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MORPHOLOGICAL AND ECOLOGICAL VARIATION IN *OTOPTERUS CARTILAGONODUS* KOCK, 1969 (MAMMALIA: CHIROPTERA: PTEROPODIDAE) FROM LUZON, PHILIPPINES

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Abstract.—Morphological variation in twenty-four characters of the skull, eight wing bones, and five characters of external morphology, as well as ecological data, are examined in the pteropodid bat, *Otopteropus cartilagonodus*, heretofore only known from six specimens. This study examines *O. cartilagonodus* from three populations: Zambales Mountains (n = 38), Mount Isarog (n = 46), and Isabela Province (n = 1). In the Zambales population, marked sexual dimorphism was found in five cranial characters associated with the feeding apparatus, as well as in overall length. Only two characters differed between sexes in the Mount Isarog population. The Zambales and Mount Isarog populations differed significantly in 21 out of 37 mensural characters, as well as in reproductive timing and embryonic development. From the segregation of sexes along an elevational gradient in the Zambales population, it is hypothesized that bats of this population may reduce intersexual competition by displaying distinct trophic and habitat preferences. This pattern of altitudinal segregation was not as marked in the Mount Isarog population. The structured, geographically and morphologically cohesive populations of *O. cartilagonodus* represent an ideal organism for elucidation of zoogeographic relationships among the different regions of the island of Luzon.

The pteropodid bat fauna of the Philippines currently is known to comprise twenty-four species in 15 genera (Heaney et al. 1987, Heaney 1991, Ingle & Heaney 1992). Of the 15 species of Pteropodidae endemic to the Philippines, only *Otopteropus cartilagonodus* Kock, 1969, is restricted to the island of Luzon. Until recently, only six specimens of this species were known: five from the Cordillera Central Mountains of northwestern Luzon (Kock 1969), and one from the Sierra Madre Mountains, northeastern Luzon (Mudar & Allen 1986). An additional reported specimen (University of Michigan Museum of Zoology no. 156689) was misidentified, and actually represents *Haplonycteris fischeri* (Heideman et al. 1993; LAR, pers. obs.). More recently, Heideman et al. (1993) reported on the reproductive timing and early development of this species based on a sample of seven males and twenty-two females from Mount Isarog, southern Luzon Island. The specimens forming the basis of that report now are at the United States National Museum, and form part of the basis for this report.

Recently, an inventory of the fauna of the Philippines was undertaken jointly by the Cincinnati Museum of Natural History (CMNH), the National Museum of the Philippines (NMP), and the University of the Philippines at Los Baños (UPLB), to provide baseline data on the distribution and conservation status of major vertebrate groups in the Philippines and to promote the conservation of centers of biological diversity. A portion of that survey was carried out along an elevational gradient in west central Luzon Island. During that time, several specimens of *O. cartilagonodus* were secured, allowing us the opportunity to examine morphological and ecological variation in this species in greater detail than heretofore possible. We also examined some ecological factors that may influence intraspecific altitudinal zonation in the species.

Methods

Field studies in the Zambales Mountains were conducted from 17 February to 8 March 1992. The Zambales were chosen as a study area because the fauna was relatively unknown (only studies by Johnson 1962 and Ripley & Marshall 1967 are known to us, both conducted in the foothills of the Zambales Mountains in and around the former Clark Air Force Base), and because they constitute a large, "insular" mountain, presently isolated from the other montane areas of Luzon. In addition, Dickerson (1924) suggested that the Zambales Mountains may have constituted an island separated from Luzon for much of the Tertiary and Quaternary.

Mist nets were set up along an elevational gradient extending from 125 m to 1900 m. Forty standard 12 m four-rung 25 mm mesh mist nets were used at each of three sites and run for seven consecutive nights; *O. cartilagonodus* were caught at two of these sites (described below). At both sites, a single "wall net" was set, consisting of four (Site 1) and three (Site 2) superimposed nets extending from ground level to the top of the canopy. At Site 1, an additional three sets were "doublehigh" nets, consisting of two superimposed nets. Mist nets were checked for bats and birds at dawn, every three to four hours during the course of the day, at dusk, and at least twice at two-hour intervals after dusk.

Twenty-four cranial measurements of *O. cartilagonodus* were taken to the nearest 0.01 mm using a Fowler Max-Cal digital caliper (measurements defined by Freeman 1981). These included greatest length of skull (GLS), length of rostrum (ROSL), length of palate (PALL), length of maxillary toothrow (MAXTL), length of upper molariform row (UPMOLL), rostral breadth (ROSW), least interorbital breadth (IOB; = postorbital breadth, POST ORB, of Freeman 1981), zygomatic breadth (ZB), breadth of braincase (BB), height of braincase (HB), breadth between upper canines (INTCB), breadth between M2 (INTMB), width between anterior pterygoids (APTB), width between posterior pterygoids (PPTB), height of upper canine (HUPCAN), length of M3 (M3L), width of M3 (M3W), length of dentary (DENTL), condylocanine length (CONCANL), condyle to m1 (CONM1), length of lower toothrow (MNDTOOTH), moment arm of masseter (MAMASTR), thickness of dentary (DENTTHK), and height of lower canine (HTLWRCAN). Wing bone measurements (described by Ruedas & Bickham 1992), included forearm length (FA), length of metacarpals of digits two through five (D2M through D5M), and length of proximal phalanges of digits two through five (D2P1 through D5P1). External measurements included total length, length of hind foot, length of ear, and weight.

Statistical analyses were carried out using the Statistical Analysis Software, version 6.03 (SAS Institute, Inc. 1988a, 1988b). Standard univariate statistics were obtained using the UNIVARIATE procedure; pairwise comparisons were evaluated using the TTEST procedure. The significance of the moment statistics (skewness, g_1; and kurtosis, g_2) was calculated by hand using the method of Sokal and Rohlf (1981:174–175).

Species diversity was measured using the Shannon diversity index, H' (Shannon 1948). Differences between diversity indices of the two sites were evaluated using the t test approach of Hutcheson (1970) for the Shannon formula, as described by Zar (1984). Community similarity was examined using the Horn index of community overlap (Horn 1966, Brower & Zar 1984).

Evenness of abundance of species was calculated as the ratio of the Shannon index, H', to the maximum possible diversity, H'_{max} (Pielou 1969). These measures of diversity and community similarity (heterogeneity indices sensu Peet 1974) are preferred herein over species abundance models because they are distribution independent (Magurran 1988, Peet 1974; but see Graham 1983 for a contrasting opinion).

