Bat species diversity and distribution in three vegetation communities of Meru National Park, Kenya

Paul W. Webala[1]*, Nicholas O. Oguge[2] and Afework Bekele[3]

[1]National Museums of Kenya, PO Box 40658 Nairobi, Kenya, [2]Kenyatta University, PO Box 43844 Nairobi, Kenya and [3]Department of Biology, Addis Ababa University, PO Box 1176 Addis Ababa, Ethiopia

Abstract

Diversity and distribution of bats was determined in four vegetation types in and around Meru National Park, Kenya between September 2000 and February 2001. Bat-habitat studies were based on plant species dominance, cover and farming activities. Bats were captured using standard mist nets (18 m long × 2 m high) erected on poles averaging 3 m. Vegetation was broadly grouped as *Acacia* or *Combretum* wooded grassland, or *Acacia–Commiphora* bushland and studied using the Braun-Blanquet method. Analysis of floristic similarity showed five vegetation species assemblages in the three broad categories. Four hundred and ninety-five bats representing eleven genera in seven families were recorded. These were *Epomophorus labiatus*, *E. wahlbergi*, *Cardioderma cor*, *Lavia frons*, *Myotis welwitschii*, *Scotoecus hirundo*, *S. leucogaster*, *Pipistrellus kuhlii*, *Mops condylurus*, *Chaerephon bemmeleni*, *Mormopterus* sp., *Hipposideros caffer*, *H. commersoni*, *Nycteris arge* and *Rhinolophus landeri*. This was the first record of *N. arge*, *M. welwitschii*, *C. bemmeleni* and a *Mormopterus* species in eastern Kenya. The *Combretum* community was most equitable ($E = 0.51$) with nine bat species records, while farming areas had only four. The low species richness and increased dominance of a few generalist species on farms may be indicative of different levels of disturbance.

Key words: bat, diversity, distribution, habitat, Meru, Kenya

Résumé

On a déterminé la diversité et la distribution des chauves-souris dans quatre types de végétation dans et autour du Parc National de Meru, au Kenya, entre septembre 2000 et février 2001. Les études de l'habitat des chauves-souris se basaient sur la dominance et le couvert de certaines espèces végétales et sur les activités agricoles. On a capturé les chauves-souris en utilisant les filets standards (18m de long sur 2 m de haut) fixés sur des piquets d'environ 3 m de haut. La végétation fut grossièrement regroupée en prairie arborée à Acacia ou à Combretum, ou en brousse à Acacia-Commiphora, et étudiée suivant la méthode Braun-Blanquet. L'analyse des similarités floristiques a montré cinq assemblages d'espèces végétales dans ces trois grandes catégories. On a relevé 495 chauves-souris représentant onze genres appartenant à sept familles. Ce sont: *Epomophorus labiatus*, *E. wahlberghi*, *Cardioderma cor*, *Lavia frons*, *Myotis welwitschii*, *Scotoecus hirundo*, *Scotophilus leucogaster*, *Pipistrellus kuhlii*, *Mops condylurus*, *Chaerephon bemmeleni*, *Mormopterus* sp., *Hipposideros caffer*, *H. commersoni*, *Nycteris arge* et *Rhinolophus landeri*. Ce sont les premiers cas rapportés pour *N. arge*, *M. welwitschii*, *C. bemmemeni* et pour une espèce de *Mormopterus* dans l'est du Kenya. La communauté à Combretum était la plus équitable ($E = 0,51$), avec neuf espèces de chauves-souris rapportées, alors que les aires cultivées n'en comptaient que quatre. La faible richesse en espèces et la dominance croissante de quelques espèces généralistes dans les fermes pourraient indiquer divers degrés de perturbation.

Introduction

Savannah woodlands cover most of sub-Saharan Africa and support a diverse bat fauna (White, 1983). These ecosystems are increasingly being affected by human settlement, land-use practices, and fuel-wood off take [World Resources Institute (WRI), 1992]. Ecosystem disturbance can reduce biodiversity and modify community structures (Lawton *et al.*, 1998). In the fragile savannah woodlands, fires, humans or elephants may contribute to such perturbations. Although little is known about the specific char-

Correspondence: Tel: +254 20 3741424; Fax: +254 20 3742161; E-mail: pwebala@hotmail.com

acteristics of roost sites, the loss of large trees and snags because of above factors is expected to decrease roosting sites of bats and increase distances to foraging areas (Fenton *et al.*, 1998). Movement between roosting and foraging sites may demand high energetic costs affecting reproductive success (Barclay, 1989). Because of size and mobility, bats are variously susceptible to disturbance and like in other mammalian groups, larger species tend to have bigger home ranges than smaller ones (Fenton, 1997).

