaceae	1	-	-	-	-	-
16	Meliaceae	3	1	2	-	-	-
17	Memecylaceae	-	-	1	-	-	-
18	Moraceae	11	-	2	-	-	-
19	Myristicaceae	-	-	2	-	-	-
20	Myrtaceae	1	-	-	1	-	-
21	Oleaceae	-	1	-	-	-	-
22	Piperaceae	-	-	-	-	1	-
23	Podocarpaceae	-	1	-	-	-	-
24	Rosaceae	1	-	-	-	-	-
25	Rubiaceae	-	1	-	-	-	-
26	Rutaceae	-	-	-	1	-	-
27	Sterculiaceae	-	3	-	-	-	-
28	Symplocaceae	-	1	-	-	-	-
29	Theaceae	-	1	-	-	-	-
30	Ulmaceae	-	2	-	-	-	-
31	Unknown	-	-	-	-	-	7
	Total	26	26	15	2	8	7

Table 4. Number of species bearing ripe fruits corresponding with their availability during the hornbill annual life cycle at Khao Yai National Park 1993-2000: EN = early nesting period, NP = nesting period, LNF =late nesting to early flocking period, FP = flocking period

No.	Family	EN	NP	LNF	FP
1	Alangiaceae	-	-	1	1
2	Anacardiaceae	-	1	1	-
3	Annonaceae	3	4	2	4
4	Aquifoliaceae	-	-	-	1
5	Arecaceae	1	1	-	1
6	Burseraceae	1	1	-	1
7	Celastraceae	-	1	-	-
8	Cornaceae	-	-	-	1
9	Elaeagnaceae	1	1	-	-
10	Euphorbiaceae	-	1	-	1
11	Flacourtiaceae	-	-	1	2
12	Gnetaceae	-	1	1	1
13	Icacinaceae	-	1	1	1
14	Lauraceae		9	5	7
15	Magnoliaceae	-	1	1	1
16	Meliaceae	2	6	4	-
17	Memecylaceae	-	1	1	-
18	Moraceae	12	13	12	11
19	Myristicaceae	-	2	2	-
20	Myrtaceae	1	1	1	-
21	Oleaceae	1	1	-	-
22	Piperaceae	-	1	1	1
23	Podocarpaceae	-	1	1	1
24	Rosaceae	-	1	1	-
25	Rubiaceae	-	1	-	-
26	Rutaceae	-	1	1	-
27	Sterculiaceae	-	3	3	-
28	Symplocaceae	-	1	1	-
29	Theaceae	-	1	1	-
30	Ulmaceae	-	-	2	2
31	Unknown	-	7	3	-
	Total identified species	22	56	44	37
	Total	22	63	47	37

DISCUSSION

Our study confirmed the importance of fruit food during the chick rearing period (Appendix 1 and Table 4). Fruit food choice may be related to the nature of the habit of hornbill food plants and to the abundance of the plants in the study area (Kitamura 2000). Fruits of climbers appear to be a relatively important food source when the relative abundance of the plants is considered. Therefore, the choice of fruits of large and medium plants may reflect the abundance of such plant habits or life forms.

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Appendix 1. Monthly of ripe fruits at Khao Yai National Park, 1993-2000.

Family	No.	Scientific name	Month											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Alangiaceae	1	*Alangium kurzii* Craib						---	---					
Anacardiaceae	2	*Buchanania glabra* Wall.			---	---	---							
Annonaceae	3	*Alphonsea elliptica* Hk. f.& Th.					---	---						
	4	*Anomianthus dulcis* Sincl.					---	---						
	5	*Cyathostemma micranthum* (A.DC.) Sincl.							---	---	---			
	6	*Desmos chinensis* Lour.	---	---								---		
	7	*Polyalthia clemensorum* Alston							---	---				
	8	*Polyalthia jucunda* Finet et Gagnep.		---	---	---								
	9	*Polyalthia viridis* Craib			---	---	---							
	10	*Uvaria cordata* Alston	---								---	---		
	11	*U. lurida* HK. f. & th.								---	---	---		
Aquifoliaceae	12	*Ilex* sp. 1							---	---	---			
Arecaceae	13	*Livistona speciosa* Kurz.	---	---	---					---	---	---		
Burseraceae	14	*Canarium euphyllum* Kurz.	---	---						---	---	---		
Celastraceae	15	*Bhesa robusta* Ding Hou.		---	---	---								
Cornaceae	16	*Mastixia pentandra* Bl.							---	---				
Elaeagnaceae	17	*Elaeagnus latifolia* Linn.	---	---	---									
Euphorbiaceae	18	*Bischofia javanica* Bl							---	---				
	19	*Bridelia retusa* sprong			---	---								
Flacourtiaceae	20	*Casearia grewiaefolia* Vent.					---	---						
	21	*Casearia* sp.1						---	---					
Gnetaceae	22	*Gnetum montanum* Markger				---	---	---						
Icacinaceae	23	*Platea latifolia* Bl.					---	---						
Lauraceae	24	*Actinodaphne* sp. 1				---	---							
	25	*Beilschmiedia balansae*			---	---	---							

Appendix 1. (cont'd)

Family	No.	Scientific name	Month											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Lauraceae	26	*Beilschmiedia maingayi* Hk.f.			----------	----------	----------							
	27	*B. roxburghiana* N.				----------	----------							
	28	*B. villosa* Craib				----------	----------							
	29	*Cinnamomum glaucescens* Drury								----------	----------			
	30	*C. iners* Reinw		----------	----------	----------								
	31	*C. subavenium* Miq.			----------	----------	----------							
	32	*Cryptocarya impressa* Hook.f.		----------	----------	----------								
	33	*C. kurzii* Hk.f.						----------	----------	----------				
	34	*Litsea monopetala* (Roxb.) Pers					----------	----------						
	35	*L. martabonica* Hk.f. & Th.							----------	----------				
	36	*Neolitsea latifolia* M.Mon.								----------	----------			
	37	*Nothaphoebe reticulata* Gamble					----------	----------	----------					
	38	*Persea gamblei* Kosterm.			----------	----------	----------	----------						
	39	*Phoebe cathia* (D.Don.) Kosterm.								----------	----------			
Magnoliaceae	40	*Paramichelia baillonii* Hu.			----------	----------	----------	----------	----------					
Meliaceae	41	*Aglaia lawii* (Wight) Saldanha ex Ramanoorth			----------	----------	----------							
	42	*A. spectabilis* S.S. Jain & Bennet.				----------	----------							
	43	*Aphanamixis polystachya* (Wall.) R. Parker	----------	----------	----------									
	44	*Dysoxylum cyrtobotryum* Miq.				----------	----------							
	45	*D. densiflorum* (Bl.) Miq.				----------	----------							
	46	*Dysoxylum* sp.	----------	----------	----------									
Memecylaceae	47	*Memecylon plebejum* Kurz			----------	----------	----------							
Moraceae	48	*Antiaris toxicaria* Lesch.	----------	----------	----------									
	49	*Artocarpus lakoocha* Roxb.					----------	----------						

Appendix 1. (cont'd)

Family	No.	Scientific name	Month											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Moraceae	50	*Ficus albipila* Bl.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	51	*F. altissima* Bl.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	52	*F. annulata* Bl.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	53	*F. benjamina* L.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	54	*F. genniculata* Kurz.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	55	*F. glaberrima* Kurz.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	56	*F. kurzii* King	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	57	*F. microcarpa* L.f.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	58	*F. nervosa* Heyne	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	59	*F. stricta* Miq.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
	60	*F. superba* (Miq.) Miq.	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------		
Myristicaceae	61	*Horsfieldia glabra* Warb.			----------	----------								
	62	*Knema erratica* Warb.			----------	----------								
Myrtaceae	63	*Decaspermum parviflorum*	----------	----------								----------		
	64	*Syzygium* sp. 1					----------							
Oleaceae	65	*Chionanthus ramiflorus* Roxb.	----------	----------	----------									
Piperaceae	66	*Piper ribesioides* Wall.					----------	----------						
Podocarpaceae	67	*Podocarpus neriifolius* D. Don.					----------	----------						
Rosaceae	68	*Prunus arborea* var. *montana* Kalkm.			----------	----------								
Rubiaceae	69	*Canthium glabrum* Bl.		----------	----------	----------								
Rutaceae	70	*Micromelum minutun* Wight & Arn.			----------	----------	----------							
Sterculiaceae	71	*Sterculia balanghas* Linn.			----------	----------								
	72	*Sterculia* sp. 1			----------	----------								
	73	*Sterculia* sp. 2			----------	----------								

Appendix 1. (cont'd)

Family	No.	Scientific name	Month Jan	 Feb	 Mar	 Apr	 May	 Jun	 Jul	 Aug	 Sep	 Oct	 Nov	 Dec
Symplocaceae	74	*Symplocos cochinchinensis* spp. *laurina* (Retz.) Noot.			----------	----------	----------							
Theaceae	75	*Ternstroemia wallichiana* Engler			----------	----------	----------							
Ulmaceae	76	*Celtis hamiltonii*					----------	----------	----------					
	77	*C. tetrandra* Roxb.					----------	----------	----------					
Unidentified	78	Unknown 1			----------	----------								
	79	Unknown 2				----------	----------							
	80	Unknown 3				----------								
	81	Unknown 4			----------	----------								
	82	Unknown 5			----------	----------								
	83	Unknown 6				----------								
	84	Unknown 7				----------	----------							
		Total	21	23	31	42	46	46	29	22	22	22	18	17

PART III: HORNBILL SURVEYS

PART III: INTRODUCTION

The 1st International Asian Hornbill Workshop held in 1992 in Bangkok was dedicated to determining the status and distribution of hornbill species across Asia. One might therefore wonder why it is necessary to include a section on survey data when we already have abundant information on the status of hornbills in Asia (for Africa, see Alan Kemp's chapter in the section on Conservation in this volume).

At the time of the 1st Workshop, some of the participating countries reported very up-to-date information that had been based upon on long-term studies. Other nations, however, presented reports based on incomplete survey data or upon information that either was not accurate on a fine geographic scale or had not been updated for a number of years. For both kinds of situations, follow-up surveys on a regular basis would be an ideal.

Surveys work to establish accurate distribution and abundance data, and permit monitoring of populations over time and an understanding of their dynamics. Even where hornbill distributions and numbers are known, regular monitoring is needed in order to ascertain changes in abundance and whether species are extant in various parts of their presumed range. Furthermore, as all Asian and many African hornbill species inhabit forests, periodic surveying is critical given the rate of loss, fragmentation, alteration, and disturbance to the mature stands of tropical forest upon which hornbills are dependent. In the case of locally or globally endangered hornbill species the need for periodic and detailed surveys rises even more.

There are of course methodological and logistic challenges facing anyone attempting a survey of animals as mobile as hornbills are. Charles, in his survey of hornbills in Brunei conducted on foot and by automobile, proposes survey methods that might be attempted by those with limited manpower resources at their disposal. He also addresses the issue of what constitutes an optimal transect length for recording hornbills, thereby striking a balance between recording accurate information without expending excessive time or effort.

Lakim and Biun assess the status of hornbills in the East Malaysian state of Sabah in what is the first systematic hornbill survey conducted there. Sabah has a string of National Parks where hornbills enjoy complete protection. Lakim and Biun's survey was an attempt not only to document the current status of hornbills in Sabah Parks, but also to guide them in the direction of more detailed ecological studies of the birds in the State. Lakim and Biun's survey is the first step in what could be an integrated hornbill conservation strategy involving National Parks and other protected areas across a rather large geographic range.

Hornbills, to the surprise of some, range into southern China, particularly in the southern and western portions of Yunnan Province which border Vietnam, Laos and Myanmar. Wen provides an update on the occurrence of hornbills in Yunnan, where there have been dramatic land-use changes since the 1960s, when the earliest hornbill surveys took place. Not surprisingly, perhaps, hornbills have disappeared from parts of the Xishuangbanna National Park Reserve. Wen makes a case for combining field surveys with the use of geographic information systems such as Gap Analysis. In addition, Wen advocates that minimum area requirements be estimated for various hornbill species so as to better facilitate their protection and the management of their habitats.

All animals, including hornbills, share their habitats with other animals and with increasing numbers of people. Elevated human activity in and around hornbill habitats must be taken into account in formulating conservation strategies for these birds. Is hornbill survey information sufficient as-is, or is there more to be extracted from the data through the use of other methods? In his paper on the modeling of hornbills and other wildlife distributions at Khao Yai National Park, Thailand, Yongyut Trisurat demonstrates that the value of field surveys can be greatly augmented through the employment of various computer-based techniques. He uses a method known as kriging to interpolate sampled data collected from various parts of Khao Yai National Park, with interesting results. Trisurat's methods could be applied elsewhere in the region to help develop improved plans for the conservation of hornbills and other wildlife.

To close out this section, we include a note presented at the 3rd International Hornbill Workshop by Hugo Rainey, then a graduate student at the University of St. Andrews. Rainey points out the flaws in standard field survey techniques such as point counts. These include their relative inefficiency or inaccuracy in capturing data, or their invasiveness. Rainey proposed that the analysis of hornbill vocalizations could be a more feasible and potentially more powerful survey tool than traditional survey methods. Moreover, inter-individual variations in hornbill calls could make it possible to use vocal-based surveys as a kind of "mark-recapture" method as well.

Taken together, these papers form a complete and well-integrated whole. The papers comprise results, different survey methods and applications, and include suggestions for integrating survey data with the formulation of conservation proposals. Their value goes far beyond the already valuable census data presented.

Relative abundance of hornbills in Brunei Darussalam

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Abstract Eight hornbill species occur in Brunei Darussalam. Relative abundance of each species was assessed in six different habitat types. In general, it seems that an extensive undisturbed region like Belalong with its mixed dipterocarp-alluvial forests or a rich mosaic of undisturbed forest types will support the highest diversity of hornbills. The diversity of habitats in a mosaic provides hornbills with a varied and constant supply of food, as well as resting, roosting and breeding sites. A quick census method for hornbills is proposed.

INTRODUCTION

The occurrence of hornbills in different forest types in Brunei Darussalam has been documented (Bennett *et al*. 1987; Mann 1987) and discussed in relation to forest mosaics (Charles 1996). No attempt has been made yet to assess Hornbill densities in Brunei. Eight hornbill species occur here, the Rhinoceros Hornbill (*Buceros rhinoceros*), the Helmeted Hornbill (*Rhinoplax vigil*), the Wreathed Hornbill (*Aceros undulatus*), the Wrinkled Hornbill (*A. corrugatus*), the White-crowned Hornbill (*Berenicornis comatus*), the Black Hornbill (*Anthracoceros malayanus*), the Bushy-crested Hornbill (*Anorrhinus galeritus*) and the Oriental Pied Hornbill (*A. albirostris*) Telemetry shows that hornbills range over very large areas (Poonswad and Tsuji 1993), their movements influenced mainly by the sporadic occurrence of fruiting trees. In Brunei, the range of any hornbill includes a mosaic of various forest types that may include disturbed secondary forests, kerangas (tropical heath forests), both mixed freshwater and peat swamps, mangroves, alluvial forests, or lowland mixed dipterocarp forests (MDF). Many forests today are exposed to extensive anthropogenic interference and the abundance of hornbills can vary dramatically when only disturbed habitats are surveyed.

The Fourier series technique (Burnham *et al.* 1980), employed to assess densities of primates, is not applicable to hornbills, since the presence of hornbills in an area is usually inferred from calls. Exact locations from the transect line are not always possible. Errors arising from this method make those density measures unreliable. This paper suggests that data obtained from repeated simple linear transects in forest mosaics can be used to express relative abundance as numbers per km, besides the usual density measures, especially in situations when density estimates become unreliable.

METHODOLOGY

Study localities and transects

Six different regions of Brunei Darussalam were surveyed for hornbill abundance (Table 1). Whenever an access route is not available in a forest area, a transect was established. In areas where a regular dirt track or paved road traversed the forest, this was used as a transect route and the entire distance was measured.

Table 1. Species of hornbills found in various transect localities and forest types

Transect Locality	Forest Mosaic	Species of Hornbills								Species Richness
		Rhinoceros	Wreathed	Wrinkled	Black	Helmeted	Pied	Bushy–cr.	White-cr.	
Belalong	Mixed Lowland Dipterocarp (MDF)	*	*	*	*	*	*	*	*	8
Sungai Ingei	Kerangas (Tropical heath)/ Dipterocarp	*	*	*	*					4
Sungai Burung	Disturbed forests, MDF, Peat swamp	*		*	*	*	*	*		6 (fruiting of figs) 3 (during other periods)
Pipe-line Road Lumut	Kerangas, Mixed swamp, MDF			*	*		*			3
Kuala Balai Road Belait	Peat swamp, Disturbed forests, Mangrove, Mixed swamp	*	*	*	*		*			5
Panaga, Seria	Residential area with golf course, gardens, secondary forests, mixed swamp			* #			*			2

* Present
\# 1 pair recorded in 2002

Localities chosen for transects showed a range of environmental disturbances. Belalong in the Ulu Temburong National Park and Sungai Ingei were undisturbed. Sungai Burung sustained regular vegetation clearing and burning and is on the periphery of a logged forest. The Pipe-line Road in Lumut was extensively damaged by the burning of kerangas and mixed swamp forests and clearing for the construction of a highway. The Kuala Balai Road in Belait district suffered extensive burning of peat and mixed swamp forests to make way for residential areas. Wildfires in early 1998 severely affected extensive areas of both the Lumut Pipe-line and Kuala Balai Roads. The Panaga area in Seria is a township with gardens, a golf course, and patches of secondary forests, with burnt peat and mixed swamp forests on the periphery.

All transects commenced at sunrise and were walked at a rate of 10 minutes per 100 m. Surveys lasted for 3-4 hours. During the walk, the forest canopy was constantly scanned for movement of branches and leaves. The identity and numbers of hornbills were noted when seen or estimated from calls when they were unseen. Care was taken to avoid double counting. “Walk” transects were 2 km or 4 km long. “Drive” transects were too long to be walked and were surveyed by driving a car and stopping every 0.8 km for a 10 minute circular scan with a radius of 0.4 km. Thus the whole length of the transect was covered. This was possible as the forests had been extensively disturbed and open areas were common. These transects were more or less straight. Most transects in Belalong were carried out in 1991-1992 and 1996-1997 and in all the other localities from 1996-1998 except in Panaga (2000-2001).

In the Lowland Mixed Dipterocarp Forest of Belalong (Ulu Temburong National Park), transects of 2 km and 4 km were walked along the East Ridge (average altitude of 300 m) and 2 km transects along the West Ridge at similar altitude. The 2 km and 4 km transects along the East Ridge were used to assess whether a longer transect gave a higher measure of hornbill density.

Other 2 km transects were carried out in the Sungai Ingei Conservation Forest in the Belait District. These had both Kerangas and Lowland Dipterocarp forest elements. In the Sungai Burung area of Lamunin, Tutong District, transects passed through a disturbed secondary forest and mixed lowland dipterocarp forest, and in Panaga (part of Seria town, Belait District) through residential areas with a golf course, gardens, orchards, secondary forests and mixed swamp. Transects in the last two areas used paved roads.

“Drive” transects along the Lumut Pipe-line Road (Belait District, 12.56 km) passed through Kerangas, Mixed Swamp and Mixed Dipterocarp forests. Along the 28 km Kuala Balai Road (Belait District) vegetation included peat and mixed swamp, disturbed forest and mangrove. An independent survey of the abundance of Rhinoceros Hornbills in the Mixed Lowland Dipterocarp Forest of Belalong was carried out in November 1991 (Cranbrook and Edwards 1994).

Forest mosaics

The forest types in a forest mosaic for a 2 km or 4 km transect were identified from a vegetation map of Brunei Darussalam using an area 6 km x 6 km around the transect. For the 12.56-km transect of the Lumut Pipe-line Road, the area that was used to identify the forest types was 13 km x 3 km. For the 28 km transect along the Kuala Balai road, the area used was 28 km x 3 km. Details of the forest mosaics are given in Table 1.

3) Relative abundance

Relative abundance of hornbills was expressed in two ways: as “numbers per km” and “numbers per km^2 or density”. The former measure was obtained by counting the number of hornbills seen perched within about 20 m from the transect line. Hornbills were not actually found on the open road or track of a transect and we assume that our counts represent those that would have been on the transect, if the road had not been cut and the habitat disturbed.

These 40 m wide transects were not used for calculating density. For estimating hornbill density, we counted all hornbills in a strip of 250 m either side of a transect. In nearly all situations, the hornbills were seen, but on some occasions, calls were used to detect their presence and location. The strip of 250 m reflects the limit of detection of hornbills in a forest. All locations of hornbills from the transect were measured by using Leica Geovid 7 x 42BDA binoculars.

RESULTS

2 km and 4 km transects in the East Ridge, Belalong

The relative abundance of hornbills expressed as numbers per km was compared between thirty 2 km transects and twelve 4 km transects carried out in the same area of the East Ridge in Belalong (Table 2). There was no significant difference (t = 2.021, $P>0.05$) in the abundance of Rhinoceros (t = 1.064, $P>0.05$), Wreathed (t = 0, $P>0.05$), Helmeted (t = -0.2727, $P>0.05$), Bushy-crested (t = 0.0348, $P>0.05$), and White-crested Hornbills (t = 0.522, $P>0.05$). The 4 km transect showed the presence of the Black Hornbill, which was not recorded in the 2 km transects.

Relative abundance of hornbills as numbers per km in different parts of Brunei Darussalam

The abundance figures for hornbills in Belalong are based on forty-three 2 km transects carried out on both the East and West Ridges (thirteen transects for the West Ridge and thirty for the East Ridge, Table 3). The figure for the Black Hornbill obtained during the 4 km transects in the East Ridge was included in this Table for comparison with the rest. The number of transects carried out for other areas are indicated in the Tables.

The Rhinoceros Hornbill occurred in four areas, with the highest abundance in Belalong (1.7) followed by Sungai Burung (1.5). The Wreathed Hornbill was seen in three localities and was abundant in Sungai Ingei (0.7) and Belalong (0.5). The Wrinkled Hornbill occurred in all six areas (Table 1) but was only recorded in five transects, being abundant in Sungai Ingei (1.0) Sungai Burung (0.7) and Pipe-line Road (0.5). The Black Hornbill was recorded in five areas and was abundant in Sungai Burung (1.8) and Sungai Ingei (0.8). The Helmeted Hornbill occurred in two areas and was most abundant in Belalong (0.5). The Oriental Pied Hornbill was recorded in five areas, being most abundant in Panaga (12.5) and least common in Belalong. The Bushy-crested Hornbill occurred in two transects, namely Sungai Burung (2.8) and Belalong (1.5). The White-crested Hornbill was only seen in Belalong (0.2).

