

SHORT COMMUNICATION

Altitudinal variation in the subcanopy fruit bat guild in Bioko Island, Equatorial Guinea, Central Africa

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Changes in a community or a guild along an environmental gradient reflect the effects of historical and ecological factors (Graham 1983). Knowledge of altitudinal changes in diversity, abundance and species composition of a biota improve our understanding of the environment/species interactions and altitudinal structuring of communities. The decline with altitude of species abundance and richness is described as a regular feature in natural communities. This observation has been explained by variations in environmental conditions, abrupt changes in habitats, reduction in food availability and competition (Graham 1983, 1990, Navarro 1991, Stevens 1992, Terborgh 1971, 1977) although the response to these variables seems to be specific for each group that has been considered (Owen 1990).

Studies relating bat communities to environmental gradients are rare, especially in tropical environments. In the Neotropics, Graham (1983, 1990) and Koopman (1978) considered biogeographical and evolutionary aspects of bat community changes along a gradient in the Peruvian Andes. Heaney *et al.* (1989) studied the elevational zonation of fruit bats in the Philippines, emphasizing the value of examining pteropodids in addressing ecological questions. There is no information on altitudinal variation in bat communities from Africa, but there are a few references to distributional ranges in altitude for some chiropteran taxa (e.g. Coe 1975, Eisentraut 1963, 1964, Verschuren 1976) and one detailed study at Mount Nimba (Liberia) (Wolton *et al.* 1982).

In this study we analyse variations in bat composition and richness within the subcanopy guild of fruit bats (Pteropodidae) in an altitudinal gradient on Bioko Island (Equatorial Guinea, Central Africa). This island, lying only 32 km

from the coast of Cameroon at 3° 48'–3° 12' N and 8° 25'–8° 57' E, shows a considerable altitudinal variation (over 3000 m) and supports a simplified bat community compared with the near-by mainland (Cameroon).

Bioko (2007 km²) is a volcanic island that emerged during the Pleistocene (Eisentraut 1963) associated with a rift that stretches across the Gulf of Guinea (Fuster 1955). This island has been connected to the continent several times in the recent past (Juste & Ibáñez 1993, Thys van den Andenauerde 1967) and, consequently, exhibits a noticeable continental character. The landscape is young with deep valleys and steep slopes reaching upwards to 3011 m on the Basilé peak (IGNE 1983).

The climate is typically equatorial with an annual average temperature around 25°C at sea level and over 5°C in the Basilé peak (Capuz 1961). Mean annual rainfall varies with local topography and altitude, and ranges from 10,000 mm in the southern slopes to 2000 mm in the north. Rainfall is concentrated mainly between June and October (Terán 1962).

Bioko's vegetation is structured along altitudinal rings and includes mainly the following associations (Butynski & Koster 1989, Guinea 1951, 1968, Juste 1992):

1. Lowland rainforest (0–800 m): the richest and most diverse formation with a canopy height reaching 40 m. The dominant tree species are *Ceiba pentandra*, *Pycnanthus angolensis*, *Erythrina senegalensis*, *Staudtia gabonensis*, *Sterculia acuminata*, *Clorophora excelsa* and several *Ficus* spp., all of which support lianes and a moderate epiphyte community. Most of this vegetation has been cleared and transformed into cacao agrosystems or food plantations including *Musa* spp, *Carica papaya*, *Mangifera indica* and other succulent fruit trees.
2. Montane forest (800–1400 m): a forest with a lower canopy than the former, relatively less diverse and nearly undisturbed by human activities. The dominant tree species include *Pycnanthus microcephala*, *Coelocaryon preusii*, *Sterculia oblonga* and *Clorophora regia*, with a proportional increase in lianes, epiphytes and tree ferns (*Cyathea usambarensis* and *C. manniana*).
3. Mossy forest (1400–2500 m): a low and dense forest typically composed of *Schefflera mannii*, *S. hierniana*, *Dracaena frangans* and *Ficus toningli*.
4. Shrubs (>2500 m): an area of dense vegetation up to 4 m in height, mainly consisting of *Hypericum lanceolatum*, *Agauria salicifolia* and *Philippia mannii*, which are carpeted with abundant mosses and lichens.