Specimens Examined

Otopteropus cartilagonodus.—Philippines: Luzon Island; Camarines Sur Province; 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N, 123°20'E, 475 m; external and cranial characters of 4 males (U.S. National Museum of Natural History [USNM] 573439, 573444–573446) and 6 females (USNM 573440–573443, 573447, 573448); external characters of 1 male (USNM 573684) and 2 females (USNM 573680, 573682). Philippines, Luzon Island; Camarines Sur Province; 4 km N, 21 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1350 m; external and cranial characters of 1 female (USNM 570503), external characters of 1 female (USNM 573713) and 2 males (USNM 573712, 573715). Philippines: Luzon Island; Camarines Sur Province; 5 km N, 20 km E Naga, Mt. Isarog, 13°40'N, 123°21'E, 900 m; external characters of 3 males (USNM 573694, 573696, 573704) and 20 females (USNM 573685–573693, 573695, 573697–573703, 573705–573707). Philippines: Luzon Island; Camarines Sur Province; 4.5 km N, 20.5 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1125 m; external characters of 4 females (USNM 573708–573711). Philippines: Luzon Island; Camarines Sur Province; 4 km N, 21.5 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1550 m; external characters of 1 male (USNM 573715). Philippines: Luzon Island; Camarines Sur Province; 4 km N, 22 km E Naga, Mt. Isarog, 13°40'N, 123°22'E, 1750 m; external characters of 1 male (USNM 573716). Philippines: Luzon Island; Isabela Province; 3 km W mouth of Blos River, 17°30'N, 122°10'E, elev. 50 m (precise locality illustrated in Fig. 1, Mudar & Allen 1986:220; external and cranial characters of 1 female (University of Michigan Museum of Zoology [UMMZ] 156972). Philippines: Luzon Island; Zambales Province; Zambales Mountains, 15°35'N, 120°09'E, 1140 m; external and cranial characters of 7 females (National Museum of the Philippines/Cincinnati Museum of Natural History field numbers [NMP/CMNH] 22, 39, 75, 139, 140, 148, 149); external characters of 3 females (NMP/CMNH 45, 106, 141). Philippines: Luzon Island; Zambales Province; Zambales Mountains, 15°30'N, 120°08'E, 1500 m; external and cranial characters of 3 females (NMP/CMNH 354, 388, 407) and 9 males (NMP/CMNH 304, 312, 356, 362, 364–366, 390, 391); external characters of 4 females (NMP/CMNH 321, 332, 389, 408) and 12 males (NMP/CMNH 302, 307, 314, 318, 322, 335, 336, 355, 357, 363, 378, 409). These specimens will be assigned permanent museum numbers as soon as the division of specimens between CMNH and NMP takes place.

Specimens from the National Museum of the Philippines were examined by RVS, but the measurements are not included to maintain consistency of measurer and instrument. Specimens are identified by collection date because of lack of museum number, as follows: Luzon Isl.; Laguna Prov.; Balian; 1 female (col. 16 Jul 1964). Luzon Isl.; Nueva Viscaya Prov.; Dalton; 1 male (col. 20 Apr 1966), 4 females (col. 20 and 21 Apr 1966; 3 Jun 1970; 29 Oct 1970). Luzon Isl.; Quezon Prov.; Real, National Botanic Garden (University of the Philippines Land Grant); 2 males (3 and 8 Jun 1974). Three specimens (two males, one female) were collected at this last site by Andres L. Dans and Pedro L. Alviola, III, in May 1983, but were lost during a fire at the University of the Philippines at Los Baños on 10 May 1990 (A. L. Dans, in litt.). One additional male was collected during May 1992 by two students of A. L. Dans in Luzon Isl.; Cagayan Prov.; Mount Cetaceo, Sierra Madre, elev. 1500 m (A. L. Dans, in litt.) The exact whereabouts of this specimen are unknown.

The type series was not examined, but includes the holotype (Senckenberg Museum, Frankfurt [SMF] No. 28462, male) and three paratypes (SMF 28852–28854, 2 males, 1 female) from Philippines: Luzon Island; Mountain Province; Sitio Pactil; paratype, SMF 35750, female, Luzon Island: Abra Province; Massisiat Resthouse; and paratype, SMF 35749, female, "Philippines," no specific locality. No elevations, latitude, or longitude are noted in the description.

Study Sites

Specimens from Mount Isarog were collected by L. R. Heaney and his coworkers. These sites are described and illustrated by Goodman & Gonzales (1990) and Rickart et al. (1991); one *O. cartilagonodus* from that locality is illustrated in Heaney & Rickart (1990). The collection locality of the single specimen from Isabela Province (UMMZ 156972), also collected by L. R. Heaney, is described by Mudar & Allen (1986). The Zambales Mountains specimens were collected by LAR and JRD and coworkers.

The Zambales Mountains (Fig. 1) are an isolated mountain range encompassing approximately 6960 km^2 in west central Luzon. Including the volcanoes of the Bataan Peninsula, the Zambales extend approximately 200 km in length, running about 20° west of due north; the southern end (Bataan Peninsula) begins approximately 55 km west of the city of Manila, across Manila Bay. The greatest width of the range is about 60 km. To the east, the Zambales Mountains are isolated from the Cordillera Central (the nearest mountain range) by the extensive plains of Tarlac, also known as the Great Valley of Luzon, a wide expanse of alluvial, fluviatile, lacustrine and other sedimentary deposits (including beach and coralline), now consisting primarily of rice fields. To the west and north, the mountains end in the South China Sea; to the south, they separate Subic Bay from Manila Bay.

Rainfall patterns in the area display clearly demarcated dry and wet seasons. Data collected between 1951 and 1970 in Iba, a coastal town in the Zambales Province near the study area, indicate rainfall maxima in late July or August (ca. 1025 mm monthly average) and minima in late January or February (ca. 20 mm monthly average; data from Philippine Council, 1977).

Site 1.—Zambales Mountains, 15°35′N, 120°09′E, 1140 m. Sampled 17 to 26 Feb 1992. The altitudinal transect at this site was situated along a steep South facing ridge of Mount Apoy between 1050 m and 1265 m. During our stay at this camp, nighttime low temperatures averaged 10°C, while daytime highs rarely exceeded 23°C. This site was characteristic of the tropical moist deciduous forest type of Whitmore (1984), specifically, tropical lower montane rain forest; toward the top end of the transect were found elements transitional to a mossy forest type. Relatively untouched forest begins in the area only above approximately 1030 m (LAR, pers. obs.); below this elevation, extensive thickets of bamboo and other secondary growth predominate. The forest had two stories, but moving from the lower to higher elevations, the canopy gradually decreased in height above ground from 15–16 m to 11–13 m, and the subcanopy became increasingly broken and less conspicuous. Due to the high number of tree falls and boulders (the latter often 4–5 m wide) at either end of the transect, the canopy at the extremes of the transect was broken and uneven, while the canopy between the extremes was closed and continuous. Vegetation varied depending on exactly where the nets were set. Nets set along a ridge near the camp (ca. 1170 m) were in a moderately to dry habitat, with volcanic ash from the explosion of Mount Pinatubo in