Table 2. The mean number of hornbills per km using 2 km and 4 km transects lengths along the East Ridge, Belalong

Transect Locality	Transect		Number of hornbills (Mean±S.D.)								Forest Mosaic
	Length	Number	Rhinoceros	Wreathed	Wrinkled	Black	Helmeted	Pied	Bushy-cr.	White-cr.	
East Ridge Belalong	2 km x 40 m	30	1.9±0.91	0.3±0.67	0	0	0.6±0.82	0	1.1±1.18	0.2±0.48	Lowland Mixed Dipterocarp
East Ridge Belalong	4 km x 40 m	12	1.6±0. 64	0.3±0.36	0	0.1±0.2	0.7±0.78	0	1.1±0.59	0.1±0.21	Lowland Mixed Dipterocarp
t - test			1.064	0	-	-	-0.2727	-	0.0348	0.522	

Critical value = 2.021 at 5% significance level

Table 3. The mean number of hornbills per km in different transect localities in Brunei Darussalam

Transect Locality	Transect		Number of Hornbills (Mean±S.D.)							
	Length	Number	Rhinoceros	Wreathed	Wrinkled	Black	Helmeted	Pied	Bushy-cr.	White-cr.
Belalong (East and West Ridges)	2 km x 40 m	43	1.7±0.95	0.5±0.83	0.04±0.13	0.1± 0.31	0.5±0.63	0.08±0.14	1.6±1.71	0.2±0.47
Sungai Ingei	2 km x 40 m	3	1.0±0.0	0.7±0.47	1.0±0.0	0.8±0.24	-	-	-	-
Sungai Burung	2 km x 40 m	3	1.5±0.71	-	0.7±0.47	1.8±0.62	0.3±0.47	1.0±0.0	2.8±0.47	-
Pipe-line Road Lumut	12.56 km x 40 m	4	-		0.5±0.34	0.4±0.15	-	1.0±0.11	-	-
Kuala Balai Road Belait	17.39 km x 40 m	6	0.1±0.1	0.2±0.25	0.3±0.19	0.3±0.28	-	0.8±0.58	-	-
Panaga, Seria	4.02 km x 40 m	2	-	-	-	-	-	12.5±1.37	-	-

Relative abundance of hornbills (as density) in different parts of Brunei Darussalam

The density measures for the various species of hornbills followed the same trend as the numbers per km (Table 4). The independent survey of the density of Rhinoceros Hornbills (Cranbrook and Edwards 1994) yielded a density of 3.4 hornbills per km^2, comparable to the figure of 3.3 per km^2 obtained using 2 km transects (Table 4).

Species richness in the forest mosaics

All eight hornbill species are found in Belalong, mainly a Mixed Lowland Dipterocarp forest with riverine forests along the rivers Sungai Belalong and Sungai Temburung. Sungai Ingei Conservation Forest has three forest types (fresh water swamp, kerangas and mixed dipterocarp) and all eight hornbill species are expected to be found there. However, the site where the transect was carried out had a mixture of kerangas and mixed dipterocarp forest elements and only four hornbill species were seen (Table 1).

Sungai Burung, comprising a mosaic of disturbed forests, peat swamp and mixed dipterocarp forest usually, has three species of hornbills, the Wrinkled, Black and the Oriental Pied. During the transect periods, fig trees in the vicinity were fruiting and this evidently attracted three more species, the Rhinoceros, Helmeted and Bushy-crested, known to travel long distances in the forest in search of fruiting fig trees.

The Lumut Pipe-line Road with its mosaic of extensively disturbed swamp, mixed dipterocarp forests and kerangas (or tropical heath) had only three hornbill species. The mosaic of disturbed forests, peat and mixed swamp forests with mangroves around the Kuala Balai Road had five hornbill species. The Oriental Pied hornbill was the only species recorded in transects in Panaga, a residential area with mixed swamp and disturbed secondary forests. Teo (2002) recorded a pair of Wrinkled Hornbills here.

DISCUSSION

The usefulness of expressing hornbill abundance as numbers per km

This paper has expressed the abundance of hornbills as numbers per km as well as numbers per km^2, the usual practice (Kemp and Kemp 1974; Leighton 1986). Expressing abundance as numbers per km can be an alternative measure to density, especially in situations when the latter measurement becomes unreliable. It is useful when different habitats (or forest mosaics) are compared at different periods of time, e.g. before and after an ecological disaster like fire, or when a quick assessment of abundance is needed.

Optimal transect length

Comparing between a 2 km and a 4 km transects in Belalong, the results show no significant difference. However, the 4 km transect did identify the presence of an additional hornbill species. Thus, while two different transect lengths may yield comparable abundance measures, longer transects may be more accurate. These results are from a forest dominated by one vegetation type. In a forest mosaic, however it is important that a transect goes through all different forest types. But if all the vegetation types can be covered only in a longer transect as seen in the Kuala Balai Road or the Lumut Pipe-line Road, then a transect longer than 4 km should be considered.

Table 4. Density of hornbills in Brunei Darussalam

Transect Locality	Transect		Density (no. hornbills/ km^2)							
	Length	Number	Rhinoceros	Wreathed	Wrinkled	Black	Helmeted	Pied	Bushy-cr.	White-cr.
Belalong (East and West Ridges)	2 km x 500m	43	3.3	0.9	0.08	0.2	1.0	0.2	3.1	0.5
Sungai Ingei	2 km x 500 m	3	2.0	1.33	2.0	1.67				
Sungai Burung	2 km x 500 m	3	3.0		1.33	3.67	0.67	2.0	5.67	
Pipe-line Road Lumut	12.56 km x 500 m	4			1.0	0.8		2.0		
Kuala Balai Road Belait	17.39 km x 500 m	6	0.2	0.4	0.6	0.6		1.6		
Panaga, Seria	4.02 km x 500 m	2						25.1		

Relationship between occurrence of hornbill species and forest mosaics

The transect data shows that all eight hornbill species occur in the pristine, undisturbed forests of the Ulu Temburong National Park, dominated by lowland mixed dipterocarp forests (MDF) and patches of alluvial forests along river banks. Rhinoceros, Helmeted and White-crowned Hornbills have the highest densities there. The White-crowned and the Helmeted Hornbills occur only in this habitat. Their absence from kerangas, peat swamps and disturbed forests is striking.

The Wreathed and the Wrinkled Hornbills were most abundant in the Sungei Ingei undisturbed forest mosaic of MDF, kerangas and mixed swamp. Presence of fruiting trees during the transects in Sungei Burung influenced the occurrence of six species of hornbills where normally three species (Wrinkled, Black and Oriental Pied) are seen. The Sungei Burung surveys have shown that the presence of fruiting fig trees in a highly disturbed and degraded forest mosaic can attract hornbill species from afar, though they may not be usually seen in that mosaic.

The Lumut Pipe-line Road, with its highly disturbed forest mosaic, had only the Wrinkled, Black and Oriental Pied hornbills. The Oriental Pied Hornbill had a very low density in the undisturbed forests of Belalong but appeared to thrive in disturbed habitats, reaching a very high density in disturbed forest mosaics close to human habitation in Panaga. This is curious since their usual breeding sites appear to be in the swamp forests. A recent study has recorded Oriental Pied Hornbill nest sites in Panaga (Teo 2002). The Black Hornbill appears to be a successful forest edge species as seen in Sungai Burung but it is uncommon in pristine Belalong and less common in disturbed, burnt areas. The mosaic around Kuala Balai Road, though badly damaged owing to fires and logging, still has five hornbill species.

In general, it seems that an extensive undisturbed region like Belalong with a mosaic of MDF-alluvial forests or a rich mosaic of undisturbed forests types (e.g. MDF, mixed and peat swamp, alluvial, and kerangas forests, as seen in the Sungai Ingei Conservation Area), will support the highest diversity of hornbills. The diversity of habitats in a mosaic provides hornbills with a varied and constant supply of food, and resting, roosting and breeding sites.

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A preliminary survey of hornbills within National Parks of Sabah, Malaysia

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Abstract National Parks in Sabah harbor all eight species of hornbill recorded in Borneo. A survey was initiated to evaluate the distribution and density of hornbill populations within these various tropical forest habitats. A preliminary survey over the two-year period January 1999 to December 2000 involved general observation and line transect surveys in the Crocker Range, Tawau Hills and Pulau Tiga Parks. Seven species of hornbills were recorded from these Parks during the survey. Occurrence, distribution and density estimates for hornbill species varied between sites according to different habitat types in the Parks. The full protection of Parks within Sabah will preserve the last remaining forested areas vital for the survival of hornbills.

INTRODUCTION

Eight species of hornbills are present in Sabah, Malaysian Borneo, but specific studies on these species are lacking, sporadic or uncoordinated. Recent information on population density, distribution and biological aspects of hornbills in Sabah is not available, while information from surveys conducted in the early 1980s (Davies and Payne 1982) may not reflect the current situation as several forest clearances have altered the original habitat in certain areas. Current understanding of the ecology of hornbills is also limited, with little known about habitat preferences or adaptations of hornbills to disturbed forest habitats. Hornbills are vulnerable to habitat loss due to forest clearance for human development, which happens at present almost throughout Sabah. Evaluation is therefore necessary to know the current status of hornbill populations and their importance for conservation.

The terrestrial Parks of Kinabalu, Tawau Hills and Crocker Range are believed to harbor all eight species of hornbill recorded in Borneo, while the larger marine parks on the Tiga and Gaya islands are also home to one species of hornbill. Since the Parks are fully protected from any form of forest clearance, they provide some insurance for the conservation of hornbills and also suitable sites for hornbill research. Hornbills are the easiest representatives of the fauna to survey, through use of visible and audible means of identification.

This study aimed to evaluate the occurrence, distribution and density of hornbill populations in various habitats throughout the Parks of Sabah and to compare this to the ecology and behavior of various hornbill species from other tropical forest habitats. This preliminary study was used as a pilot survey for more comprehensive research work on hornbills in the future that will subsequently highlight the importance of hornbill conservation.

METHODOLOGY

Study area

The study was conducted at three localities with slightly different habitats in each of three different Parks, Pulau Tiga, Crocker Range and Tawau Hills (Fig. 1). These areas covered marine habitats on the west coast, crossed through the Crocker Range area and ended on the east coast of Sabah. They provided surveys at various altitudes and therefore within different habitat types.

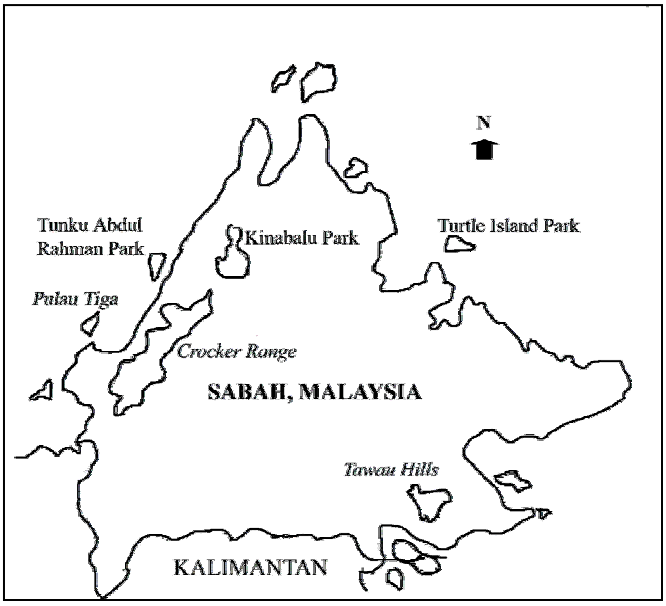

Figure 1. Map showing localities of national parks throughout Sabah, with survey sites marked in italics.

Pulau Tiga Park, a marine park situated off the west coast of Sabah, consists of three islands approximately 9 km from the nearest point on the mainland at Kuala Penyu. It covers an area of 158.64 km^2 and was gazetted as a park in 1978 (Phillipps 1988). Tiga Island is the largest, with an area of 7.25 km^2, whereas Kalampunian Damit and Kalampunian Besar are small islets of sand. Tiga Island, located at 5°42′N and 115°39′E, is covered by pristine coastal tropical rainforest and consists of 12 plant communities that includes mangroves, shrubs and palms. The island receives an average annual rainfall of 244 cm (Phillipps 1988) and was the survey site.

Crocker Range Park, a terrestrial park located on the west coast of Sabah, was gazetted in 1984 and with an area of 1399 km^2, is the largest terrestrial park in Sabah. It comprises a range of altitudes, from lowland (300 m) to lower montane (1400 m), and is covered with extensive tropical rainforest. The submontane areas, dominated by mixed dipterocarp and submontane forests, have a lower mean daily air temperature and higher relative humidity than lowland rain forest. This park receives an annual rainfall of 230-300 cm (Phillipps 1988). The study site was located in the center of the Park (5°27.369′N and 116° 0.434′E) at elevations of 300-1200 m and was accessible through the gravelled Kimanis Trunk Road.

Tawau Hills Park, a terrestrial park situated on the southeast corner of Sabah, was gazetted in 1979 and has an area of 279.72 km^2. It consists mainly of lowland tropical rainforest at elevations of 200-300 m dominated by lowland and hill dipterocarp forest (Phillipps 1988), and with an average annual rainfall of 180-235 cm with no apparent seasons. The mean daily temperature is 25-30°C with a moderate relative humidity of 50-70%. The park is bordered by oil palm plantation in the south and by a forest reserve to the north. The study was conducted within a long-term ecological research site, located at the southern tip of the park around Bombalai Hill (Maklarin, in press).

METHODOLOGY

This study was conducted over the 2-year period January 1999 to December 2000, during which each study site was visited during each quarter for 4-7 days of data collection in the field. The transect method employed to estimate hornbill populations within study sites (Mikol 1980; Marsh and Wilson 1981; Rodgers 1991) required at least two persons to walk slowly along a trail between 0600 to 1800 hours. Trails of approximately 6 km in length were identified and used for surveys at each study once or, in most cases, twice during each visit.

Data recorded during each survey included: location, date, time, weather, species encountered (directly or indirectly), number of individuals (seen or estimated), perpendicular distance from trail, canopy layer occupied (emergent, upper, middle, lower, understory), activity at first sight (feeding, foraging, flying, grooming, resting, calling, others) and other feeding ecology (food identity, feeding site). Special attention was paid to hornbills, but other animals encountered were also recorded and birds identified (using King *et al*. 1975; MacKinnon and Phillipps 1993; Smythies 1999). Observations were made with the aid of Leica 10 x 40BA binoculars: other equipment included camera, compass, altimeter, GPS, wrist watch, map of study site, data sheets/notebooks, pen/pencil, marker pen, and flagging ribbon.

RESULTS

Five visits were made to each study site in the period January 1999 to December 2000, during which a total of 27 transects were conducted (Table 1), with similar numbers for each study site as a basis for comparisons between sites. Months of visits to each site were more or less distributed throughout the annual cycle for monitoring seasonal changes in hornbill populations. However, habitats types covered by the survey trails differed between sites.

Table 1. Numbers and months of hornbill transect surveys at three study sites in Sabah, Malaysia

Locality	No. of transect	Month of visit	Forest type
Pulau Tiga Park (PTP)	9	February, May, June, August, November1999.	Coastal vegetation
Crocker Range Park(CRP)	10	May 1999; March, June, July, November 2000.	Lowland and lower Montane forest
Tawau Hills Park (THP)	8	March, June1999; February, August, November 2000.	Lowland tropical rainforest
Total	27		

Seven species of hornbills were observed at least once during the surveys, seven in Tawau Hills Park, five in Crocker Range Park and one in Pulau Tiga Park. Their frequency of occurrence was also recorded (Table 2). The Wrinkled Hornbill (*Aceros corrugatus*) was the only Bornean hornbill species not recorded. The Oriental Pied Hornbill (*Anthrococeros albirostris*) monopolised Pulau Tiga Park whereas the Rhinoceros Hornbill (*Buceros rhinoceros*) was the most frequently observed hornbill species at the terrestrial Parks.

Table 2. Occurrence and frequency of observation of hornbills at the three study sites in Sabah, Malaysia. Numbers of individuals observed are in parentheses. (PTP-Pulau Tiga Park; CRP-Crocker Range Park; THP-Tawau Hills Park)

Species of hornbill	Frequency of observation/ encounter			Total
	PTP	CRP	THP	
White-crested Hornbill (*Berenicornis comatus*)	-	-	1 (1)	1 (1)
Wreathed Hornbill (*Aceros undulatus*)	-	10 (21)	15 (31)	25 (52)
Wrinkled Hornbill (*Aceros corrugatus*)	-	-	-	-
Bushy-crested Hornbill (*Anorrhinus galeritus*)	-	15 (35)	2 (19)	17 (54)
Asian Black Hornbill (*Anthracoceros malayanus*)	-	11 (30)	6 (15)	17(45)
Oriental Pied Hornbill (*Anthracoceros albirostris*)	77 (156)	-	1 (8)	78 (164)
Helmeted Hornbill (*Rhinoplax vigil*)	-	8 (9)	18 (19)	26 (28)
Rhinoceros Hornbill (*Buceros rhinoceros*)	-	30 (53)	27 (50)	57 (103)
Total	77 (156)	74 (148)	70 (143)	221 (447)

The coastal Oriental Pied Hornbill was abundant and quite easily-encountered on Pulau Tiga. Of 77 encounters with 156 individuals, 39% were of singletons, 45% were of pairs and while larger flocks of 10, 9, 6 and 5 individuals were also observed once each. A nest discovered in May 1999 in a dead tree stump of 65 cm dbh was the only evidence of breeding discovered during the survey, but nesting was unsuccessful when the tree was blown down.

The most frequent of five species recorded at Crocker Range Park was the Rhinoceros Hornbill, followed by the Bushy-crested, Asian Black, Wreathed and Helmeted Hornbills. Other than the Wrinkled Hornbill, White-crested and Oriental Pied Hornbills were also not recorded from Crocker Range Park. Most species were recorded in pairs, except for the Helmeted Hornbill that was most often recorded singly when vocalizing at a distance. The largest flocks observed at Crocker Range Park were single records of six Asian Black Hornbills foraging in the middle canopy and five Bushy-crested Hornbills.

The most frequently encountered of seven species at Tawau Hills Park was the Rhinoceros Hornbill followed by the Helmeted, Wreathed, Asian Black, Oriental Pied, and White-crested Hornbills. The Wrinkled Hornbill was also observed at a remote site in this Park. Helmeted and Wreathed Hornbills were relatively more abundant in Tawau Hills compared to Crocker Range Park due to the lower elevation of the former site. Most sightings were also of pairs, with the largest hornbill flocks at Tawau Hills a group of 15 Bushy-crested Hornbills foraging in an unidentified tree in the middle canopy, and five Rhinoceros and five Asian Black Hornbills observed on separate occasions.

Data were too few for the estimation of densities using statistical procedures since frequency histograms could not be drawn to determine the effective transect width. However, the density of all hornbill species recorded was estimated based on a mean perpendicular distance as the transect width. The mean perpendicular distance varied between surveys. Since transect length was fixed at 6 km, the sampling area for each species was then calculated and used in density estimates (Table 3).

Table 3. Density estimates for hornbill species at three study sites in Sabah, Malaysia where density, D = n/2XY (n = number of birds observed; X = mean perpendicular distance; Y = total length of transect). See also text for statistical assumptions

Species of hornbill	Density estimates (indiv./km^2)		
	PTP	CRP	THP
White-crested Hornbill	-	-	0.84
Wreathed Hornbill	-	1.18	11.15
Wrinkled Hornbill	-	-	-
Bushy-crested Hornbill	-	1.60	26.39
Asian Black Hornbill	-	2.32	7.08
Oriental Pied Hornbill	19.65	-	2.22
Helmeted Hornbill	-	0.19	0.60
Rhinoceros Hornbill	-	0.94	5.67

Hornbill density was greatest in Tawau Hills Park (Bushy-crested 26.4/km^2, Wreathed 11.2/km^2, Asian Black 7.1/km^2) and lower in Crocker Range Park (Asian Black 2.3/km^2, Bushy-crested 1.6/km^2, Wreathed 1.2/km^2), while Oriental Pied Hornbills were at high density (19.7/km^2) at Pulau Tiga Park. Subject to all assumptions related to transect methodology, and assuming uniform habitat throughout each Park, a total of 142 Oriental Pied Hornbills were present in Pulau Tiga Park, 3,119 Wreathed Hornbills in Tawau Hills Park, and 3245 Asian Black Hornbills in Crocker Range Park.

DISCUSSION

The only Bornean hornbill species not recorded during the surveys in Sabah was the Wrinkled Hornbill, but this species is now rare and was previously only reported from the east coast (Davies and Payne 1982; Robson 2000). Wrinkled hornbills are also known to occur at Danum Valley in Lahad Datu (Mohammed-Zakaria 1994) and were also observed at a more remote site in Tawau Hills Park on several occasions outside of this survey. The White-crested Hornbill, recorded only once in Tawau Hills Park and not detected in Crocker Range Park during this survey, is also rare and difficult to find but has been reported from the southern part of the Crocker Range (Davies and Payne 1982) and is known to be present in Kinabalu Park (MBL, pers. obs.).

The abundant Oriental Pied Hornbill on Tiga Island has enjoyed full protection within this forest reserve since 1933, well before it was gazetted as a park in 1978, and so possesses undisturbed virgin forest habitat. A population of this hornbill is also found on Gaya Island, part of Tunku Abdul Rahman Park near Kota Kinabalu. The adjacent mainland, including the south-west portion of Crocker Range Park, is also believed to harbor this coastal hornbill species, while its presence at Tawau Hills Park in the east is due to having the coast only 10 km away and linked to the Park by vast riverine habitats. A survey made in the early 1980s further indicates the distribution of this species on the east coast of Sabah (Davies and Payne 1982).

All species of hornbill in Sabah may be sympatric, coexisting in a given area at the same time, but occupying their own niches for space, food and activities. The breeding season of most species is usually between January to June, supported by the Oriental Pied Hornbill nest found in May 1999, but it differs between species (Robson 2000) and requires more intensive and longer-term study in the future.

Differences in habitat types covered between sites during this survey contributed to differences in species composition at the three localities. Hornbill species are known to differ in their habitat preferences (Poonswad 1995). This survey was intended to measure occurrence as well as density of hornbills in selected areas with slightly different environments, but our density estimates may not reflect the actual population in the field. For instance, the Rhinoceros and Helmeted Hornbills may appear relatively less densely distributed in their respective habitats, despite being frequently recorded through their conspicuous vocalizations. This is the effect of longer perpendicular distances from transects which enlarged the sampling area and consequently decreased their densities.

All wildlife within Sabah Parks is fully protected from any kind of encroachment under the Parks Enactment, 1984. Moreover, all species of hornbills are listed in Schedule 2 of the Wildlife Conservation Enactment, 1997, which requires people to have permits to possess as well as to hunt them. Such legal protection is useless if enforcement measures are not taken and pockets of hunting activities persist in several terrestrial parks. Such acts may not pose a serious threat, however, as compared to habitat destruction through logging activities, which are the main factor that threatens wild animals of the tropical rainforest. Conservation efforts through enforcement, protection of habitat as well as conservation research are obviously vital and the fully protected Parks of Sabah will serve as important refuges for hornbill survival.

ACKNOWLEDGMENTS

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Recent hornbill surveys in Yunnan, China: a review and recommendation for future research

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Abstract Yunnan is a province located in southwestern China. Its southern and western parts are the major range of hornbills in China. No dedicated hornbill survey has been conducted in the past decade, although hornbills are a group of birds which have always received special attention in previous wildlife surveys. A new recorded species of hornbill for China, the Wreathed Hornbill (*Aceros undulatus*), was found at Tongbiguan Nature Reserve, western Yunnan, in 1996. Two skulls (one mature and one immature) were obtained from local hunters near the Reserve, and one male was seen clearly in the Reserve in April 1996. Special attention was paid to hornbills in a wildlife survey in Xishuangbanna National Nature Reserve in 1997, and populations of hornbills in each part of the Reserve was estimated based on information from local villagers. Among the five isolated parts of the Xishuangbanna National Park Reserve, hornbills were only found in three areas with size larger than 30,000 ha and may have disappeared from one small and highly fragmented area where they used to occur in the 1960s. A bird inventory in Jinggu County, Yunnan Province in 1997 showed that the Oriental Pied Hornbill still occurs in some remote mountain areas of the County, and two individuals were seen at Banpo Township. Gap analysis, a new method to predict the distribution of wildlife on a large-scale area, should be urgently applied in Yunnan immediately in order to identify the current range of hornbills. Due to the high degree of fragmentation of their habitats in Yunnan, the minimal area requirement (MAR) of each species should also be a focus of future studies in order to ensure the sustainability of hornbill populations.