Relatively little literature is available on the ecology and conservation of Kenyan small mammals (Aggundey & Schlitter, 1984). This is particularly true for bats where most of the literature is in checklists and museum voucher specimens where information on taxonomy and geographic distribution may be inferred. Bats are difficult to survey thoroughly and apparent patterns might result as much from sampling bias or fragmentary distributional information as from real differences in species richness across sub-regions (Lim & Engstrom, 2001).

Meru National Park is one of the 27 conservation areas under the management of the Kenya Wildlife Service. This park of 870 km^2 constitutes a highly heterogeneous ecosystem, as evidenced by different vegetation communities that support a wide array of herbivores, carnivores and about 300 species of birds. It occurs in an area with one of the highest human population densities in the country and a population largely dependent on subsistence agriculture. This has led to continual breaches of park regulations by the local community seeking out bush-meat, honey, medicinal plants and wood products, thereby enhancing uncontrolled fires in the park. Our study examined the effects of vegetation disturbance on the distribution and diversity of bats in this conservation area. In particular, we explored differences in bat abundance and diversity in different plant communities. Herein, we report results of our survey of bats in three vegetation communities in the park and on farmed lands in adjacent areas with implications for the conservation of this park.

Materials and methods

Bat survey

This report stems from fieldwork carried out from September 2000 to February 2001 in Meru National Park (0°20′N and 0°10′S; 38°0′E and 38°25′E). Six representative sites for bat surveys were selected from each of three natural vegetation types in the park: (i) *Acacia–Commiphora* bushland, (ii) *Combretum* wooded grassland and (iii) *Acacia* wooded grassland (Ament, 1975); and six adjacent agro-systems [i.e. banana, vegetable, *Catha edulis* (Vahl) Forssk. ex Endl., sorghum, maize and a grazing field] (Fig. 1). Each site in the natural vegetation was subdivided into six trapping stations, 100 m apart giving 36 stations per community type. Bats were captured using mist nets set in the different microhabitats. Bats flying below 3 m were caught with two-ply braided nets with a 36-mm mesh of 50-denier nylon (18 m long × 2 m high) erected on poles. Because of a limited number of nets available, sampling was systematic between and within habitats. Save for the *Combretum* community that had a trap-line of 360 m, other vegetation communities and agrosystems had a total of 576 m each. Nets were typically set across flyways such as streams or dry riverbeds, trails, clearings or forest gaps. Nets were opened between 18.00 and 22.00 h at each site for two consecutive trapping nights.

Captured bats were identified to species level (Meester & Setzer, 1971; Kingdon, 1997) and sample specimen collected for identity confirmation. All specimens have been deposited at the National Museums Kenya (NMK). Morphometric measurements (in mm) and mass (in g) were obtained from all captures. These included the total length (TL), length of tail (LT), length of hind foot (HF), length of forearm (FA), length of ear (E) and mass (M) (Nagorsen & Peterson, 1980). Sex, age, and reproductive condition were also obtained from the collected specimen. Fluid-preserved specimens were fixed in 10% buffered (sodium phosphate) paraformaldehyde and preserved in 70% ethyl alcohol. Tissue samples of collected specimens are preserved in 25% dimethyl sulfoxide (DMSO)/EDTA in concentrated sodium chloride and are available for DNA studies. The netting site and the microhabitat type were recorded for each animal.

Microhabitat and species diversity studies

A transect was established in each of the three vegetation communities. Along each transect, fifteen sampling plots, each 20 × 10 m, were randomly selected giving 45 sampling plots for the entire park. Using the modified Braun-Blanquet cover/abundance scale, each plant species (shrubs and trees) in each plot was assigned a cover/abundance rating (Mueller-Dombois & Ellenberg, 1974; Green, 1979).

