

Bat species diversity and distribution in a disturbed regime at the Lake Bogoria National Reserve, Kenya

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Abstract

Human population growth drives intrusion and progressive conversion of natural habitats for agriculture. We evaluated human impacts on bat species diversity and distribution among four vegetation types in and around Lake Bogoria National Reserve between November 2012 and July 2013. Plants were surveyed using the Braun–Blanquet cover/abundance method, whereas bats were sampled using standard mist nets erected on poles at ground level. Floristic similarity analysis revealed three broad vegetation assemblages, namely riverine vegetation, farmland and *Acacia* woodland/*Acacia–Commiphora* woodland. Two hundred and 33 bats representing eleven species in eleven genera and seven families were recorded. These were *Epomophorus minimus*, *Rhinolophus landeri*, *Hipposideros caffer*, *Cardioderma cor*, *Lavia frons*, *Nycteris hispida*, *Chaerephon pumilus*, *Mops condylurus*, *Neoromicia capensis*, *Scotoecus hirundo* and *Scotophilus dinganii*. Species richness estimators indicated that sampling for bats at ground level was exhaustive. Bat species richness and diversity were highest in the more structurally complex *Acacia* woodland compared to more homogenous farmlands where we recorded only common and generalist species that often occur in open habitats. The higher bat species richness and diversity in the *Acacia* woodland as compared to farmland underscore the importance of remnant natural savannah woodlands in the conservation of bats and other elements of biodiversity.

Key words: abundance, bats, Bogoria, disturbance, species diversity

Résumé

La croissance démographique entraîne des intrusions et une conversion progressive d'habitats naturels en terres

agricoles. Nous avons évalué les impacts humains sur la diversité et la distribution d'espèces de chauves-souris dans quatre types de végétation dans et autour de la Réserve Nationale du Lac Bogoria, entre novembre 2012 et juillet 2013. Les plantes ont été étudiées par la méthode d'abondance-dominance de Braun-Blanquet, et les chauves-souris ont été échantillonnées au moyen de filets japonais fixés sur des piquets au niveau du sol. Une analyse de similarité floristique a révélé l'existence de trois grands assemblages de végétation, à savoir une végétation riveraine, des exploitations agricoles et des forêts soit à *Acacia* seul, soit mêlées *Acacia-Commiphora*. Nous avons enregistré 233 chauves-souris représentant 11 espèces de 11 genres et sept familles. Ce sont *Epomophorus minimus*, *Rhinolophus landeri*, *Hipposideros caffer*, *Cardioderma cor*, *Lavia frons*, *Nycteris hispida*, *Chaerephon pumilus*, *Mops condylurus*, *Neoromicia capensis*, *Scotoecus hirundo* et *Scotophilus dinganii*. Des estimateurs de richesses en espèces ont indiqué qu'un échantillonnage de chauves-souris au niveau du sol était exhaustif. La richesse et la diversité des espèces de chauves-souris étaient les plus élevées dans la forêt d'acacias, structurellement plus complexe, par rapport aux terres agricoles, plus homogènes, où nous n'avons enregistré que des espèces communes et généralistes que l'on trouve souvent dans des habitats ouverts. La richesse et la diversité plus élevées dans la forêt à acacias que sur les terres agricoles soulignent l'importance des vestiges de forêts naturelles de savane pour la conservation des chauves-souris et d'autres éléments de la biodiversité.

Introduction

One of the most universal features of global biodiversity is the variability of species richness across different regions. Bats represent more than 20% of all mammal species

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(Simmons, 2005), making them the second largest mammal group with over 1,300 species currently known worldwide (Fenton & Simmons, 2014). As the only group of mammals capable of sustained flight with diversified foraging and dispersal capabilities, bats can exploit many ecological resources (Kunz & Pierson, 1994; Patterson, Willig & Stevens, 2003; Denzinger & Schnitzler, 2013). Nevertheless, they remain poorly studied (Monadjem *et al.*, 2010) and misunderstood, particularly in Africa (Voigt & Kingston, 2016). For instance, detailed data on bat ecology, including distributional patterns, are usually poorly known (Happold & Happold, 2013). Yet, knowledge about species richness and diversity is crucial for conservation and management of biodiversity (Margules & Pressey, 2000). An urgent need is for more precision in the measurement of biodiversity and more consistency in mapping it across regions and biomes. To address this gap, there is need to allocate more resources to the collection of field records of species and other biodiversity features (Margules & Pressey, 2000).