INTRODUCTION

Asian hornbills are a group of large tropical forest birds. Four species of them were recorded in China before 1996. The White-throated Brown Hornbill *Anorrhinus* (*Ptilolaemus*) *austeni* was recorded in Xishuangbanna, Yunnan, Rufous-necked Hornbill (*Aceros nipalensis*) in Medog, Xizang and Xishuangbanna, Yunnan, the Oriented Pied Hornbill *Anthracoceros albirostris* in western and southern parts of Yunnan and southern part of Guangxi, and the Great Hornbill *Buceros bicornis* in western and southern parts of Yunnan (Cheng Tso-hsin 1987; Yang and Wen 1995). In 1996, a newly recorded species of hornbill for China, the Wreathed Hornbill *Aceros undulatus*, was found at Tongbiguan Nature Reserve, western Yunnan (Qu and Yang 1998). Therefore, five species of hornbill have been recorded in China thus far.

Yunnan province is located in southwestern China and borders Vietnam and Laos in the south and Myanmar to the west and southwest. Tropical forests and subtropical evergreen forests occur in the southern and the western parts of the province. All five species of hornbill occur within the province (Yang *et al*. 1995; Qu and Yang 1998). Among these five species, four species were recorded in the southern part and four species recorded in the western part making these two geographical regions the most important areas for the conservation of hornbills in China.

In the winter of 1992, Juangbianzai, located in the western part of the Mengyang Nature Reserve, was selected as a sampling site for a wildlife survey in the Xishuangbanna National Nature Reserve. The sampling area size was about 500 ha and the main vegetation type there was tropical rainforest. This site, away from local communities, experiences limited human disturbance. Out of the 11 days of the survey, the Oriental Pied Hornbill was seen on three days. This seemed to suggest that the status of Oriental Pied Hornbill in that area was relatively good.

Previously there were surveys carried out on wildlife, including hornbills, in the southern and western parts of Yunnan. Although all species of hornbills have been listed in the second category of protected species, there have been no specific studies or surveys on hornbills conducted in the last decade.

METHODOLOGY

Study area

Surveys were conducted in the following nature reserves:

1. Xishuangbanna National Nature Reserve (XNNR) which comprises five isolated areas, namely Mangao, Mengyang, Menglun, Mengla and Shangyong, were surveyed between January and June 1997 (Fig. 1 a, b). Hornbill surveys were a part of the field survey of protected animals in these reserves. Some physical characteristics of these reserves are shown in Table 1. Survey methods used included line-transect sampling to estimate hornbill densities, and interviews of local people, including Reserve staff, forest guards and villagers, to determine the presence and abundance of hornbill species. The number of transect lines laid and number of villagers visited for interviews are also presented in Table 1.

2. Weiyuanjiang Nature Reserve in Jinggu County was surveyed in May 1997. Weiyuanjiang Nature Reserve is located at $23^o06'$-$23^o17'$N and $100^o31'$-$100^o35'$E and covers a total area of 7,653 ha (Fig. 1a). The dominant vegetation type is Simao Pine (*Pinus simaoensis*) forest, which accounts for 88.6% of the total forested area. The remaining vegetation type is broad-leaved evergreen monsoon forest, which is scattered among the pine forest in valleys.

3. Tongbiguan Nature Reserve in Yingjiang County in Western Yunnan was surveyed in various periods. Tongbiguan Nature Reserve is located in western Yunnan ($23^o54'$-$24^o51'$N, $97^o31'$-$97^o46'$E; Fig. 1a). It consists of four separate parts with a total area of 30,711 ha. One part is in Yingjiang County with an area of 19,265 ha, one in Longchuan County with an area of 3174 ha, and two in Ruili county with a combined area of 8,272 ha (Fig. 1c). The elevation of the reserve ranges from 210 m to 2,595 m. Due to the great difference in elevation, many types of vegetation exist in the reserve, including rainforest, monsoon forest and broad-leaved evergreen forest in the valleys. Information was obtained from both the literature and field surveys, which included interviews with local people.

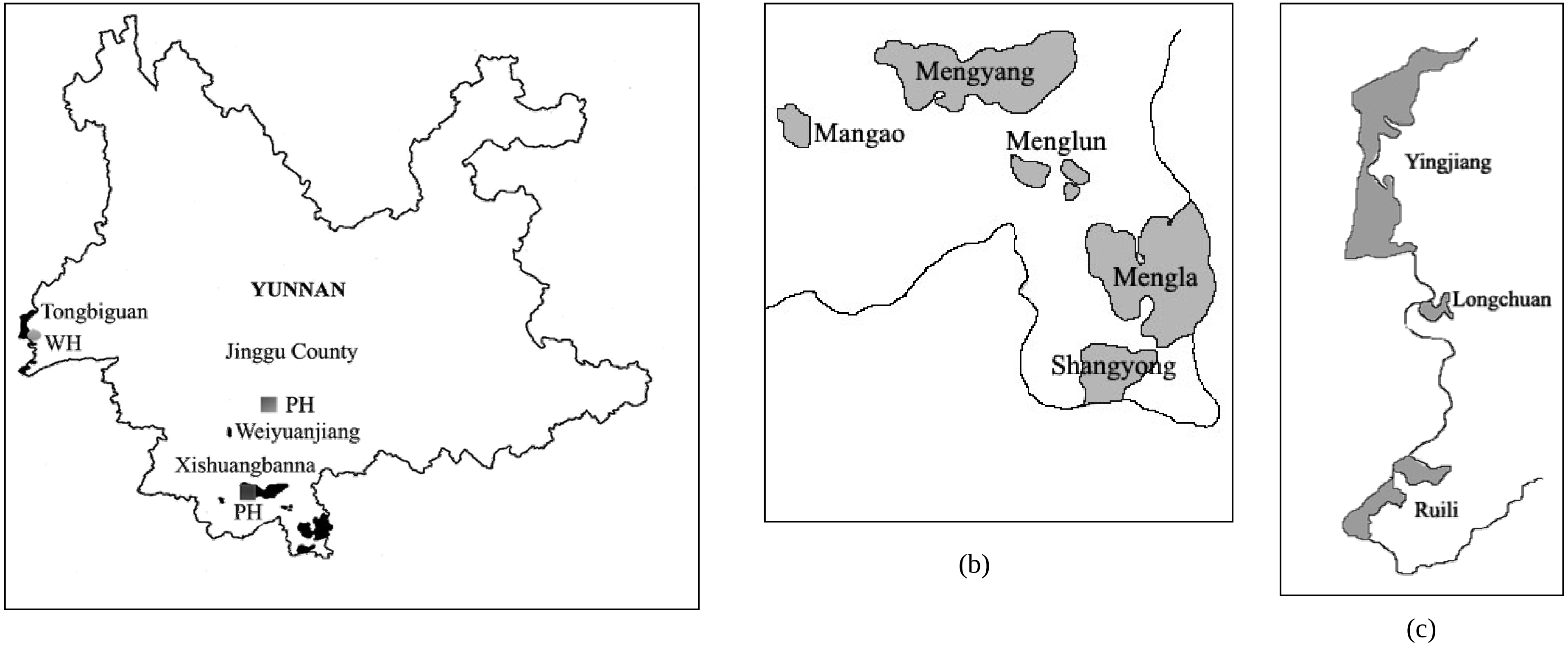

Figure 1. (a) Locations of nature reserves where hornbill surveys were conducted.
(b) Locations and relative size of five areas in Xishuangbanna National Nature Reserve.
(c) Locations and relative sizes of four areas of the Tongbiguan Nature Reserve (Modified from Forestry Surveying and Planning Institute 1989).

● Wreathed Hornbill ■ Oriental Pied Hornbill

Table 1. Size and altitude of five major areas surveyed for hornbills in Xishuangbanna National Nature Reserve (during the Expedition of Xishuangbanna Nature Reserve 1987), and the number of transect lines and villages visited for interviews during the field survey in the Reserve in 1997

	Surveyed area				
	Mengyang	Menglun	Mengla	Shangyong	Mangao
Size (ha)	99,760	11,242	92,932	30,538	7,340
Altitude (m)	590-1,600	550-1,340	650-2,007	610-1,691	1,084-1,771
Habitat status	Contiguous	3 isolated fragments	Contiguous	Contiguous	Contiguous
No. of transect lines	24	4	11	6	3
Total length (km)	12.26	1.135	8.34	4.68	0.77
No. of villages visited	52	12	26	9	9

RESULTS

Surveys in Xishuangbanna

No hornbill was seen by field researchers during the survey of protected animals in Xishuangbanna National Nature Reserve in 1997. This suggests that the populations of hornbills in Xishuangbanna National Nature Reserve are very small now. However, hornbills are still known to occur in some parts of the Reserve based on information obtained from local people. Table 2 shows the distribution and estimated populations of hornbills in the Reserve (see also Fig. 1b) and their current populations that were estimated based on the interviews of local villagers.

Surveys in Weiyuanjiang Nature Reserve, Jinggu County

Information gathered from local people revealed that Oriental Pied Hornbills can be still found in Banpo, Eisai and Mengban Townships and the Weiyuanjiang Nature Reserve. We also saw two birds in the evergreen broad-leaved forests of the mountain along the Mekong River on May 14, 1997 (see Fig. 1a) at an elevation of about 1,000 m. This was the first scientific record of the Oriental Pied Hornbill in Jinggu.

Surveys in Tongbiguan Nature Reserve

Based on the literature and on field surveys, four species of hornbills, the Rufous-necked, Wreathed, Oriental Pied, and Great Hornbills were recorded in the Reserve (Southwest Forestry College *et al*. 2000). The Wreathed Hornbill (*Aceros undulatus*) was a newly recorded species of hornbills in China (Qu and Yang, 1998; Fig. 1).

Table 2. The distribution and estimated populations (individuals) of four hornbill species in five areas of Xishuangbanna National Nature Reserve. * specimens were collected in the area between 1959 and 1960; ? the species is still believed to occur in Mengyang, with uncertain population size based on the information from local villagers

English name	Scientific name	Surveyed area				
		Mengyang	Menglun	Mengla	Shangyong	Mangao
White-throated Brown Hornbill	*Anorrhinus austeni*	50-150	*	90-100	40-50*	-
Rufous-necked Hornbill	*Aceros nipalensis*	-	-	30-40	20-30*	-
Oriental Pied Hornbill	*Anthracoceros albirostris*	?	*	About 100	50-60	-
Great Hornbill	*Buceros bicornis*	50	*	20-30*	About 20	-

In April 1992, a Wreathed Hornbill skull with some feathers remaining at the base of the bill was obtained from a local villager at the southern point of the Tongbiguan Nature Reserve. The skull was identified as a juvenile female from the two ridges on its casque and no corrugation on both upper and lower mandibles being visible (Poonswad and Kemp 1993; Fig. 2). The owner confessed that he had shot the bird on a mountain slope, more than one km north of his village, in August 1990. On April 6, 1996, an adult male skull was obtained from another local villager. There were six ridges on the casque and six clear corrugations on both upper and lower mandibles (Fig. 2). Both skulls are stored at the Southwest Forest College. On April 8, 1996 a male Wreathed Hornbill was seen in the nature reserve (Qu, pers. comm.) suggesting it was a breeding male (Poonswad *et al*. 1987).

A very similar species, the Plain-pouched Hornbill (*Aceros subruficollis*) is known to occur in northern Myanmar adjacent to western Yunnan (Poonswad and Kemp 1993). Table 3 shows a comparison of the bill length of skulls we obtained with that of Wreathed and Plain-pouched Hornbills.

Although the Wreathed and Plain-pouched Hornbills are very similar in appearance, the Plain-pouched Hornbill is the smaller than the Wreathed Hornbill (Poonswad and Kemp 1993). Moreover, the adult Wreathed Hornbill has corrugations on both upper and lower mandibles while the Plain-pouched Hornbill does not (Poonswad and Kemp 1993; Robson 2000). The bill length of the skulls obtained from western Yunnan was much longer than that of the Plain-pouched and fell within the range of the bill length of Wreathed Hornbills. The adult skull had six clear corrugations and the immature had indistinct corrugations on both upper and lower mandibles. Thus, we confirmed the identity of this newly recorded species occurring in western Yunnan to be the Wreathed Hornbill.

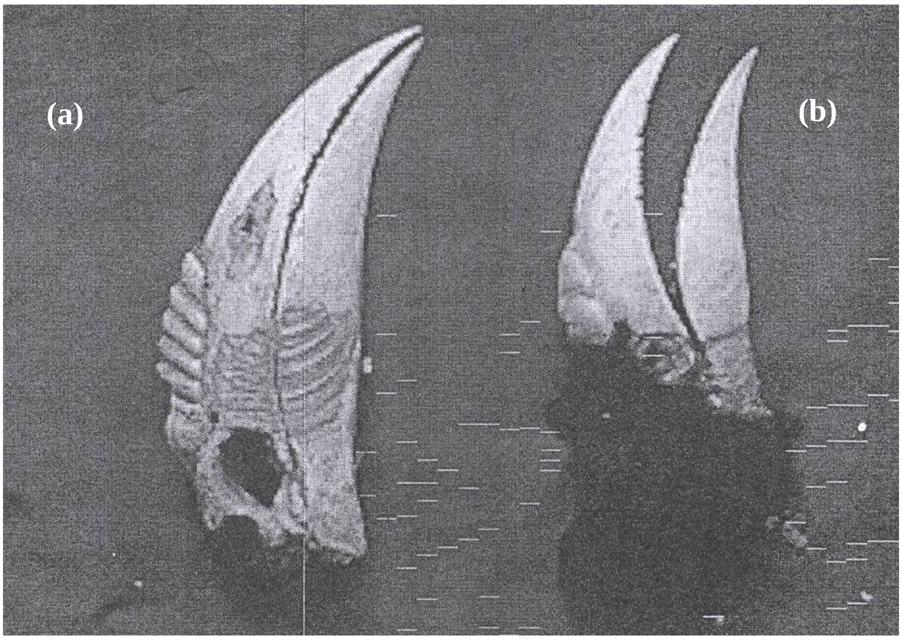

Figure 2. Skulls of the Wreathed Hornbill (*Aceros undulatus*).
(a) adult male and (b) a juvenile female.

Table 3. Comparison of bill length of Wreathed and Plain-pouched Hornbill from Poonswad and Kemp (1993) and the present skull of Wreathed Hornbills

	Sex	Bill from nostril	Bill from skull
Wreathed[1]	Male	189 (155-238)	215 (173-259)
	Female	150 (125-176)	165 (152-192)
Plain-pouched[1]	Female	109	158
Our skulls	Male	213	242
	Female	159	181

[1] From Poonswad and Kemp (1993)

DISCUSSION

Hornbills are tropical old-growth forest species. Their breeding habits such as nesting site selection and large home range requirement make them very sensitive to the fragmentation of tropical old-growth forests. Three species of hornbills were once found at Menglun in the 1960s, but they now seem to have disappeared from there. This local extinction may be related to the high degree of forest fragmentation in this area. The size of the nature reserve at Menglun is only 11,242 ha, but it was divided into three completely isolated parts. The inability to locate hornbills in Mangao might be related to the high elevation of the nature reserve. Hornbills are mostly found below 1000 m above sea level in China.

Although many wildlife surveys have previously been conducted in southwestern China, many areas still remain unexplored. A number of sites were explored by scientists several decades ago, but habitats there have greatly changed since then. Even in areas previously surveyed, new species may turn up, as in the case of the Wreathed Hornbill at Tongbiguan. As the species may have moved between contiguous forest of the Tongbiguan Nature Reserve and the forests of Myanmar, a method should be applied for identifying the potential range and habitat status of wildlife on a larger scale in order to protect them.

Gap analysis, a new geographic information system, is a method of identifying gaps in the protection of biodiversity on a large-scale, from a province or state to a country or even an international scale. A “gap” is defined by the US Geological Survey (USGS) as “the lack of representation or under-representation of an element of biodiversity (plant community or animal species) in an area intended for its long-term maintenance.” The gaps then can be filled with changes in land-use practices or the establishment of new protected areas after gap analysis. It uses satellite imagery, combining other information such as aerial photos, aerial videography and local expert knowledge to map the vegetation, and then predicts the distribution of animals based mainly on the habitat preferences of the animals.

The map of predicted distribution of a species is not drawn directly from specimen locality records, so it includes unexplored regions of suitable habitat and excludes unsuitable habitats within the overall range limit of a species (Scott *et al*. 1993). This process helps identify the gaps for the protection of hornbills. Conservation efforts and land use practices can be subsequently improved to fill the gaps.

Xishuangbanna used to be the home of four hornbill species and held the largest populations of hornbills in China. Comparing present information with historical data from the beginning of the 1960s, hornbills have become locally extinct in some areas. Mengyuan, a township where four species of hornbills were known to occur, has been replaced by a large rubber plantation and all hornbills have been extirpated there. The Tongbiguan Nature Reserve, which comprises isolated areas, supports populations of four hornbill species including the newly recorded Wreathed Hornbill, but their populations are apparently very small.

The small habitat patch can only hold limited populations of each species of wildlife, especially for large forest birds such as hornbills because they need a large home range or territories during the breeding season. Inbreeding usually cannot be avoided in small populations. The presumption that inbreeding increases the risk of extinction in naturally outbreeding species was validated (Frankham 1995). The minimal viable population in a patch should be studied, and then the minimal area requirement for this population can be estimated based on their home range. These kinds of studies on hornbills are essential for the planning and management of nature reserves, such as the expansion of existing nature reserves, restoration of habitat and even the establishment of connections between each part of a reserve of between reserves.

CONCLUSIONS

Five species of hornbill known from China, with the Wreathed Hornbill being a new record. All species can still be found in Yunnan with at least small populations, although they have disappeared from certain areas.

In order to identify the areas for protection, the application of gap analysis is proposed. Conservation efforts and improved land use practices can then be used to fill the gaps. Minimal area requirements for hornbills should be studied so that the protected areas can be efficiently managed.

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Modeling of hornbill and other wildlife distributions in a forested landscape at Khao Yai National Park, Thailand

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Abstract Biodiversity hot spots are defined as places that support high numbers of species. By identifying such hot spots and implementing appropriate interventions, park officials can manage natural resources effectively and biodiversity conservation can be sustained. A number of intensive and extensive techniques for mapping species richness and biodiversity over local to global scales have become available in the last two decades. Each technique has its own advantages and disadvantages. The objectives of this paper are to assess the geographical distribution of six threatened wildlife species in a tropical forested landscape of Khao Yai National Park, Thailand, and to apply the results for biological conservation efforts in the park. Khao Yai is Thailand's oldest protected area and is of national and international heritage value but poaching and other human disturbances threaten to reduce the wildlife populations and the overall biological diversity of the park. A universal kriging method and a Geographic Information System (GIS) were used to interpolate the sampled data of relative wildlife abundance collected throughout the park. The results showed that distributions of relative wildlife abundance generated from universal kriging were similar to those generated for the same species by independent camera-trapping undertaken by the Wildlife Conservation Society (WCS). By considering wildlife distribution maps along with information on human use of the forest from camera-trapping, sign surveys, and interviews with villagers, it is possible to formulate specific management activities to reduce poaching of threatened species and to stabilize or reverse the erosion of biodiversity at Khao Yai National Park. A wildlife monitoring program at the scale of the entire park is required to test and modify the model. The approach taken at Khao Yai may have relevance to other protected areas in Thailand, and elsewhere in the region.

INTRODUCTION

Mapping species-rich hot spots of biodiversity, locations where a plethora of key species live (Wilson 1996), is ideally derived by combining information on the distributions of these different species. However, the task requires reliable data and much effort. In situations where the required data are not yet available, species distributions are frequently represented on maps either by points, continuous distributions, or by the presence or absence of species on grids (Prance 1990).

The Royal Thai Forest Department has recently used point coverage to determine the presence of large mammals both within and outside protected areas. Researchers at the Natural History Museum in the U.K. used WORLDMAP GIS software, which was designed to record thousands of species while maintaining the speed required for analysis. The output map showed species-richness in lowest-rank taxa (either species or subspecies) plotted for cells in a 1° latitude-longitude grid (Williams 1996). Habitat requirements, such as food, cover and water data can also be used to determine wildlife suitability maps (Patton 1992). For example, Scott *et al*. (1987) used GIS to successfully integrate and analyze a number of field point data for various species. They correlated this data with environmental factors to estimate areas of potential distribution of those species. In addition, the MacKinnon-Ali

Software Stem (MASS) can predict lists of species likely to be found in protected conservation areas in Thailand based on general habitat requirements (MacKinnon 1992).

Each technique clearly generates a different thematic map of wildlife distribution. Maps prepared by using point data can present only a few observations found in the entire landscape. Plotting continuous distributions over a large area or the simple presence or absence of species from a grid cell have little or no ecological meaning. This is because the location precision of the original observations is lost to a greater or lesser extent through the process of generalization (Grainger *et al*. 1995; Stoms 1992). These results eventually affect conservation planning strategies of biodiversity.

However, there is exists the potential to derive more sophisticated measures and to integrate GIS techniques with geostatistics to identify patterns that take into account actual species presence and their abundance. Application techniques for analysis of geographical distribution of species abundance are available from the literature on spatial statistics but they are not yet in general use among ecologists and biogeographers (Oliver *et al*. 1990). For example, Webster *et al*. (1989) analyzed and mapped the annual mean concentrations of acidity and major ions in precipitation using the General Regionalized Variable Model (GRVM). Burgess and Webster (1980) applied semi-variogram and punctual kriging to interpolate soil properties.

Typically regeneralized variables are functions describing natural phenomena that have geographical distribution, which use semi-variance to express the rate of change of a regeneralized variable spatially correlated over short distances (Davis 1986). Thus, if variables of natural phenomena are spatially correlated in some manner, then sampled data can be used to estimate unsampled data in the landscape. Regeneralized variables seem to be an appropriate model to describe spatial variation in wildlife abundance (Maurer 1994).

The objective of this paper is to assess geographical distributions of six threatened wildlife species including two species of hornbills in tropical forested landscape of Khao Yai National Park, Thailand, and to apply the results for biological conservation efforts in the park. This is because wildlife poaching is a major threat to large mammal and bird species in the park, many of which may be headed toward local extinction (Lynam, pers. comm.). Therefore, there is an urgent need to determine the status and distribution of threatened species for use by park rangers and scientists to combat poaching and maintain biodiversity over the long term. The study is a first attempt to apply a spatial model for conservation purposes at Khao Yai National Park.

METHODOLOGY

Study area

Khao Yai National Park is situated between 14°05′to 14°15′ north latitude and 101°05′ to 101°50′ east longitude in north-central Thailand, covering 2,168 km^2 (Fig. 1). The Park was established as Thailand’s first National Park in 1962. The general topography of the Park is mountainous and elevation ranges from approximately 50 m to 1,351 m above sea level. The park experiences both the southwest and northeast monsoons. The mean annual rainfall is 2,850 mm, and is 3,000 mm at higher elevations due to windward and topographic effects (Pattanakiat 1988; Tangtham 1992). Most precipitation occurs during late April to October while the driest months are December and January, with an average rainfall of less than 10 mm/month. The mean temperature is 23.2°C and the relative humidity in the Park is about 90 percent year-round except in the foothills (Royal Irrigation Department, unpublished).

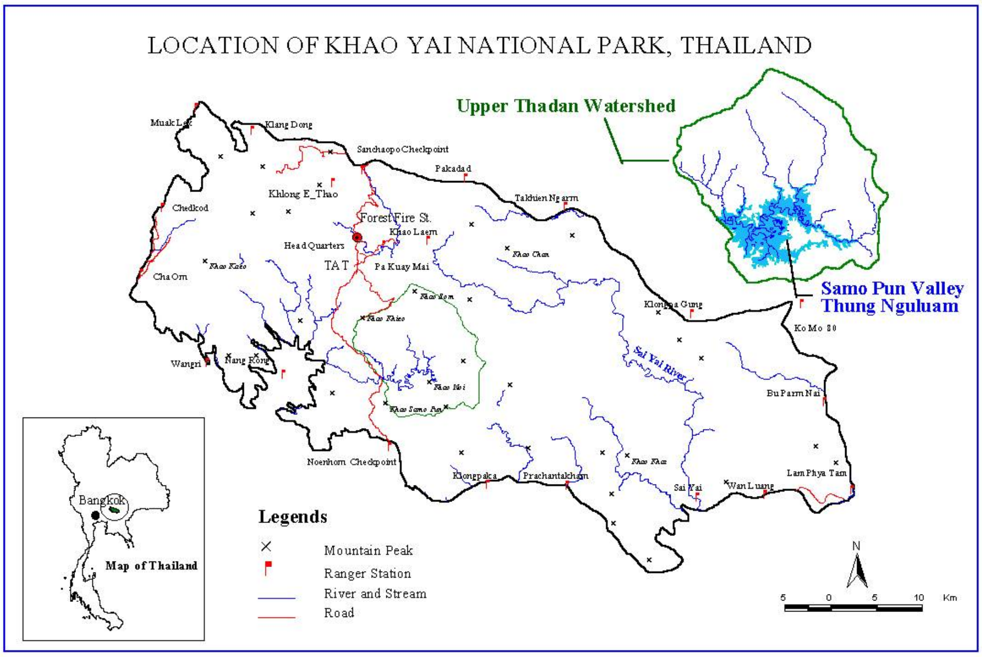


Figure 1. Location of Khao Yai National Park in Thailand.