An accumulation curve of the number of bat species against net length was plotted to assess the completeness of the survey. Species diversity for the different veget-
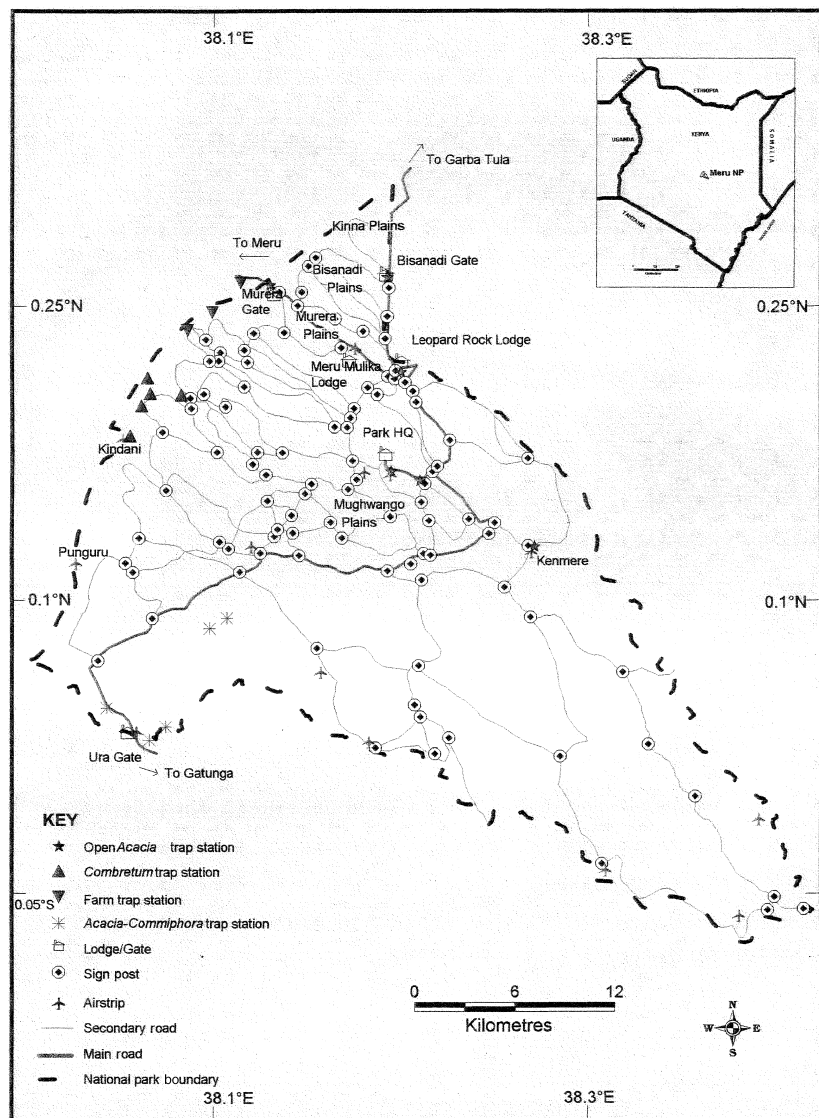
Fig 1 Map of Meru National Park showing study sites

ation communities was computed using the modified inverse of Simpson-Yule diversity of concentration, *C*, for equally abundant species (Dustan & Fox, 1996). For purposes of comparison, the Shannon's index, *H'*, was also determined. To determine similarities in vegetation (species presence/absence, abundance) at all localities, detrended correspondence analysis (DCA) was applied using CANOCO Version 4.0 (ter Braak, 1987). Further classification was made using SYNTAX (Podani, 1988). Detrended canonical correspondence analysis (DCCA) was applied in assessment of bat-habitat association (ter Braak, 1988). To determine the bat–plant species relationship, the Shannon–Wiener (*H'*) index (Krebs,

1999) was determined for plant and bat species. A correlation analysis was then used to assess any association between heterogeneity of bat communities with the five plant species assemblages identified by the SYNTAX analysis.

Bat species richness for Meru National Park was estimated using (i) the Jackknife estimate for quadrat counts (Krebs, 1999) estimated by $\hat{S} = s + (n - 1/n)k$, where $\hat{S}$ is the Jackknife estimate of species richness, *s* is the actual number observed, *n* total number of quadrat samples, and *k* number of unique species; and (ii) Chao's statistics (reviewed in Burton & Engstrom, 2001) estimated by the formula $S^* = S_{obs} + (a^2/2b)$, where S^* is the expected
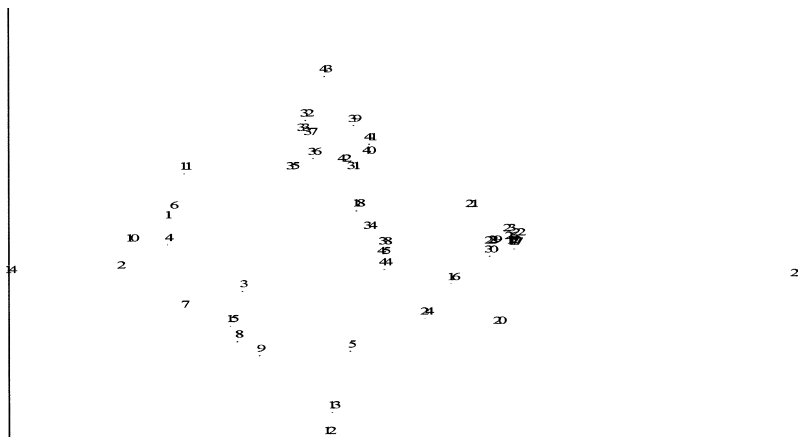
Fig 2 Detrended correspondence analysis (DCA) ordination diagram from the three vegetation communities: plots 1–15, *Acacia* Wooded Grassland; plots 16–30, *Combretum* Wooded Grassland; 31–45, *Acacia–Commiphora* bushland

number of species, S_{obs} is the actual number of species observed, a is the number of species caught only once, and b is the number of species caught only twice. In order to compare bat diversity for different vegetation communities within the park, the lognormal estimations were computed and Simpson's equitability index determined (Begon *et al.*, 1986; Krebs, 1999).