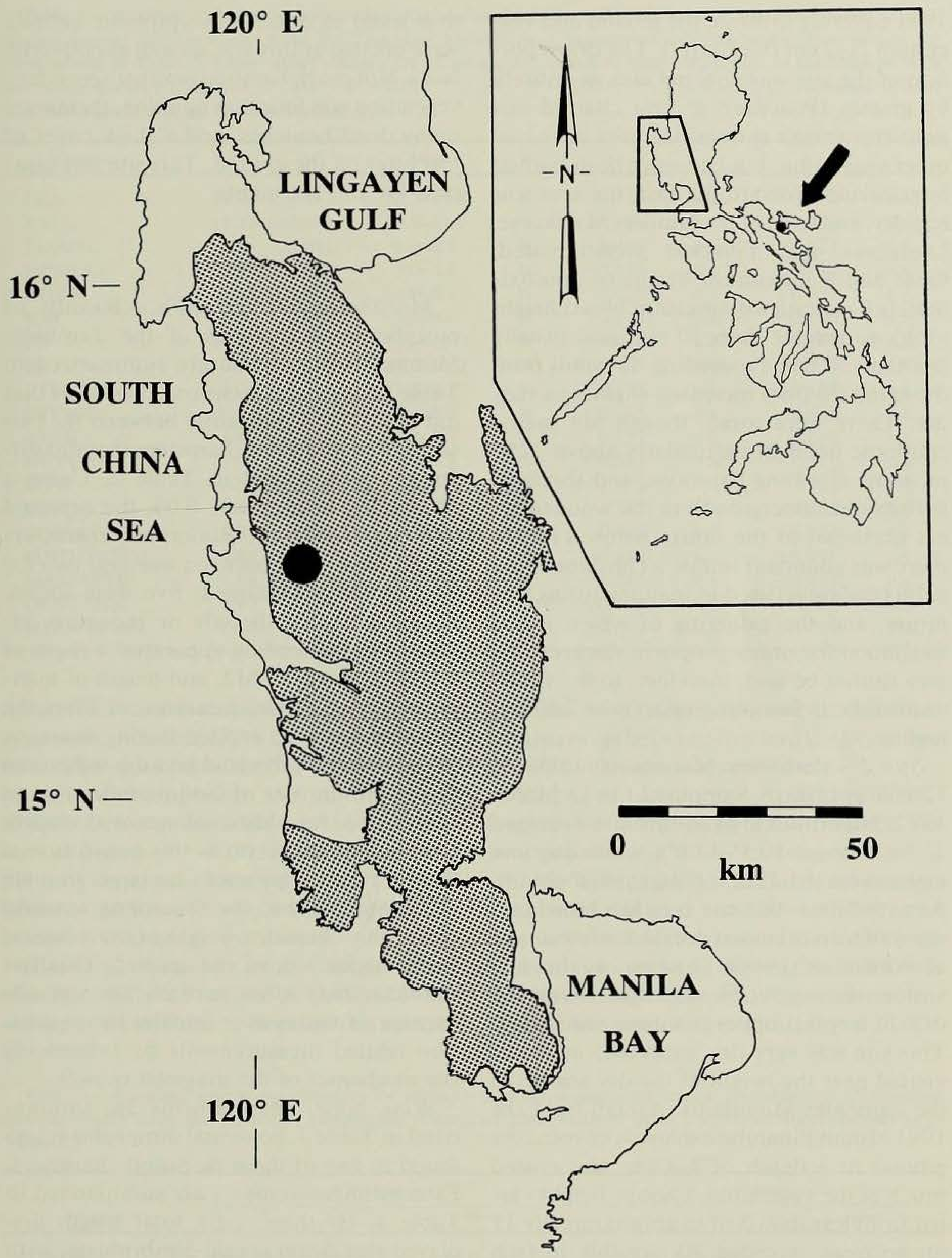

Fig. 1. Map of the geological assemblage constituting the Zambales Mountains (stippled area); the solid circle marks the study area. Inset map shows the Zambales area (box) in relation to the remainder of Luzon Island and the Philippines, with the arrow pointing to Mount Isarog, where the sample of *Otopteropus cartilagonodus* from the National Museum of Natural History originated.

1991 covering much of the ground and vegetation (1–2 cm thick layer). The driest portion of the site was covered almost entirely by grasses (Poaceae); several charred upright tree trunks showed the area once had other vegetation, but had since been burned to grassland. Toward the east, the area was less dry, and trees of the families Myrtaceae, Lauraceae, and Tiliaceae predominated; these had a maximum height of approximately 9 m, with a diameter at breast height (dbh) no greater than 50 cm, and usually less than 30 cm. Proceeding downhill from the camp (S) trees increased slightly in stature. There were some, though not many, epiphytic orchids, particularly above 1250 m; some climbing bamboos, and shrubby, herbaceous undergrowth in the wooded areas northeast of the camp. Below 1100 m there was abundant rattan, a climbing spiny palm (*Calamus*) used in manufacturing furniture, and the gathering of which is the livelihood for many people in the area; the area cannot be said, therefore, to be wholly undisturbed. Sampling effort was 240 net nights.

Site 2.—Zambales Mountains, 15°30'N, 120°08'E, 1500 m. Sampled 11 to 18 March 1992. Nighttime lows at this site averaged 12.6°C (range: 10.3°–14.0°), while daytime highs averaged 22.5°C (range: 19.8°–24.0°). As with Site 1, this site is in the broad category of tropical moist deciduous forest type of Whitmore (1984); however, at this elevation, the vegetation was more characteristic of tropical upper montane rain forest. This site was very dry, especially as it was visited near the height of the dry season in the Zambales Mountains. Ashfall from the 1991 Mount Pinatubo explosion covered the ground to a depth of 2–4 cm and coated much of the vegetation. Canopy height varied from less than 5 m to approximately 11 m; no trees exceeded 70 cm dbh: in fact, few were greater than 50 cm dbh. Predominant trees were of the families Fagaceae, Myrtaceae, Magnoliaceae, and Pinaceae, although other families also were represented to a lesser extent. Many epiphytic orchids were present at this site, as well as epiphytic ferns. Not much bamboo or other secondary vegetation was found; in addition, there were many dead branches, and a thick cover of leaf litter on the ground. This site was sampled for 200 net nights.

Results

Morphological variation.—Results of morphometric analyses of the Zambales Mountains population are summarized in Table 1 for cranial mensural characters that did not differ significantly between the two sexes. Those cranial characters that did differ are summarized in Table 2. Using a probability level of $\alpha = 0.05$, the expected number of sexually dimorphic characters would have been between one and two for 24 characters examined; five were found. All of these are directly or indirectly involved in the feeding apparatus. Length of rostrum, length of M3, and length of mandible from condyle to canine, all affect the mechanical force applied during mastication. Posterior pterygoid breadth influences the maximum size of food particles able to be ingested. An additional note with respect to sexual dimorphism in this population is that all cranial characters are larger in male *O. cartilagonodus*; the remaining sexually dimorphic character, height of braincase, is larger in females of the species. This last character may offset partially the size advantage of males over females in mastication related measurements by influencing the mechanics of the masseter muscle.