Khao Yai has been recognized internationally as a rich wildlife habitat that includes four species of hornbills (Poonswad *et al*. 1987). It has also been selected as one of the ten ASEAN Heritage Parks and Reserves since 1981 (National Park Division 1987). Vegetation types of the park have been classified into six main classes: tropical rainforest, dry evergreen forest, hill evergreen forest, dry mixed deciduous forest, grassland, and agricultural areas (Smitinand 1977; Trisurat 1997). Tropical rainforest occupies about 50 percent of the Park, followed by dry evergreen forest and mixed deciduous forest. At least 71 species of mammals, 333 species of birds and 35 species of reptiles, as well as 18 species of amphibians have been recorded (National Park Division 1987; Srikosamatara and Hansel 1996). However, comprehensive maps of wildlife distribution throughout the Park are as yet not available.

Five stages were involved in mapping geographical distributions of relative wildlife abundance in Khao Yai National Park. These procedures include 1) sampling design, 2) selection of key species, 3) estimation of key species abundances, 4) kriging and 5) mapping relative key species distributions. In addition, the models were tested with the data obtained from camera traps. A flowchart of the study and procedures of analyses is presented in Fig. 2.

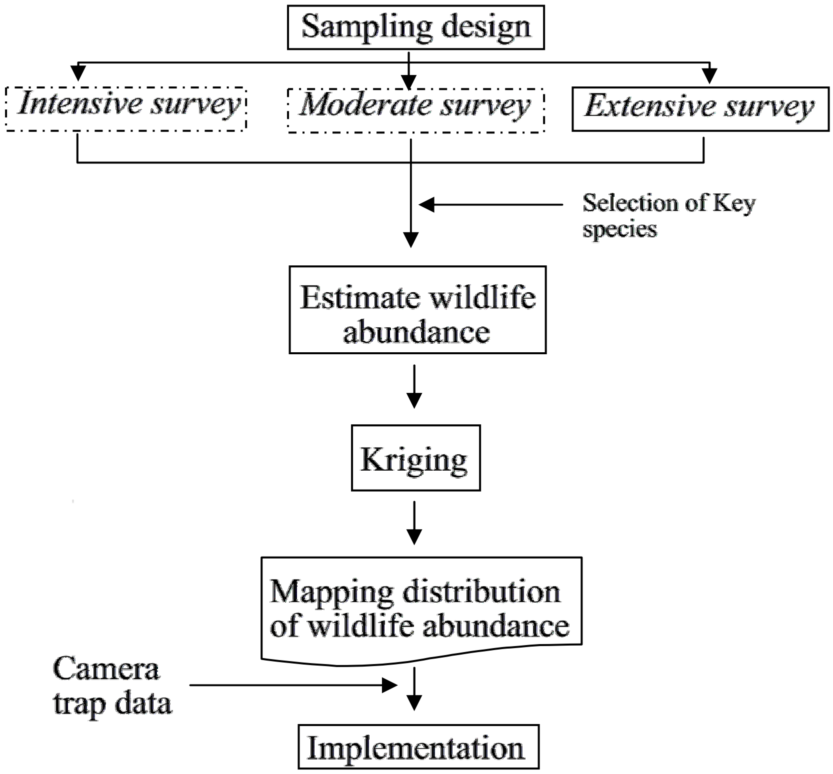


Figure 2. Study design for mapping relative wildlife abundance.

Sampling design

A wildlife survey was carried out during March-July 1996 at three scales: intensive in the Samo Pun Valley, moderate in the Upper Thadan Watershed, and extensive surveys covering all of Khao Yai (Fig. 1). This sampling design was, in fact, developed for an ecological impact assessment of proposed dam construction in Khao Yai National Park (Trisurat 1997). Sampling plots were chosen using the stratified systematic unaligned technique in order to avoid the periodicity of the systematic pattern during interpolation (Clark and Hosking 1986). In this procedure, three grid structures of 2x2 km^2, 5x5 km^2, and 10 x 10 km^2 were laid over the Samo Pun Valley, Upper Thadan Watershed and Khao Yai area, respectively. The sample sizes corresponding to the hierarchical scale are 11, 9 and 25 plots. Sample sites were accessed through animal tracks, topographic maps, hand compasses and a global positioning system (GPS).

Selection of key species

Since animal diversity in Khao Yai National Park is high, only a few threatened wildlife species were selected using several criteria for monitoring (flagship, keystone, key indicators and umbrella species). The selection of important wildlife species was first based on a list recommended by groups of conservation experts in Thailand (Brockelman and Baimai 1993). They were then finalized in consultation with the park's Superintendent and took into account practical limitations in resources and time (Table 1). The Asian Elephant *Elephas maximus* was select because it is an umbrella species, while two of gibbons *Hylobates lar* and *H. pileatus*, and bears (*Ursus thibetanus* and *U. malayanus*) are flagship species for conservation in Khao Yai National Park. Gaur (*Bos gaurus*) and deer (*Cervus unicolor*) are important prey species for tigers, and two species of hornbills (*Buceros bicornis, Aceros undulatus*) are keystone and flagship species as seed dispersers and for conservation. The tiger was not selected because it is not common in the park and furthermore, tiger surveys require considerable effort and resources.

Table 1. Selected key species for survey, conservation status and their role in ecosystem

Common name	Scientific name	Conservation status	
		National [1]	International [2]
Asian Elephant	*Elephas maximus*	CR	EN
Gaur	*Bos gaurus*	VU	VU
Sambar Deer	*Cervus unicolor*	NT	-
Asiatic Black Bear	*Ursus thibetanus*	EN	VU
Sun Bear	*U. malayanus*	EN	VU
White-handed Gibbon	*Hylobates lar*	EN	EN
Pileated Gibbon	*H. pileatus*	CR	EN
Great Hornbill	*Buceros bicornis*	NT	RA
Wreathed Hornbill	*Aceros undulatus*	NT	RA

[1] Office of Environmental Policy and Planning (1997), [2]Species Survival Commission (1994), CR - critically endangered, EN- endangered, VU – vulnerable, RA- rare, and NT- near threatened

Estimation of key species abundance

Indices of relative wildlife abundance were determined using a modified strip method with an equal amount of search effort and time at each sampling plot. This technique is simpler and more efficient in heterogeneous habitats (Brockelman and Ali 1987). At each selected sampling point, the modified 1-km transect to the north and a 1-km transect to the east were placed. Visual sightings along the transects were recorded first, while on the return walk animal signs such as droppings, mounds and calls were noted in the species recording sheets. Distances to animals or signs were measured from the transects (Srikosamatara 1993). The total abundance of each animal in the strip was estimated based on the number of signs and visual sightings using the following equation:

$$D = \frac{N}{2LW}$$

where D = total abundance of each animal in the strip
N = the number of signs or animals seen on both sides
L = total length of the transects
W = the maximum distance at which an animal is detected from the transect

Kriging

Kriging is merely a weighted moving average technique based on GRVM. It uses information on the patterns of spatial correlation among scattered sampled locations (point or grid) to estimate interpolated points. This technique has been proven to be useful and popular in many fields because it is a minimum variance estimator (Ingram, unpublished). Kriging incorporates information from a semivariogram to obtain the weights, so that patterns of the spatial autocorrelation are used explicitly (Maurer 1994). The kriging process involves the construction of a weighted moving average equation which is used to estimate the true value of a regionalized variable at specific locations. The semivariogram (γ) is half the expected squared difference between two values as in the following function:

$$\gamma\,(h) = \frac{1}{2n}\left\{\sum_{t=1} Z(\chi_i) - Z(\chi_{i+h})\right\}^2$$

Where n is the number of pairs of sample points separated by lag distance h and $Z(\chi_i)$ is the value of some property Z at position χ_i and $Z\,(\chi_{i+h})$ is the value at χ_{i+h} (Maurer 1994; ESRI 1992). In addition, the weightage assigned to each observed point is obtained by solving the following equation:

$$\sum_{j=1}^{N} W_{jk}\gamma\,(\chi_i, \chi_j) + C = \gamma(\chi_i, \chi_k)$$

Where $\gamma(\chi_i, \chi_j)$ is the semivariance between points χ_i and χ_j, and χ_k is the point to be interpolated. W_{jk} is the weightage for the point χ_k and C is the constant to insure that the solution is unbiased, by containing the weightages to sum to one (Webster *et al*. 1989). Once the weightage has been estimated, then the estimated values of numerous points or grids over the space can be interpolated by using the following equation:

$$Z(\chi_k) = WZ(\chi_i) + WZ(\chi_j)$$

Since kriging is most reliable when the data are normally distributed (Oliver and Webster 1990), the preliminary abundance of animals obtained from all sampling plots using were examined based on the frequency distributions and computed summary statistics including skewness. Transformations were used either to stabilize the variance or to achieve a known distribution, usually a normal distribution. Semi-variograms were computed and modeled with several methods and sample sizes using UNIX Arc/Info software and the best fitting model for each species was chosen.

Mapping distribution of wildlife abundance

The SURFER 6.1 PC software was employed to extrapolate maps of relative wildlife abundance as it generates good visual maps. The process began with the creation of grid coverage. Then, abundant contours were generated at intervals equal to 10 percent of the maximum abundance, and the output maps were exported to Arc/Info for final processing.

As this study was the first large scale wildlife survey for Khao Yai National Park, the results may not be comparable with data from previous studies of hornbills (Poonswad 1993), gibbons (Brockelman 1996), and sambar deer (Ngampongsai 1978) which were done on a fine scale at well-defined study areas. It may not be easy or appropriate to translate findings at this scale to the larger scale of the park. Therefore, preliminary tests of the models were compared with point data of wildlife distribution derived from camera trap surveys (153 locations) being undertaken by Wildlife Conservation Society-Thailand Program in collaboration the Thailand Royal Forest Department.

RESULTS AND DISCUSSION

Relative abundance and statistical summaries

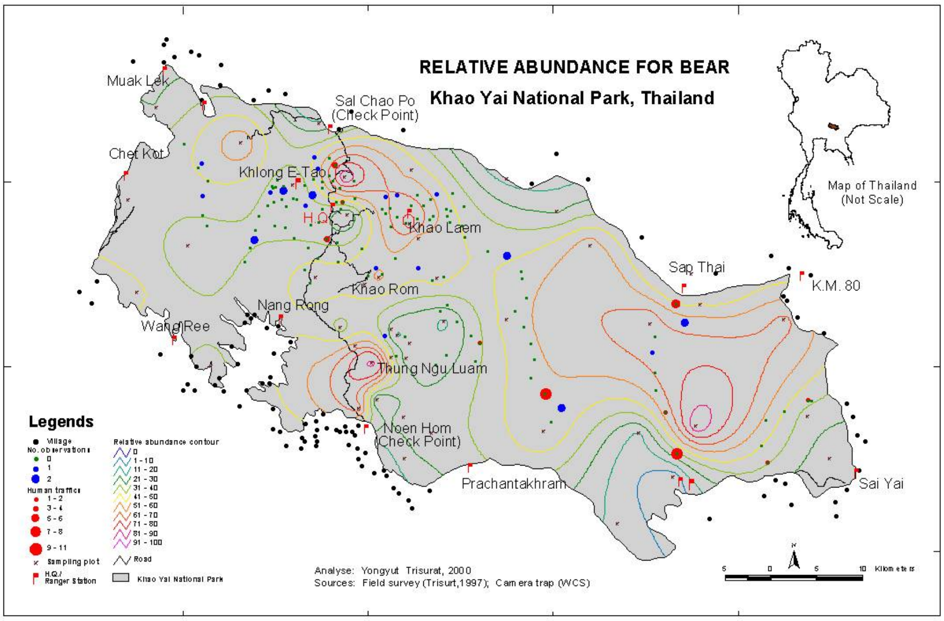
The distributions of bears, deer, elephants, gibbons and gaurs were strongly positive (Table 2). The skewness of bear distribution data (1.61) required transformation to stabilize the variance. The logarithmic transformation was applicable for deer, elephants and gaurs while a square root transformation was used to compute data on bears and gibbons. The skewness of hornbills data was asymmetrical (0.87) but not sufficient to require transformation. This may be because deer, elephants and gaurs tend to prefer habitats along available water sources in the dry and early rainy seasons more than other species (Srikosamatara and Hansel 2000).

Table 2. Statistical summary of relative abundance of key species from sampling plots

Species	Mean	Standard deviation	Skewness
Bear	204.34	214.02	1.61
√Bear	12.26	7.42	0.40
Deer	595.91	204.38	3.80
Log_{10}(deer+1)	1.22	1.09	0.90
Elephant	167	212.10	2.42
Log_{10}(elephant+1)	1.41	1.12	-0.25
Gibbon	1.25	1.94	2.12
√Gibbon	0.75	0.84	0.81
Gaur	145.92	327.09	4.31
Log_{10} (gaur+1)	1.36	1.00	-0.13
Hornbill	20.68	21.66	0.87

Maps of relative wildlife abundance

The study showed that bears are relatively abundant and widespread in Khao Yai National Park (Fig. 3), even though they are difficult to see. This may be because bears have less restricted habitat requirements. The main concentrations of bears are found in three areas: Thung Ngu Luam; forest patches near Forest Fire Control Station extending to Khao Laem Ranger Station; and the eastern part of Khao Rom Noi. They are less common in the southwest because these areas are affected by intensive human disturbance.



Analyse: Yongyut Trisurat, 2000
Sources: Field survey (Trisurt,1997); Camera trap (WCS)

Figure 3. Geographical distribution of bear relative abundance.

Deer distributions were somewhat different from those of other species. Deer tended to be more aggregated at the transition zones between grassland and evergreen forest. Higher concentrations of deer were found in Khao Laem grassland, and adjoining Khlong E-thao, Park H.Q. and the former golf course (Fig. 4; see also Fig. 1). The concentration at Thung Nguluam was relatively small but it was the core area found in the southern part of the park. Deer were less abundant in the remaining areas – places covered by dense evergreen forests with less young plant biomass generated in the undergrowth, and areas along the park boundary where the degree of human pressure is high. These results are comparable to the estimated densities of deer in Khao Yai National Park by Ngampongsai (1978) and Kutintara and Pongumphai (1982), which indicated that deer density was as high as 26 individuals/km^2 in grassland and forest edge habitats, 2.8 individuals/km^2 in dense forest, and 0.8 individual/km^2 in the areas along the park border.

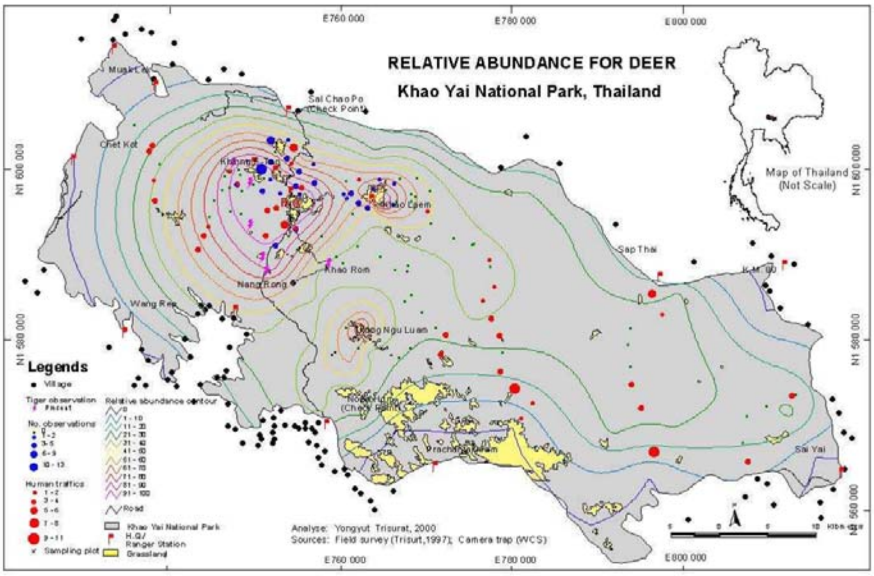


Figure 4 . Geographical distribution of Sambar Deer relative abundance.

Elephants were highly concentrated in the core area of the Park, which is covered by tropical rainforest and grassland, disturbed areas in transition zones near salt licks and guard stations, or areas that are less accessible to poachers (Fig. 5). Elephants were also abundant along the roadsides to the south of the Park Headquarters where their favourite foods, including *Imperata* grassland, *Macaranga denticulata*, and herbs in the family Zingiberaceae are abundant. In general, the pattern of elephant distribution derived from this study is similar to the preliminary elephant survey conducted by WFT (1994). Elephants are rare in the east and along the park boundaries (excluding the east) because of human disturbance and an escarpment slope, respectively.

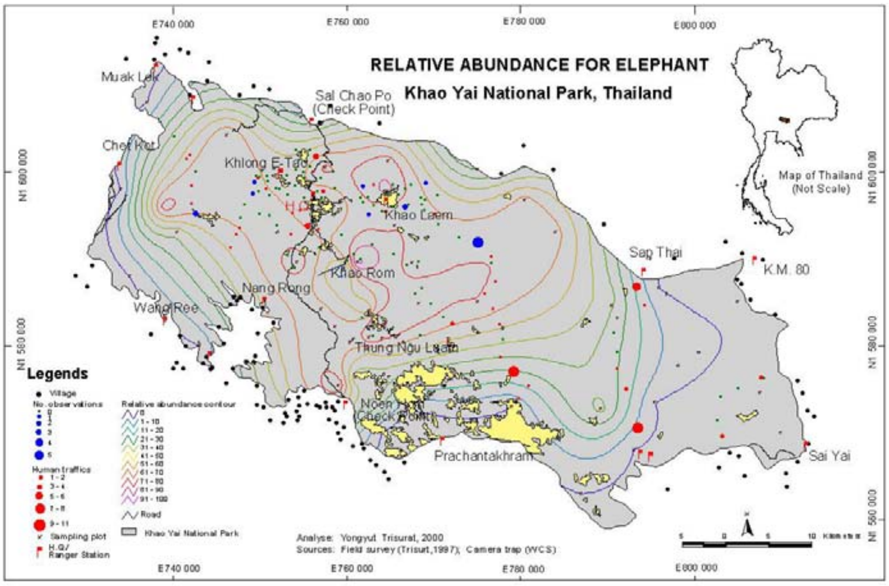


Figure 5. Geographical distribution of elephant relative abundance.

Geographical distributions of gaur were similar to those of gibbons but the extent of their distribution in the east was greater (Fig. 6). Gaur tends to prefer foraging in forests that are adjacent to open areas or bamboo forest (Srikomatara and Hansel 1996) regardless of elevation (Kutintara and Ngampongsai 1982). However, gaur is sensitive to human disturbance, and major signs and tracks are found deep inside the park. The results from field surveys and interpolation indicated that areas of concentration were at Samo Pun Valley, Khlong E-thao and in the northeast of the Park where grassland is predominant. The abundance was also high in the Khao Rom compound, Khao Samo Pun plateau, and at Khao Khat where bamboo is present. In fact, the Khao Laem grassland and TAT Golf Course are physically suitable for gaur but their relatively scarcity there may be because these areas are intensively influenced by human activities.

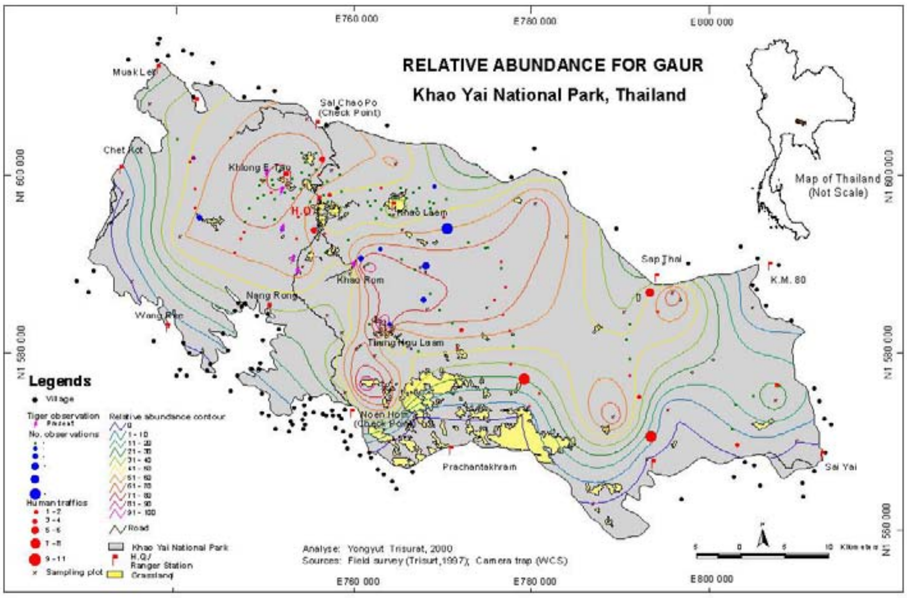


Figure 6. Geographical distribution of gaur relative abundance.

Gibbons tend to be rare in the Park (Srikomatara and Hansel 1996), even though the Park could possibly support 3,000-5,000 gibbons; this figure is much greater than the existing situation (Trisurat 1994; Brockelman, unpublished data). The pattern of gibbon distribution derived from the model (Fig. 7), which indicated the gibbons are found in evergreen forest where the elevation is less than 1000 m, agrees with the optimal habitat of gibbons (Trisurat 1994). In addition, this result was confirmed by W. Brockelman (pers. comm.) an expert on gibbons in Thailand. The map of gibbon distributions from this study also indicated that maximal abundance of gibbons was at Khlong E-thao and its surroundings, and near Thung Nguluam. The main area of concentration was at Khlong E-thao where it covered a larger area. This was perhaps the consequence of it being a well-protected area where food is abundant, particularly figs. On the other hand, gibbon abundance is low at higher altitudes and the area along the park boundaries, especially in the east. At higher altitude, in hill evergreen forest as well as in habitats to the south and east of the park, decreasing diversity and abundance of fruit food may make them suboptimal habitats for the gibbons. Meanwhile, animal poaching is still going on in areas near the park border.