Results

A cover/abundance rating (Braun-Blanquet) was recorded for 134 plant species in 45 plots, 15 each, for *Acacia* wooded grassland, *Combretum* wooded grassland and *Acacia–Commiphora* bushland. Three plant species assemblages were identified according to their floristic similarity (Fig. 2) and five from the SYNTAX analysis at dissimilarity level of above 0.7 (Fig. 3). The three corresponded to *Acacia* wooded grassland, *Combretum* wooded grassland and *Acacia–Commiphora* bushland. Dissimilarity dendrogram separated the *Combretum* (node 5) from *Acacia* (nodes 1 and 2) and *Acacia–Commiphora* (nodes 3 and 4) communities (Fig. 3). Heterogeneity (H') indices within these assemblages for nodes 1 and 2 (*Acacia*), node 3 (*Acacia–Commiphora*) and node 5 (*Combretum* community), respectively, were 2.50, 3.05, 3.81 and 3.85.

Four hundred and ninety-five bats comprising 15 species (Table 1) were recorded in 48 trap nights covering a total trap-length of 2088 m in three vegetation communities within the park and on adjacent farms. Information on the species accounts is detailed below.
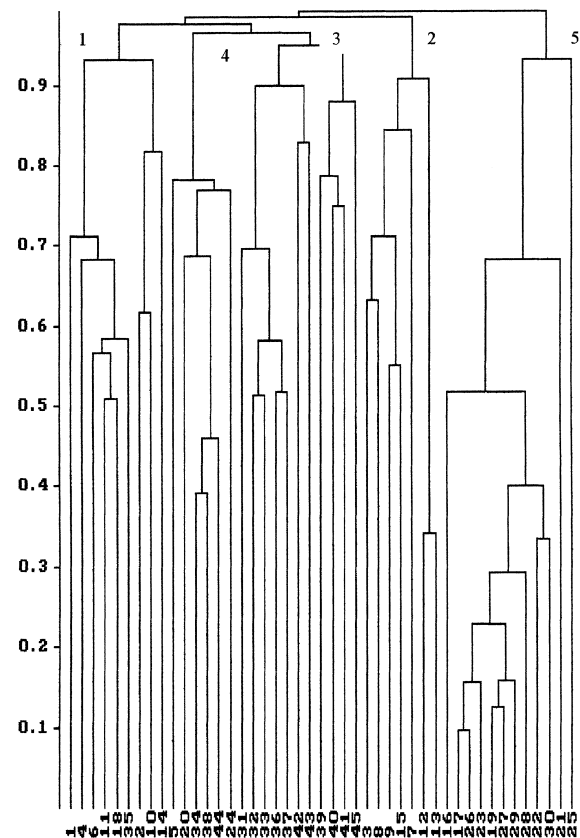

Fig 3 Dendrogram of species assemblages of vegetation (*y*-axis represents the dissimilarity level while the *x*-axis represents the assemblages). Nodes 1 and 2 refer to *Acacia* wooded grassland; nodes 3 and 4 to *Acacia–Commiphora* bushland; while node 5 to *Combretum* wooded grassland

Table 1 Distribution and proportional abundance of bats in *Acacia* woodland, *Combretum* wooded grassland, *Acacia–Commiphora* bushland and agrosystems in and around Meru National Park. Vegetation communities were grouped dependent on dominant plant species

| Family | Species | Vegetation community/farms | | | | |
		Acacia	*Combretum* community	*Acacia–Commiphora* bushland	Farms	Total
Hipposideridae	*Hipposideros caffer*	1	2	3	0	6
	Hipposideros commersoni	0	13	0	0	13
Megadermatidae	*Cardioderma cor*	5	4	11	7	27
	Lavia frons	2	0	0	0	2
Molossidae	*Chaerephon bemmeleni*	0	0	9	0	9
	Mormopterus species	0	2	0	0	2
	Mops condylurus	102	0	0	0	102
Nycteridae	*Nycteris arge*	0	0	2	0	2
Pteropodidae	*Epomophorus labiatus*	72	30	74	30	206
	Epomophorus wahlbergi	3	29	44	4	80
Rhinolophidae	*Rhinolophus landeri*	0	1	0	0	1
Vespertilionidae	*Myotis welwitschii*	0	0	1	0	1
	Scotoecus hirundo	3	31	2	0	36
	Pipistrellus kuhlii	0	0	0	3	3
	Scotophilus leucogaster	0	3	2	0	5
	Total (individuals)	188	115	148	44	495
	Observed species richness	7	9	9	4	15

Species accounts

Family Hipposideridae. Hipposideros caffer (Sundevall, 1846): specimens examined (2) – from the *Combretum* and *Acacia–Commiphora* communities.