Seven fruit bat species have been recorded in Bioko (Eisentraut 1964). The large flying foxes *Hypsignatus monstrosus* and *Eidolon helvum* forage in the canopy and sometimes fly above it. The subcanopy guild consists of five species. Among these, *Myonycteris torquata* is uncommon (Eisentraut 1964, Juste 1990). *Rousettus aegyptiacus* and *Rousettus angolensis* are similar morphologically (Coe 1975) and have been considered as a single taxon in this study. Our study of the subcanopy fruit bat guild in Bioko is represented only by the small *Megaloglossus woermanni*, *Scotonycteris zenkeri* and the middle-size *Rousettus* spp.

From January 1990 to July 1992, bats were captured using two different size mistnets (12 m × 2.5 m and 6 m × 2.5 m) set in natural forests and cultivated areas (the latter only below 800 m). Netting was centred during the dry season in a range of altitudes from sea level to 2800 m. Nets were erected across trails among trees and operated in the same place up to three consecutive nights to minimize possible trap-shy effect (see Kunz & Kurta 1988). They were deployed for at least 12 hours (1800 h–0600 h). At dawn trapped bats were identified and released by the second author at the site of capture. Mistnets are poorly detected by Old World fruit bats and thus it can be assumed that differences in capture rates reflect real differences in densities (Heaney *et al.* 1989). In fact, Heideman & Heaney (1989), in their study in the Philippines, demonstrated a high correlation between net capture rates of Old World fruit bats and their density estimates from mark-and-recapture data. Recently, differences in mistnet bat captures have been used to detect levels of habitat disruption in the Neotropics (Fenton *et al.* 1992). In the present study, capture success was used as a relative index of abundance, defined as the length of mistnet in metres needed to capture an individual in the total subcanopy for each species. Contingency tables were used to test for significance in capture differences both between forest and agricultural areas and between altitudinal vegetation types. Confidence levels were adjusted by the Bonferroni procedure in multiple comparisons (Zar 1984). Shannon diversity index (H') was calculated for each environment and differences were tested by t-test (Magurran 1988).

A total of 5774 m of mistnet, set during 75 nights, captured a total of 608 fruit bats (Table 1). The diversity index (H') was significantly higher in cultivated areas than in the lowland rainforest ($t = 5.13$, $df = 292$, $P < 0.01$). These habitats differed in the composition of the subcanopy fruit bat guild ($\chi^2 = 51.29$, $df = 2$, $P < 0.001$) but showed a similar pattern of species abundance ($\chi^2 = 0.45$, $df = 1$, $P = 0.45$). Among vegetation types, the diversity of fruit bats reached its peak in the lowland rainforest and was significantly higher ($t = 4.26$, $df = 381$, $P < 0.01$) than in the mossy forest (Table 1).

Table 1. Subcanopy fruit bats captured on Bioko Island. The capture success, considered as the total metres of mistnet needed to capture an individual, is given within parentheses.

	Cultivated areas	Lowland rainforest	Montane forest	Mossy forest	Shrubs
<i>Rousettus</i> spp.	40 (29.00)	142 (13.74)	78 (13.05)	152 (6.71)	1 (504)
<i>Scotonycteris zenkeri</i>	29 (40.00)	14 (139.47)	0 (—)	0 (—)	0 (—)
<i>Megaloglossus woermanni</i>	61 (19.01)	46 (42.19)	7 (145.39)	38 (26.88)	0 (—)
Total	130 (8.92)	202 (9.66)	85 (11.97)	190 (5.25)	1 (504)
Nights	15	23	14	15	8
Diversity (H')	1.05238	0.76969	0.28447	0.05004	0
Mistnet metres	1160	1952	1018	1020	504
No. species	3	3	2	2	1

