ALTITUDINAL DISTRIBUTION OF FRUIT BATS (PTEROPODIDAE) IN LORE LINDU NATIONAL PARK, CENTRAL SULAWESI, INDONESIA

IBNU MARYANTO¹, MUHAMAD YANI², SITI NURAMALIATI PRIJONO¹, SIGIT WIANTORO^{1*}

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¹Museum Zoologicum Bogoriense-LIPI, Jl. Raya Jakarta-Bogor KM. 46, Cibinong, Bogor, Indonesia; Corresponding author, E-mail: wiantoro@gmail.com
²Jl. Gotong Royong, Pajeruk Lombok Mataram-NTB, Indonesia.

ABSTRACT - Between March 2000 and July 2001, we studied the distribution of fruit bats in Lore Lindu National Park, Central Sulawesi, Indonesia. Vegetation types and elevation belts between 350 and 2100 m a.s.l. were combined to characterize 17 habitat types, which were surveyed using standardized mist netting. Sixteen species of Pteropodidae (fruit bats) were identified in the park. Using an Euclidian distance dissimilarity index (EDD), the 16 species were clustered into four main groups. The results of cluster analysis were supported by Principle Component Analysis, PC1 and PC2 accounting for 71.94% and 27.39% of total variance, respectively. We suggest that PC2 primarily implies an altitudinal gradient, while PC1 is probably related to the gradient of humidity.

Key words: Chiroptera, elevation, diversity, habitat preferences

RIASSUNTO - *Distribuzione altitudinale dei pipistrelli frugivori (Pteropodidae) nel Par-co Nazionale di Lore Lindu, Sulawesi, Indonesia*. Tra Marzo 2000 e Luglio 2001, abbiamo studiato la distribuzione dei pipistrelli frugivori del Parco Nazionale di Lore Lindu (Sulawesi, Indonesia). Il tipo di vegetazione e le fasc di quota individuate tra 350 e 2100 m s.l.m. sono state combinate ad identificare 17 habitat, che sono stati monitorati tramite mistnets. Sono state identificate 16 specie, che, tramite analisi dei cluster (EDD), sono state raggruppate in 4 gruppi principali. I risultati ottenuti sono stai confermati dall'Analisi delle Componenti Principali, per la quale PC1 e PC2 hanno spiegato, rispettivamente, il 71,94% e 27,39% della varianza complessiva. Riteniamo che PC2 sia legata ad un gradiente altitudinale, mentre PC1 probabilmente riflette un gradiente di umidità.

Parole chiave: Chiroptera, altitudine, diversità, preferenze ambientali

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INTRODUCTION

Sulawesi Island (Indonesia) retains high levels of endemism, particularly for mammals. As much as 30 % of the island's rats are endemic (Carleton and Musser 1984; Musser 1991), and even for more mobile mammals, such as pteropodids, levels of ca. 10% have been reported (Maryanto and Higashi in prep.). Furthermore, Sulawesi has been divided into several areas based on the distribution of endemic mammals, for instance Muridae (Musser and Dagosto 1987; Corbet and Hill 1992), squirrels (Musser et al. 2010), macaques (Fooden 1969; Supriatna 1996) and tarsiers (Shekelle and Laksono 2004), but not for Chiroptera. The geological history of the island probably played a major role in determining the high endemism rates of Sulawesi (Shekelle and Laksono 2004).

Sulawesi and neighbouring smaller islands are known to be rich in pteropodid (fruit bat) species. Bergmans and Rozendaal (1988) reported 21 species of Pteropodidae in Sulawesi and Sangihe/Sangir islands, to which, in their checklist of Indonesian mammals, Suyanto et al. (2002) added six further species, recorded on Selavar and Talaud islands (Acerodon humilis K. Andersen, 1909: Cvnopterus minutus Miller, 1906; C. sphinx (Vahl, 1797); Pteropus speciosus K. Andersen, 1908; P. pumilus Miller, 1911). A new species, Rousettus linduensis Maryanto and Yani, 2003 has been recently described from the Lore Lindu area. However, none of these studies provided any information on the habitat preferences of these bats. In other parts of Southeast Asia, Medway (1972) and Heaney et al. (1989) reported that pteropodid species richness typically decreases with height above sea level. The same pattern has been reported for Lombok Island and the Lesser Sunda Islands of Indonesia (Gunnel et al. 1996; Kitchener 1998).