External measurements and mass for the two males were: TL 81, 82; LT 31, 32; HF 8, 9; E 10, 11; FA 46, 48; M 10.

Hipposideros commersoni (E. Geoffrey, 1813): specimens examined (5) – from the *Combretum* community only.

Range of external measurements and mass for the five males are as follows: TL 152–165; LT 37–45; HF 23–25; E 29–32; FA 97–100; M 83–108.

Family Megadermatidae. Cardioderma cor (Peters, 1872): specimens examined (8) – from all vegetation communities and the farm.

Range of external measurements and mass for two females and six males, respectively, are as follows: TL 79–100, 72–112; HF 16–20, 16–21; E 40, 31–40; FA 56, 54–58; M 25–32; 22–30.

Lavia frons (E. Geoffrey, 1810): specimens examined (1) – from the *Acacia* woodland.

External measurements and mass of this male was TL 64; HF 17; E 41; FA 58; M 20.

Family Molossidae. Chaerephon bemmeleni (Jentink, 1879): specimens examined (3) – from the *Acacia–Commiphora* bushland.

Range of external measurements and mass for two females and two males, respectively, are as follows: TL106–110, 108–115; LT 46, 45–48; HF 13, 12; FA 46–47, 46–47; E 19–20, 19–21; M 17–20; 19 (one male).

Mops condylurus (A. Smith, 1833): specimens examined (17) – from the *Acacia* woodlands.

Range of external measurements and mass from eight females and nine males, respectively, are as follows: TL 107–126, 115–126; LT 43–61, 46–52; HF 12–15, 12–18; FA 44–49, 47–52; E 16–18, 17–19; M 21–24, 19–30.

Mormopterus species: specimens examined (2) – from the *Combretum* woodland.

External measurements and mass for the two males were: TL 93; LT 34–35; HF 10; FA 33–37; E 17; M 14–15.

Family Nycteridae. Nycteris arge (Thomas, 1903): specimens examined (2) – from the *Acacia–Commiphora* bushland.

External measurements and mass for the two males examined were: TL 101,100; LT 50; HF 10; FA 43, 42; E 28; M 9, 8.

Family Pteropodidae. Epomophorous labiatus (Temminck, 1837): specimens examined (7) – from all vegetation communities and farm.

Range of external measurements and mass for five females and two males, respectively, are as follows: TL 69–101, 94–97; HF 16–19, 18; FA 41–62, 58–61; E 16–21, 21; M 21–41, 40–41.

Epomophorous wahlbergi (Sundevall, 1846): specimens examined (7) – from all vegetation communities and farms.

Range of external measurements and mass for five females and two males, respectively, are as follows: TL 118–150, 125–150; HF 20–24, 19–22; FA 75–85, 78–85; E 21–25, 20–29; M 60–100, 62–106.

Family Rhinolophidae. Rhinolophus landeri (Martin, 1838): Specimens examined (1) – from the *Combretum* community.

External measurements and mass for the female are as follows: TL 78; LT 23; HF 10; FA 46; E 20; M 13.

Family Vespertilionidae. Myotis welwitschii (Gray, 1866): specimens examined (1) - from the *Acacia–Commiphora* bushland.

External measurements and mass for the female are as follows: TL 137; LT 68; HF 14; FA 58; E 22; M 15.

Pipistrellus kuhlii (Kuhl, 1817): specimens examined (3)- from the farms.

External measurements and mass for one male and two females, respectively, are as follows: TL 38, 36, 36; LT 29, 28, 28; HF 10, 10, 9; E 7, 7, 6; FA 34, 32, 30; M 7, 5, 4.

Scotoecus hirundo (de Winton, 1899): specimens examined (6) – from the three natural communities.

External measurements and mass for three females and males, respectively, are as follows: TL 41–92, 55–91; LT 27–35, 29–35; HF 7–11, 9–11; FA 31–34, 34–39; E 9–12; M 9–16, 11–13.

Scotophilus leucogaster (Cretzschmar, 1826): specimens examined (2) – from the *Combretum* and *Acacia–commiphora* communities.

External measurements and mass for two males are as follows: TL 115, 120; LT 46, 51; HF 11, 11; E 15, 16; FA 46, 49; M 19, 20.