In Africa, public perceptions of biodiversity are dominated by charismatic megafauna, overshadowing an appreciation of less conspicuous fauna that may have equal or even greater ecological importance. Bats perform important roles in agriculture (Boyles *et al.*, 2011; Kunz *et al.*, 2011; Ghanem & Voigt, 2012), forestry (Fleming & Muscarella, 2007), and may be a concern for public health (Wibbelt *et al.*, 2010; Luis *et al.*, 2013). Kenya has a diverse bat fauna; more than 108 bat species have been described and constitute a major part of Kenya's biodiversity (Patterson & Webala, 2012). Yet, little is known about their taxonomy and distribution, let alone their responses to habitat loss. As in other African countries (Fenton *et al.*, 1998), Kenyan bats face severe threats, including loss of critical roosting and foraging sites due to forest clearance, charcoal production, and logging and conversion of remnant natural habitats such as savannahs into farmlands and settlements. Numerous studies have documented bat species richness and distribution at varied scales in East Africa (e.g. Kingdon, 1974; Aggundey & Schlitter, 1984; Kityo & Kerbis, 1996; Thorn & Kerbis, 2009), West Africa (e.g. Monadjem *et al.*, 2013; Kangoyé *et al.*, 2015), Central Africa (e.g. Monadjem *et al.*, 2010) and South African countries (e.g. Taylor, 2000; Monadjem & Reside, 2008; Monadjem *et al.*, 2010). However, due to varying levels of human-induced habitat modifications, it is difficult to predict bat species diversity based on such previous studies (Gorresen & Willig, 2004; Davy, Russo & Fenton, 2007).

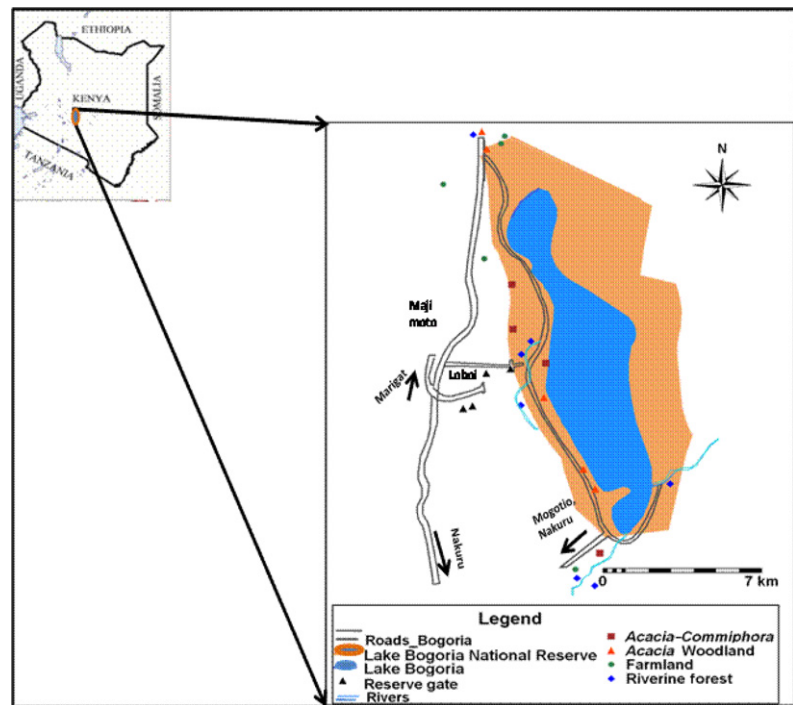
Previous studies on Kenya's bat species diversity and distribution patterns were compiled in checklists and reviews (Harrison, 1960; Aggundey & Schlitter, 1984; Patterson & Webala, 2012). Additional bat surveys were recently conducted at Meru National Park (Webala, Oguge & Bekele, 2004), eastern Lake Turkana (Webala, Carugati & Fasola, 2010) and western Kenya (Webala, Musila & Makau, 2014). Together, these studies offer the foundation to develop a more detailed and informative study to unravel knowledge gaps in bat biology. On the basis of previous studies, Kenya harbours one of Africa's richest bat faunas (Patterson & Webala, 2012). Given Kenya's high bat richness, it is imperative that more studies document bat occurrence and distribution in additional regions, including protected areas. We investigated impacts of human-induced habitat modifications on bat species richness and diversity at the Lake Bogoria National Reserve (LBNR), a protected savannah type of biome in Kenya's Rift Valley (Johansson & Svensson, 2002). The reserve is subject to immense pressures from human activities because it is an important source of medicinal plants, firewood, charcoal, timber and honey. Furthermore, overgrazing by both livestock and wild herbivores increasingly denudes the area of vegetation, a situation made worse by occasional long droughts. We compared bat species richness and diversity in four vegetation types, namely *Acacia* woodland, *Acacia-Commiphora* woodland, riverine vegetation and farmlands at LBNR, and assessed associations between the bats and plant species assemblages. We hypothesized that rich and more heterogeneous habitats should have higher bat species richness and diversity.