Species richness decreased with altitude but altitude was not significantly correlated with abundance either for the total bat abundance ($r_s = 0.085$, $z = 0.73$, $P = 0.68$) or for each species: *M. woermanni* ($r_s = 0.242$, $z = 2.08$, $P = 0.06$) and *Rousettus* spp. ($r_s = 0.03$, $z = 0.32$, $P = 0.48$). *Scotonycteris zenkeri* was netted only below 400 m, being captured more frequently in cultivated clearings ($\chi^2 = 16.43$, $df = 1$, $P < 0.001$) than in rainforests. *Megaloglossus woermanni* reached 1800 m and showed highest relative abundance also in cultivated areas compared with lowland rainforest ($\chi^2 = 17.11$, $df = 1$, $P < 0.001$). *Rousettus* spp. were present throughout the island up to 2800 m, but its abundance was significantly higher ($\chi^2 = 17.37$, $df = 1$, $P < 0.001$) in the rainforest than in the cultivated areas. Among vegetation types, the relative abundance of *M. woermanni* and *Rousettus* spp. was significantly higher ($\chi = 4.30$, $df = 1$, $P < 0.05$ and $\chi^2 = 21.29$, $df = 1$, $P < 0.001$, respectively) in the mossy forest (Table 1).

The present paucity of fruit bat species in Bioko Island is striking compared with records for the adjacent mainland of Cameroon, which is only 30 km away. The absence of *Micropteropus pusillus*, *Epomops franqueti* and other epomophorines in the Bioko's bat fauna is probably due more to extinction, related to the recent isolation of Bioko, than to competition processes (Juste 1990). Among the species present, *S. zenkeri* showed the lowest abundance and used the least ecological space. Wolton *et al.* (1982) only recorded this species below 800 m at Mount Nimba. *Megaloglossus woermanni* showed broader ecological preferences and was captured even higher (up to 2000 m) by Eisentraut (1964) than by us. *Rousettus* spp. were distributed throughout each of the plant associations and exhibited the highest ecological plasticity. Unfortunately, our data do not allow us to test for *R. angolensis* preference for high altitude as recorded elsewhere (Verschuren 1976, Wolton *et al.* 1982). Our results on subcanopy fruit bat distribution are consistent with those obtained in a former survey of Bioko fruit bats (Eisentraut 1964). Compared with altitudinal records in the nearby Mount Cameroon (Eisentraut 1963), our data show an apparent extension of the altitudinal ranges of *M. woermanni* and *Rousettus* spp. that may be due to an ecological expansion related to the impoverished fruit bat guild of Bioko. The absence of a correlation between capture success and altitude would indicate that fruit bat abundance is determined more by differences in habitat characteristics than by altitudinal variations in environmental factors. Among the different vegetation types, the two small fruit bats are clearly favoured by the high, soft food supply provided in agricultural areas, unlike *Rousettus* spp. which showed an opposite response. This could be related to a greater foraging preference (pers. obs.) upon wild fruits (mainly Moraceae). Finally, it is striking that the highest fruit bat density was reached in the mossy forest, almost twice the density observed in the lowland rainforest. As altitude does not seem to hinder fruit bat displacements (except for *S. zenkeri*), this could be explained by a relatively higher fruit production in this association during the driest months when bats were netted. Smythe (1970) found more constant availability of annual fruit crops in the highlands in a Neotropical wet forest during the dry months. Unfortunately, the

lack of phenological data on Bioko's flora impedes any verification of seasonal phenology.