Nine species were recorded in each of the *Combretum* and the *Acacia–Commiphora* bushland communities seven in *Acacia* wooded grassland and four on farms. The cumulative bat species richness in the region peaked at 15 after a trap-length of 1600 m and remained the same following another 400 m of mist net-trapping (Fig. 4).
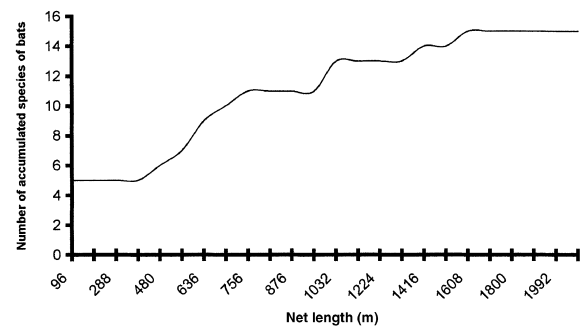

Fig 4 Species accumulation curve for bats in relation to net-length in Meru National Park and adjoining farms

Statistical prediction of total bat species richness (±SEM) based on Jackknife estimate was 21.8 (±1.44) with a range, at 95% confidence limit, of 17.2–26.3 species. The more conservative Chao's statistics gave an estimate of 15.7 species and the lognormal distribution, 17.5 species with equitability of 0.27. Lognormal species estimates and equitability for the different communities were 10.6 ($E = 0.32$), 10.1 ($E = 0.32$), 9.6 ($E = 0.51$) and 4.0 ($E = 0.5$) for *Acacia–Commiphora*, *Acacia*, *Combretum* and farmlands, respectively. Most species of bats were associated with *Combretum* wooded grassland ($H' = 3.85$, node 5 of Fig. 3), more and *Acacia–Commiphora* bushland ($H' = 3.81$, node 3) than with *Acacia* wooded grassland ($H' = 2.50$ for node 1; $H' = 3.05$ for node 2). This association was highly significant ($r = 0.99$, $P < 0.01$, n = 4).

Discussion

Five plant species assemblages identified from SYNTAX analysis and the three identified by DCA ordination corresponded closely with the broad classification of vegetation at Meru National Park by Ament (1975). These were *Acacia* wooded grassland, *Acacia–Commiphora* bushland and *Combretum* wooded.

There were 15 species of bats in seven families recorded following a net-trap length of 2088 m. These were *C. cor*, *Epomophorus labiatus*, *E. wahlbergi*, *H. caffer*, *H. commersoni*, *L. frons*, *M. welwitschii*, *N. arge*, *P. kuhlii*, *R. landeri*, *S. hirundo*, *S. leucogaster*, *M. condylurus*, *C. bemmeleni* and *Mormopterus* sp. (Table 1). We therefore report the first records of *N. arge*, *M. welwitschii*, *C. bemmeleni* and a *Mormopterus* species in eastern Kenya although further taxonomic work may be necessary for the latter species. These bats represent the only species flying up to 3 m
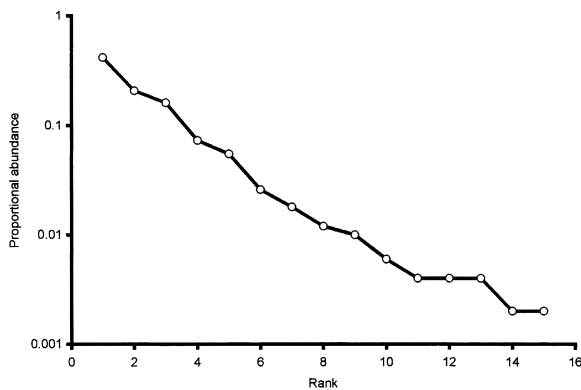
Fig 5 Analysis of the bat community of the Meru National Park, Kenya. The rank-abundance diagram shows a geometric relationship with a low equitability of 0.27

above ground. Canopy bats or those with other ranging habits may not be adequately represented.

We used a simple method to estimate relative completeness of this survey in Meru National Park. This involved a species accumulation curve based on capture effort (Fig. 4). Our curve did not only reach an asymptote but also levelled off suggesting that the species we recorded approaches the actual number of bats (Burton & Engstrom, 2001) trappable by this method. Statistical prediction based on Jackknifing, however, estimated 22 species while the more conservative estimate by Chao's technique was 16 species of bats. The lognormal estimate was 17 species and the low equitability of 0.27 suggests a more geometric than broken-stick model in explaining bat heterogeneity (Begon *et al.*, 1986) in Meru National Park (Fig. 5). An earlier study (Williams, 1981) recorded fourteen species of which eleven were recorded in the present study. Although our finding of 15 species is close to those predictable by Chao's statistics and lognormal distribution, the jackknifing statistics may provide a plausible estimate to actual bat species richness in this instance. However, As Chao's statistic provides a better estimation for relatively species poor communities (Colwell & Coddington, 1994), our sampling may be considered reasonable for species trappable up to 3 m in this savannah ecosystem. It is noteworthy that a survey of bats at ground level underestimates the presence of molossids that often forage for insects above the canopy (Rautenbach *et al.*, 1996; Fenton & Griffin, 1997; Kalko, 1997). Mist nets may also under-represent some species known to be adept fliers, such as vespertilionids (Aldridge & Rautenbach, 1987; Rautenbach *et al.*, 1996; Kalko, 1997) and emballonurids (Kalko, 1997). A study of