Material and methods

Study area

Lake Bogoria National Reserve (LBNR) (0°15'N; 36°06'E) is located within Kenya's Great Rift Valley (Fig. 1) at an elevation of 990 m above sea level. LBNR is bounded by rocky escarpments that rise to the east and west, reaching over 1500 m above sea level. The topography of the area is characterized by rugged hills, rocky outcrops, deep valleys and incised gullies some over 3 m deep and, cut into fine textured alluvial soil. The climatic conditions are harsh with mean annual temperatures of 23–25°C (Ashley *et al.*, 2002). Rainfall is erratic and highly localized. The yearly average for the foothills varies between 1000 and

Fig 1 Location of the study area and sampling sites at LBNR and adjacent farmland. Inset is a map of Kenya showing the location of Lake Bogoria National Reserve



1500 mm, and for lowlands, between 300 and 700 mm annually, with most of the rain falling from May to August and in light showers, during November and December. The combination of weather variables and physiographic location gives the lake basin a hot, semiarid climate (De Groot, Field-Juma & Hall, 1992).

The natural vegetation at LBNR is dominated by trees and shrubs and naturally vegetated grassland with some *Acacia*-dominated thorn bush, but this gradually changes to deciduous and semideciduous bushland with a number of common tree species such as *Acacia tortilis*, and *A. mellifera* and common genera such as *Commiphora*, *Terminalia* and *Combretum*. The riverine vegetation is dominated by *Ficus sycomorus* and *F. capensis* mixed with some *Acacia* and *Terminalia* tree species. Sustained grazing by livestock and wild herbivores may have contributed to encroachment of *Acacia nubica* and *A. reficiens* as well as the invasive *Prosopis juliflora* which has become thick and impenetrable in some places, and has suppressed growth of grass and most ephemeral herbaceous species (Marangu *et al.*, 2008). On the basis of species dominance, the sites were subjectively classified into three broad vegetation types: *Acacia* woodland, *Acacia-Commiphora* woodland and riverine vegetation. In contrast, the areas around LBNR are dominated by farmlands where such common

plants as maize, bananas and fruit orchards are well established.

Field methods

Vegetation surveys. We established one (4-km) transect in each of the four vegetation types within the reserve and adjacent farmland. Along each transect, ten sampling plots, each 20 m × 10 m, were randomly selected giving a total of 40 sampling plots. Each plot was at least 500 m from the nearest sampling point. A field determination of the principal plants was based on the standard field guides (Noad & Birnie, 1989; Dharani, 2002). Using the modified Braun-Blanquet Cover/Abundance Scale, each woody plant species (including shrubs and trees) in each plot was assigned a cover/abundance rating (Causton, 1988).

Bat sampling. Bats were captured between 2012 (November and December) and 2013 (January, February, March, May, June and July) using standard mist nets (12 m long × 2 m high) deployed at ground level across potential flyways (dry river beds, open vegetation gaps and trails) at four sites in each vegetation type. At each site, six mist nets (set approximately 200 m apart) were set for four

consecutive nights along the transects for vegetation surveys. Nets were opened at 1830 h and monitored at intervals of 15 min to avoid injuries and/or to reduce cases of bat predation in the nets. Sampling was carried out systematically between and within habitats. Nights with full moon or bright moonlight was avoided due to potential reduced capture rates resulting from lunar phobia by many bats (Kunz, Tidemann & Richards, 1996; Meyer, Schwarz & Jacob, 2004; Larsen *et al.*, 2007).

Bats were released at the point of capture within 12 h. Data collected from each captured bat included species, age (juvenile, subadult, adult), sex, mass (to nearest 0.2 g using a Pesola spring balance) and reproductive condition. We determined the male and female reproductive condition by examining the position of scrotum (abdominal or scrotal) and palpating the abdomen and inspecting the mammae, respectively (Racey, 1988), and determined age class by examining the degree of epiphyseal–diaphyseal fusion (Anthony, 1988). All handling techniques and sampling were carried out according to the standards established by American Society of Mammalogists (Sikes & Gannon, 2011).