Wing bone measurements are summarized in Table 3; no sexual dimorphism was found in any of these mensural characters. External measurements are summarized in Table 4. Of these, only total length displayed significant sexual dimorphism, with females being somewhat longer than males.

Mensural characters of the Mount Isarog population are summarized in Tables 5–7. Only two cranial measurements differed be-

Table 1.—Standard univariate statistics for cranial characters (in millimeters; abbreviations defined in text) of *Otopteropus cartilagonodus* from the Zambales Mountains. Characters displaying sexual dimorphism are summarized in Table 2. (Other abbreviations are: $\bar{X}$ mean; *SE,* standard error; *W,* results of the Shapiro-Wilk test for normality [N, normal; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$]; g_1, skewness statistic [n.s., not significant]; g_2, kurtosis statistic.)

Character	$\bar{X}$ SE	Range	W	g_1	t_{g1}	g_2	t_{g2}
GLS	23.02 ± 0.107	22.2–23.8	N	0.257	n.s.	−0.652	n.s.
PALL	11.35 ± 0.072	10.9–11.9	N	−0.046	n.s.	−1.308	n.s.
MAXTL	6.56 ± 0.042	6.2–6.8	N	−0.493	n.s.	−0.672	n.s.
UPMOLL	5.33 ± 0.039	5.0–5.6	N	−0.655	n.s.	−0.440	n.s.
ROSW	5.52 ± 0.956	5.0–6.1	N	0.323	n.s.	−0.716	n.s.
IOB	4.20 ± 0.051	3.7–4.6	N	−0.224	n.s.	−0.100	n.s.
ZB	14.49 ± 0.079	13.9–15.3	N	0.692	n.s.	0.504	n.s.
BB	10.65 ± 0.058	10.2–11.2	N	0.435	n.s.	−0.040	n.s.
INTCB	2.09 ± 0.034	1.8–2.4	N	0.123	n.s.	−0.633	n.s.
INTMB	4.84 ± 0.054	4.4–5.2	N	−0.253	n.s.	−0.930	n.s.
APTB	3.90 ± 0.036	3.7–4.2	N	0.157	n.s.	−1.030	n.s.
HUPCAN	1.85 ± 0.071	1.2–2.3	N	−0.335	n.s.	−0.370	n.s.
M3W	0.90 ± 0.018	0.7–1.0	*	−1.472	**	4.325	***
DENTL	16.43 ± 0.088	15.7–17.6	*	1.385	**	3.855	***
CONM1	13.26 ± 0.093	12.7–14.1	N	0.406	n.s.	−0.722	n.s.
MNDTOOTH	6.64 ± 0.043	6.3–6.9	N	−0.523	n.s.	−0.991	n.s.
MAMASTR	7.18 ± 0.079	6.5–7.8	N	−0.545	n.s.	−0.075	n.s.
DENTTHK	1.93 ± 0.029	1.6–2.2	N	−0.128	n.s.	0.797	n.s.
HTLWRCAN	1.66 ± 0.046	1.2–2.1	*	−0.001	n.s.	3.034	**

tween males and females in this population: zygomatic breadth ($P = 0.0085$) and posterior pterygoid breadth ($P = 0.0090$). With respect to the wing bones, the only one found to differ between the sexes was the first phalanx of digit 5 ($P = 0.0053$). Ear length was the only external character found to differ between the sexes ($P = 0.0117$), despite considerable overlap in the ranges.

Mensural characters of the single specimen from Isabela Province (UMMZ 156972) are reported in Table 8. Because this sample consists of a single specimen, statistical comparisons between this and the other two populations were not carried out.

Geographic variation.—Considerable differences in morphology exist between the two populations of *O. cartilagonodus* examined herein: 21 out of the 37 characters examined differed significantly between Zambales and Isarog populations. With respect to non-sexually dimorphic characters of the skull, significantly different characters include interorbital breadth ($P = 0.0000$),

Table 2.—Standard univariate statistics for sexually dimorphic mensural cranial characters of *Otopteropus cartilagonodus* from the Zambales Mountains. (Character abbreviations as in text; other abbreviations as in Table 1.)

Character	Males		Females	
	$\bar{X}$ SE	Range	$\bar{X}$ SE	Range
ROSL	10.67 ± 0.116	10.0–11.1	10.12 ± 0.118	9.7–10.7
HB	8.93 ± 0.098	8.8–9.8	9.34 ± 0.102	8.8–9.8
PPTB	3.48 ± 0.048	3.3–3.7	3.27 ± 0.058	3.0–3.6
M3L	1.12 ± 0.022	1.1–1.2	1.04 ± 0.020	0.9–1.1
CONCANL	15.82 ± 0.105	15.4–16.3	15.50 ± 0.096	15.1–16.0

Table 3.—Wing bone measurements, in millimeters, for *Otopteropus cartilagonodus* from the Zambales Mountains. (Character abbreviations as in text; other abbreviations as in Table 1.)

Character	$\bar{X}$ ± *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
D2M	22.41 ± 0.138	20.1–24.1	N	−0.433	*	0.864	n.s.
D2P1	5.23 ± 0.055	4.6–5.8	*	−0.012	n.s.	−1.274	n.s.
D3M	32.88 ± 0.173	30.0–35.2	N	−0.467	n.s.	0.500	n.s.
D3P1	24.78 ± 0.161	22.1–26.9	N	−0.361	n.s.	0.919	n.s.
D4M	30.58 ± 0.183	27.2–33.5	N	−0.076	n.s.	2.046	**
D4P1	17.82 ± 0.145	15.0–19.9	N	−0.453	n.s.	1.985	**
D5M	32.25 ± 0.181	28.3–34.0	*	−1.103	**	3.769	***
D5P1	15.44 ± 0.106	14.0–16.4	N	−0.576	n.s.	−0.388	n.s.

height of upper canine ($P = 0.0000$), length of dentary ($P = 0.0052$), length of condyle to M1 ($P = 0.0001$), length of mandibular toothrow ($P = 0.0000$), and height of lower canine ($P = 0.0047$). In sexually dimorphic characters, females differ between the two populations in length of rostrum ($P = 0.0005$), zygomatic breadth ($P = 0.0003$), posterior pterygoid breadth ($P = 0.0370$), and condylocanine length ($P = 0.0201$), while males differ in posterior pterygoid breadth only ($P = 0.0397$). Every wing bone measurement differs significantly between the two populations (FA, D2M, D3M, D4M, D4P1, D5M, $P = 0.0000$; D3P1, $P = 0.0093$; D5P1, females, $P = 0.0000$, males, $P = 0.0005$). Finally, with respect to external characters, the two populations differ in length of hind foot ($P = 0.0001$), mass ($P = 0.0001$), and total length (females, $P = 0.0001$, males, $P = 0.0091$). The specimen from Isabela Province (Table 8) is closest to Mount Isarog specimens rather than to Zambales specimens in all characters examined, albeit without statistical confirmation.