acoustic versus capture techniques (mist nets and double frame harp-traps) in the south-western United States also found that captures accounted for 63.5% and acoustic sampling 86.9% of the combined species present (O'Farrell & Gannon, 1996). Thus, for an exhaustive survey of bats, a combination of techniques, including acoustic sampling, is necessary.

Our study of bat distribution and abundance indicate that *R. landeri* and *M. welwitschii* were rare spatially and numerically, being represented by only one individual each in *Combretum* and *Acacia–Commiphora* communities, respectively (Table 1). *Lavia frons*, *Mormopterus* sp. and *P. kuhlii* were similarly unique with two or three individuals being captured in the *Acacia* and *Combretum* communities and the farmland, respectively. *Mops condylurus*, *H. commersoni* and *C. bemmeleni* showed clumped distribution being recorded, respectively, in the *Acacia*, *Combretum* and *Acacia–Commiphora* communities yet relatively abundant locally. Three species, *C. cor*, *E. labiatus*, and *E. wahlbergi* were widespread and common.

We measured heterogeneity between vegetation communities using the lognormal distribution (Krebs, 1999). This predicted even distribution comprising 10 species within the different vegetation communities but only four in farmlands. Sampling of bats in the *Acacia* wooded grassland was done after a long period of drought that may explain the observed lower species richness. In a study in the Miombo Woodlands of northern Zimbabwe, bat species composition did not differ significantly between intact and impacted sites (Fenton *et al.*, 1998). However, smaller species (<10 g) were affected more by the loss of canopy trees than larger ones. In the present study, such species were only captured in natural vegetation but not on farms. The DCCA ordination analysis showed that bats were associated more with *Combretum* wooded grassland and *Acacia–Commiphora* bushland than with *Acacia* wooded grassland. This may be an artefact of the temporal factors associated with our study but may also indicate relative levels of disturbances among vegetation communities in the park. In general, bat species diversity increased with increasing plant species diversity in four of the five vegetation assemblages recorded (Table 2). This association could be explained best by an exponential model ($r = 0.99$, $P < 0.01$, n = 4) and demonstrate the importance of vegetation diversity in the maintenance of diverse chiropteran assemblages.

Our study has shown significant reduction of bat diversity in farming systems outside Meru National Park

Table 2 Relationship between bat and plant species diversity

Plant species assemblage	Community type	Bat Species Diversity (H')	Plant Species Diversity (H')
1	*Acacia*	0.85	3.05
2	*Acacia*	0.78	2.50
3	*A. -Commiphora*	1.36	3.81
4	–	–	2.88
5	*Combretum*	1.70	3.85

compared with natural communities within it. This may be an indication of habitat disturbance involving removal of key bat resources such as canopy trees and snags leading to loss of optimal roosting sites near foraging sites. As different species respond differently to habitat modification or disturbance, the more generalist ones have colonized all habitat types including farms. The more specialized species showed characteristics of rarity in space and abundance. Such species are likely to be more affected by environmental perturbations, especially those driven anthropologically. One such impact includes uncontrolled burning because of illegal activities such as bush meat extraction or wood product harvesting. Controlled burning to allow regeneration of grasses and herbs for herbivores also needs to be carefully planned to preserve unique microhabitats. As our work is not exhaustive, future work should include a variety of techniques including (i) sub-canopy and canopy trapping, (ii) roost locations using radio-tracking techniques, and (iii) echolocation. This may help elucidate the direct effects of canopy cover removal on bats and other vertebrates.

Acknowledgements

References

AGGUNDEY, I.R. & SCHLITTER, D.A. (1984) Annotated Checklist of the Mammals of Kenya: Chiroptera. *Ann. Carn. Mus.* **53**, 119–161.

ALDRIDGE, H.D.J.N. & RAUTENBACH, L.I. (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* **56**, 763–778.

AMENT, J.G. (1975) The vascular plants of Meru National Park, Kenya: Part 1. A preliminary survey of the vegetation. *J. East Africa Nat. Hist. Soc. Nat. Mus.* **154**, 1–10.

BARCLAY, R.M.R. (1989) The effect of reproductive condition on the foraging behaviour of female hoary bats, Lasiurus cinereus. *Behav. Ecol. Sociol.* **24**, 31–37.