The distribution and diversity of bats are influenced by microclimate, elevation, habitat types and food resources (Maryanto and Yani 2003; Hodgkison et al. 2004; Campbell et al. 2007). In the Philippine archipelago, Heaney *et* *al.* (2005) showed that species associated with disturbed habitats tend to be widely distributed and show higher rates of gene flow between populations than species associated with rain forests, which tend to be endemic. This study was designed to provide detailed information on the distribution and habitat preferences of fruit bats in a mountainous region of Central Sulawesi.

MATERIALS AND METHODS

Lore Lindu National Park is the largest protected area on the island (ca. 231000 ha; Fig.1). The Park has a rugged topography, altitude ranging from 250 to 2340 m a. s. l. The area is mainly mountainous, 90% of the park being above 1000 m, while lower areas occur only next to the north-western park boundaries (Wirawan 1981). Ten land system use types and 11 major vegetation types have been distinguished (Maryanto and Yani 2001). According to Watling and Mulvana (1981), in Lore Lindu lowland forest species grow up to 1500 m a.s.l., the transition to mountain forest occurring at about 1000 m a.s.l. In contrast, Musser and Dagosto (1987) reported that, in Central Sulawesi, above 1300 m a.s.l. the lowland evergreen forest gives way to the lower mountain rain forest, and that this transition entails a reduction in mean canopy height, number of buttressed trunks and creepers, and ambient temperature. Biological diversity generally decreases with increasing elevation (Whitmore, 1984).

According to Maryanto and Yani (2001), vegetation cover was divided into 11 types: cloud forest (Cf), upper mountain forest (Um), mountain forest (Mo), lower mountain forest (Lm), lower mountain moist forest (Lmm), marsh (Ma), mixed garden (Mg), monsoon forest (Ms), swamp forest (Sf), lowland forest (Lf), and degraded lowland forest (Df). We divided the study area

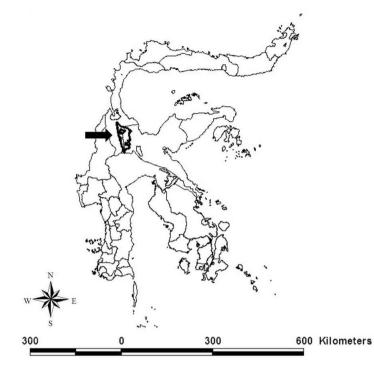


Figure 1 - Study area: Lore Lindu National Park, Central Sulawesi, Indonesia.

into seven altitudinal zones: 300-599 m (L2), 600-899 m (L1), 900-1199 m (M2), 1200-1499 m (M1), 1500-1799 m (H2), 1800-2099 m (H1) and above 2100 m a.s.l. (T). From the combination of the 11 vegetation types and 7 altitudinal zones, we obtained 17 habitats (Tab. 1). As an example, L2Ms is monsoon forest at 300-599 m a.s.l. Between March 2000 and July 2001, a total of 40 sampling sites were set up in the different habitats. Each sampling site was sampled for four nights by using four mist nets (lengths of 6, 9, 12, 18 m, each with a height of 2.7 m and four shelves). Mist nets were set up among the lower tree canopies and checked at 21:00 and 06:00 the following day. Survey data were entered into a Geographical Information System (GIS) (Arcview 3.2). Shannon-Wiener's index and Evenness (Krebs 1989) were used to compare bat assemblages. To define different clusters of species in relation to habitat variables, the Euclidian distance dissimilarity coefficient (EDD; Krebs 1989) was used and dendrograms were clustered by the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). Cluster analyses and dendrograms of dissimilarity were produced using NTSYSpc 2.10. Principle Component Analysis (PCA) was employed to group bats according to habitat preferences (Tab. 1).