Captured bats were held individually in cloth bags and identified from external characters using available taxonomic nomenclature (e.g. Patterson & Webala, 2012). However, because it was not possible to accurately identify all species in the field, a few individuals of each species were collected and retained as museum vouchers to document captured species and to clarify their identification. Voucher specimens are deposited in the collection of the Mammalogy Section of the National Museums of Kenya. For each specimen, morphometric measurements were taken, which include total length (including tail), head-and-body length (excluding tail), tail length, hind foot length, forearm length, ear length and tragus length, all to the nearest millimetre (following Webala, Oguege & Bekele, 2004).

Data analyses

To determine similarities in vegetation (species presence, abundance) at all localities, cluster analysis was applied. A correlation analysis was then used to assess the relationship between bat assemblages and identified plant species assemblages. Bat species diversity for the different vegetation types was computed using the modified inverse of Simpson–Yule diversity of concentration, C , for equally abundant species calculated as:

$D = \frac{1}{\sum p_i^2}$ (Dustan & Fox, 1996), where D = Simpson's diversity index, p_i is the proportional abundance of the i th species, given by $p_i = n_i/N$, $i = 1, 2, 3 \dots S$. S = species richness which equals to the total number of species in a community, n = number of individuals of i species and N = total number of individuals.

Evenness of each assemblage was calculated using indices derived from the reciprocal Simpson index ($E_{1/D}$), where evenness is expressed as a number between 0 (only one species present) and 1 (all species equally abundant):

$$D = 1 - \left[\frac{\sum n(n-1)}{N(N-1)} \right].$$

Estimates of species richness at all study sites were based on capture data using five models (Jackknife 1, ACE, Bootstrap, Chao1 and Chao2) from the program EstimateS 9.0; (Colwell, 2005). All indices were corrected for sampling bias using the jackknife technique (Magurran, 2004), and 95% confidence intervals (CI) computed accordingly. Differences in bats captures in the four broad vegetation types were assessed using one-way ANOVA, with vegetation type and bat captures as the predictor and dependent variables, respectively. To assess the completeness of the survey and standardize comparisons of different species, an accumulation curve of the number of bat species against number of sites was plotted.

Results

Vegetation structure

Field determinations of the principal plants revealed 52 plant species (Table 1). Three plant species assemblages were identified according to their floristic similarity using cluster analysis. While riverine vegetation (node 1) and farmland (node 2) grouped separately, *Acacia* woodland is grouped together with *Acacia–Commiphora* woodland (node 3) (Fig. 2). Indeed, heterogeneity for Simpson and Shannon indices within the four prior assemblages of riverine vegetation, *Acacia* woodland, *Acacia–Commiphora* woodland and farmland was 2.580 (0.863), 2.962 (0.906), 2.917 (0.915) and 1.646 (0.778), respectively (Table 1). Further support for the similarity in plant diversity between the four vegetation types assessed was found in the Simpson evenness measures and equitability indices (Table 1).

Bat records

Two hundred and 33 bats comprising eleven species from seven families were recorded during 64 trapping nights in

Table 1 Plant species sampled in different vegetation types at the LBNR and farmland

Plant species	<i>Acacia</i> woodland	<i>Acacia-Commiphora</i>	Riverine Vegetation	Farmland
<i>Acacia brevispica</i>	—	*	*	—
<i>A. gerrardii</i>	*	*	—	—
<i>A. mellifera</i>	*	*	*	—
<i>A. nilotica</i>	*	*	*	—
<i>A. senegal</i>	*	*	—	—
<i>A. tortilis</i>	*	*	*	*
<i>A. ruficiens</i>	*	*	*	—
<i>Prosopis juliflora</i>	*	—	*	—
<i>Terminalia brownii</i>	—	—	*	—
<i>T. kilimandscharica</i>	*	*	—	—
<i>T. spinosa</i>	*	*	*	—
<i>Salvadora persica</i>	*	*	*	*
<i>Warburgia ugandensis</i>	*	*	—	—
<i>Gardenia ternifolia</i>	*	*	—	—
<i>Cissus rotundifolia</i>	*	*	*	—
<i>Sesbania sesban</i>	*	*	—	—
<i>Tamarindus Indica</i>	*	*	*	—
<i>Commiphora africana</i>	*	*	—	—
<i>C. edulis</i>	—	*	—	—
<i>C. samharansis</i>	*	*	*	—
<i>Pistacia aethiopica</i>	*	*	—	—
<i>Maerua angolensis</i>	—	—	*	—
<i>Euphorbia scarlatina</i>	*	*	—	—
<i>Ziziphus mucronata</i>	*	—	*	—
<i>Rhus natalensis</i>	*	—	—	—
<i>Olea europaea</i>	*	*	*	*
<i>Euphorbia tirucalli</i>	—	—	*	—
<i>Ficus capensis</i>	—	—	*	—
<i>F. sycomorus</i>	—	—	*	—
<i>Hibiscus indica</i>	—	—	*	—
<i>Kigelia africana</i>	*	*	*	—
<i>Cissus quadrangularis</i>	*	*	*	—
<i>Ipomoea spp</i>	*	*	—	—
<i>Senna singueana</i>	—	*	*	—
<i>Boscia salicifolia</i>	*	—	—	—
<i>Vepris glomerata</i>	*	—	—	—
<i>Indigofera sp</i>	—	—	*	—
<i>Cordia africana</i>	*	*	*	—
<i>Zanthoxylum gillettii</i>	—	—	*	—
<i>Croton dichogamous</i>	*	—	*	—
<i>Musa sapientum</i>	—	—	—	*
<i>Capparis fascicularis</i>	*	—	—	—
<i>Mangifera indica</i>	—	—	—	*
<i>Lantana camara</i>	*	—	*	*
<i>Crateva adansonii</i>	—	—	*	—
<i>Combretum molle</i>	—	*	—	—
<i>Aloe vera</i>	*	*	*	—
<i>Opuntia stricta</i>	*	*	*	—
<i>Adenia venenata</i>	*	—	*	—