BEGON, M., HARPER, J.L. & TOWNSEND, C.R. (1986) *Ecology: Individuals, Populations and Communities*. Sinauer Associates Inc., Sunderland.

TER BRAAK, C.J.F. (1987) The Analysis of vegetation-environment relationship by canonical correspondence analysis. *Vegetation* **69**, 69–77.

TER BRAAK, C.J.F. (1988) Canoco – a FORTRAN Program for Canonical Community Ordination by (partial) (detrended) (canonical) Correspondence Analysis, Principal Component Analysis, and Redundancy Analysis (Version 2.1). Technical report LWA-88–02. Agricultural Mathematics Group, Wageningen.

BURTON, K.L. & ENGSTROM, M.D. (2001) Species diversity of bats (Mammalia: Chiroptera) in Iwokrama Forest, Guyana, and the Guianan subregion: implications for conservation. *Biodiv. Cons.* **10**, 613–657.

COLWELL, R.K. & CODDINGTON, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B.* **345**, 101–118

DUSTAN, C.E. & FOX, B.J. (1996) The effects of fragmentation and disturbance of rainforests on ground dwelling small mammals on the Robertson Plateau New south Wales Australia. *J. Biogeogr.* **23**, 187–201.

FENTON, M.B. (1997) Science and the conservation of bats. *J. Mammal.* **78**, 1–14.

FENTON, M.B. & GRIFFIN, D.R. (1997) High-altitude pursuit of insects by echolocating bats. *J. Mammal.* **78**, 247–250.

FENTON, M.B., CUMMING, D.H.M., TAYLOR, D.R., RAUTENBACH, L.I., CUMMING, S.G., CUMMING, S.M., FORD, G., DUNLOP, J., HOVORKA, D.M., JOHNSTON, S.D., PORTFORS, V.C., KALCOUNIS, C.M. & MAHLANGA, Z. (1998) Bats and the loss of tree canopy in African woodlands. *Cons. Biol.* **12**, 399–407.

GREEN, R.H. (1979) *Sampling Design and Statistical Methods for Environmental Biologists*. Wiley, New York.

KALKO, E.K.V. (1997) Diversity in tropical bats. Tropical biodiversity and Systematics. In: *Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems* (Ed. H. ULRICH). pp. 13–43. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

KINGDON, J. (1997) *The Kingdon Field Guide to African Mammals.* Harcourt Brace and Company. pp. 364.

KREBS, C. (1999) *Ecological Methodology*, 2nd edn. Benjamin Cummings, Menlo Park.

LAWTON, J.H., BIGNELL, D.E., BOLTON, B., BLOEMERS, G.F., EGGLETON, P., HAMMOND, P.M., HODDA, M., HOLTS, R.D., LARSEN, T.B., MAWDSLEY, N.A., STORK, N.E., SRIVSTAVA, D.S. & WATT, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391, 72–75.

LIM, B.K. & ENGSTROM, M.D. (2001) Species diversity of bats (Mammalia: Chiroptera) in Iwokrama Forest, Guyana, and Guianan subregion: implications for conservation. *Biodiv. Cons.* 10, 613–657

MEESTER, J. & SETZER, W.H. (1971) *The Mammals of Africa, an Identification Manual.* Smithsonian Institution Press, Washington, USA.

MUELLER-DOMBOIS, D. & ELLENBERG, H. (1974) *Aims and Methods of Vegetation Ecology.* John Wiley & Sons, Uppsala, Sweden.

NAGORSEN, D.W. & PETERSON, L.R. (1980) *Mammal Collector's Manual. A Guide for Collecting, Documenting, and Preparing Mammal Specimens for Scientific Research.* Life Sciences Miscellaneous Publications, Royal Ontario Museum, Toronto. pp. 79.

O'FARRELL, J.M. & GANNON, L.W. (1996) A comparison of acoustic versus capture techniques for the inventory of bats. *J. Mammal.* 80, 24–30.

PODANI, N. (1988) Syntax III. A package of program for data analysis in community ecology and Systematics. *Coe.* 3, 111–119.

RAUTENBACH, I.L., FENTON, M.B. & WHITING, M.J. (1996) Bats in riverine forest and woodlands: a latitudinal transect in southern Africa. *Can. J. Zool.* 74, 312–322.

WHITE, F. (1983) *The Vegetation of Africa.* United Nations Educational, Scientific and Cultural Organization, Paris, France.

WILLIAMS, J. (1981) *National Parks of East Africa.* William Collins Sons & Co Ltd., London, UK.

World Resources Institute (WRI). (1992) *World Resources 1992–1993.* Oxford University Press, New York and Oxford.

(Manuscript accepted 23 July 2003)