Ecological notes.—Thirty-eight specimens of *O. cartilagonodus* were collected in mist nets set near Sites 1 and 2. Ten individuals, all females, were collected at Site 1 in seven nets set between 1130 and 1235 m. Four were caught in two nets, set at 1140 m and 1180 m; the remaining six were caught singly. All individuals were flying between 125 and 270 cm above the ground when captured. Of these ten females, nine were pregnant, with embryos averaging 9.22 mm in crown rump length (mode, 12 mm; range 5–13 mm; *SE*, ± 0.969).

At Site 2, 15 males and 9 females were collected. Two nets, set at 1579 m, and 1613 m, each caught two; one net set at 1594 m resulted in three; remaining bats were caught singly in nets at elevations between 1365 m

Table 4.—Standard external measurements for *Otopteropus cartilagonodus* from the Zambales Mountains. Total length was the only external measurement found to be sexually dimorphic. (Mass expressed in grams; all other measurements in millimeters; abbreviations as in Table 1.)

Character	$\bar{X}$ ± *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
Hind foot	10.66 ± 0.102	9–12	***	−0.294	n.s.	0.189	n.s.
Ear length	13.80 ± 0.150	11–16	***	−0.646	n.s.	1.887	*
Forearm	44.55 ± 0.213	41–47	N	−0.835	*	0.864	n.s.
Mass	13.55 ± 0.099	12–15	*	−0.025	n.s.	0.192	n.s.
Total length							
Females	69.47 ± 0.515	65–74	N	0.088	n.s.	−0.344	n.s.
Males	68.10 ± 0.350	66–70	*	−0.092	n.s.	−1.422	n.s.

Table 5.—Standard univariate statistics for mensural cranial characters of *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S. National Museum of Natural History, U.S.N.M.), in millimeters. (Abbreviations are as in Table 1.)

Character	$\bar{X}$ ± *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
GLS	23.18 ± 0.123	22.4–23.9	N	−0.374	n.s.	0.723	n.s.
ROSL	10.79 ± 0.078	10.4–11.1	N	−0.454	n.s.	−1.625	n.s.
PALL	11.89 ± 0.077	11.4–12.3	N	−0.364	n.s.	−0.134	n.s.
MAXTL	6.76 ± 0.112	6.2–7.5	N	0.518	n.s.	0.976	n.s.
UPMOLL	5.45 ± 0.068	5.0–5.7	N	−1.271	n.s.	0.921	n.s.
ROSW	5.72 ± 0.140	5.1–6.5	N	0.232	n.s.	−0.878	n.s.
IOB	3.73 ± 0.071	3.4–4.0	N	0.006	n.s.	−1.606	n.s.
BB	10.85 ± 0.094	10.2–11.2	N	−1.144	n.s.	0.897	n.s.
HB	9.52 ± 0.091	9.0–10.2	N	0.844	n.s.	1.485	n.s.
INTCB	2.20 ± 0.045	1.9–2.4	N	−0.802	n.s.	0.361	n.s.
INTMB	4.77 ± 0.064	4.4–5.1	N	−0.081	n.s.	−0.779	n.s.
APTB	3.81 ± 0.027	3.7–4.0	N	0.944	n.s.	2.110	n.s.
HUPCAN	2.53 ± 0.077	2.0–2.8	N	−0.759	n.s.	0.466	n.s.
M3L	1.09 ± 0.016	1.0–1.1	N	−0.503	n.s.	−1.168	n.s.
M3W	0.91 ± 0.021	0.8–1.0	N	0.675	n.s.	0.309	n.s.
DENTL	16.89 ± 0.124	16.2–17.7	N	0.172	n.s.	0.706	n.s.
CONCANL	16.10 ± 0.141	15.0–16.6	N	−1.128	n.s.	1.947	n.s.
CONM1	13.92 ± 0.114	13.1–14.5	N	−0.828	n.s.	1.247	n.s.
MNDTOOTH	7.03 ± 0.068	6.7–7.5	N	0.421	n.s.	0.768	n.s.
MAMASTR	7.23 ± 0.079	6.6–7.6	N	−1.112	n.s.	1.552	n.s.
DENTTHK	1.91 ± 0.045	1.7–2.2	N	0.300	n.s.	−0.372	n.s.
HTLWRCAN	1.90 ± 0.053	1.6–2.3	N	0.612	n.s.	0.516	n.s.
ZB (females)	15.10 ± 0.086	14.8–15.5	N	0.066	n.s.	0.385	n.s.
ZB (males)	14.51 ± 0.180	14.2–15.0	N	1.635	n.s.	2.999	n.s.
PPTB (females)	3.09 ± 0.043	2.9–3.3	N	0.360	n.s.	−0.701	n.s.
PPTB (males)	3.30 ± 0.035	3.2–3.4	N	−1.414	n.s.	1.500	n.s.

Table 6.—Wing bone measurements, in millimeters, for the *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S.N.M.); 33 females and 8 males comprise the sample. The only measurement differing at $\alpha = 0.05$ was that of the first phalanx of digit 5 (D5P1; $P = 0.0053$); however, D3M, D3P1, and D4P1 all had P values between 0.05 and 0.10. (Character abbreviations as in text; other abbreviations as in Table 1.)

Character	$\bar{X}$ ± *SE*	Range	*W*	g_1	t_{g1}	g_2	t_{g2}
D2M (♀)	23.94 ± 0.183	21.4–25.8	N	−0.038	n.s.	−0.170	n.s.
D2M (♂)	23.44 ± 0.529	21.1–25.5	N	−0.346	n.s.	0.382	n.s.
D3M (♀)	34.56 ± 0.191	32.3–36.7	N	−0.123	n.s.	−0.739	n.s.
D3M (♂)	33.78 ± 0.333	32.6–35.1	N	0.016	n.s.	−1.702	n.s.
D3P1 (♀)	25.45 ± 0.143	23.8–27.2	N	−0.045	n.s.	−0.673	n.s.
D3P1 (♂)	24.82 ± 0.277	23.5–25.8	N	−0.688	n.s.	−0.412	n.s.
D4M (♀)	32.98 ± 0.181	30.0–35.2	N	−0.402	n.s.	1.059	n.s.
D4M (♂)	32.56 ± 0.469	30.8–34.7	N	0.351	n.s.	−0.673	n.s.
D4P1 (♀)	19.28 ± 0.188	17.7–23.9	***	2.509	***	10.050	***
D4P1 (♂)	18.55 ± 0.245	17.5–19.4	N	−0.279	n.s.	−1.210	n.s.
D5M (♀)	33.48 ± 0.214	31.0–35.3	N	−0.206	n.s.	−0.803	n.s.
D5M (♂)	33.09 ± 0.389	31.6–35.0	N	0.502	n.s.	−0.072	n.s.
D5P1 (♀)	17.12 ± 0.120	15.8–18.8	N	0.149	n.s.	0.498	n.s.
D5P1 (♂)	16.36 ± 0.177	15.6–17.2	N	0.281	n.s.	0.593	n.s.