RESULTS

1. Composition and diversity of bat assemblages

A total of 3799 fruit bats were captured. The sample included 16 species and 11 genera (Tab. 1), 62% of Sulawesian fruit bat species. Dominant species (90.8% of the whole bat assemblage) included *Thoopterus nigrescens* (Gray, 1870) (2075 individuals), *Rou*-

settus celebensis K. Andersen, 1907 (1309 individuals), Macroglossus minimus (E. Geoffroy, 1810) (200 individuals), and Cynopterus luzoniensis (Peters, 1861) (187 individuals). Two species. Rousettus (Boneia) bidens (Jentink, 1879) and R. linduensis were rarely netted and were represented by only nine and four (0.241% and 0.11%) individuals each. Seven of the 16 species (44%), C. luzoniensis, Dobsonia exoleta K. Andersen, 1909, R. (Boneia) bidens. R. celebensis. R. linduensis. Styloctenium wallacei (Gray, 1866), and Harpvionvcteris celebensis Miller and Hollister, 1921 are endemic to Sulawesi and adjacent islands (Kitchener and Maharadatunkamsi 1991; Corbet and Hill 1992).

The number of individuals captured for each altitudinal zone ranged from 48 (L2Ms) to 627 (M2Lm), due to variation in the abundance of dominant and eurytopic species. Shannon-Weiner's diversity curve was rather stable between 300 and 1500 m a.s.l. and then progressively decreased down to 0.18 at the highest elevations, while evenness ranged between 0.2 and 0.4 at 300-1800 m a.s.l. and then increased up to 0.53 at the highest elevations (Fig. 2). The decrease in Shannon-Weiner index at the summit of the mountain mainly depended on low species richness, bat assemblages being sharply dominated by *Thoopterus nigrescens* (Tab. 1).

2. Habitat preferences

The 16 species were clustered into groups at EDD =1.9, subgroups at EDD = 1.4 and subsets at EDD = 1.2 (Fig. 3).

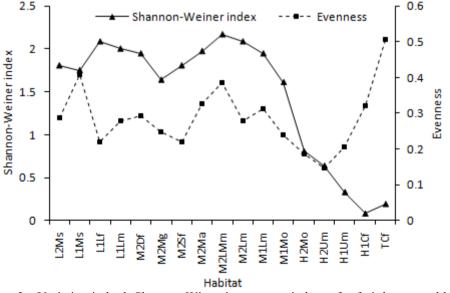


Figure 2 - Variation in both Shannon-Wiener's evenness indexes for fruit bat assemblages in different habitats in relation to the height a.s.l. (see the methods for habitat abbreviations).

National Park, Central Sulawesi. Abbreviations of species names: Chironax melanocephalus (Chm), Cynopterus brachyotis (Cb), C. luzo-
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Habitat	C_{nm}	භි	ڻ ت	Ğ	Ъ°*	Es	H_{c}^{*}	Mc	Mm	Ра	<i>S</i> ₩*	Ra	Rb *	Rc^*	R*	Тл	Totalspecies
TCf	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	5	2
HICF	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	254	ы
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HZUm	S	-	1	1	0	0	4	0	9	0	0	0	0	1	0	271	∞
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di Mb	۲	-	ч	0	ч	0	9	0	14	0	0	0	0	34	0	116	6
MI Lm	۲		0	0	0	0	1	7	17	0	-	0	0	8	0	S	6
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v2Lm	11	ଞ	62	16	9	0	ο	щ	18	0	7	0	0	292	0	180	11
M2Lmm	Ś	~	4	Ś	0	0	1	0	7	0	0	0	0	Ś	0	32	∞
MZMa	0	1	м	0	м	0	0	0	8	0	7	0	п	141	7	7	6
MZME	0	0	0	~	Ś	0	7	1	7	1	0	0	0	53	0	54	6
LILF	7	8	51	18	19	0	m	1	Я	0	7	0	0	151	0	8	11
MZSF	1	4	Ś	т	8	1	4	m	я	0	0	m	0	246	0	8	12
LlLm	00	18	25	4	m	0	4	0	9	0	0	м	0	16	0	8	10
LIMS	0	м	Ś	~	0	0	0	0	0	0	0	1	0	Я	0	ò	9
L2MS	0	S	0	м		0	0	0	1	0		7	0	8	0	Ś	∞
Total	46	8	12	74	89	-	É	5	С.	-	0	:	o	1200	ç	70.7	

Fruit bats in Indonesia

Maryanto et al.

