

# Effects of habitat fragmentation on the bats of Kakamega Forest, western Kenya

Paul W. Webala<sup>1,\*</sup> , Jeremiah Mwaura<sup>2</sup>, Joseph M. Mware<sup>2</sup>, George G. Ndiritu<sup>2</sup> and Bruce D. Patterson<sup>3</sup>

## Research Article

**Cite this article:** Webala PW, Mwaura J, Mware JM, Ndiritu GG, and Patterson BD. Effects of habitat fragmentation on the bats of Kakamega Forest, western Kenya. *Journal of Tropical Ecology* <https://doi.org/10.1017/S0266467419000221>

Received: 13 September 2018

Revised: 25 June 2019

Accepted: 25 June 2019

### Keywords:

Bats; foraging mode; forest use; habitat fragmentation; tropical rain forest

### Author for correspondence:

\*Paul W. Webala,  
Email: [paul.webala@gmail.com](mailto:paul.webala@gmail.com)

<sup>1</sup>Maasai Mara University, Department of Forestry and Wildlife Management, P.O. Box 861, Narok 20500, Kenya; <sup>2</sup>Karatina University, School of Natural Resources and Environmental Studies, P.O. Box 1957, Karatina 10101, Kenya and <sup>3</sup>Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA

### Abstract

Habitat loss and fragmentation are major threats to biodiversity worldwide, and little is known about their effects on bats in Africa. We investigated effects of forest fragmentation on bat assemblages at Kakamega Forest, western Kenya, examining captures at edge and interior locations in three forest fragments (Buyangu, 3950 ha; Kisere, 400 ha; and Malava, 100 ha) varying in forest area and human-use regimes. Basal area, canopy cover, tree density and intensity of human use were used as predictors of bat abundance and species richness. A total of 3456 mist-net hours and 3168 harp-trap hours resulted in the capture of 4983 bats representing 26 species, eight families and four foraging ensembles (frugivores, forest-interior insectivores, forest-edge insectivores and open-space insectivores). Frugivores were frequently captured at the edges of the larger, better-protected forests, but also in the interior of the smaller, more open fragment. Forest-interior insectivores and narrow-space foragers predominated in the interiors of larger fragments but avoided the smallest one. Forest specialists showed positive associations with forest variables (canopy cover, basal area and tree density), whereas frugivores responded positively to the human-use indicators. On these bases, specialist species appear to be especially vulnerable to forest fragmentation.

## Introduction

Globally, tropical forests are being lost at unprecedented rates (Hansen *et al.* 2013), leading to fragmentation, degradation and loss of habitat for many organisms (Barlow *et al.* 2016). Such changes influence the structure and composition of biological communities, often reducing local species richness and diversity, habitat connectivity, and consequently gene flow, the adaptive capacity of species and the integrity of ecosystems (Fahrig 2003, Laurance *et al.* 2011). Landscape-level effects of deforestation are manifested in smaller fragment areas, greater isolation and a proliferation of edge effects (Andr n 1994, Ewers & Didham 2006). Additionally, the remaining forest fragments may be continually degraded by such practices as selective logging (Hill & Hamer 2004, Morris 2010).

Bats (Mammalia: Chiroptera) are taxonomically and ecologically diverse, especially in the tropics. They utilize diverse roosting structures and a wide range of diets (Kunz & Pierson 1994, Meyer *et al.* 2008) and their sensitivity to anthropogenic alterations in habitat quality makes bats valuable indicators of habitat disruption (Jones *et al.* 2009, Sherwin *et al.* 2013). Forest fragmentation, selective logging and other forms of human disturbance can induce major changes in the distribution and abundance of bat species (Meyer *et al.* 2016). At the landscape scale, remaining patches of forest may become too small, too isolated, and too influenced by edge effects to maintain viable populations of some bat species (Meyer *et al.* 2008). However, not all bat species or functional groups are disadvantaged by human influences, and some species remain unaffected (Presley *et al.* 2008) or may even benefit from human disturbance (Farneda *et al.* 2015, Garc a-Garc a *et al.* 2014, Gorresen & Willig 2004). Most studies of fragmentation effects on tropical bats have been concentrated in South and Central America and on the New World family Phyllostomidae (Meyer *et al.* 2016). Effects of habitat fragmentation on the diverse bat assemblages in tropical Africa, where deforestation rates are high (Hansen *et al.* 2013), remain poorly understood (Meyer *et al.* 2016).