Table 7.—Standard external measurements for *Otopteropus cartilagonodus* from Mt. Isarog (specimens at the U.S.N.M.); 40 females and 14 males comprise the sample. Ear length was the only external measurement found to be sexually dimorphic ($P = 0.0117$). (Mass expressed in grams; all other measurements in millimeters; abbreviations as in Table 1.)

Character	$\bar{X}$ ± SE	Range	W	g_1	t_{s1}	g_2	t_{s2}
Total length							
Females	74.67 ± 0.989	65–87	N	0.196	n.s.	−0.861	n.s.
Males	72.28 ± 1.348	65–79	N	−0.175	n.s.	−1.422	n.s.
Hind foot							
Females	13.78 ± 0.494	11–20	***	1.058	**	−0.658	n.s.
Males	12.88 ± 0.670	11–19	***	1.931	**	2.892	*
Ear length							
Females	14.00 ± 0.095	12–15	***	−0.753	*	2.789	***
Males	13.21 ± 0.260	12–15	N	0.089	n.s.	−1.026	n.s.
Forearm							
Females	48.75 ± 0.256	44–52	N	−0.190	n.s.	0.650	n.s.
Males	47.86 ± 0.404	45–51	N	0.124	n.s.	0.494	n.s.
Mass							
Females	15.98 ± 0.245	13–19	N	0.109	n.s.	−0.706	n.s.
Males	16.36 ± 0.360	15–20	*	1.615	**	3.369	**

and 1643 m. At this site bats were flying between 30 and 210 cm above the ground when caught. Only three of the nine females were pregnant; two embryos measured 8 and 14 mm, the third female was fluid preserved intact and determined to be pregnant by external inspection (fide JRD). All males captured exhibited abdominal testes; habit-

Table 8.—Measurements of the single specimen of *Otopteropus cartilagonodus* (UMMZ 156972) from Isabela Province, Luzon Island, Philippines. (Mass expressed in grams, all other measurements in millimeters.)

Cranial measurements			
Greatest length of skull	23.3	Anterior pterygoid breadth	3.7
Length of rostrum	10.7	Posterior pterygoid breadth	3.0
Length of palate	12.2	Height of upper canine	2.6
Length of maxillary toothrow	7.2	Length of M3	1.0
Length of upper molariform row	6.1	Width of M3	0.9
Rostral breadth	4.8	Length of dentary	17.7
Interorbital breadth	3.5	Condylocanine length	15.7
Zygomatic breadth	15.4	Condyle to m1	14.3
Breadth of braincase	10.9	Length of mandibular toothrow	6.7
Height of braincase	9.4	Moment arm of masseter	7.8
Breadth between upper canines	2.2	Thickness of dentary	2.0
Breadth between M3	4.8	Height of lower canine	2.0
Wing bone measurements			
D3M 32.6	D4M 31.3	D5M 32.3	
D3P1 26.0	D4P1 18.7	D5P1 16.3	
FA 47.6			
External measurements (from specimen label)			
Total length	70	Length of hind foot	11
Length of ear	14	Mass	17

ually, this would indicate the organism is not breeding, however, many bats are able to move their testes in and out of their abdominal cavity, apparently at will. For 14 males where such data were taken, testes measurements averaged 3.3 by 2.4 mm.

A single net set for one night just below Mt. High Peak (15°29′N, 120°07′E) at ca. 1900 m caught four male *O. cartilagonodus* with abdominal testes, averaging 3.2 by 2.5 mm. The nighttime low at this camp reached at least 7°C.

Geographic variation.—The altitudinal segregation of sexes found in the Zambales sample was not present in the sample from Mount Isarog, as no statistically significant differences were found between capture elevations in males versus females. The trend, however, was for a greater number of females than males at the lower elevations: three males and twenty females were captured at 900 m, only females at 1125 m, one female and two males were captured at 1350 m, but only males of the species were captured at 1550 and 1750 m (one at each elevation). The two populations also appear to differ in reproductive timing. Heideman et al. (1993) found that the Mount Isarog sample displayed synchrony of embryological development, with small uterine swellings in March, and 15–20 mm embryos in females captured in May; they extrapolated birth dates in late May or June. In contrast, the sample from the Zambales Mountains (collected mid-February to early March) contains a mixture of pregnant and non-pregnant females with embryos from 5 to 14 mm in crown rump length.

Other chiropteran species.—An additional 12 species of bats were collected in the same two localities where *O. cartilagonodus* was found to be present (Table 9). The Shannon diversity index for the chiropteran fauna of Site 1 was $H'_1 = 0.648$, while that for Site 2 was $H'_2 = 0.585$. The t test for the Shannon formula (Hutcheson 1970), indicated there was no significant difference between species diversities at the two sites ($P \gg 0.05$). Because diversity indices usually are not calculated for particular subsections of a fauna (Chiroptera in this instance), we calculated the relative diversity, or evenness, J', as a proportion of H'_n to the theoretical maximum value for H', or $H'_{n\,max}$, thereby yielding a value constrained between 0 and 1. For Site 1, $H'_{1\,max} = 1.079$, while for Site 2, $H'_{2\,max} = 0.845$. Thus, for Site 1, $J'_1 = 0.600$, while for Site 2, $J'_2 = 0.692$. The Horn index of community similarity ("community overlap"), R_0, also constrained between 0.0 (when the two communities under consideration have no species in common) and 1.0 (when species compositions and relative abundances are identical between the two sites) calculated for Sites 1 and 2 was $R_0 = 0.637$; the overlap between the chiropteran faunas of the two sites was thus on the order of 64%.

What may not readily be apparent from these indices is that there is at least one major difference between the two sites, that being in the abundances of three species:

Table 9.—List of bats caught at the two localities where *Otopteropus cartilagonodus* also were captured[1].