(continued)

Table 1 (continued)

Plant species	<i>Acacia</i> woodland	<i>Acacia-Commiphora</i>	Riverine Vegetation	Farmland
<i>Themeda triandra</i>	*	*	*	
<i>Phyllanthus sepialis</i>	*	*	–	–
<i>Zea mays</i>	–	–	–	*
Taxa_S	36	31	32	7
Individuals	141	115	125	44
Shannon_H	2.962	2.917	2.580	1.646
Simpson_1-D	0.906	0.915	0.863	0.778
Evenness_e ^{H/S}	0.537	0.596	0.413	0.741
Pielou's Evenness: <i>J'</i>	0.827	0.850	0.745	0.846

*species present, -species absent.

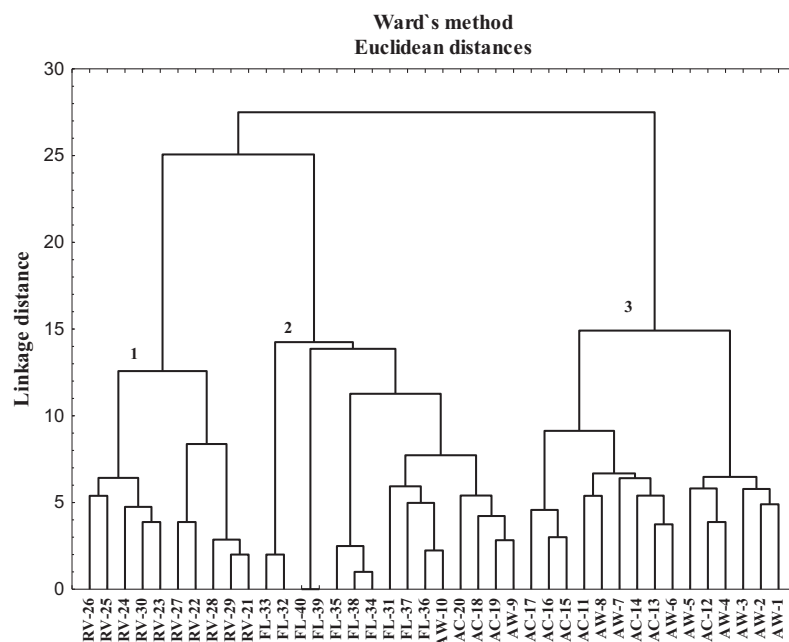


Fig 2 Dendrogram of species assemblages of vegetation (*y*-axis represents the dissimilarity level, while the *x*-axis represents the assemblages). Node 1 clusters riverine vegetation (RV) sites; node 2 farmland (FL); node 3 *Acacia* woodland/*Acacia-Commiphora* woodland (AW and AC respectively)

three vegetation types within LBNR and farmland (Table 3). The range of morphometrics and mass of different sexes for each species are shown in Table 2. In all, ten species were recorded in *Acacia* woodland, six in *Acacia-Commiphora* woodland, seven in riverine vegetation and five from the farmlands (Table 3).