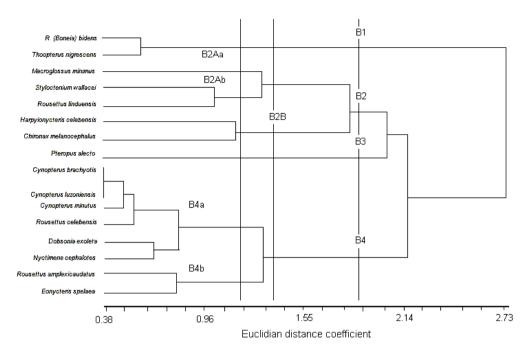


Figure 3 - Clustering of bats species captured at Lore Lindu National Park, Central Sulawesi by Euclidian dissimilarity index and UPGMA.

Group B1: Upper mountain association (1800-2100 m a.s.l.): consisted of *R*. (Boneia) bidens and *T. nigrescens*. The first is a rare and probably stenotopic species, while *T. nigrescens* is a eury-topic species. However, both of them are associated with the upper mountain forest.

Group B2: Lowland & mountain forest association (600-1800 m a.s.l.): consisted of two Subgroups. Subgroup B2A: Nectarivores, included *M. minimus*, *S. wallacei* and *R. linduensis*. In particular, *M. minimus* (Subset B2Aa) is a more specialized nectarivore than the other two species. *R. linduensis* was also captured in swamp forest at 930 m a.s.l. Subgroup B2B: included of *H. celebensis* and *C. melanocephalus* which are mainly frugivores (Corbet and Hill, 1992). Group B3: included only one individual *Pteropus alecto*, a migrant species, which was captured in a marsh using mistnets that were set up about 9 m above the ground.

Group B4: Lowland and lowermountain association (300-1200 a.s.l.): consisted of two Subgroups, B4a: frugivores (C. brachyotis, C. luzoniensis, C. minutus, R. celebensis, D. exoleta and N. cephalotes); and B4b: nectarivores (R. amplexicaudatus and E. spelaea), mainly associated with lowland forests at 300-600 m a.s.l. (Corbet and Hill 1992). Except for R. celebensis, the eight species of Group B4 are widespread, indicating that endemic species are mainly distributed at high altitudes.

The results of clustering analysis are supported by PCA (Fig. 4, Tab. 2), for

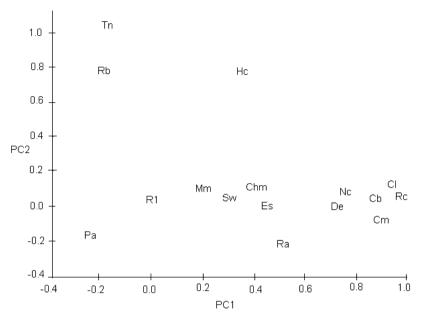


Figure 4 - Principle Component Analysis. PC1 and PC2 explain 71.94%, and 27.39% of total variance. Species name abbreviations are as in Table 1.

Habitat	Factor 1	Factor 2	Factor 3
TCf	-0.64449	-0.64143	-0.79372
H1Cf	-0.62667	0.63681	-0.91862
H1Um	-0.74569	2.85406	-0.42391
H2Um	-0.6208	0.84672	-0.48849
H2Mo	-0.78214	1.03824	0.57678
M1Mo	-0.74557	-0.54158	0.4933
M1Mo	-0.57096	-0.09283	0.35539
M2Sf	-0.00731	-0.07363	2.69962
M2Lm	2.47036	0.88395	-0.28367
M2Lmm	-0.47871	-0.97322	-1.14078
M2D1	0.6102	-0.36647	0.20854
M2Ma	-0.98804	-0.7665	1.57638
M2Mg	0.82951	-0.35562	-0.20075
L1Ms	-0.20684	-1.08587	-1.06841
L1Lf	1.7756	-0.19181	0.52512
L1Lm	1.04591	-0.10739	-0.30729
L2MS	-0.31436	-1.06344	-0.80949