Species (Site:)	Site 1, Zambales, 1100 m (n)	Site 2, Zambales, 1500 m (n)
Rhinolophidae		
Rhinolophus arcuatus	59	39
Rhinolophus subrufus	36	2
Rhinolophus philippinensis	1	3
Hipposideros bicolor	0	1
Vespertilionidae		
Myotis muricola	2	20
Murina cyclotis	1	1
Pteropodidae		
Cynopterus brachyotis	1	0
Eonycteris spelaea	1	0
Haplonycteris fischeri	1	0
Macroglossus minimus	1	0
Otopteropus cartilagonodus	10	24
Ptenochirus jagori	5	0
Rousettus amplexicaudatus	19	0

[1] Four *O. cartilagonodus* and two *R. arcuatus* that were caught in a net set at 1900 m are not included in the totals.

Myotis muricola, Rhinolophus subrufus, and *Rousettus amplexicaudatus.* This last species is particularly noteworthy because it previously has been associated with disturbed areas, either natural or anthropogenic (Heideman & Heaney 1989). Its presence at Site 1 reinforces our perception of this site as disturbed, either by rattan gathering, or by the Mount Pinatubo ashfall, or a combination of both factors. The few known specimens of *R. subrufus* have been collected from caves (Heaney et al. 1987); their presence at Site 1 but not Site 2 may be more indicative of the proximity of a cave, rather than of any specific habitat preference.

Discussion

With respect to morphological variation, we found that 21 out of the 37 mensural characters examined in the Zambales and Isarog populations differed significantly between the two populations. They are most readily separated by forearm length (Isarog, 45–52 mm; Zambales, 41–46 mm), and length of upper and lower canines. The differences in dental characters may be indicative of differences in diet. There also are marked differences in reproductive timing and embryonic development between the Zambales and Isarog samples. Although the two populations constitute readily identifiable clusters of individual organisms (sensu Cracraft 1983, McKitrick & Zink 1988), we prefer at this time not to make any hard and fast taxonomic decision with respect to *Otopteropus,* since this might obscure the fact that we still know very little about the biology of these bats, which still are known from very small samples. We were unable to examine the type series, although from measurements provided in Kock (1969), the holotype and adult paratypes most closely resemble the specimens from Mount Isarog than the geographically closer Zambales specimens. The specimen from Isabela Province also is most similar to the Isarog and type series. The specimens from the Cordillera Central and Sierra Madre Mountains are closer in multivariate morphological space to the Mount Isarog population (based on the available material) than they are to the Zambales population.

In our Zambales Mountain study population of *O. cartilagonodus* we found a greater number of sexually dimorphic mensural characters in the skull than expected by chance alone. All differences found were in characters that affect the feeding apparatus, and thereby potentially trophic behavior as well; these may also impact male competition in this probably harem-polygynous species. Although there is sexual dimorphism in characters associated with feeding and mastication, there is no difference in mass between the sexes, and only a slight (but significant) difference in total length. Four of the five dimorphic characters of the skull were larger in males than females; however, males are significantly smaller than females in overall length. Because there is no difference in mass between the sexes, and only the difference in overall length is very small, we hypothesize that the intersexual differences in masticatory characters affect (or are affected by) food preferences, rather than resulting from an overall size component.

Latitudinal species succession, or succession of species with temperature variation is a long known phenomenon (Fleming 1973, McCoy & Connor 1980, Rapoport 1982, Pianka 1983). Recently, however, more attention has been paid to an expected corollary of this phenomenon, that is, to elevational zonation of species. The underlying processes controlling this phenomenon remain unclear because of the extensive variation in geographic, taxonomic, and trophic parameters (Terborg 1971, Heaney et al. 1989, Patterson et al. 1989, Rickart et al. 1991). One reason for the uncertainty underlying the patterns and processes of altitudinal distribution may be that most research has focused on faunal subsets, such as mammals (Heaney et al. 1989, Heaney & Rickart 1990), small mammals (Patterson et al. 1989, Rickart et al. 1991), bats (Graham 1983), or birds (Goodman & Gonzales 1990; Terborgh 1971, 1977), rather than on individual species. It is possible that the different faunas, and indeed, different species within a faunal assemblage, may be prescribed by a specific paradigm governing different factors, or characteristics, of their elevational distribution and, consequently, altitudinal patterns of replacement. Furthermore, in habitats considered less "heterogeneous" (where there may be fewer resources available to species), there may be mechanisms for reducing intraspecific competition (or intersexual competition); this sort of intraspecific zonation may be a confounding variable when it comes to examining the elevational distribution of taxa and faunas.

We found such an apparent segregation of sexes by habitat along an elevational gradient. At lower elevations (ca. 1100 m), only females, most (90%) of them pregnant, were found. At elevations surrounding the 1500 m site, a ratio of 3 females to 8 males existed and only 30% of the females were pregnant. Within the confines of a limited sampling effort, only males were found at 1900 m. A major supposition here is that capture site is correlated with day roost site, which not always is the case in bats mist netted in the mountains. However, since the nets were set in recognizably discrete habitat types at each elevation (lower and upper montane forest), the hypothesis that intraspecific sexual segragation takes place may confidently be stated.

It has been remarked that in contrast to rodents, bats decrease in relative abundance and species richness with elevation (Graham 1983, Heaney et al. 1989, Heaney & Rickart 1990). Possibly, the metabolic demands imposed by flight on bats (Burton et al. 1989, McNab 1989), in contrast to other mammals, together with reduced availability of trophic resources for insectivorous and frugivorous organisms at higher elevations, may increase the competition for resources at these elevations.

Traditional definitions of competition divided this population phenomenon into exploitative (indirect, i.e., resource depletion) and interference competition (direct, i.e., fighting or predation [e.g., Park 1962]). An alternative taxonomy of competition was proposed by Schoener (1983). Here, "consumptive competition designates consumption of resources that deprives other individuals of those resources, whereas preemptive competition occurs when a unit of space is passively occupied by an individual, thereby causing other individuals not to occupy that space before the original occupant disappears" (Schoener 1988:256).

We hypothesize that *O. cartilagonodus* from the Zambales Mountains may reduce competition between sexes by two means: consumptive competition is reduced by adjusting to differences in food preferences (based on cranial morphometric data), and preemptive competition is reduced by adjusting habitat preferences between the sexes (based on capture data). A test of these hypotheses will necessitate further study involving examination of stomach contents from freshly captured individuals, and more extensive sampling along an elevational gradient. The data from Mount Isarog, currently under study by L. R. Heaney and coworkers may serve as an additional test of these hypotheses.

Clearly, the variation exhibited by this species is not a case of ordinary, clinal geographic variation. The data therefore lend themselves to a number of alternative hypotheses to be tested with respect to the relationships among the various populations. Given the exhibited pattern of morphological variation, it may well be that the Zambales population represents a long isolated population. Additional specimens will be needed to distinguish among competing hypotheses, including additional sampling from the Laguna and Batangas Provinces' montane areas, from which only a few specimens are known (and none closely scrutinized), as well as a greater number of specimens from the type locality (in Cordillera Central) and from the Sierra Madre Mountains. Until such a time as the regional populational differences are resolved, the structured, geographically and morphologically cohesive populations of *O. cartilagonodus* appear to represent an ideal study case for elucidation of zoogeographic relationships among different regions of the island of Luzon.