Equatorial African bat faunas include four functional groups or foraging ensembles: frugivores, forest-interior insectivores, forest-edge insectivores and open-space insectivores. The forest-interior insectivores show specializations for narrow-space foraging and appear dependent on forest interiors (Kingston *et al.* 2003). We compared bat abundance and species richness in forest habitats varying in fragment size and/or level of degradation. We expected that different bat species and ensembles would respond differentially (Barlow *et al.* 2007, Pardini *et al.* 2009), according to their ecomorphology, foraging strategy and echolocation call attributes

(Denzinger & Schnitzler 2013, Kingston *et al.* 2003, Schnitzler *et al.* 2003). Specifically, we predicted that (1) forest-interior insectivores are strongly associated with the interior of the larger, more intact forests; and (2) frugivores and forest-edge or open-space insectivores are more strongly associated with edges and smaller, more degraded forest fragments.

## Methods

### Study site

Kakamega Forest (0°07' 0°27' N, 34°46' 34°57' E; Figure 1) is a mid-elevation rain forest (1400–1700 m asl). Rainfall averages 2000 mm y<sup>-1</sup> and daily temperatures range from 11°C to 26°C (Glenday 2006). Kakamega is the easternmost outlier of the Guineo-Congolese rain forest (Wagner *et al.* 2008). 'Kakamega Forest' is used to refer to both the main forest block (8600 ha) and its two satellite fragments, Kisere (400 ha) and Malava (100 ha). Kakamega Forest is managed by two different parastatals, Kenya Forest Service (KFS) and Kenya Wildlife Service (KWS). This study was carried in the northern section of the main Kakamega Forest block (also called Buyangu, ~3950 ha) and Kisere fragment, both managed by KWS as Kakamega National Reserve; KFS manages the southern part of the main Kakamega Forest block (4695 ha) and Malava forest. Malava and Kisere fragments are separated from Buyangu Forest by 9.2 and 1.6 km, respectively, while Malava and Kisere forests are 6.3 km apart. Kisere and Malava forest fragments have been disconnected from the main block for at least 50 y (Mitchell *et al.* 2009), separated by a high-contrast matrix of dense human settlements (> 578 people km<sup>-2</sup>), subsistence agriculture, exotic forest plantations of *Pinus* and *Eucalyptus*, and regenerating forest and pastures (Kokwaro 1988, Müller & Mburu 2009). The dense human population and widespread poverty place unsustainable demands on the forest for timber, charcoal and fuel wood for domestic uses, livestock grazing and conversion for croplands (Guthiga *et al.* 2008).

### Experimental design

We assessed bat species richness and relative abundance at each forest fragment using captures. A two-factor orthogonal experimental design was employed that included three forest fragments (Buyangu, Kisere and Malava) and captures made at edge and interior. We defined forest edge as an area within 100 m of any disturbance (i.e. agricultural crop or pasture, roads) whereas forest interior was an area in the forest interior that showed no detectable edge influence (Harper *et al.* 2005). Forest interior sites were at least 100 m (Buyangu: 125 ± 5.62 m; Malava: 103 ± 1.62 m; Kisere: 111 ± 2.51 m) from a forest/non-forest boundary (mean ± SE).

We sampled six edge and six interior locations per fragment, and sampled from two sites (≥ 500 m apart) at each location. Locations were > 2 km apart to minimize pseudoreplication and interspersed with respect to the three fragments (Figure 1). Accordingly, captures were conducted at 12 sites per fragment, making a total of 36 sampling sites.