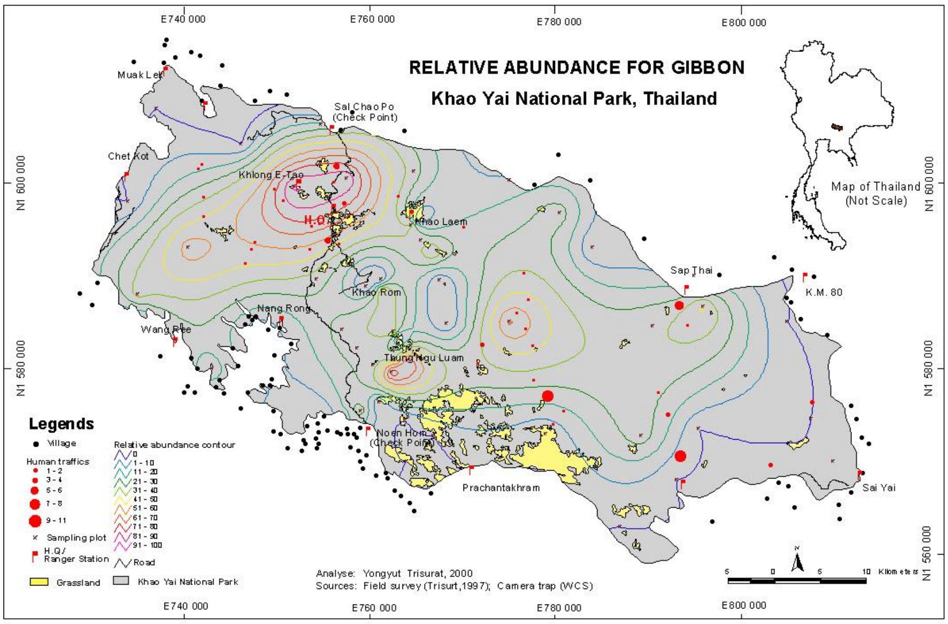


Figure 7. Geographical distribution of gibbon relative abundance.

Like other species, hornbills are most common in the core area, extending to the western region of the park. The potential habitats of hornbills are found in Khlong E-thao and its surrounding areas, the eastern part of Khao Rom Noi and Thung Nguluam. A high concentration of hornbills was in fact found at Khlong E-thao (Fig. 8). Hornbills are less common or absent along the park boundaries, especially in the east and the south where poachers can easily access the park. In addition, hornbills are rare at higher elevations, perhaps because there are fewer large trees for nesting and limited fruit trees for food. This result is supported by Poonswad (1993). Since this survey was carried out in the breeding season of hornbills (January-June), concentrations of hornbills were narrower than they are in the non-breeding season. Home ranges of all hornbill species in the breeding season are approximately one-third of the range sizes during the non-breeding season (Poonswad 1993). Thus, it is predicted that the spatial distribution of hornbill concentrations would be broader after the breeding season.

Preliminary testing of the kriging model

The results from Table 3 show that the distribution of deer and gaur are consistent with camera trap survey results. For example, the area of highest relative abundance for sambar deer (80-100 %) was covered with 4.9 pictures/10 km^2, while the lower gradients were covered with 2.82 pictures/10 km^2 and 2.99 pictures/10 km^2, respectively. Meanwhile, the gradient abundance of gaur is also compatible with the density obtained from camera traps. Interestingly, the camera trap surveys also show that tigers, the main predator of deer and gaur, were found in this area.

On the other hand, elephant distribution was only moderately compatible with the data from camera traps while bear distribution also was not wholly compatible with this data. This inconsistency may be because cameras recorded only visual sightings while the data used in the kriging model were obtained from a combination of signs and footprints.

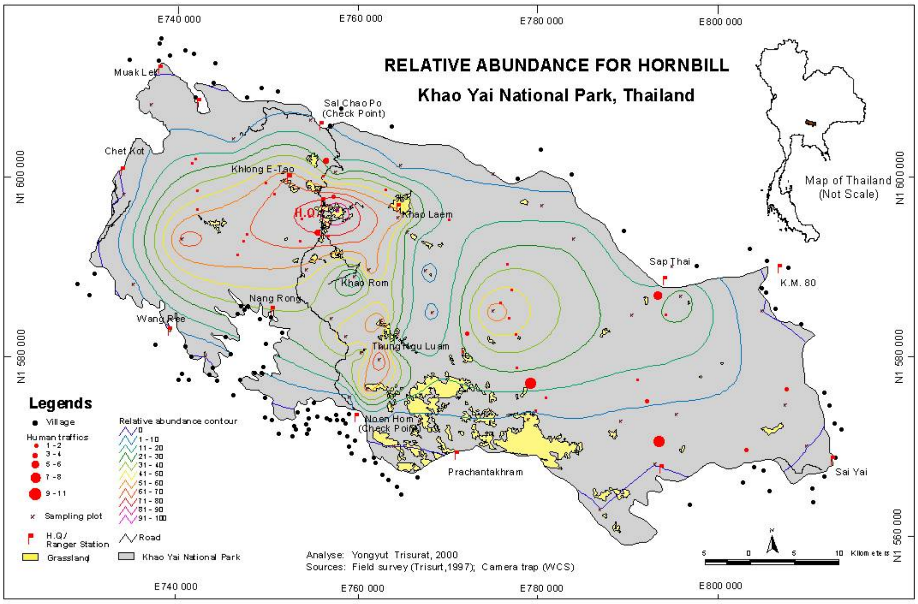


Figure 8. Geographical distribution of relative abundance for hornbills

CONCLUSION

Bear, deer, elephant, gaur, gibbon and hornbill – all species threatened by poaching – were selected for the mapping of their relative abundances at Khao Yai National Park, Thailand. Some of these species are considered endangered both nationally and internationally, which makes it very important to protect them in their wild habitats. About 50 sampling plots were laid for hierarchical analyses of wildlife abundance. In addition, surveys were done once in each transect to determine the relative abundance for each species with an equal amount of search effort and time. Therefore, concentrations of wildlife species may vary according to the season or when human activities and ecological factors are changed.

Maps of geographical wildlife distribution were prepared using universal kriging. UNIX Arc/Info was the main software used to calculate semi-variance and to interpolate relative wildlife distribution maps. The results showed that interpolated data of deer and gaur were highly correlated with camera trap surveys, which were recorded independently, while elephant and bear data were not significantly correlated. The distributions of two other animals (hornbill and gibbons) were confirmed by wildlife experts and bio-physical factors in the park.

Considering the geographical distribution of relative abundance for all species, the threatened species tended to be concentrated in the western portion of the park, where park officials have implemented strict protection measures. Deer distribution was concentrated in optimal regions (grassland and forest edge), which were mainly found at the Khlong E-thao area and the Park Headquarters. Hornbills revealed moderately stationary distributions due to their restricted habitat requirement, poaching, and narrow home ranges in the breeding season. Other species are dispersed throughout the park landscape except in the areas along the park boundaries and in the eastern and southern parts of the park. This may be due to intensive human pressure such as poaching and habitat conversion, as well as grazing by domesticated animals. Threatened species are concentrated in Khlong

E-thao and its surrounding areas. The Thung Nguluam area and eastern end of Khao Rom Noi are considered the second and the third most suitable areas for the threatened species, respectively.

The results suggest that universal kriging is a promising technique with potential application for identifying patterns of wildlife distribution and hot spots of biodiversity in protected areas. This is because this method does not require intensive surveys throughout the landscape. By identifying such hot spots, or concentrations of threatened species, park officials can effectively manage biological resources. This could lead to cost-effective conservation of biodiversity in protected areas. It should be noted that the patterns of wildlife concentrations are not static and may change periodically (Srikosamatara, pers. comm.). Therefore, these maps may not provide any detailed information on how wildlife species select habitat features, but may provide information on the range of ecological conditions within a landscape that a species is capable of using. It is recommended that future research should expand to cover monitoring surveys of a wider range of wildlife species as well as to train park staff. Monitoring should also cover seasonal variation in order to identify concentrations of threatened species in other seasons as well.

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SHORT NOTE

Hornbill surveys: too much effort?

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Abstract A very high proportion of hornbill species are globally threatened. Many populations of hornbills still remaining have not been studied and their status lies undetermined. Hornbills are very important for forest ecology as they disperse a large number of seeds from many different tree species. Often they are the sole large animals remaining which are involved in seed dispersal in Asian or African forests as other species may have been removed by hunting. They are also potential flagship species for helping to focus conservation action. Current techniques for estimating population sizes are often very time-consuming and require access to all regions and habitats of a study area. This can be a problem where terrain is difficult and the forest impenetrable. In particular, point counts which are currently used, may not be sensitive enough to detect variations in populations at very low densities. Many hornbills are rare so this is a major problem. Hornbills are very vocal and there is evidence that there is some consistent inter-individual variation in calls. If this is so, then recordings can be made of hornbill calls in a study area. They can be digitized and the spectrograms distinguished visually or by discriminant function analysis. This technique will allow a population to be censused. This may reduce the time required in the field and the number of skilled fieldworkers needed. It is a non-invasive technique so birds will be disturbed less by the cutting of vegetation for transects and the birds can be recorded remotely. Identification of individuals increases the value of data because when surveys are repeated it allows capture-mark-recapture studies and also analysis of survival rates. This technique will be tested to analyze its effectiveness and efficiency.

INTRODUCTION

Kemp (1995) recognizes 54 species of hornbill. Of these an enormously high proportion (21 species, nearly 40%) are listed as globally threatened and near-threatened (Collar *et al.* 1994) (Table 1). Their populations are often declining rapidly as a result of both habitat losses from agricultural clearance and logging and as target species for hunting. The populations that remain are often poorly known and in remote areas so surveys of their status are needed to establish their viability.

The threats to their populations are of great concern because hornbills are such valuable species. They are very important for forest dynamics and ecology as they disperse many species of tree seeds (Holbrook and Smith 2000; Jensch and Ellenberg 1999; Kinnaird *et al.* 1996; Whitney *et al.* 1998; Whitney and Smith 1998). Black and White Casqued Hornbills (*Ceratogymna subcylindricus*) in Kibale Forest National Park (NP), Uganda consumed the fruit of 67 tree species (Kalina 1988) and in Cameroon, three hornbill species consumed fruit from 59 species of tree, 22% of the total tree assemblage (Whitney *et al.* 1998). Jensch and Ellenberg (1999) found the seeds of 20% of the area's fruit-bearing trees under Pied Hornbill (*Tockus fasciatus*) roosts in Ivory Coast.

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Table 1. List of the threatened species of hornbill with threat status

Hornbill species		Threatened status (Collar *et al*. 1994)
Sulu Hornbill	*Anthracoceros montani*	Critical
Visayan Hornbill	*Penelopides panini*	Critical
Writhed-billed Hornbill	*Aceros waldeni*	Critical
Mindoro Hornbill	*Penelopides mindorensis*	Endangered
Writhed Hornbill	*Aceros leucocephalus*	Endangered
Rufous-necked Hornbill	*Aceros nipalensis*	Vulnerable
Wrinkled Hornbill	*Aceros corrugatus*	Vulnerable
Narcondam Hornbill	*Aceros narcondam*	Vulnerable
Sumba Hornbill	*Aceros everetii*	Vulnerable
Plain-pouched Hornbill	*Aceros subruficollis*	Vulnerable
Malabar Grey Hornbill	*Ocyeros griseus*	Near-threatened
Malabar Pied Hornbill	*Anthracoceros coronatus*	Near-threatened
Black Hornbill	*Anthracoceros malayanus*	Near-threatened
Rufous Hornbill	*Buceros hydrocorax*	Near-threatened
Helmeted Hornbill	*Rhinoplax vigil*	Near-threatened
Brown Hornbill	*Anorrhinus tickelli*	Near-threatened
Luzon Hornbill	*Penelopides manillae*	Near-threatened
Samar Hornbill	*Penelopides samarensis*	Near-threatened
Mindanao Hornbill	*Penelopides affinis*	Near-threatened
Brown-cheeked Hornbill	*Ceratogymna cylindricus*	Near-threatened
Yellow-casqued Hornbill	*Ceratogymna elata*	Near-threatened

Large mammalian seed dispersers are very scarce in many areas, especially in West African forests (the region in which I propose to work) where both hunting and habitat fragmentation are critical problems (Barnes 1996, 1999; Chatelain *et al*. 1996; Fa *et al*. 1995; Oates *et al*. 2000). Hornbills may therefore be the sole large vertebrates involved in seed dispersal that remain in many West African forests (Whitney *et al*. 1998) and other areas. Whitney *et al*. (1998) did show that there was little overlap in the species of seeds dispersed between hornbills and some other animals, e.g. African Elephant (*Loxodonta Africana*) and Gorilla (*Gorilla gorilla*) but it is likely that they could disperse some seeds of fruits which they normally consume only occasionally.

Hornbills are often the most obvious large animals in a forest due to their noisy behavior and their coloration. They are also charismatic, if not very beautiful, birds and so it is possible that they can be used as focal flagship species for conservation in protected areas. This places further emphasis on their importance for forest conservation.

HORNBILL SURVEY TECHNIQUES

The importance of hornbills for conservation has made them a target for conservation action and a survey protocol to assess their population has been adapted for them (Marsden 1999). This technique is based on using the variable circular plot method where counts are made from points. A flaw with Marsden's technique and for point counting methods in general is a huge number of point counts may be needed and, for very rare species, the method may not be appropriate (Marsden 1999). As travel and count time at each point can take 15 minutes and counting can only take place in the morning (Marsden 1999), this means that only approximately 20 counts can be undertaken per person per day. To reduce standard errors of bird density estimates to 20%, Marsden found that 212 point counts were needed for the Sumba Hornbill and 1,452 for the Papuan Hornbill (for the Purple-naped Lory *Lorius domicella*, a parrot, 2860 counts were required). At 20 counts per day, counting the Papuan Hornbill would take 70 days for one habitat type.

The number of trained and experienced ornithologists in many parts of the world is not sufficiently great to permit such intensive surveys and the technique may not even be sensitive enough to detect variations in populations of the very species that are being studied (Marsden 1999). Some species may have been reduced to such low population densities that it is not an appropriate survey technique. Hornbills often occur in large flocks and although point counts can compensate for this when estimating densities, if flocks are very rarely encountered then this may distort density estimates and it is also an inefficient way of collecting data. Another problem in some areas is that habitat variation may be so great that many different surveys need to be carried out to assess the population density for a particular site. For example, Mont Péko National Park in Ivory Coast, one of my proposed study sites, ranges from 250 to over 1,000 m. It contains bare rock, low scrubby forest, swamp, secondary, primary, and riverine forest. Many of these features can occur together in a small area. Surveys would be needed in each of these habitats to assess their quality for hornbills. Another problem for this site is that the forest is so dense in many places and the terrain so steep that it is practically inaccessible, making transects for point counts almost impossible.

Other techniques can be considered. The "look-down" method involves counting every bird within an area from a vantage point overlooking forest (Lambert 1983). This relies on there being suitable vantage points so this may be a limitation, and it also require that the species being studied fly above the canopy. This could be a consideration for some areas of Mont Péko but for the lowland area it would not be possible. Territory mapping could be a suitable technique for population estimates of the territorial savanna hornbills but for most forest species it would be ineffective as so many do not defend exclusive territories.

Vocalizations

Hornbills are amongst the most vocal and noisy of all bird species, with even their wing noise being used in communication (Brosset and Erard 1986; Kemp 1995). Alexander *et al.* (1994) showed that the casque in various species of hornbills might have some acoustic function as the resonant frequency of the casque corresponded closely to the fundamental frequency of the call. Kemp (1995) suggests that the casque and bill structure in conjunction with other morphological features may have some role in communicating information about the age, sex and status of an individual. P. Jones (pers. comm.) observed male Silvery-cheeked Hornbills (*Ceratogymna brevis*) in Tanzania with varying sizes of casques. It is not known whether these were immature males but amongst Black and White Casqued Hornbills the casque was still growing at 1 year old (Kilham 1956). The size of the casque could assist estimates of age and variation in casque coloration could aid individual recognition (Kalina 1988). In two Asian species (Great *Buceros bicornis* and Rhinoceros Hornbills *B. rhinoceros*), the casque was still growing at 5 years and 8.5 years old respectively (Frith and Frith 1983; Tickell 1864). All this evidence suggests that there is likely to be considerable inter-individual variation in calls because of the effect of casque size on call structure. This inter-individual variation between calls is likely to be consistent as the casque is a rigid structure and this is an important basis for using the calls for individual recognition (Falls 1982).

Kalina (1988) was able to distinguish the calls of some male hornbills by ear. More sophisticated analysis of calls is possible by digitising them. Differences between the calls of individuals may be more apparent using this technique.

METHODOLOGY

As explained above, there are currently no techniques which are efficient for assessing populations of hornbills and their habitat requirements. A new technique would be of great value for the study and management of hornbills. Marsden (1998) suggests using vocalizations to detect elusive species in bird surveys. The basis of my new technique is the recognition and distinction of individual calls. If calls can be distinguished then they can be used to census populations. This technique has been used successfully for a number of species (Beightol and Samuel 1973; Galeotti and Pavan 1991; Gilbert *et al.* 1994; McGregor and Byle 1992; Saunders and Wooller 1988) and may prove particularly effective for hornbills as will be shown below.

The basic technique is very simple. Each call of a suitable type that is heard in the study area will be recorded. The location of the caller should be estimated and can be plotted on a map of the area. Recorded calls can then be digitized and compared with calls of other individuals in the area. The identity of the caller can either be discerned by studying the spectrogram visually or by the more time-consuming method of measuring the components of the spectrogram and then using discriminant function analysis to distinguish individuals (Gilbert *et al.* 1994).

RESULTS

It may be possible to reach an absolute total for the hornbill population in the area as individuals can be distinguished. A map of the locations of hornbill individuals can be constructed which can be compared to habitat availability and other features of the area such as hunting pressure. As calls are individually distinct, estimates of the population size can be made using the capture-mark-recapture technique if surveys are repeated. Survival estimates can also be made if a population is resurveyed in subsequent periods, as the rate of turnover can be estimated by comparing captures of known to new individuals. It is likely that only males produce the type of call which will be suitable for analysis. This is a limitation but would still allow an assessment of the number of breeding pairs or groups.

DISCUSSION AND CONCLUSIONS

There are a number of advantages of this method compared to point counts.

1) It may reduce the amount of fieldwork required for estimation of the size of a population as it can be carried out at the same time as other work. Alternatively, hornbill calls could be elicited by playing back calls and recording their responses. This may prove to be an efficient method of collecting recordings.
2) The technique is non-invasive. Point counts involve cutting transects and paths to points which can be very noisy so birds may be disturbed and missed before the point is reached. Calls may travel 2 km and so can be recorded at some distance from the calling bird (Kalina 1988; Kemp 1995). This may be especially important in some areas where hunting pressure is high as birds can be very wary making approach difficult.
3) Point counts require systematic surveys of all parts of a study area. Calls can be recorded at some distance from the bird which may be important in areas where there is very rough terrain or inaccessible forest.
4) Identification of individuals increases the value of the data collected as explained above by allowing capture-mark-recapture studies. Survival estimates can also be made if the study is repeated in subsequent seasons.

Although behavioral studies are often criticized for their lack of application to conservation, this may often be related to a belief by those studying animal behavior that they do not have an important role to play in conservation (Sutherland 1998). The development of this technique shows how developments in pure research can be used to help solve practical problems. This paper has arisen as a result of my postgraduate work on the acoustic communication and behavioral ecology of African hornbills.

Field trials

This technique must be tested to assess its potential and effectiveness. In particular the ease with which individuals can be distinguished must be assessed. The types of call suitable for analysis must be chosen from the range of calls produced. These will differ between species but the function of the suitable calls is likely to be similar across species. Attenuation of calls and components of calls will increase with distance from the caller. The greatest distance at which calls can be recorded and distinguished must also be assessed. I will be working in Mont Péko and Marahoué National Parks, Ivory Coast to test the technique.

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PART IV: HORNBILL CONSERVATION

PART IV: INTRODUCTION

This entire volume can be said to be about hornbill conservation. With the rapid rate at which forests are being cleared and the sensitivity of most hornbills to habitat fragmentation and the loss of big trees, even "basic" research that attempts to better understand the biology of hornbills may provide information that could be vital for their conservation. In reading through the various papers in this volume, one cannot help but to wonder how the many interesting findings presented can be applied to the management and protection of hornbill populations.

This section features papers which highlight three broad areas of importance for conservation, be it for hornbills or any other species – compiling all relevant information from previous systematic, ecological and behavioral studies on a group of taxa, sorting out the nomenclatural and systematic status of the taxa concerned, and managing the species or habitat with the help of local communities and a successful outreach program.

Alan Kemp summarizes over 70 years of hornbill studies in Africa in his overview. After consulting over 800 references, it was possible for him to notice trends in research interest over the years and to identify well-studied as well as under-studied species and topics. The challenges for hornbill conservation in Africa, as well as in Asia, are many, but comprehensive literature reviews help provide an indispensable starting point for conservation efforts.

How does one tackle the problem of species and subspecies delimitation, especially in instances where it may make a difference in the conservation status of a group in question? Wayne Delport addresses this issue using a multi-disciplinary approach involving morphological, behavioral, breeding biology, and molecular studies. His work is relevant to the field of evolutionary biology, but also addresses the real-world needs of the conservation biologist.

It goes without saying that hornbills, by virtue of their conspicuousness, the critical ecological role that they play, and their vulnerability to habitat loss are a symbol for conservation in Africa and Asia. There is nevertheless a need to educate others about hornbills – what they do, why they are important, why we need to protect them, and how we can help save them. Outreach efforts of this sort are never easy, especially if a target audience have had limited exposure to the animals and/or know very little about them. Visits, both to the field site as well as to a virtual one, can drive home the conservation message. In the case of visits to the field, can they be organized such that they do not degrade the habitat or disturb the animals? There is an additional vital factor – how can a local community be inspired to participate or even spearhead conservation efforts?

In their case study of ecotourism on the World Natural Heritage-recognized Japanese island of Yakushima, Tetsuka and Yumoto provide a prototype of how it might be possible to organize an outreach and ecotourism effort to help save hornbills and other threatened species. In order to be successful, such an effort must be sustainable and fulfil the needs of tourists, local communities, and perhaps most importantly, the natural habitat. Yakushima also boasts a virtual museum called the Yakushima Open Field Museum, designed for the benefit of researchers, residents, and visitors alike. Could this be a model for hornbill conservation as well?

At the conclusion of the 3rd International Hornbill Workshop, participants unanimously expressed grave concern over the future of the world's tropical forests and the implications for hornbills should these forests be further reduced in size and species richness. The participants were resolved to work towards highlighting the ecological importance and the sensitivity of hornbills to habitat disturbance, both to policy makers as well as the general public. Although a hoped-for Hornbill Conservation Action Plan was not formulated, all left the Workshop prepared to further advance both hornbill research and conservation. We hope that the findings presented in this volume will make their way beyond the circle of Workshop participants and inspire others to help better understand and protect hornbills and the habitats they live in.

An Overview of Hornbill Studies in Africa

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Abstract This paper summarizes published references to the 23 species of African hornbills. 837 references have been analyzed to provide a picture of the extent of taxonomic, geographic and biological knowledge of these species. The first detailed studies of any hornbills were conducted in Africa in the 1930s, by such workers as Ranger (Crowned Hornbill *Tockus alboterminatus*, Trumpeter Hornbill *Ceratogymna bucinator*) and the Moreaus (Silvery-cheeked Hornbill *C. brevis*) and later by Kilham (Grey-cheeked Hornbill *C. subcylindricus*). Compared to Asia, a high proportion of African species occupy savanna and open forest habitats, making observations relatively easy. Representative species of the genera *Bucorvus* (Southern Ground Hornbill *B. leadbeateri*), *Tockus* (African Grey Hornbill *T. nasutus,* Monteiro's Hornbill *T. monteiri,* African Red-billed Hornbill *T. erythrorhynchus,* Southern Yellow-billed Hornbill *T. flavirostris*) and *Ceratogymna* (*C. brevis, C. subcylindricus*) have been studied in detail. However in each genus, those species least studied occur in tropical lowland rainforest, mainly in West Africa. The unusual nesting biology has been studied in most detail, for a number of species, followed by much less detail on feeding biology. There have been few studies of ecology or genetics and there is scope for several taxonomic studies. Only recently have studies of movements, range utilization and communication been attempted. All this information would be essential for good conservation planning and management, yet projects aimed specifically at hornbill conservation have been undertaken only recently.