Bat species richness and diversity

Sorensen classic indices (0.80) show bat diversity across habitat sites varied significantly ($F_{3, 15} = 3.698$ $P = 0.043$). Although it had a relatively low number of captures, *Acacia*

woodland recorded the highest bat species diversity and evenness. In contrast, farmlands recorded the lowest species richness diversity and evenness but with highest number of captures of only two generalist species, *Epomophorus minimus* and *Cardioderma cor* (Table 3). Estimations of total bat species richness for the area were Jackknife 1 mean (11.94), abundance-based cover estimate means (11.34), bootstrap (11.66), Chao1 (11) and Chao2 (11). The species accumulation curves for all sampled sites combined did not reach an asymptote but had begun to level off (Fig. 3). Differences in bat captures among the four vegetation types were insignificant ($F_{3, 15} = 6.908$).

Table 2 Range of external measurements of specimens collected from LBNR for both males and females (n = number of specimens, FA = forearm length, TTL = total length, TL = tail length, RHF = right hind foot length, EL = ear length, Tr = tragus length, all in mm, and WT = weight of specimen in grams)

Family	Species	n	Sex	FA	TTL	TL	RHF	EL	Tr	WT
Pteropodidae	<i>Epomophorus minimus</i>	41	M	54–63	86–117	–	18–20	18–20	–	23–44
		36	F	54–64	83–107	–	18–19	18–20	–	21–40
Rhinolophidae	<i>Rhinolophus landeri</i>	2	M	44–45	71–77	24–27	9–10	17–18	7–8	6–8
Hipposideridae	<i>Hipposideros caffer</i>	1	F	50	84	36	8	17	–	8
Megadermatidae	<i>Cardioderma cor</i>	47	M	53–57	63–80	–	18–21	35–38	17–20	18–34
		59	F	53–60	67–80	–	18–21	35–39	17–20	21–37
		4	M	57–61	63–73	–	16–19	36–39	26–28	18–28
	<i>Lavia frons</i>	8	F	57–64	63–71	–	17–19	35–38	27	19–25
Nycteridae	<i>Nycteris hispidus</i>	3	M	43–44	35–51	30	9–10	28	5–6	6–8
		2	F	43–45	50	31	10	28–29	5–8	8–9
Molossidae	<i>Chaerephon pumilus</i>	9	M	30–46	78–113	31–42	7–13	16	1–3	9–22
		4	F	37–47	79–111	31–40	9–13	15–18	1–3	9–23
		4	M	45–48	103–107	33–36	9–14	10–13	–	19–26
Vespertilionidae	<i>Neoromicia capensis</i>	1	M	33	79	34	8	4	–	4
		1	F	31	82	31	7	7	–	4
	<i>Scotoecus hirundo</i>	6	M	32–33	87–90	28–36	7–8	5–6	–	4–9
		2	M	51–52	126–127	54	9	7	3	22–23
	<i>Scotophilus dinganii</i>	3	F	53–56	129–131	54	7–12	7–9	2	17–22

Association between bat species and plant species assemblages

Analysis of plant species diversity (Table 1) for the three vegetation types within LBNR and farmland showed comparatively similar diversities (*Acacia* woodland, $D = 2.962$; *Acacia-Commiphora* woodland, $D = 2.917$; riverine vegetation, $D = 2.580$). Conversely, the plant diversity on adjacent farmland was lower ($D = 1.646$). Lack of correlation between plant and bat diversities ($r = 0.17$, $n = 16$, $P = 0.5 > 0.05$) indicated no significant difference between vegetation types.

Discussion

Three broad plant species assemblages identified by cluster analysis were riverine vegetation, farmland and *Acacia* woodland/*Acacia-Commiphora* woodland. However, from preliminary observations, the latter was comprised of sections where plants of the genus *Acacia* were dominant and others consisted of a mixture of both *Acacia* and *Commiphora* plants. Results of the bat species richness and diversity at LBNR are therefore discussed following the aforementioned coarse vegetation classification.

Eleven bat species belonging to eleven genera and seven families were confirmed to occur at LBNR. These were *Epomophorus minimus*, *Rhinolophus landeri*, *Hipposideros*

caffer, *Cardioderma cor*, *Lavia frons*, *Nycteris hispidus*, *Chaerephon pumilus*, *Mops condylurus*, *Neoromicia capensis*, *Scotoecus hirundo* and *Scotophilus dinganii*.