### Vegetation and forest-use characteristics

At all 36 capture sites, vegetation and human-use parameters were measured in four 0.04-ha (20 × 20-m) plots. Inside each plot, all trees (≥ 10 cm diameter at breast height - dbh) were counted, their dbh measured and used to calculate basal area, BA (the space

covered by tree stems) (Mueller-Dombois & Ellenberg 1974). BA values were combined for all species per location by summing the basal areas of individual trees. Mean canopy cover was estimated from four measurements taken with a concave spherical densiometer, 1.5 m from the centre of the plot in each of the four cardinal directions. Finally, as indicators of human forest use, forest degradation values were indexed in each plot as simple counts of cut tree stumps, charcoal kilns and footpaths.

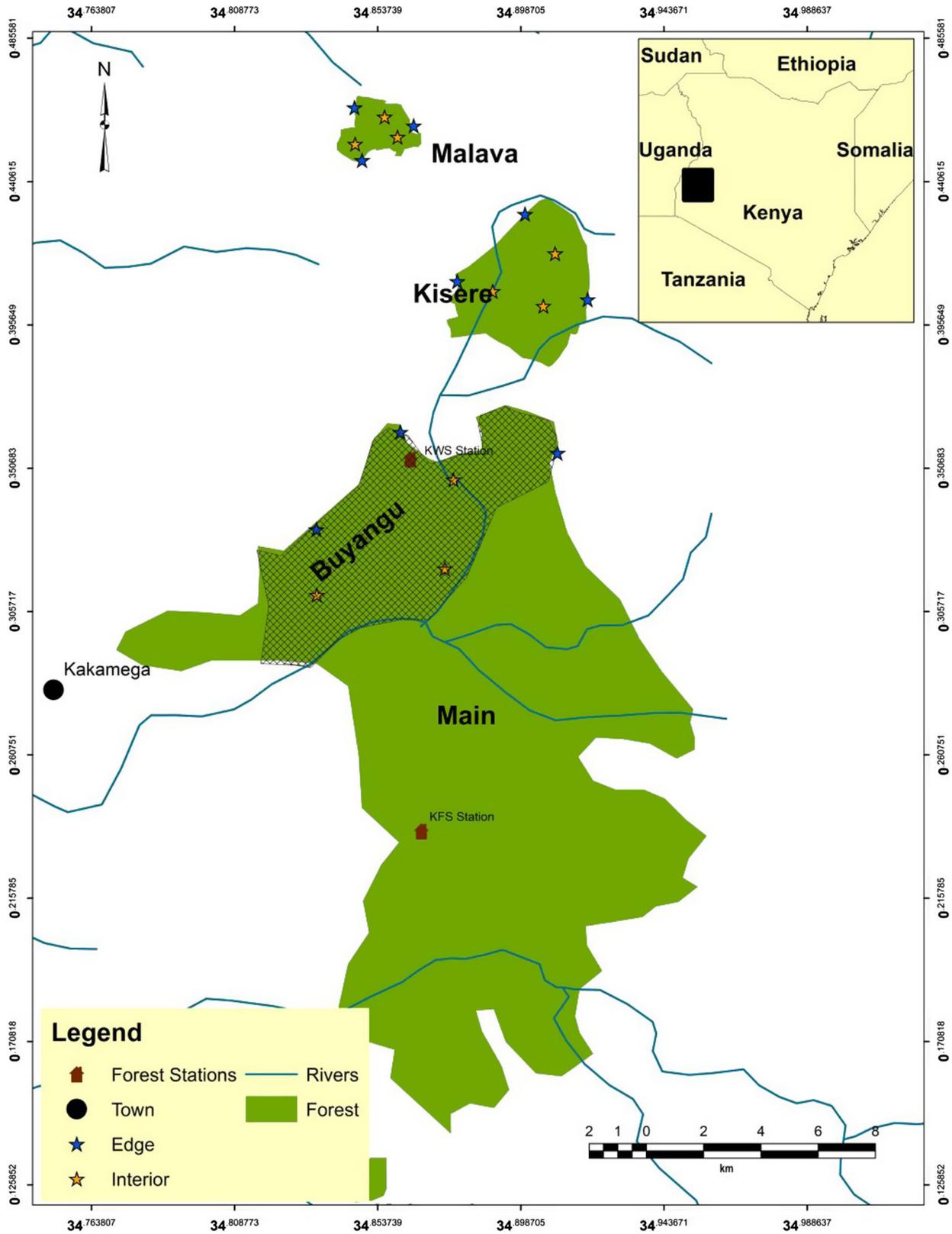
### Bat trapping

Fieldwork was carried out from May 2013 to April 2014, amounting to 144 sampling nights. Sites were visited in randomized order within each forest fragment, but interior and edge locations were paired during sampling to minimize variation in habitat use, as this may vary temporally due to prey availability and weather conditions. At each sampling site, six monofilament mist nets (6 × 2.5 m or 9 × 2.5 m, denier 75/2, mesh 16 × 16 mm, five shelves - Ecotone, Inc., Poland) and two harp traps (two-bank 4.2 m<sup>2</sup>; Austbat Research Equipment, Victoria, Australia) were set across trails and spaced ~50 m apart. Each site was sampled over three two-night surveys that were separated by at least 2 weeks. Mist nets were open between 19h00 and 23h00 and checked at 15-min intervals. Harp traps were operational between 19h00 and 06h00 at each site and were checked at 30-min intervals after dark until 23h00 and again at 06h00 the next day. Nights with rain and immediately before, during and after the full moon were not sampled to minimize potential bias (Saldana-Vázquez & Munguía-Rosas 2013). Except for subadults (Anthony 1988), captured bats were marked using coloured and numbered plastic bands placed on the forearm (Handley *et al.* 1991). A few bats were retained as voucher specimens and deposited at the National Museums of Kenya to both facilitate and document identifications; identifications and nomenclature followed Patterson & Webala (2012). Insectivorous species were assigned to one of three foraging modes (ensembles) depending on habitat use (Denzinger & Schnitzler 2013, Kingston *et al.* 2003, Schnitzler & Kalko 2001). Forest-interior species were considered specialists because they forage exclusively in spatially complex environments (Marinello & Bernard 2014). Non-echolocating frugivores were categorized in a separate ensemble.