INTRODUCTION

Some of the earliest and most detailed biological studies of hornbills ever conducted were on African species (Ranger 1931-1952; Moreau 1934-1938; Moreau and Moreau 1940-1941; Kilham 1956-1957), at about the same time that similar work started in Southeast Asia (Bartels and Bartels 1937). Currently, an incomplete but comprehensive bibliography of the 23 species of African hornbill includes 837 published references (Kemp unpublished, available on the hornbill website: http://www/nfi.org.za /birds/ground %20Hornbill/ hornbill%20Bibliography.doc). This does not include many regional and national fieldguides, handbooks, and research articles on birds or other topics that include but do not make special mention of hornbills. Five major works over the last half-century cover African hornbills in detail (Sanft 1960; Fry *et al*. 1988; Forshaw and Cooper 1994; Kemp 1995; del Hoyo *et al*. 2001). All except Fry *et al*. (1988) also treat the 30 species of Asian hornbills in equal detail. In this paper we use published references to review the extent of research on African hornbills by taxon, region, subject, and date. It is an attempt to identify important gaps and possibilities; it also complements another recent publication that examines the conservation biology of African hornbills (Kemp in press).

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METHODOLOGY

A comprehensive bibliography of hornbills, current to the end of 2000, was used to compile the texts and systematic arrangement for the *Handbook of Birds of the World*, Volume 6 (del Hoyo *et al*. 2001). An analysis of this bibliography provided an index of the coverage of African hornbills by taxon, region, subject and date, although the assessment of this coverage remains subjective, given the variance in the length, content, detail and significance of each reference.

The taxon and region covered by each reference were taken from the title and/or journal in which they were published, so that only a subset of the total references was included. However, all references were allocated to a category of subject matter, based again mainly on the title of the article. The dates on which the references or each of their parts were published, rather than the date of the study, was also analyzed.

RESULTS

Analysis by taxon

The number of published articles and post-graduate theses recorded for each taxon show uneven coverage (Table 1). One third of the references pertain only to the two large and spectacular species in the genus *Bucorvus*, half refer to the 14 species in the genus *Tockus*, and only one fifth to the seven species in the genus *Ceratogymna*. Species of lowland rainforest are least studied. Only six species have been the subject of post-graduate theses, yet *T. erythrorhynchus* has attracted no less than four thesis studies.

Analysis by country and region

The coverage of references by region within Africa is also uneven, with 16% of references pertaining to West Africa, 10% to North East Africa, 19% to East Africa, 15% to Central Africa and 36% to Southern Africa (Table 2). These figures show no obvious relationship to land surface area or density of hornbill species, but seem rather to reflect the higher level of research activity in Southern, East and West Africa. Of the post-graduate theses, three were done in Southern Africa (Kemp 1976; Knight 1990; Delport 2001) two in East Africa (Wambuguh 1987; Kalina 1988) and two in West Africa (Diop 1993; Jensch 1995). Even the important historical studies were done only in South Africa (Ranger 1931-52) and East Africa (Moreau, 1934-38; Moreau and Moreau, 1940-41; Kilham 1956-57). Studies in countries that support mainly tropical lowland rainforest were once again poorly represented, with only 23% of the references, only one post-graduate thesis and no important historical studies.

Table 1. Numbers of references by genus and species, and post-graduate theses, in which a taxon of African hornbill is the principal subject. The full citation details of all references are not provided, except for the theses which may not be easily located, but all major references to each taxon are listed in del Hoyo *et al*. (2001)

Taxon		References		Total		Post-graduate
		Nos	%	Nos	%	
Bucorvus				78	32	
	abyssinicus	29	12			Knight 1990
Tockus				115	47	
	alboterminatus	18	7			
	bradfieldi	7	3			
	fasciatus	2	1			Jensch 1995
	hemprichii	4	2			
	nasutus	23	9			Kemp 1976
	pallidirostris	1	<1			
	monteiri	4	2			
	erythrorhynchus	34	14			Kemp 1976 Wambuguh 1987 Diop 1993 Delport 2001
	leucomelas	9	4			Kemp 1976
	flavirostris	3	1			
	deckeni	9	4			
	albocristatus	0	0			
	hartlaubi	0	0			
	camurus	1	<1			
Ceratogymna				53	22	
	sharpii	3	1			
	bucinator	17	7			
	cylindricus	0	0			
	subcylindricus	17	7			Kalina 1988
	brevis	12	5			
	atrata	3	1			
	elata	1	<1			
Total:		246	100	246	100	

Table 2. Numbers of references pertaining to a country or region. Major references are listed under each taxon in del Hoyo *et al*. (2001) or on the bibliographies presented on the hornbill website http://www.nfi.org.za/birds/hornbill

Region	References						Total	
	Country	Nos.	%	Country	Nos.	%	Nos.	%
All Africa, general		23	4				563	100
West Africa, general		13	2				89	16
	Senegal	11	2	Gambia	4	1		
	Burkina Faso	3	1	Guinea	7	1		
	Sierra Leone	3	1	Liberia	5	1		
	Ivory Coast	8	1	Ghana	8	1		
	Togo	4	1	Benin	1	<1		
	Nigeria	19	3	Mali	1	<1		
	Niger	2	<1					
Central Africa, general		11	2				82	15
	Cameroon	24	4	Fernando Po	4	1		
	Gabon	5	1	Congo	3	1		
	D.R. Congo	27	5	Cen. Afr. Rep.	7	1		
	Chad	1	<1					
North East Africa, general		6	1					
	Sudan	14	3	Ethiopia	13	2		
	Somalia	14	3	Eritrea	1	<1		
	Saudi Arabia	5	1	Yemen	2	<1		
	Egypt	1	<1					
East Africa, general		28	5					
	Kenya	35	6	Uganda	27	5		
	Tanzania	15	3	Rwanda/ Burundi	2	<1		
Southern Africa, general		11	2				206	37
	Angola	17	3	Zambia	20	4		
	Malawi	12	2	Mozambique	10	2		
	Namibia	22	4	Boswana	12	2		
	Zimbawe	29	5	South Africa	73	13		
Total							563	100

Analysis by subject

Most references containing significant amounts of information on hornbills are either regional or local survey reports (40%, Table 3). A further 11% refer to studies of hornbills in captivity. The remaining half of the references are observations made on hornbills in their natural habitat. Of these, about one fifth (10% of the total) refer mainly to the special breeding biology of hornbills, one half (24%) to various aspects of non-breeding biology, especially diet, and one quarter (13%) to distribution, biogeography and taxonomy. A paltry 3% of the total references refer specifically to the conservation biology of African hornbills.

Analysis by date

The number of references published per decade during the Twentieth Century is summarized in Table 4. Half the total references (49%) were published after 1970. It is not clear if the slight decline in the 1990s is due to a decrease in output or an incomplete bibliography. References for 2000 onwards have not been included since many smaller regional publications have not yet been searched.

DISCUSSION

Analysis of published and unpublished references to African hornbills provides an objective starting point for what has been studied to date. However, it can be misleading without additional information. For example, the two species of *Bucorvus* ground hornbill both appear to have been well studied (Table 1). However, the northern *B. abyssinicus* has been studied mainly in captivity, where it breeds quite readily, while the southern *B. leadbeateri* has been the subject of long-term field studies, but only in South Africa, and only because it appears not to breed easily in captivity. Comparative studies on the species, which have quite different social systems would be important for both their wild and captive conservation but are lacking. There appears to be no easy substitute for an intimate knowledge of the literature to assess the coverage of a particular hornbill species, geographical region or research topic.

Therefore, the following comments provide an assessment based both on the analyses above and on our personal knowledge of the literature. The comments are directed at two main audiences, conservationists who want to decide what to do next, and researchers who want interesting and relevant topics to study. A comparison with references for Asian hornbills would be instructive.

Conservationsts have the least information on hornbill species of lowland tropical rainforest (Table 2), despite this being the most threatened habitat and containing the greatest number of threatened African hornbills, especially in West Africa (Kemp, in press). Techniques developed in Asian rainforests (Poonswad and Kemp 1993; Poonswad 1998) need to be applied in Africa. The work of Whitney and Smith in Cameroon (Whitney and Smith 1998; Whitney *et al*. 1998) on the large *Ceratogymna* species and their role in fruit dispersal and forest conservation, is pioneering in this respect, as is the work of Jensch (1995) in Ivory Coast. A major gap remains in the study of the smallest and most unusual hornbill species, *Tockus hartlaubi, T. camurus and T. albocristatus*, within the rainforest habitat. Several taxonomic studies are also necessary before conservation priorities can be assigned to other hornbill populations and their habitats (Kemp, in press), of which the recent work of Huebner *et al*. (in press) and Delport (this volume) are excellent examples. However, species in need of even the most basic studies are already apparent (Table 1).

Researchers have concentrated mainly on the breeding biology of hornbills, both wild and captive (Table 3), and on the population ecology of a few savanna species (Kemp 1976, 1988; Wambuguh 1987; Knight 1990; Diop 1993). Exceptions are Kalina's (1988), Jensch's (1995) and Whitney's (Whitney and Smith 1998; Whitney *et al*. 1998) work on the ecology of a forest species, and Delport's (this volume) communication, an ecological and molecular study on the taxonomy of a savanna species. These studies have recently been augmented by the use of artificial nest boxes in the more arid and treeless habitats of Namibia, facilitating access to data that was previously difficult to acquire on the fertility (Boix-Hinzen *et al*. 2000) and energetics (Klaassen and Brenninkmeijer 1997) of breeding hornbills. Studies on population dynamics, population genetics and communication are notably few. Several new studies are underway or being planned, suggesting that the volume of published results will resume after the slight decline in the 1990s (Table 4).

CONCLUSION

A wide range of published studies form a foundation for future studies on African hornbills. Our personal interpretation of existing coverage suggests the need for two main initiatives. First, a study of the population ecology of rainforest species, in particular the larger frugivores, of which the West African *C. c. cylindricus* and *C. elata* are conservation priorities, and the small forest insectivores, especially *T. hartlaubi* and *T. camurus*. Second, a study of the role of hornbills as seed dispersers in the forests and as predators on the savannas, to extend the work already done in Cameroon (Whitney and Smith 1998; Whitney *et al*. 1998) and South Africa (Kemp 1976, 1988) respectively.

Finally, we advertise with pleasure the projects that are underway on the molecular systematics of hornbills (Stephan Hübner, smhuebner@gmx.de; Wayne Delport, simdel@icon.co.za), on population studies using nest boxes (Christian Boix-Hinzen, cboix@botzoo.uct.ac.za) and on the harvest of redundant second-hatched chicks and their re-introduction in ground hornbills (Hendri Coetzee and Anne Turner, project@groundhornbill.org.za). We thank the organizers of this workshop for their support while in Thailand. ACK thanks the Northern Flagship Institution for permission to attend and the National Research Foundation for the airfare from South Africa.

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When should subspecies be evaluated to species?
A multidisciplinary approach to determining Hornbill taxonomic status

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Abstract Many avian species have geographic variants described as subspecies. These generally have consistent morphological features and are geographically subdivided from their sister taxa. Although such characteristics suggest that some subspecies should be elevated to specific status, the elevation of subspecies to species is not necessarily a simple task. Evolutionary biologists seldom agree on a particular species concept, and therefore the assignment of a new species under a particular species concept is rarely accepted universally. This paper summarizes research into the taxonomic status of the Damaraland Red-billed Hornbill (*Tockus erythrorhynchus damarensis*), endemic to Namibia. We used a multidisciplinary approach, including morphological, behavioral, breeding and molecular data, to determine taxonomic status. Furthermore, we did not adopt a species concept prior to the research, but rather collated ideas from several species concepts. Therefore, data collection and analyses were not exclusive to a particular notion of how the speciation process occurs. We advocate this approach, using several lines of evidence without an *a priori* defined species concept, as advantageous to taxonomists, aviculturalists, zoo curators and conservationists alike. We do not intend to negate the debate over species concepts. However, while such debates have their role in the field of evolutionary biology, taxonomic decisions need to be made in other fields that do not necessarily need the adoption of a process-oriented species concept.

INTRODUCTION

> "Geographic speciation is thinkable only, if subspecies are incipient species. This of course, does not mean that every subspecies will eventually develop into a good species. Far from it! All this statement implies is that every good species that developed through geographic speciation had to pass through the subspecies stage"
>
> E. Mayr 1942

Approximately six decades after the publication of Mayr's (1942) *Systematics and the Origin of the Species* the debate over how to define a good species is still largely unresolved. A major factor contributing to the species concept debate is the diverse array of scientists that need a workable species concept. Evolutionary biologists require species concepts to address the processes of evolution and speciation. Conservation biologists require species concepts to determine which species are endangered or have limited distributions and therefore require conservation attention. Peterson and Navarro-Sigüenza (1999) have demonstrated that numbers of avian endemics differed according to which species concept was adopted. Moreover, the authors call for conservationists and systematists to collaborate when conservation priorities need to be determined. Finally, zoo biologists require species concepts to identify whether the breeding programs they are conducting are representative of what occurs naturally. This diversity of biologists that require or have addressed species concepts has led to the development of two major species concept philosophies. Both Ferguson (1998) and Templeton (1998) have identified these philosophies as either process- or pattern-orientated species concepts.

The Biological Species Concept (BSC) (Dobzhansky 1970; Mayr 1970) defines species as populations that are reproductively isolated from one another. This isolation is proposed to be the result of natural selection leading to isolating mechanisms that prevent mating between different species. The BSC is therefore process-orientated since it uses a hypothesis about how speciation occurs to define species. A philosophical problem some have with the BSC is that if speciation occurs in allopatry and the evolutionary process has no power of foresight, how do these isolating mechanisms evolve for the purpose of preventing mating between geographically subdivided populations?

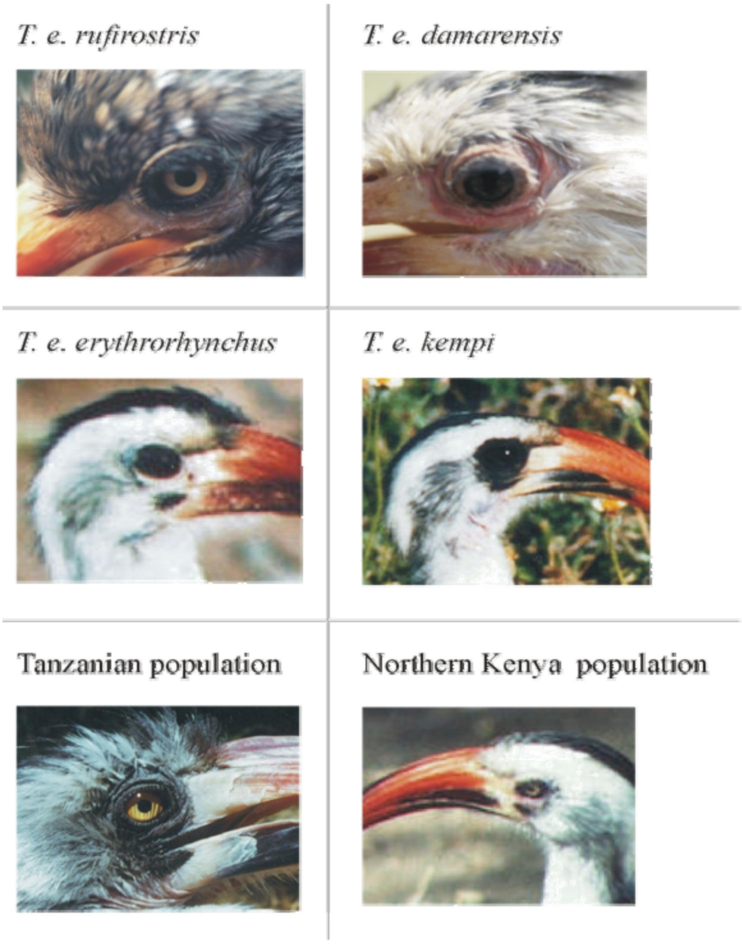
This philosophical problem of the BSC made way for another process-orientated species concept. Paterson’s (1985) Recognition Species Concept (RSC) defines species as populations that share a common fertilization system. However, such a system has arisen for the purpose of communication between individuals and has the prevention of mating between species as a fortuitous consequence.

The proliferation of molecular methods in recent years has led to the development of a new species concept, the Phylogenetic Species Concept (Cracraft 1989). The Phylogenetic Species is a population of organisms that have consistently diagnosable traits, whether of a morphological or molecular nature. Species in this case are essentially defined using the patterns that are the culmination of the speciation process.

Templeton (1989) has combined pattern and process into a single concept, the Cohesion Species Concept (CSC). The CSC comprises a series of testable hypotheses that deal with diagnosability on morphological and molecular grounds, gene flow between populations, and hybrid infertility. In this paper we demonstrate how we determined the taxonomic status of the Damaraland Red-billed Hornbill (*Tockus erythrorhynchus damarensis*) using a collation of ideas from the above species concepts.

The African Red-billed Hornbill subspecies complex (*Tockus erythrorhynchus*) comprises four recognized subspecies and two additional undescribed variants (Kemp 1995). The North African Red-billed Hornbill (*T. e. erythrorhynchus*), the Southern African Red-billed Hornbill (*T. e. rufirostris*), the Damaraland Red-billed Hornbill in Namibia, and the West African Red-billed Hornbill (*T. e. kempi*) (Tréca and Erard 2000) exhibit morphological differences (Fig. 1) that allow reliable discrimination between them. The additional populations that occur in northern Kenya and southern Tanzania also show sufficient morphological differences for reliable discrimination (Kemp 1995; Fig. 1).

This study investigated whether two of the African Red-billed Hornbill subspecies, *T. e. rufirostris* and *T. e. damarensis*, should be considered independent species. These two subspecies have overlapping distributions in northern Namibia (Fig. 1), where hybridization occurs (Delport 2000b). Hybridization between divergent populations would define these two subspecies as a single species under the Biological Species Concept. However, hybridization does occur between several bird species (Grant and Grant 1992), some of which are not sister taxa. Therefore, combining hybridizing populations into a single species may not reflect the true evolutionary history of the group.



T. e. rufirostris

T. e. damarensis

T. e. erythrorhynchus

T. e. kempi

Tanzanian population

Northern Kenya population

Figure 1. Morphological characteristics of the subspecies of African Red-billed Hornbill. The subspecies of African Red-billed Hornbill exhibit morphological differences in both eye color and circumorbital skin color.

We address the problem of identifying the taxonomic status of hybridizing subspecies with divergent characters consistent within each of their geographic ranges. In order to address the question at hand we collected morphometric, behavioral, breeding and molecular data from populations of both subspecies. We demonstrate the advantages of collecting and interpreting such data without the *a priori* adoption of a species concept.

MATERIALS AND METHODOLOGY

Study areas

The two subspecies, *T. e. rufirostris* and *T. e. damarensis*, occur in sympatry over a narrow contact zone in northern Namibia (19º20′S, 17º21′E). *Tockus e. rufirostris* occurs northeast of this contact zone in forest savannah and woodland habitat, whereas *T. e. damarensis* occurs southwest of the contact zone in mopane and thornbush savannah. We collected breeding and molecular data within this contact zone and morphometric, behavioral and molecular data from allopatric populations of both subspecies.

Morphometric data collection and analyses

The purpose of the morphometric analysis was to determine if allopatric populations of both subspecies are diagnosable as distinct. We measured bill length, bill width and tarsus length (to the nearest 0.1 mm using a vernier caliper) from ten allopatric *T. e. damarensis* females, thirteen allopatric *T. e. damarensis* males, fifteen allopatric *T. e. rufirostris* females, and twenty-five allopatric *T. e. rufirostris* males. These morphometric measures were included in statistical analyses (i) that identified whether morphological characters were consistent within allopatric populations (PCA and ANOVA) and (ii) that indicated the reliability of the morphometric discrimination between the subspecies (ANOVA, Discriminant Function Analysis).

Vocalization data collection and analyses

The presence of species-specific signals is a notion common to several species concepts. We collected data that would determine if the courtship vocalizations of Red-billed Hornbills were significantly different between the two subspecies. We recorded twenty-nine *T. e. damarensis* vocalizations from four allopatric populations and sixteen *T. e. rufirostris* vocalizations from four allopatric populations. We digitized recorded vocalizations on an Apple Macintosh Power PC using Canary 2.1 (Cornell Laboratory of Ornithology) and generated independent sonograms for temporal and frequency measurements respectively (temporal: FFT = 256, frequency: FFT = 512). Twelve call variables were measured from the sonograms (Fig. 2, Table 1). The statistical analyses we conducted aimed (i) to determine if the calls of a single subspecies were consistent between geographically isolated populations (MANOVA) and (ii) to determine if there were significant differences between the calls of the two subspecies of Red-billed Hornbill (Discriminant Function Analysis and ANOVA).

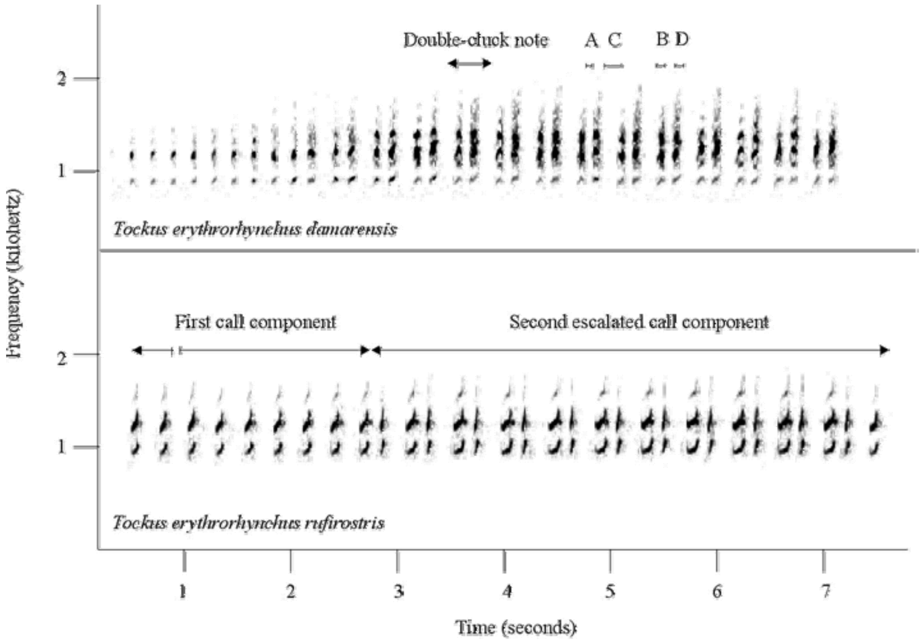


Figure 2. Sonograms of the courtship call of two subspecies of African Red-billed Hornbill, *Tockus erythrorhynchus damarensis,* and *Tockus erythrorhynchus rufirostris*. The call terminology used is represented, as are some of the variables used in the multivariate analyses. The first call component arrow is broken since the call starts earlier than represented.

Table 1. Variables measured from sonograms and used in multivariate analyses of recordings. Mean values and standard deviations (in parentheses) are presented (*T. e. r* = *Tockus erythrorhynchus rufirostris*, *T. e. d* = *Tockus erythrorhynchus damarensis*)

Mnemonic	Variable	Units	Taxon mean (standard deviation)	
DUR	Total duration of call	s	9.3 (2.4)	9.4 (2.4)
PRO_1	Proportion of call comprising the first component	%	46.5 (14.6)	48.3 (10.5)
PRO_2	Proportion of call comprising the second escalated component	%	49.8 (15.0)	51.8 (10.5)
MDUR_C1	Mean duration of all the notes in the first call component	s	0.053 (0.012)	0.054 (0.011)
MDUR_BC1	Mean duration between all successive notes in the first call component	s	0.159 (0.030)	0.162 (0.032)
N_C1	Number of notes in first call component	n	18.0 (7.35)	21.1 (9.3)
N_C2	Number of notes in the second escalated call component	n	34.7 (13.4)	31.2 (9.6)
A*	Mean duration within double-clucks	s	0.048 (0.010)	0.065 (0.009)
B*	Mean duration of the first notes of double-clucks	s	0.074 (0.015)	0.072 (0.005)
C*	Mean duration between double-clucks	s	0.114 (0.021)	0.114 (0.020)
D*	Mean duration of the second notes of double-clucks	s	0.063 (0.010)	0.066 (0.016)
C – A	The duration mean A subtracted from the duration mean C	s	0.064 (0.016)	0.052 (0.020)
B – D	The duration mean D subtracted from the duration mean B	s	0.016 (0.023)	0.004 (0.013)
C_RATE1	Rate at which notes are uttered in the first call component	notes.s^{-1}	0.043 (0.008)	0.045 (0.007)
C_RATE2	Rate at which notes are uttered in the second escalated call component	notes.s^{-1}	0.083 (0.034)	0.065 (0.012)
EM_FREQ	Emphasized frequency (frequency emitted at the loudest amplitude) of the call	Hz	1096.8 (182.2)	1037.3 (154.9)

* Measurements that were not included in the analyses, but were used to calculate some variables.