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Literature Cited

Brower, J. E., & J. H. Zar. 1984. Field and laboratory methods for general ecology, 2nd. ed. Wm. C. Brown Publishers, Dubuque, Iowa, xi + 226 pp.

Bureau of Mines, Philippines, in coordination with the Board of Technical Surveys and Maps. 1963. Geological map of the Philippines, edition 1. Single sheet map.

Burton, D. W., J. W. Bickham, & H. H. Genoways. 1989. Flow-cytometric analyses of nuclear DNA content in four families of neotropical bats.—Evolution 43(4):756–765.

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 *in* R. F. Johnston, ed., Current ornithology, Volume 1. Plenum Press, New York, xvi + 425 pp.

Dickerson, R. E. 1924. Tertiary paleogeography of the Philippines.—Philippine Journal of Science 25:11–50, pls. 1–4.

Fleming, T. H. 1973. The number of mammal species in several North and Central American forest communities.—Ecology 54:555–563.

Freeman, P. W. 1981. A multivariate study of the family Molossidae (Mammalia: Chiroptera): morphology, ecology, evolution.—Fieldiana, Zoology, New Series, No. 7, vii + 173 pp.

Goodman, S. M., & P. C. Gonzales. 1990. The birds of Mt. Isarog National Park, Southern Luzon, Philippines, with particular reference to altitudinal distribution.—Fieldiana, Zoology, New Series, No. 60, iv + 39 pp.

Graham, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes.—Journal of Mammalogy 64:559–571.

Heaney, L. R. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae).—Bulletin of the American Museum of Natural History, 206:145–167.

———, & E. A. Rickart. 1990. Correlations of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321–332 *in* G. Peters and R. Hutterer, eds., Vertebrates in the tropics. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 424 pp.

———, P. C. Gonzales, & A. C. Alcala. 1987. An annotated checklist of the taxonomic and conservation status of land mammals in the Philippines.—Silliman Journal 34:32–66.

———, P. D. Heideman, E. A. Rickart, R. B. Utzurrum, & J. S. H. Klompen. 1989. Elevational zonation of mammals in the central Philippines.—Journal of Tropical Ecology 5:259–280.

Heideman, P. D., & L. R. Heaney. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rainforest.—Journal of Zoology, London 218:556–586.

———, J. A. Cummings, & L. R. Heaney. 1993. Reproductive timing and early development in an Old World Fruit Bat, *Otopteropus cartilagonodus* (Megachiroptera).—Journal of Mammalogy 74:621–630.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies.—American Naturalist 100:419–424.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula.—Journal of Theoretical Biology 29:151–154.

Ingle, N. R., & L. R. Heaney. 1992. A key to the bats of the Philippines.—Fieldiana, Zoology, New Series, No. 69, iv + 44 pp.

Johnson, D. H. 1962. Two new murine rodents.—Proceedings of the Biological Society of Washington 75:317–319.

Kock, D. 1969. Eine bemerkenswerte neue gattung und art flughunde von Luzon, Philippinen.—Senckenbergiana Biologica 50:329–338.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, x + 179 pp.

Margalef, R. 1972. Homage to Evelyn Hutchinson, or why is there an upper limit to diversity.—Transactions of the Connecticut Academy of Arts and Sciences 44:211–235.

McCoy, E. D., & E. F. Connor. 1980. Latitudinal gradients in the species diversity of North American mammals.—Evolution 34:193–203.

McKitrick, M. C., & R. M. Zink. 1988. Species concepts in ornithology.—The Condor 90:1–14.

McNab, B. K. 1989. Temperature regulation and rate of metabolism in three Bornean bats.—Journal of Mammalogy 70:153–161.

Mudar, K. M., & M. S. Allen. 1986. A list of bats from northeastern Luzon, Philippines.—Mammalia 50:219–225.

Park, T. 1962. Beetles, competition and populations.—Science 138:1369–1375.

Patterson, B. D., P. L. Meserve, & B. K. Lang. 1989. Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile.—Journal of Mammalogy 70: 67–78.

Peet, R. K. 1974. The measurement of species diversity.—Annual Review of Ecology and Systematics 5:285–307.

Philippine Council for Agriculture and Resources Research, Soil and Water Resources Research Division. 1977. Map of monthly rainfall and cyclones in the Philippines, 2nd ed.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley Interscience, New York, 286 pp.

Pianka, E. R. 1983. Evolutionary ecology. Third edition. Harper & Row Publishers, Cambridge, Massachusetts, xii + 416 pp.

Rapoport, E. 1982. Areography: geographical strategies of species. Pergamon Press, New York, xvi + 269 pp.

Rickart, E. A., L. R. Heaney, & R. C. B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in Southeastern Luzon, Philippines.—Journal of Mammalogy 72:458–469.

Ripley, S. D., & J. T. Marshall, Jr. 1967. A new subspecies of flycatcher from Luzon, Philippine Islands (Aves, Muscicapinae).—Proceedings of the Biological Society of Washington 80:243–244.

Ruedas, L. A., & J. W. Bickham. 1992. Morphological differentiation between *Rhogeessa minutilla* and *R. tumida* (Mammalia: Chiroptera: Vespertilionidae).—Proceedings of the Biological Society of Washington 105:403–409.

SAS Institute, Inc. 1988a. SAS/STAT user's guide, release 6.03 edition. Cary, North Carolina, SAS Institute, Inc., 1028 pp.

———. 1988b. SAS procedures guide, release 6.03 edition. Cary, North Carolina, SAS Institute, Inc., 441 pp.

Schoener, T. W. 1983. Field experiments on interspecific competition.—American Naturalist 122: 240–285.

———. 1988. Ecological interactions. Pp. 255–297 *in* A. A. Myers and P. S. Giller, eds., Analytical biogeography; an integrated approach to the study of animal and plant populations. Chapman and Hall, New York, xiii + 578 pp.

Shannon, C. E. 1948. A mathematical theory of communication.—Bell System Technical Journal 27: 379–423.

Simpson, E. H. 1949. Measurement of diversity.—Nature 163:688.

Sokal, R. R., & F. J. Rohlf. 1981. Biometry, second edition. W. H. Freeman and Co., New York, xviii + 859 pp.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru.—Ecology 52: 23–40.

———. 1977. Bird species diversity on an Andean elevational gradient.—Ecology 58:1007–1019.

UNESCO/ECAFE. 1971. Geologic map of southeast Asia. United Nations Publication No. 69-30632.

Whitmore, T. C. 1984. Tropical rain forests of the Far East. Clarendon Press, Oxford, England, xvi + 352 pp.

Zar, J. H. 1984. Biostatistical analysis, 2nd. ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, xiv + 718 pp.

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