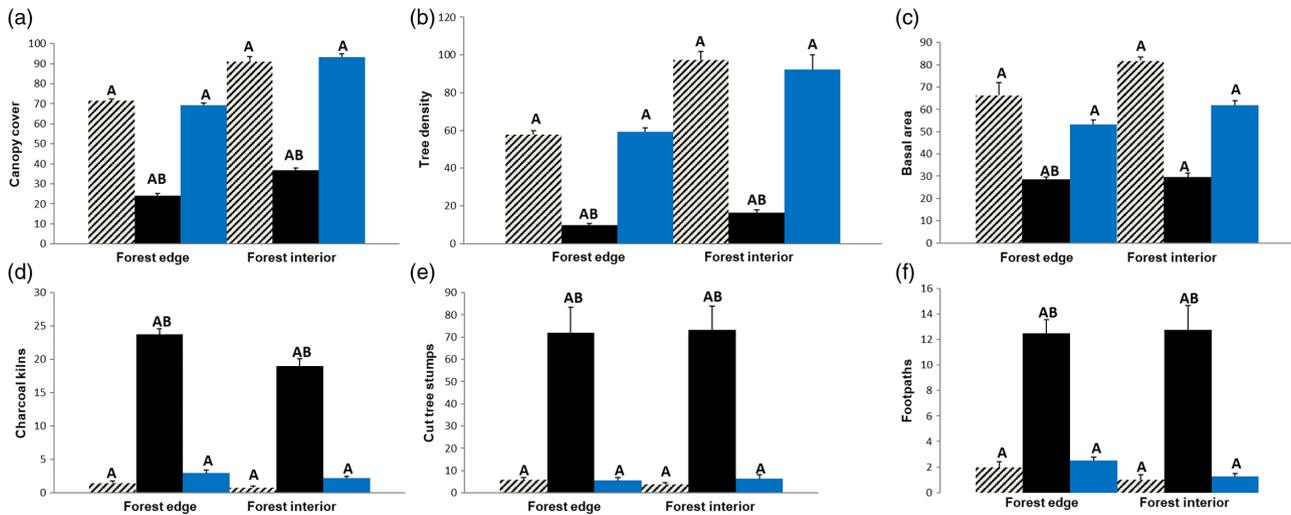
### Statistical analyses

Prior to analyses, all data were transformed [ $\log(x + 1)$ ] and tested for normality by the Shapiro-Wilk Test. Non-parametric tests were applied when transformations failed to render a variable both normal and homoscedastic. All means are presented ± SE. Two-way multivariate ANOVAs were used to test for differences in tree density, canopy cover, basal area and tree stumps among forest fragments and between capture locations (edges and interiors), with the four variables as dependent variables and forest fragments and capture locations as fixed factors. This was followed by post hoc pairwise comparisons of means using Tukey tests (Day & Quinn 1989). Similarly, differences in number of charcoal kilns and footpaths between treatments were tested using the Kruskal-Wallis test and subsequent multiple comparison tests.

Bat assemblages across the three forest fragments and capture locations were described individually with Simpson's index,  $D$  (Simpson 1949) and Pielou's evenness:  $J'$  (Pielou 1975). Simpson's index was used because it provides a good estimate of diversity even for small sample sizes (Magurran 2004). Bat compositional similarity among forests was gauged by Bray-Curtis similarity using PRIMER software package (Clarke & Gorley 2001).



**Figure 1.** Map of Kakamega Forest showing the spatial arrangement of sampling locations (stars) and studied forest fragments: Buyangu, Kisere and Malava forests. Inset is the map of Kenya showing the location of the study area.



**Figure 2.** Differences in vegetation canopy cover (a), tree density (b), basal area (c) – and disturbance characteristics – charcoal kilns (d), cut tree stumps (e) and footpaths (f) – (units ha<sup>-1</sup>; untransformed mean ± SE) in three forest fragments (Buyangu forest = stripes, Malava forest = black, and Kisere forest = blue), and at forest edges and interiors. Different letters denote significant differences at  $P < 0.05$ .

We tested for differences between forest fragments and locations (edge, interior) in bat abundance (captures) of common species ( $n > 30$ ) using two-way ANOVAs, with abundance as the dependent variable and forest fragment and location as fixed factors. Spearman's rank correlation was used to relate bat abundance and the distribution measures (Gorresen & Willig 2004, Sokal & Rohlf 1995). Both ANOVA and correlation analyses were conducted using Statistica v.7.0 (www.statsoft.com).

Direct interactions between bat abundance and vegetation/forest-use parameters were explored with Canonical Correspondence Analysis (CCA) in CANOCO 4.5 (Lepš & Šmilauer 2003) and thereafter Monte-Carlo permutation tests ( $n = 999$ ) performed to determine which vegetation/forest-use parameters significantly influenced bat distribution at  $P < 0.05$ , using conditional automatic forwarding options (Lepš & Šmilauer 2003). We also tested for significance of the first three canonical axes. Highly correlated vegetation/forest-use parameters were not used in the CCA because highly correlated variables tend to cause redundancy in the set of explanatory variables (Lepš & Šmilauer 2003).