Table 2 - Factors' scores of Principle Component Analysis (see methods for abbreviations).

which the inspection of the eigenvalues revealed that PC1, PC2 and PC3 accounted for 71.94%, 27.39% and 0.34% of total variance, respectively. PC3 was subsequently excluded from the analysis. On PC1, the two dominant species, T. nigrescens and R. celebensis, are positioned on opposite margins, suggesting that PC1 was associated with some factor which is very different between mountain and lowland areas. It should be noted that the group of T. nigrescens and R. (Boneia) bidens is joined by P. alecto which was captured only in a marsh. Humidity being higher in mountain forests than in lowland forests, PC1 may be related to the gradient of humidity. For PC2, mountain species such as T. nigrescens, R. bidens and H. celebensis are positioned on the positive margin, while lowland species, R. amplexicaudatus, C. minutus. P. alecto and R. celebensis are on the negative one, suggesting that PC2 primarily describes an altitudinal gradient.

DISCUSSION

Our results agree with previous studies of fruit bats in suggesting that species richness decreases with altitude (Heaney et al. 1989; Medway 1972; Azlan 2003), although in the Rinjani Mountain area of Lombok richness declined between 200-400 m (Gunnel 1998). Bat abundance is thought to be influenced by habitat types and, consequently, food availability. Accordingly, the diversity of fruit trees decreases from lowland areas to mountain peaks (Whitmore 1984).

Over 450 species of fruit-bearing plants, including many economically

important trees in tropical rain forests are associated with bats (Marshall, 1985; Fujita and Tuttle, 1991), which are considered to play a major role in the maintenance of many forest ecosystems. Shilton (1999) studied seed dispersal and pollination by bats in the Krakatau Islands and demonstrated rapid transit times, generally less than 30 minutes, whilst Tidemann et al. (1990) reported that in Cvnopterus sphinx gut retention of food, including viable fig seeds, can be more than 12 hours. Macroglossus, Eonycteris and Rousettus bats mainly feed at flowers (Marvati et al. 2008; Soegiharto et al. 2010) and may play a major role in the pollination of several tree species in Sulawesi.

Six fruit bats species found in Lore Lindu National Park are widespread throughout Southeast Asia (C. brachvotis. C. minutus. M. minimus. C. melanocephalus. R. amplexicaudatus and E. spelaea). Heaney et al. (2005) suggested that widespread species occur also in disturbed habitats, whilst endemic species are rarely found far from primary rain forest. Accordingly, in our study area R. amplexicaudatus, C. brachyotis, C. minutus were strongly associated with disturbed lowland habitats. In contrast, the ability of these species to tolerate disturbed habitats and low humidity in highland habitats may be quite limited (Abdullah et al. 1997; Azlan 2000; 2003).

In Sri Lanka, *C. brachyotis* has been reported to be rare and restricted to forest habitat (Mapatuna et al. 2002), therefore this species is potentially threatened by deforestation. In contrast, in Peninsular Malaysia and Sarawak, *C. brachyotis* has two 'morphs': one usually found in forest and the other in disturbed habitats (Campbell et al. 2004; 2006; 2007). In Lore Lindu, *C. brachyotis* and *C. minutus* are sympatric with the endemic *R. celebensis and C. luzoniensis* in lowland or open habitats.

M. minimus has been reported to be a strong flier with wide distribution, from lowlands to upper mountain elevations (Suvanto 1994). In Lore Lindu, it was usually found in open secondary forests and was rather common in marsh and swamp forest. It is sympatric with the Sulawesian eurytopic species R. celebensis and T. nigrescens. R. bidens occurred at high elevations, R. linduensis and *M. minimus* at middle elevations and R. amplexicaudatus and E. spelaea in lowlands. In contrast, Bergmans and Rozendaal (1988) recorded R. (Boneia) bidens in lowland forests, between 200 and 500 m a.s.l., of Tambun and Lembeh Island. Pteropus alecto has so far been reported also for Bawean, Maluku and Irian (West Papua).

Based on this survey, habitat overlap and niche breadth deserve additional future studies to clarify the ecology and biogeography of bats in Sulawesi.

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