A species accumulation curve of the number of bat species plotted against number of sites did not reach an asymptote but had begun to level off, suggesting that the species recorded approximate number trappable by this method (Colwell, Mao & Chang, 2004). Statistical estimations of total bat species richness were close to the actual number of species recorded in this study, suggesting that the sampling was adequate for species that are trappable using ground-based mist nets. Subcanopy and canopy bats or even high fliers that forage beyond the canopy may not be adequately represented or be absent altogether because they flew above ground-level mist nets (Simmons & Voss, 1998; Meyer *et al.*, 2011). Furthermore, an important assumption used in many mist nets studies is that all bat species have the same likelihood of capture. The reality, though, is that not all bat species have the same probability of being trapped due to differences in behaviour among species (e.g. Kunz, Tidemann & Richards, 1996; Kuenzi & Morrison, 1998). Mist nets are known to be biased against some species groups (Lang *et al.*, 2004) such as rhinolophids, nycterids, some hipposiderids and vespertilionids that are adept at detecting and avoiding

Table 3 Distribution and proportional abundance of bats in four broad vegetation types at Lake Bogoria National Reserve, November 2012–July 2013

Family	Species	Acacia woodland	Acacia-Commiphora woodland	Riverine vegetation	Farmland	Total
Pteropodidae	<i>Epomophorus minimus</i> Claesen and De Vree, 1991	7	8	35	27	77
Rhinolophidae	<i>Rhinolophus landeri</i> Martin, 1838	2	0	0	0	2
Hipposideridae	<i>Hipposideros caffer</i> (Sundevall, 1846)	0	1	0	0	1
Megadermatidae	<i>Cardioderma cor</i> (Peters, 1872)	13	26	10	57	106
	<i>Lavia frons</i> (E. Geoffroy, 1810)	5	3	4	0	12
Nycteridae	<i>Nycteris hispida</i> (Schreber, 1775)	1	0	3	1	5
Molossidae	<i>Chaerephon pumilus</i> (Cretzschmar, 1830–1831)	10	1	2	0	13
	<i>Mops condylurus</i> (A. Smith, 1833)	4	0	0	0	4
Vespertilionidae	<i>Neoromicia capensis</i> (A. Smith, 1829)	1	1	0	0	2
	<i>Scotoecus hirundo</i> (de Winton, 1899)	1	0	3	2	6
	<i>Scotophilus dinganii</i> (A. Smith, 1833)	2	0	2	1	5
	Total (individuals)	46	40	59	88	233
	Observed species richness (S)	10	6	7	5	11
	D	5.72	2.13	2.55	1.94	3.09
	Evenness (E)	0.847	0.599	0.681	0.517	0.614

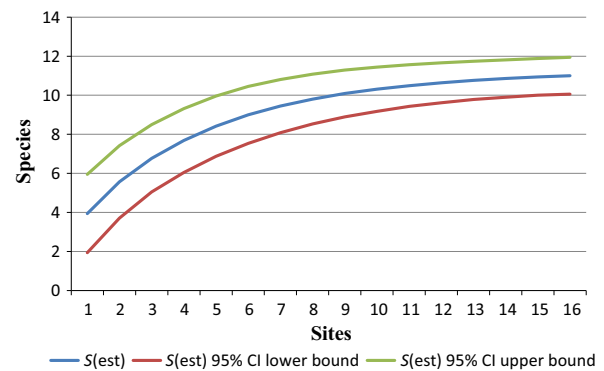


Fig 3 Site-based rarefaction curve of species accumulation at the LBNR and adjacent farmland, between November 2012 and July 2013

mist nets (Kunz, Tidemann & Richards, 1996; MacSwiney *et al.*, 2008). Therefore, a combination of methods, including acoustic sampling using bat detectors, and use of harp traps as suggested by O'Farrell & Gannon (1999) and Meyer *et al.*, 2011, could have provided a more complete characterization of the bat species assemblage at LBNR.

This study indicated that *Hipposideros caffer*, *Rhinolophus landeri* and *Neoromicia capensis* were all numerically and spatially rare but all are known to be highly adept at avoiding mist nets (Aldridge & Rautenbach, 1987). This result may therefore be an artefact of sampling bias where patchily distributed species may appear rare if sampling fails (Kingston *et al.*, 2003), or may also be indicative of relative levels of anthropogenic disturbances among vegetation types and/or sites. Disturbance may limit the availability of suitable roosting and/or foraging sites (Medellín, Equihua & Amin, 2000). However, depending on size, flight mobility allows bats to forage in a mosaic of habitats, making roost sites crucial for the survival of bats in an area (Brigham & Fenton, 1986; Vonhof & Barclay, 1996). Different bat species roost in different structures but common roosts include caves, tree hollows, under tree bark, in tree foliage and rock crevices, among others (Kunz, 1982). At LBNR, older trees with hollows and defoliating bark are selectively cut for charcoal burning, and this could certainly affect roost sites for species such as *Neoromicia capensis*. Likewise, the occasional rising water levels of the lake lead to submerged sections of vegetation cover, causing tree suffocation.