## Results

### Vegetation and forest-use intensity characteristics

Vegetation and forest-use characteristics differed significantly between forest fragments: tree density ( $F_{2,18} = 277$ ,  $P < 0.001$ ), canopy cover ( $F_{2,18} = 554$ ,  $P < 0.001$ ), basal area ( $F_{2,18} = 104$ ,  $P = 0.001$ ), cut tree stumps ( $F_{2,18} = 57.6$ ,  $P = 0.001$ ), charcoal kilns ( $H_{5,24} = 21.3$ ,  $P = 0.05$ ) and footpaths ( $H_{5,24} = 19.0$ ,  $P = 0.05$ ). Tree density, canopy cover, basal area did not differ between Buyangu and Kisere forests ( $P > 0.05$ ), but all were significantly higher than at Malava forest ( $P < 0.001$ ). Conversely, cut tree stumps, charcoal kilns and footpaths did not differ between Buyangu and Kisere forests ( $P > 0.05$ ), but were all significantly lower than at Malava forest ( $P < 0.001$ , Figure 2). Tree density ( $F_{1,18} = 48.4$ ,  $P < 0.001$ ), canopy cover ( $F_{1,18} = 46.5$ ,  $P < 0.001$ ) and basal area ( $F_{1,18} = 7.42$ ,  $P = 0.018$ ) differed between edge and interior locations, with higher values of each in the interior. Canopy cover

differed more at interior than edge locations, resulting in a significant fragment × location interaction ( $F_{2,18} = 5.34$ ,  $P = 0.022$ ).

### Bat abundance responses to fragmentation

A total of 3456 mist-net h and 3168 harp-trap h yielded 4983 unique bat captures representing 26 species, eight families and all four foraging ensembles (Table 1). We recaptured 204 bats but excluded recaptures from analyses.

More captures were made at Buyangu forest, whereas the fewest were made at Malava forest (Appendix 1). Bat captures differed significantly between the forests ( $F_{2,18} = 352$ ,  $P < 0.001$ ), as well as between forest edges and interiors ( $F_{1,18} = 63.3$ ,  $P < 0.001$ ), with a significant forest × location interaction ( $F_{2,18} = 23.7$ ,  $P < 0.001$ ) (Table 1). Mean captures of bats did not differ ( $P > 0.05$ ) at Buyangu ( $119 \pm 37.2$ ) and Kisere ( $57.4 \pm 21.5$ ) forests, but each differed significantly from Malava forest ( $14.8 \pm 7.91$ ;  $P < 0.001$ ). At the edges, captures were significantly lower at Malava forest than at Buyangu and Kisere forests, with no difference between the latter two. Similarly, the interiors of the three forests differed significantly in bat captures ( $F_{2,18} = 3.62$ ,  $P = 0.036$ ), with fewer captures at Malava forest ( $14.2 \pm 4.20$ ) than at either Buyangu ( $69.9 \pm 28.1$ ) or Kisere forest ( $40.8 \pm 4.69$ ), which did not differ significantly ( $P > 0.05$ ).

Frugivores made up 52% of all captures, although most (89%) were of two dominant species, *Epomophorus wahlbergi* ( $n = 1185$ ) and *Epomophorus labiatus* ( $n = 1158$ ). These two and *Neoromicia capensis* ( $n = 510$ ) were widely distributed on the edges of all three forests. While captures of *E. wahlbergi* and *N. capensis* did not differ at the edges of the three forests ( $P > 0.05$ ), captures of *E. labiatus* were significantly lower at the edges of Kisere ( $P < 0.05$ ) than at the edges of either Buyangu and Malava forests, with no significant difference between the latter two ( $P = 0.943$ ). Captures at Malava forest were dominated by the two disturbance-adapted frugivores, *Epomophorus labiatus* and *E. wahlbergi*. Two forest-interior insectivores, *Kerivoula cuprosa* ( $n = 504$ ) and *Hipposideros beatus* ( $n = 435$ ), were also fairly common, and were captured mainly in harp traps and exclusively in the interiors of the Buyangu and Kisere forests. Overall, forest-interior insectivores such as *Doryrhina camerunensis*, *Hipposideros beatus*, *H. ruber*, *Nycteris*

**Table 1.** *F*-values from two-way ANOVAs for effects of forest fragment and capture location on captures of common bat species at Kakamega Forest, western Kenya ( $n > 30$ ), with captures as the dependent variable and forest fragment and capture location as fixed factors. Significant results are denoted by asterisks. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