Breeding biology data collection and analyses

The frequencies of breeding pair combinations in the contact zone would indicate whether pair formation is non-random, which could be the result of failure of the communication system between heterospecifics. Frequency data of homo-and heterospecific breeding pairs (n = 117) were collected from the central 100 km of the contact zone. We only used the central 100 km since only here would *T. e. damarensis* and *T. e. rufirostris* individuals have approximately equal opportunities to mate with either of the subspecies. We proceeded with statistics that tested for randomness of mating (exact test, Haldane 1954 modified by Louis and Dempster 1987) and for asymmetry in hybrid pair formation (binomial probability test).

Deleterious effects of hybridization between recognized species can be manifested at any stage of the life cycle, however they are most likely to affect the early development or fertility of hybrid phenotypes (Moore and Koenig 1986). Therefore, we collected data that might identify any deleterious effects of hybridization between the Red-billed Hornbill subspecies. We monitored thirty-eight breeding boxes in the contact zone during the 1999 and 2000 breeding seasons. For each breeding female we recorded the subspecies of both sexes of the breeding pair, female mass after laying (with Salter 0-100 g, Salter 0-200 g and Pesola 0-300 g balances), female morphometrics, egg volume (calculated according to Hoyt's (1979) formula from egg breadth and height), clutch size and brood size. The statistical tests we conducted were intended to (i) identify if there were differences in breeding success between homo- and heterospecific pairs (ANOVA) and (ii) to determine if any of these differences were related to female fitness attributes (ANCOVA).

Molecular data collection and analyses

Finally, the occurrence or non-occurrence of gene flow between two populations is an important component to consider when determining taxonomic status. Therefore, we collected data to determine the extent of gene flow between the two African Red-billed Hornbill subspecies. We obtained genetic material from seven *T. e. rufirostris* individuals, four *T. e. damarensis* individuals, and four hybrid individuals in the northern Namibia contact zone, as well as genetic material from four allopatric *T. e. damarensis* individuals and four allopatric *T. e. rufirostris* individuals. We extracted genomic DNA from these samples, amplified the 5' domain of the mitochondrial DNA control region in a polymerase chain reaction and sequenced 627 base pairs of the control region (Delport 2000c). The statistical analysis we conducted (Excoffier's 1992 ϕ_{st}) aimed to determine the extent of gene flow between allopatric and sympatric populations of both subspecies of Red-billed Hornbill.

These morphological, behavioral, breeding biology and molecular data were used to determine the taxonomic status of the endemic Damaraland Red-billed Hornbill, *Tockus erythrorhynchus damarensis*, without the *a priori* adoption of a species concept.

RESULTS

Morphometric data

From the morphometric measurements it is clear that there are morphological differences between both males and females of the two subspecies (Table 2). Principal Component Analysis (PCA) of male and female morphometric data and the subsequent ANOVA of the first principal component yielded a highly significant result ($F_{3,\,59} = 34.31$, $P < 0.001$). Furthermore, the post hoc analysis indicated that significant differences occur between all taxonomic groups (female *T. e. damarensis*, female *T. e. rufirostris*, male *T. e. damarensis* and male *T. e. damarensis*) except between the male *T. e. rufirostris* and female *T. e. damarensis* groups. The discriminant function analysis of male and female morphometrics resulted in classification successes of 81% and 89% respectively.

Vocalization data

The statistical tests of vocalization indicated that call variables were consistent between geographically separated allopatric populations within both subspecies (MANOVA: Wilks' Lambda = 0.0073, Rao's R = 2.81, $df_1 = 84$, $df_2 = 191$, $P < 0.001$). However call variables were not consistent between populations of different subspecies (Delport 2000b). The forward-discriminant function analysis included five of the twelve variables in the discrimination model. Three of the five variables (C_RATE2, C-A and B-D) contributed significantly to the model ($F_{1,43} = 12.9$, $P < 0.001$; $F_{1,42} = 6.2$, $P < 0.05$; $F_{1,41} = 6.5$, $P < 0.05$, respectively). Moreover, a classification success of 85% was achieved in the forward-stepwise discriminant function analysis and an ANOVA of the canonical root scores indicated that the subspecies calls were significantly different ($F_{1,43} = 42.9$, $P < 0.001$).

Table 2. Mean values (and standard deviations in parenthesis) of bill length (BL), bill width (BW) and tarsus length (TAR) from allopatric males and females of both subspecies (*T. e. d = Tockus erythrorhynchus damarensis*, *T. e. r = Tockus erythrorhynchus rufirostris*). *n* = sample size

	Female allopatric *T.e.d*	Female allopatric *T.e.r*	Male allopatric *T.e.d*	Male allopatric *T.e.r*
BL	74.6 (2.9)	62.8 (4.0)	89.1 (3.0)	86.02 (4.2)
BW	19.2 (0.7)	17.4 (0.2)	21.1 (1.2)	20.6 (0.9)
TAR	38.2 (3.1)	35.3 (0.2)	40.5 (1.2)	40.6 (1.8)
n	10	15	13	25

Breeding biology data

The observed breeding pair combinations indicated that hybridization in the contact zone is not symmetrical (Table 3; Delport 2000b). Observed breeding pair combinations were significantly different from that expected in a random mating population ($P = 0.000367$). Moreover, there was a significantly larger proportion of *T. e. rufirostris* males in heterospecific pairs than *T. e. rufirostris* females (k = 34, n = 53, p = 0.5, $P < 0.05$, Delport 2000b).

The statistical tests of differences in clutch size, brood size and hatching success indicated that only hatching success was significantly different between homo- and heterospecific pairs ($F_{1,36} = 7.03$, $P < 0.05$, Delport 2000b). Hatching success was lower in hetero- than in homospecific pairs (homospecific = 98%, heterospecific = 90%). Furthermore, hatching success was still significantly different when female fitness attributes were included as covariates ($F_{1, 36} = 4.33$, $P < 0.05$, Delport 2000b).

Molecular data

Gene flow between allopatric *T. e. damarensis* and allopatric *T. e. rufirostris* is significantly lower than that expected at random (Fig. 3).

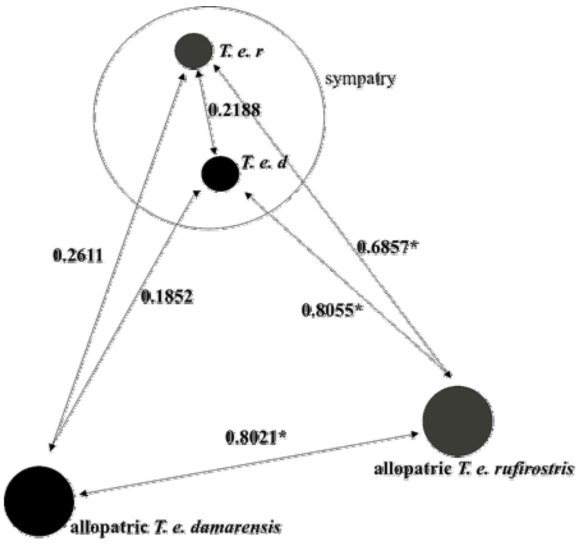


Fig. 3**.** Gene flow between populations of *T. e. damarensis* and *T. e. rufirostris*.
Values represented are Excoffier's 1992 ϕ_{st}. Large values indicate low levels of gene flow and similarly small values indicate high levels of gene flow. An asterisk after the ϕ_{st} value indicates significant differences between populations at the 95% level (based on 1000 permutations). (*T. e. d = Tockus erythrorhynchus damarensis*, *T. e. r = Tockus erythrorhynchus rufirostris*).

Populations of allopatric and sympatric *T. e. damarensis* are not significantly different, whereas allopatric and sympatric *T. e. rufirostris* were significantly different (Fig. 3). This result was expected since a larger geographic distance separates the allopatric and sympatric *T. e. rufirostris* populations than the allopatric and sympatric *T. e. damarensis* populations. Gene flow between allopatric *T. e. damarensis* and sympatric *T. e. damarensis* is greater than between the former and sympatric *T. e. rufirostris* (Fig. 3), even though the sympatric populations of both subspecies are separated from the allopatric *T. e. damarensis* by an equivalent distance. Finally, gene flow between the two subspecies within the contact zone is less than that between the allopatric and sympatric *T. e. damarensis* populations, even though the opportunity for random mating exists within the contact zone.

Table 3 Composition of breeding pairs from the central 100km of the hybrid zone in northern Namibia. These data were used in the exact test of randomness of mating and in the calculation of hybridization asymmetry between the sexes. O = observed number of each pair combination, E = expected number of each pair combination based on the number of individuals of each subspecies observed in the contact zone. Blocked cells indicate the pure breeding pair combinations of both subspecies

	Male *T. e. r*		Male hybrid		Male *T. e. d*		
	O	E	O	E	O	E	
Female *T. e. r*	37	34.5	3	3.5	16	25.5	56
Female hybrid	10	3.5	0	0.36	0	2.6	10
Female *T. e. d*	24	25.5	0	2.6	27	18.9	51
Total pairs							117

DISCUSSION

Morphological variation

It is clear that there is considerable morphological variation between the subspecies of Red-billed Hornbill (Fig. 1). Delport (2000b) has determined that there is far less morphological variation within allopatric populations of each of the two subspecies we have considered. Moreover, the two subspecies considered here exhibit significant differences in the morphometric characters we measured.

Vocalization variation

The vocal characteristics of the subspecies (i) are consistent between populations of the same subspecies and (ii) are consistently different between populations of different subspecies. In addition, the Discriminant Function Analysis classified vocalizations with 85% success. The misclassifications are probably the result of hybridization in the contact zone (Delport 2000b). When populations close to the contact zone were excluded from the analysis a much higher classification success of 95% was achieved (Delport 2000b). It is clear that there are significant differences in the calls of the two subspecies of Red-billed Hornbill considered. However, whether these differences play a role in communication between individuals remains to be tested.

Breeding biology

It is thought that mating between species may result in the reduced fitness of hybrids (Mayr 1963; Dobzhansky 1970; Butlin 1989). There is reduced fitness in heterospecific pairs of Red-billed Hornbill. This reduced fitness is most likely the result of some incompatibility in breeding between the two subspecies. Hybrid pair formation is less than expected and there exists a predominance of pure pairs of both subspecies. In addition, the formation of hybrid pairs is asymmetrical with more *T. e. damarensis* female -*T. e. rufirostris* male pairs occurring than vice versa, a result that was statistically significant in the binomial probability test. This asymmetry is probably the result of communication failure within one of the two types of hybrid pair combinations, rather than the result of Reinforcement (Dobzhansky 1940) and selection against hybridization in the contact zone. However this notion remains to be tested experimentally.

Gene flow between subspecies

Gene flow between allopatric populations of *T. e. rufirostris* and *T. e. damarensis* is limited, although this result is expected on the basis of distance between the allopatric population sample localities. However, there are lower levels of gene flow and greater sequence divergence between allopatric *T. e. damarensis* and sympatric *T. e. rufirostris* than between allopatric and sympatric *T. e. damarensis* populations. Gene flow between subspecies within the contact zone is less than that between allopatric and sympatric populations of a single subspecies that are separated by approximately 400 km. These observations suggest there is some barrier to gene flow between the subspecies in the contact zone.

CONCLUSIONS

We have determined that there are consistent morphological differences between allopatric populations of these two subspecies. Furthermore, we have determined that there is reduced gene flow of mtDNA between *T. e. rufirostris* and *T. e. damarensis* in the contact zone. In addition, molecular characters that are consistent within allopatric populations of a single subspecies are not shared between subspecies (Delport 2000c). Diagnosability on the grounds of both morphological and molecular data provides support for the assignment of separate species under the Phylogenetic Species Concept (Cracraft 1989). Other species concepts such as the Biological Species Concept (Mayr 1963; Dobzhansky 1970), the Recognition Species concept (Paterson 1985) and the Cohesion Species Concept (Templeton 1989) define species in terms of processes and not patterns as in the Phylogenetic Species Concept (Cracraft 1989). We have determined that allopatric populations of *T. e. damarensis* and *T. e. rufirostris* have vocalizations that are consistently distinct from one another. These vocalizations may therefore be a conspecific signal that has the fortuitous consequence of the prevention of mating between heterospecifics that result in reduced gene flow between the two subspecies in the zone of sympatry. Species-specific vocalizations would provide support for the identification of independent species under both the Cohesion Species Concept (Templeton, 1989) and the Recognition Species Concept (Paterson 1985), yet the Biological Species Concept further requires that there be no mating between heterospecifics.

The two subspecies of Red-billed Hornbill considered hybridize (Delport 2000b). However, it is well documented that several avian species hybridize (Grant and Grant, 1992). Ehrlich and Raven’s (1969) modification of the Biological Species Concept includes a balance between gene flow and other evolutionary forces in the definition of a species. One of these evolutionary forces or effects of hybridization in the Red-billed Hornbills is the reduced fitness of heterospecific pairs. In the context of Ehrlich and Raven’s (1969) version of the Biological Species Concept, the two subspecies of Red-billed Hornbill would be considered independent species. Therefore subspecies that have morphological, behavioral and genetic differences combined with reduced heterospecific gene flow and hybridization incompatibility are true species under any of the above species definitions.

The multidisciplinary approach used in this study has enabled us to determine the taxonomic status of the Damaraland Red-billed Hornbill, *Tockus erythrorhynchus damarensis*, without first adopting a species concept. One advantage of this approach is that no discussion of the speciation process is necessary even though the multidisciplinary approach does allow one to consider the factors that may contribute to the process of speciation. Moreover, data collection under this multidisciplinary approach is not limited by a particular species concept, resulting in a better understanding of the taxonomic group. However, the question of how to begin to collect data for a multidisciplinary approach needs to be addressed.

In our opinion, a morphological, behavioral and molecular analysis is required before embarking on an analysis of breeding biology. The reasons for this are twofold. Firstly, a morphological, behavioral and molecular analysis would determine whether the particular taxa are diagnosable as distinct, in the sense of the Phylogenetic Species Concept (Cracraft 1989). Therefore, this preliminary analysis would determine if further research were necessary or sensible. Secondly, the logistics of a good analysis of breeding biology is both time consuming and intensive and would be wasteful if the taxa under consideration were not diagnosable.

Another problematic issue that may arise is the non-congruence of results of the several data sources. In the analyses of the Damaraland Red-billed Hornbill the several sources of data were congruent, in that each data set demonstrated that the subspecies had species-specific characteristics. In our opinion, the occurrence of reduced gene flow between taxa that occur sympatrically and non-random breeding of these taxa in sympatry hold the most weight in these analyses. Therefore, in light of non-congruence between data sets we advocate the placement of most weight on these data sources.

The purpose of this manuscript is not to ignore species concepts, whether pattern- or process-orientated. Rather we wish to demonstrate that taxonomists, aviculturalists, zoo curators and conservationists need to adopt a similar approach to determining taxonomic status, whilst evolutionary biologists continue to disentangle the intricacies of the speciation process.

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Ecotourism on Yakushima Island, southern Japan: an idea for the sustainable use of nature in a World Heritage site

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Abstract Yakushima Island (ca. 503 km^2) is one of the UNESCO World Natural Heritage sites, and is widely known as an island having the highest mountains in the Kyushu district, southern Japan. The flora of the island contains 1,136 species of seed plants and 388 species of ferns and fern allies, including 45 endemic species and 31 endemic varieties. The island was originally covered by several types of temperate rainforests, but has been logged by the government since the 16th century. In the 1970s, island residents and researchers protested against the Japanese Forestry Agency to gain complete protection for the conservation of the vertical distribution of natural vegetation from sea level to 1,800 m.

As the preciousness of the island as a nature reserve is widely recognized, especially after its inclusion as a World Natural Heritage site in 1993, local government and the private sector began to realize need for development which is oriented to the sustainable use of natural resources. One of the possible eco-oriented industries is ecotourism. The ecotourism industry in Yakushima is now being developed and is expected to increase future opportunities for employment. In the future, ecotourism should change from “ecotours” in which tourists merely enjoy experiences in nature, to an “ecomuseum” experience, where they learn biodiversity and ecology as well as the tradition and way of life of local people who have been living with nature.

The problem is how to assure the sustainability of ecotours. Training courses for tour guides on safety supervision, knowledge about natural history, and environmental ethics are required. Moreover, monitoring changes to areas targeted by ecotours needs to be done properly. In such operations, community-based programs cooperating with national and international networks should be stressed. An idea to realize such a network that costs less and is utilized more was to build a virtual museum in a website, called the Yakushima Open Field Museum.

INTRODUCTION

Yakushima Island is located 60 km south of Kyushu, one of the four main islands in Japan. It is a roughly circular island with a circumference of ca. 132 km, and its area is ca. 503 km^2 (Fig. 1). This island is known for its mountainous terrain which features seven high peaks over 1,800 m in height, including Mt. Miyanoura (1,935 m), the highest peak in the Kyushu district, which comprises Kyushu and surrounding islands

Yakushima was originally covered by several types of temperate rainforests, including the source of the extremely expensive wood Yakusugi (*Cryptomeria japonica*, Taxodiaceae, especially those aged older than 1,000 years). The biggest Yakusugi, known as the Jomonsugi, is 25.3 m in height, 5.22 m in diameter, and 16.4 m in trunk circumference, and it is variously estimated to be 2,600 to 7,200 years old. These beautiful Yakusugi woods, however, have been logged by local and national governments since the 16th century.

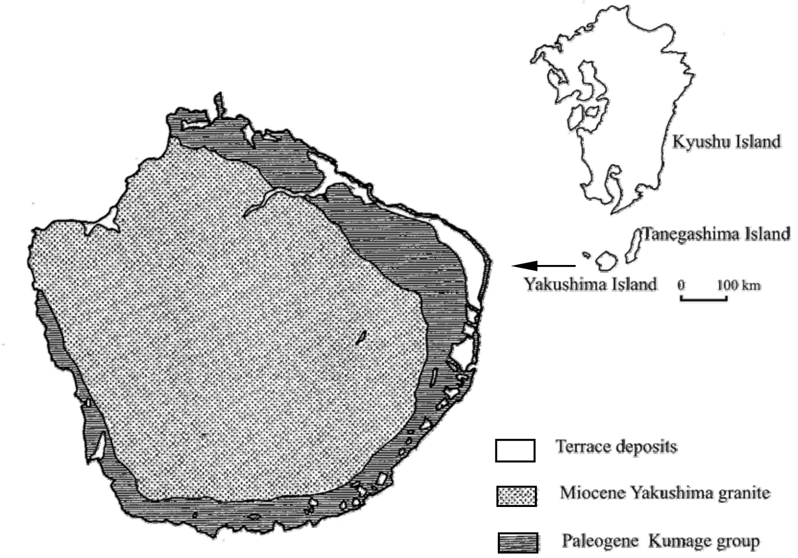

Figure 1. Geological sketch map of Yakushima Island.

For more than 300 years, logging was the main industry on the island. As the area where the natural timber could be easily harvested became smaller because of overuse, the logging industry declined. Accordingly, the population of the island also decreased. Like most isolated Japanese islands, young people cannot find any jobs on the island and leave for large cities in central Japan.

In 1993, Yakushima Island was added to the list of UNESCO World Natural Heritage sites. Since then, the forest in Yakushima began to attract many tourists, showing that ecotourism could become a major industry on this island. This paper intends to show the value of nature in Yakushima and the possibility of ecotourism as a sustainable use of nature.

NATURAL ENVIRONMENT AND VEGETATION

Although Yakushima Island has high mountains, it is not volcanic. Yakushima has a base of sedimentary rock, including sandstone and shale, which is distributed around the island. This stratum is called the Kumage group, accumulated from deposits of sand and mud on the ocean floor 60 million years ago. About 14 million years ago, granite magma intruded the Kumage group stratum. Now the greater part of the island is comprised of granite, and in particular the central area (Fig. 1). The subterranean granite rose at the speed of about one-meter every thousand years (Iwamatsu and Ogawauchi 1984).

Heavy rainfall is a feature of the climate of Yakushima (Fig. 2). The coastal area annually receives 4,200 mm precipitation on its eastern side and 2,600 mm on its western side, respectively. This is because warm low pressure fronts and typhoons pass over the island on winds from southeast, bringing heavy precipitation to the southeast and eastern perimeters of the island (Eguchi 1984). Rainfall changes dramatically according to the slope. The lee side of the wind is usually much drier. More than 8,000 mm of rain per annum is recorded from mountainous areas. The annual average temperature is 19.4^{o}C and the coldest monthly average temperature is 11.6°C in the coastal areas, so that there is no frost and rarely snow along the coast. However, the summit suffers cold weather, the estimated annual average temperature is ca. 8°C and the coldest monthly average temperature is -1°C.

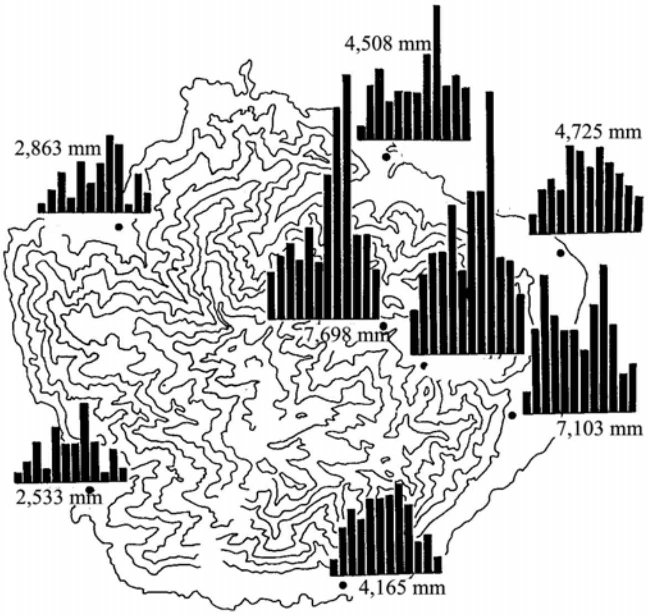

Figure 2. Variation of monthly precipitation (1982) in Yakushima Island. Numerals show the annual precipitation at each site.

This distinctive topography has created a wide climatic range on the island, from subtropical in the coastal area to cold mountainous areas. There are two typical types of natural forest, a warm temperate evergreen broad-leaved forest at lower altitudes (100 m - 800 m) and a cool temperate mixed coniferous and broad-leaved forest at high altitudes (1,200 m-1,600 m) (Fig. 3). The forest in lower altitudes below 800 m is dominated by *Dystlium racemosum, Quercus salicina, Castanopsis cuspidata* var. *sieboldii*, and Lauraceae species. At higher altitudes over 1,200 m the forest is dominated by *Cryptomeria japonica* and *Tsuga sieboldii* with broad-leaved species in the understory. Besides these two forest types, two transitional zones are recognized: subtropical to warm temperate (0 m-100 m) and warm temperate to cool temperate (800 m – 1,200 m). Over 1,600 m above sea level, wind-blown, shrubby vegetation with dwarf bamboo (*Pseudosasa owatarii*) covers the summit area (Kimura, Yoda 1984).