Differences in actual bat species richness and diversity were quite evident, perhaps reflecting differential levels of

human disturbance in the area. The *Acacia* woodland recorded the highest number of species, evenness and diversity. This can be attributed to higher habitat variability that included more foraging and roosting sites. Conversely, farmlands recorded the least number of species, evenness and diversity. The farms were less diverse in terms of habitats and plant species (Table 1), with only a few isolated trees within crop monocultures of bananas and maize, probably providing few roosting sites near suitable foraging sites. There were no significant differences in total number of captured bats ($P > 0.05$) among the four vegetation types. However, *Cardioderma cor* and *Epomophorus minimus* were ubiquitous and the most commonly caught species, occurring at all of the four vegetation types. Both species are generalists, adapted to a wide range of environmental circumstances and food sources (Mickleburgh, Hutson & Bergmans, 2001), and neither is adept at avoiding mist nets and thus are easy to capture using mist nets. *C. cor* is known to roost in single groups of up to 80 individuals on their own or with other species in caves (Csada, 1996) and hollow trees (Vaughan, 1976) and exploits a wide range of food items ranging from small vertebrates such as smaller bats and frogs to moths, beetles and even centipedes and scorpions (Vaughan, 1976). Similarly, *E. minimus* is distributed widely in dry savannah habitats and feeds on a wide variety of fruits (Mickleburgh, Hutson & Bergmans, 2001). In this study, *E. minimus* was abundant in the farmland but also in the riverine vegetation probably because of the availability of fruit orchards and fruiting trees, especially of the genus *Ficus*, which may allow large populations to persist in the area (Mickleburgh, Hutson & Bergmans, 2001). These two generalist species may be more prevalent in modified habitats as they are less likely to be affected by habitat disturbance or are more likely to recolonize after disturbance (Hansson, 1991). The ecosystem at LBNR favoured these common generalists, with other species rarer, perhaps because they were sampled in suboptimal habitats (Grindal & Brigham, 1998). *Nycteris hispida*, *Scotoecus hirundo* and *Scotophilus dinganii* were also distributed widely, albeit in small numbers, in all vegetation types. The presence of *Nycteris hispida* species in all vegetation types may be explained by the availability of roost sites, while *Scotoecus hirundo* and *Scotophilus dinganii* may have been commuting looking for food sources. Clutter-sensitive species (e.g. rhinolophids and hipposiderids) are, however, generally more sensitive to habitat disturbance (Furey, Mackie & Racey, 2010). Even

though some species such as *H. caffer* and *S. dinganii* are known to utilize roosts in abandoned man-made structures, their susceptibility to landscape fragmentation (Medellín, Equihua & Amin, 2000) could explain their rarity or low numbers at the LBNR. Up until the late 2000s, LBNR experienced intense grazing pressure through livestock farming. Such activities often result in dense clumps of woody vegetation through bush encroachment among other anthropogenic disturbances. However, sampling considerations for rare, elusive and nocturnal animals preclude an incontrovertible conclusion.

This study also showed that more heterogeneous vegetation types with higher plant species diversity supported higher bat species diversity. For instance, *Acacia* woodland, with higher plant species diversity, also recorded highest bat species diversity. In general, however, there was no significant difference in bat species richness and distribution patterns, suggesting that despite differing disturbance levels, bats can persist in such modified habitats. These findings corroborate with other studies where many bat species can persist in disturbed landscapes (Schulze, Seavy & Whitacre, 2000). This apparent tolerance to human-driven habitat disturbance is explained by the ability of bats to cross habitat boundaries and to fly over open areas to reach resources that are patchy in space and time (Fenton, 1997).

In conclusion, there were substantial differences in species richness and diversity at LBNR with *Acacia* woodland recording especially rare and more specialist species than farmlands, which recorded only generalist species. The presence of only a few generalist species on the farmlands may be an indication of habitat disturbance, where key bat resources such as cavity bearing trees are removed, leading to loss of suitable roosting sites near foraging sites (Fenton *et al.*, 1998). While the more generalist species colonized all habitat types including farms, specialized ones exhibited characteristics of rarity in space and abundance. Such species are likely to be more affected by environmental perturbations, especially those driven anthropologically (Webala, Oguge & Bekele, 2004).

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