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LITERATURE CITED

- BUTYNSKI, T. & KOSTER, S. 1989. The status and conservation of forest and primates on Bioko Island (Fernando Poo), Equatorial Guinea. Unpublished WWF Report, Uganda. 64 pp.
- CAPUZ, R. 1961. *Guía Meteorológica de las Provincias de Guinea*. Instituto de Estudios Africanos (Consejo Superior de Investigaciones Científicas), Madrid. 65 pp.
- COE, M. 1975. Mammalian ecological studies on Mount Nimba, Liberia. *Mammalia* 39:523-581.
- EISENTRAUT, M. 1963. *Die Wirbeltiere des Kamerungebirges*. Verlag P. Parey, Hamburg & Berlin. 353 pp.
- EISENTRAUT, M. 1964. La faune de chiroptères de Fernando-Po. *Mammalia* 28:529-552.
- FENTON, M. B., ACHARYA, L., AUDET, D., HICKEY, M. B. C., MERRIMAN, C., OBRIST, M. K., SYME, D. M. & ADKINS, B. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24:440-446.
- FUSTER, J. M. 1955. Vulcanología del Atlántico meridional. *Archivos Instituto Estudios Africanos* 33:67-79.
- GRAHAM, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64:559-571.
- GRAHAM, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* 17:657-668.
- GUINEA, E. 1951. Esquema de la vegetación de Fernando Po. *Conferencia Internacional de Africanistas Occidentales* (IV):41-45.
- GUINEA, E. 1968. Fernando Po. In Hedberg I. & Hedberg O. (eds). Conservation of vegetation in Africa south of the Sahara. *Acta Phytogeographica Suecica* 54:130-132.
- HEANEY, L., HEIDEMAN, P. D., RICART, E. A., UTZURRUM, R. B. & KLOMPEN, S. S. H. 1989. Elevational zonation of mammals in the Central Philippines. *Journal of Tropical Ecology* 5:259-280.
- HEIDEMAN, P. D. & HEANEY, L. R. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rainforest. *Journal of Zoology, London* 218:565-586.
- IGNE. 1983. *Mapa General de la República de Guinea Ecuatorial*. Instituto Geográfico Nacional de España. Madrid.
- JUSTE, J. 1990. Sistemática de los murciélagos de las islas oceánicas del golfo de Guinea. Unpublished PhD dissertation, University of Santiago. 362 pp.
- JUSTE, J. 1992. Zonación ecológica y evaluación del impacto ambiental de los usos actuales en la isla de Bioko. Unpublished FAO Report, Malabo. 75 pp.
- JUSTE, J. & IBAÑEZ, C. 1993. Geographic variation and taxonomy of *Rousettus aegyptiacus* (Mammalia: Megachiroptera) in the islands of the Gulf of Guinea. *Zoological Journal of the Linnean Society* 17:117-129.
- KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum Novitates* 2651:1-33.
- KUNZ, T. H. & KURTA, A. 1988. Capture methods and holding devices. Pp. 1-29 in Kunz, T. H. (ed.). *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC. 533 pp.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Croom Helm Limited, London. 179 pp.
- NAVARRO, S. A. G. 1991. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. *The Condor* 94:29-39.

- OWEN, J. G. 1990. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. *Journal of Mammalogy* 71:1-13.
- SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in Neotropical forest. *The American Naturalist* 104:25-35.
- STEVENS, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapaport's latitudinal rule to altitude. *The American Naturalist* 140:893-911.
- TERÁN De, M. 1962. *Síntesis geográfica de Fernando Poo*. Instituto de Estudios Africanos & I. Juan Sebastián Elcano (Consejo Superior de Investigaciones Científicas), Madrid. 117 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.
- TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.
- THYS VAN DEN ANDENAUERDE, D. F. E. 1967. The freshwater fishes of Fernando Poo. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen. Afdeling natuurkunde* 29:1-167.
- VERSCHUREN, J. 1976. Les cheiroptères du Mont Nimba (Liberia). *Mammalia* 40:615-632.
- WOLTON, R. J., ARAK, P. A., GODFRAY, H. C. J. & WILSON, R. P. 1982. Ecological and behavioral studies of the Megachiroptera at Mount Nimba, Liberia, with notes on Microchiroptera. *Mammalia* 46:421-448.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall International Editions, Englewood Cliffs, New Jersey. 718 pp.

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