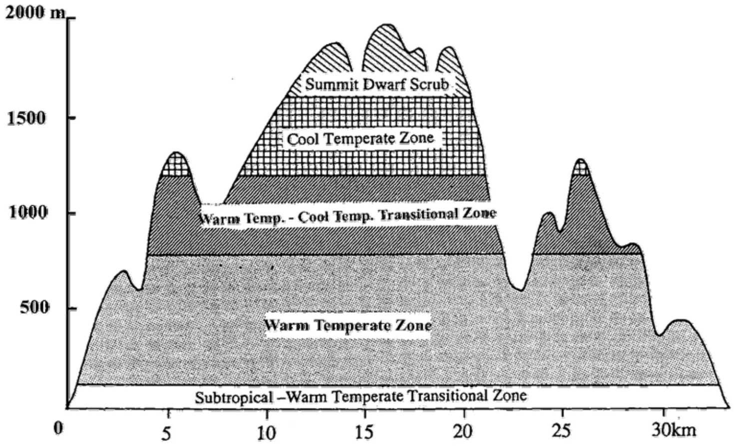

Figure 3. Vertical distribution of the main forest types of Yakushima Island.

ENDEMIC PLANTS AND WILDLIFE

On Yakushima, 1,136 species of seed plants (angiosperms and gymnosperms) and 388 spp. of ferns and fern allies are recorded (Mitsuta and Nagamasu 1984), meaning that more than one-fifth of the Japanese flora occurs on this island. Also, 45 endemic species and 31 endemic varieties are found (Yahara *et al*. 1987). This number of endemic plants is extraordinary for a continental island which was once connected to the main islands of Japan.

Yakushima has only 11 species of mammals except for bats and three of them are subspecies of Kyushu Island’s dwellers: the Yakushima monkey (*Macaca fuscata yakui*), Yaku deer (*Cervus nippon yakushimae*), and Yakushima weasel (*Mustela sibirica sho*) (Morita 1984). These three subspecies are much smaller in body size than those occurring in the main islands of Japan.

In the Japanese Archipelago, Yakushima occupies a special geographical location (Fig. 4). On the island of Honshu in central Japan, there are high mountain ranges over 3,000 m above sea level. However, between Kyushu and Taiwan, no mountains over 1,800 m exist, except for those on Yakushima. During the Ice Ages, Kyushu and Yakushima were connected at least three times during periods of cooler climate, at which time many plants and animals could have entered the island (Fig. 5; Kizaki 1980). As the sea advanced when the climate became warmer, populations of plants and animals were isolated from the main island populations. In all islands without high mountains, plants adapted to cool climates have disappeared, but populations on Yakushima survived on its high mountains and have speciated to a certain degree. The typical cases of subspecies formation in Yakushima Island are those which have sibling species in northern Japan and are assumed to have originated and become isolated from the northern populations.

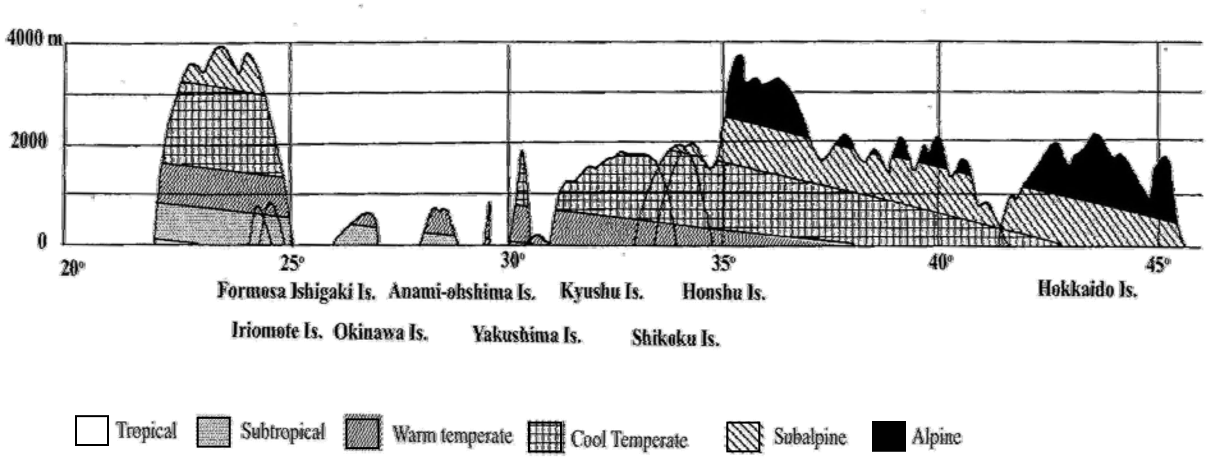

Figure 4. Horizontal and vertical distribution of main vegetations types in Formosa and the Japanese Archipelago.

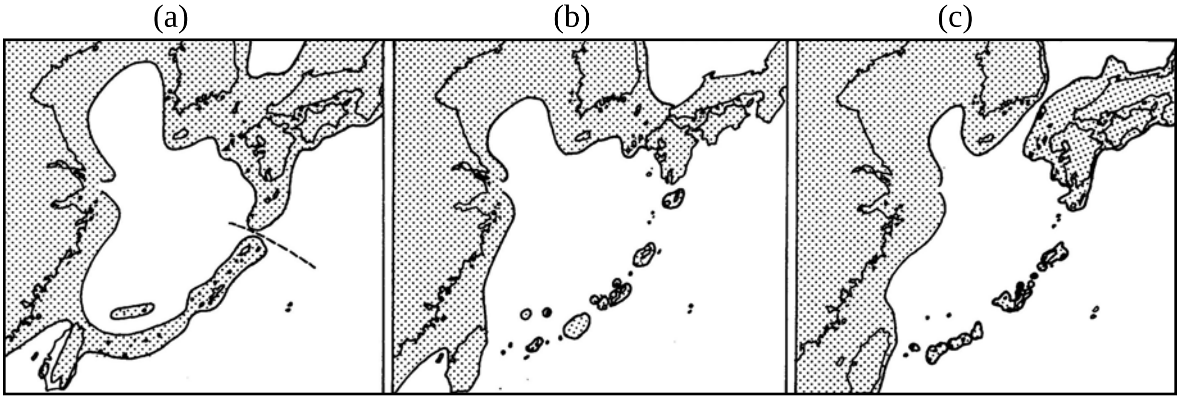

Figure 5. Paleogeography in southern Japan. a) early Pleistocene (1.5 million years ago); b) middle Pleiocene (0.5 million years ago); c) late Pleiocene (20 thousand years ago).

Volcanic ash and pyroclastic flows are believed to have covered almost all of Yakushima 6,300 years ago because of the eruption of the Kikai Caldera which is situated 40 km from the island (Iwamatsu and Ogawauchi 1984). Some researchers have argued that all organisms in the island were killed by heat of 300 - 400°C. However, the degree of speciation of the Yakushima flora and fauna suggests that small populations of plants and animals must have survived even through this volcanic catastrophe.

HISTORY OF LAND MANAGEMENT

Archeological evidence shows that people inhabited Yakushima between 2000-1000 BC. According to old documents, a deep and open river mouth was used as a stopover for vessels making the long distance voyage from mainland China to Japan since the 7th century. At that time, local people survived mainly on fishing. People cut trees only when needed in villages for construction materials and firewood, and land use was limited to the coast.

In the 16th century, the Daimyo (Lord) of the Shimazu family who governed in southern Kyushu conducted a survey of Yakusugi as potential material for building. At that time, they concluded that it was too difficult to transport the wood from the island to central Japan. A hundred years later, the Shimazu established the Yakusugi harvest system in the middle of the 17th century. They found that using the timber for making Hiragi (roof tiles) made transport much easier. Hiragi were cut into pieces 48 cm long, 10 cm wide, and 7 mm thick. Yakusugi contains a great deal of resin and so does not decay for a long time, making it an ideal material for roofing. People of Yakushima Island had to pay the tax per capita by roof tiles instead of rice as in other districts in Japan. Therefore, only the old Yakusugi with a hollow inside or a twisted trunk survived because these trees were not suitable for roof tiles. This harvesting system continued until the Meiji era of the 19th century.

After the Meiji Restoration, 98% of Yakushima Island was designated as state-owned in 1874. As a result, people were banned from using timber and firewood as they used to. A long struggle ensued for the rights of possession. In 1921 the national government established the General Principles of Yakushima National Forest Administration and finally released parts of the state-owned forest from government control. Known as the Yakushima Constitution, the Principles guaranteed livelihood for the local people.

However, logging by the government continued. Especially during World War II, a huge amount of timber was logged and exported to the main islands. After World War II, logging still continued. After 1956, when the motorized saw was introduced to the island, both

Yakusugi and broad-leaved trees were completely logged in almost 80% of state-owned forests.

In 1964 38% of Yakushima was gazetted as National Park, but the Totally Protected Area included only 12% of the island. At this time, the Japanese Ministry of Welfare which managed National Parks in Japan intended to extend the Totally Protected Area in Yakushima. However, very strong resistance from the Japanese Forestry Agency made the Ministry of Welfare reverse their decision.

In the 1970s, resident people and researchers protested against the Forestry Agency to secure Totally Protected Area status for more areas, including a vertical distribution of natural vegetation from sea level to 1800 m (Fig. 6). In 1987, Yakushima was listed in the MAB (Man and the Biosphere) program of UNESCO, and the value of nature began to be recognized nationwide.

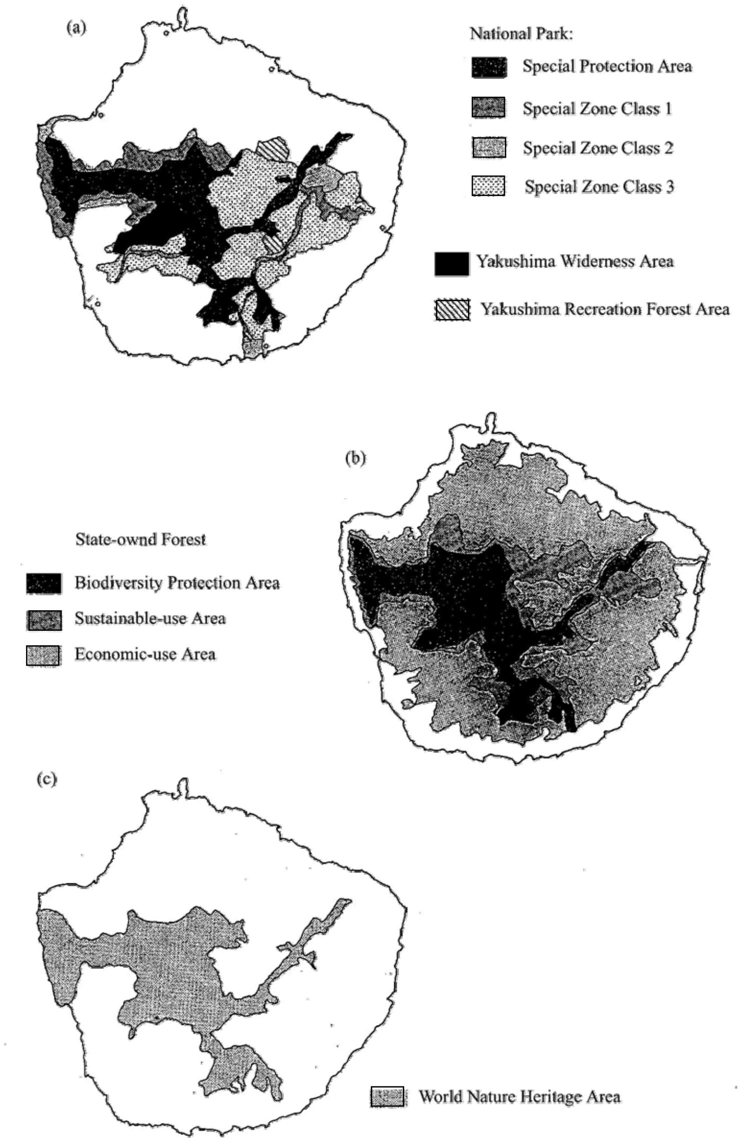

Figure 6. Zoning of a) National Park, b) State-owned Forest and c) World Heritage Area.

As the logging industry declined because the area where natural woods could be harvested became smaller, the population of the island also declined. In 1930 the population numbered 17,462 and it increased up 24,010 in 1955 when the logging of Yakusugi was at its peak. Afterward, it began to decrease, especially between 1955 and 1965, when the population decline was 6,634 within 10 years (Fig. 7).

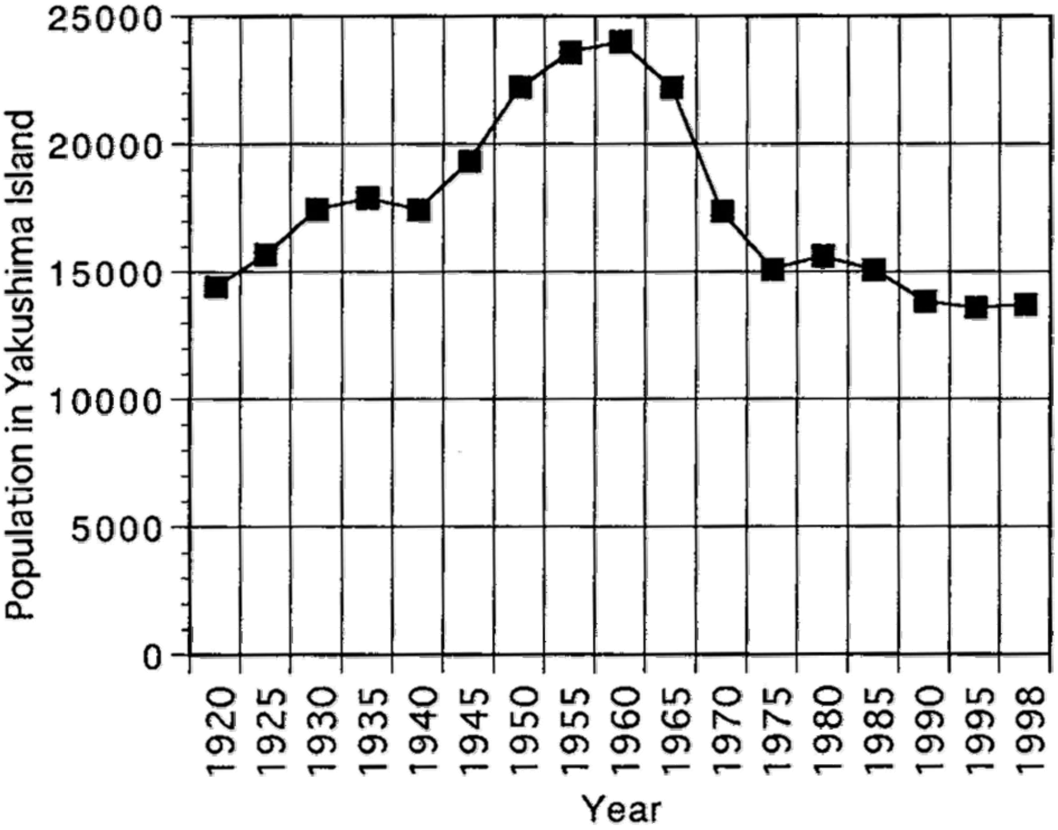

Figure 7. Change in population in Yakushima Island from 1920 to 1998.

WORLD HERITAGE AND ECOTOURISM

Out of the 505 km^2 of Yakushima Island, 107.5 km^2 was set aside as a World Natural Heritage site in December 1993. Reasons for inclusion include its unique forest flora, Yakusugi of several thousands of years of age, and the intact vertical distribution of natural vegetation. As the preciousness of the island as a nature reserve became widely recognized, local government and the private sector began to realize the importance of development which is oriented to the sustainable use of natural resources.

One possible environment-oriented industry is ecotourism. The World Heritage Center of UNESCO mentions that the new industry of ecotourism should be promoted (1) to educate youth and the general public in appreciation of World Heritage, (2) to increase the employment opportunities in World Heritage sites, and (3) to make the people who live in the sites realize the importance of conserving World Heritage.

"Ecotourism" is defined as one of the sustainable uses of nature, and each activity based on the idea of ecotourism can be called an "ecotour". The principles of ecotourism are (1) that tourism cannot be sustainable without the sustainable use of natural resources, (2) the sustainable use of the natural resources cannot be achieved without the participation of local people and (3) the participation of local people cannot be expected without economic motivation. The ecotourism industry in Yakushima is now under development and is expected to create opportunities for greatly increased employment. The first private company for ecotourism on Yakushima was established in July 1993 and the second one in 1995. Now more than 40 people are engaged as tour guides.

Eco-tourism activities include forest walks, water sports such as rapids kayaking and diving, and the interpretation of Yakushima's natural, historical, and cultural heritage. In 1999, the Yakushima Guide Association was launched to exchange ideas and information among independent tour guides.

With renewed economic opportunities, the population once again began to increase. It was 13,850 in 1990 and 13,593 in 1995, but it increased a little to 13,723 in 1998 after the island's listing as a World Heritage site. Young people could remain on the island to engage in jobs, and many people who admire nature began to immigrate from the main islands of Japan. An increasing or even stable population is quite uncommon among the 200 or so inhabited islands south of Kyushu.

VIRTUAL MUSEUM MEETS ECOTOURISM

The problems for ecotourism are how to maintain the quality of tour guides and how to monitor and assure the sustainability of ecotours. A training course for tour guides on safety supervision, knowledge about natural history, and environmental ethics is required. Moreover monitoring changes to the areas targeted by ecotours is needed, with the appropriate response where needed – for example, limiting the number of visitors if overuse is predicted. In such operations, community-based programs in cooperation with national and international networks are quite important.

In the near future, we think that ecotourism should be changed from "ecotours" in which tourists merely enjoy experiences in nature, to an "ecomuseum" approach, where they learn biodiversity and ecology as well as the traditions and lifestyles of local people who have lived with nature. The ecomuseum concept is an idea developed in the 1970s in France, of which the aim is sustainable development based on the conservation of nature and culture. Traditionally museums have three roles: collection, education and research. But the ecomuseum minimizes the activity of collection and instead utilizes and conserves the materials while using them in a living state.

An ecomuseum without a large collection does not need a large building. A sizeable museum with a big building requires huge amounts of money not only for the building but also for hiring researchers and for maintenance. Moreover, such a large museum can create a considerable environmental burden. We started the virtual Yakushima Open Field Museum in 1999. The Yakushima Open Field Museum is a non-profit organization which is operated by volunteer researchers. The web-based museum is totally virtual, (http://www.dab.hi-ho.ne.jp/yakuofm/index.html), but we aim to list 200 volunteer researchers, not only natural scientists but social scientists as well. Most of the volunteer researchers have their jobs in national and private universities and museums, and are specialists on a particular aspect of Yakushima Island. Volunteer researchers just put their name and specialty on the list and engage in some activities of a museum, such as to answer the questions which come from visitors via the internet.

In addition, volunteer researchers can teach their specialty directly to people. We have already conducted three Yakushima Field Science Courses operated by volunteer researchers for international and national college students. The course contains several sub-courses: field primatology and ornithology, research on forests and botany, relationships between nature and people, and so on.

When the ecotour is combined with an ecomuseum, tourists as well as tour guides can be educated through the Yakushima Open Field Museum. Tourists can form an image about Yakushima before visiting and tour guides can obtain the latest information and discoveries from researchers. The Yakushima Open Field Museum provides opportunities for learning not only for tourists, but also for people who live on the island. People in Yakushima live very close to nature and almost every activity affects and can be affected by nature, such that they often need some suggestions from specialists on topics including natural energy, waste recycling, organic agriculture, and restoration of natural vegetation. Volunteer researchers can give advice to people who need them via the internet. The Yakushima Open Field Museum can be a directory to search for specialists on any particular field pertaining to Yakushima Island. The Japanese Ministry of Education, Science and Technology decided to provide internet facilities for every primary and junior high school by 2003 all over Japan. School pupils will be able to access the Yakushima Open Field Museum much more easily. We have begun to negotiate with the local government to provide internet facilities for each village and to have a training course on computer literacy for villagers.

Yakushima provides an interesting case study for the conservation of priceless natural heritage through sustainable resource use and prudent economic activity. While early industries on Yakushima tended to deplete the resource base upon which the island's residents depended, ecotourism now opens the possibility of conserving and perhaps even enhancing the same resources, while providing ever-increasing economic opportunities for the island's residents. The Yakushima Open Field Museum was a concept designed to extend an awareness of the island's heritage to both residents and those from beyond Yakushima's shores who wish to learn more about this unique World Heritage site. The Open Museum concept coupled with ecologically sensitive development could possibly help resolve the traditional dichotomy between conservation of a precious habitat and the interests of local stakeholders.

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APPENDIX I: LIST OF COUNTRIES OF PARTICIPANTS OF THE INTERNATIONAL HORNBILL WORKSHOPS

	Country	No. participants		
		1st International Asian Hornbill Workshop (6-10 April 1992)	2nd International Asian Hornbill Workshop (10-18 April 1996)	3rd International Hornbill Workshop (9-18 May 2001)
1	Austria	-	1	1
2	Brunei Darussalam	-	1	1
3	Cambodia	-	1	1
4	Germany	1	-	2
5	India	1	1	4
6	Indonesia	1	2	1
7	Japan	4	7	8
8	Lao PDR	1	1	-
9	Malaysia	3	5	2
10	Myanmar	-	1	-
11	Nepal	1	1	-
12	Singapore	1	9	7
13	South Africa	1	3	4
14	Spain	-	2	2
15	Sri Lanka	1	1	2
16	Thailand	25	85	107
17	The Netherlands	1	-	-
18	The People's Republic of China	2	-	1
19	The Philippines	2	-	-
20	United States of America	1	8	9
21	United Kingdom	-	1	2
22	Vietnam	1	-	-
23	Zimbabwe	-	-	1
	TOTAL	**47**	**130**	**155**

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APPENDIX III. PAPERS PRESENTED AT THE 3RD INTERNATIONAL HORNBILL WORKSHOP PUBLISHED IN INTERNATIONAL JOURNALS

No.	Title and Journal	Author (s)
	Ostrich – Journal of African Ornithology 74: 39-47 (2003)	
1.	Biogeographical zonation of African hornbills and their biotic and geographic characterizations	R Munoz, R Real, J Olivero, A Marqiez, J Guerrero, S Barcena, J Vargas
	Bird Conservation International 14: S5-88 (2004)	
2.	The status and conservation in hornbills in Cambodia	T Setha
3.	Habitat fragmentation in north Thailand: a case study	A Pattanavibool, P Dearden, U Kutintara
4.	Size matters: the effects of forest fragmentation and resource availability on the endemic Sumba Hornbill *Aceros everetti*	A Sitompul, M Kinnaird, T O′Brien
5.	Nest-site selection and nesting success of three hornbill species in Arunachal Pradesh, north-east India: Great Hornbill *Buceros bicornis,* Wreathed Hornbill *Aceros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris*	A Datta, G Rawat
6.	Foraging characteristics of an assemblage of four Sumatran hornbill species	Y Hadiprakarsa, M Kinnaird, A Msimanga
7.	Breeding biology of Southern Ground Hornbill *Bucorvus leadbeateri* in Zimbabwe: impacts of human activities	A Msimanga
8.	Fruit preferences of Malabar Pied Hornbill *Anthracoceros coronatus* in Western Ghats, India	P Balasubramanian, R. Saravanan, B. Maheswaran
9.	Characteristics of hornbill-dispersed fruit in a tropical seasonal forest in Thailand	S Kitamura, T Yumoto, P Poonswad, P Chuailua, K Plongmai
	Ornithological Science 3: 99-112 (2004)	
10.	Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand	P Poonswad, A Tsuji, N Jiratkavi
	Biological Conservation 122: 385-393 (2005)	
11.	Comparison of cavity modification and community involvement as strategies for hornbill conservation in Thailand	P Poonswad, C Sukkasem, S Phataramata, S Hayeemuida, K Plongmai, P Chuailua, P Thiensongrusamee, N Jirawatkavi

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