Species	Fragment (F) ( $F_{2, 18}$ )	Location (L) ( $F_{1, 18}$ )	F × L ( $F_{2, 18}$ )
Overall captures	352***	63.3***	23.7***
<i>Epomophorus labiatus</i>	14.1**	958***	134***
<i>E. wahlbergi</i>	1.4	1016***	104***
<i>Hypsignathus monstrosus</i>	157***	225***	60.4***
<i>Myonycteris angolensis</i>	42.1***	91.9***	24.7***
<i>Doryrhina camerunensis</i>	22.8***	112***	22.8***
<i>Hipposideros beatus</i>	476***	717***	203***
<i>H. ruber</i>	21.1***	43.9***	2.7
<i>Nycteris arge</i>	31.7***	48.7***	12.6**
<i>N. thebaica</i>	4.1*	47.7***	2.1
<i>Chaerephon pumilus</i>	0.4	356***	0.4
<i>Hypsugo crassulus</i>	37.9***	113***	28.6***
<i>Kerivoula cuprosa</i>	333***	974***	267***
<i>Myotis bocagii</i>	213***	846***	213***
<i>Neoromicia capensis</i>	86.6***	486***	14.9**
<i>N. nana</i>	5.1*	62.5***	8.6**
<i>Scotophilus dinganii</i>	86.3***	325***	86.3***

*arge*, *Glauconycteris humeralis*, *Hypsugo crassulus* and *K. cuprosa* were captured more often in harp traps ( $203 \pm 86.2$ ) than in mist nets ( $11.8 \pm 4.70$ ;  $F_{1,13} = 6.11$ ,  $P < 0.05$ ).

Further analyses of comparison of bat species composition between capture locations showed different degrees of similarities. The degree of similarity was high for the pairwise comparisons of edges (87.5%) and interiors (77.0%) of Buyangu versus Kisere forests as well as edges (70.6%) of Malava and Kisere forests. On the other hand, species similarities were far lower between Buyangu edges with interiors of Buyangu (19.1%) and Kisere (32.4%).

### Assemblage-level responses to fragmentation

Buyangu and Kisere forest samples contained more than thrice ( $n = 26$ ) and twice ( $n = 22$ ) as many species as Malava forest ( $n = 8$ ). The three forests and capture locations differed in both evenness ( $F_{5,12} = 5.20$ ,  $P < 0.05$ ) and species diversity ( $F_{5,12} = 11.2$ ,  $P < 0.05$ ). While the edges of the three forests did not differ significantly in species diversity ( $P > 0.05$ ), post hoc tests showed that the interior of Kisere forest had significantly higher species diversity than the interiors of either Buyangu ( $P < 0.05$ ) or Malava ( $P < 0.001$ ); the latter two forests also differed significantly ( $P < 0.001$ ).

### Relationship of bats to vegetation and disturbance

Spearman rank correlation showed bat abundance, species richness and diversity were positively correlated with canopy cover, tree density and basal area, and negatively correlated with cut tree stumps, charcoal kilns and footpaths (Table 2). Permutation

analyses of the CCA revealed that bats were significantly influenced by canopy cover ( $F = 11.7$ ,  $P = 0.002$ ), basal area ( $F = 10.3$ ,  $P = 0.002$ ) and tree density ( $F = 2.9$ ,  $P = 0.04$ ). As predicted, the CCA biplot ordered bat species into three major groups related to their forest utilization (Figure 3). The first group is comprised of the forest-interior insectivores *Doryrhina camerunensis*, *Hipposideros beatus*, *H. ruber*, *Nycteris arge* and *Kerivoula cuprosa*. These species were strongly associated with the less-disturbed interior sites of Buyangu and Kisere forests. The second group was associated with forest edges and included both frugivores (*Eidolon helvum*, *Myonycteris angolensis*, *Hypsignathus monstrosus* and *Micropteropus pusillus*) and edge-tolerant insectivores (*Nycteris thebaica*, *Chaerephon major*, *Miniopterus inflatus*, *Glauconycteris argentata*, *Myotis bocagii*, *M. welwitschii*, *Neoromicia capensis*, *N. nana*, *Scotophilus dinganii* and *S. nux*). The third group included the open-space insectivore *Chaerephon pumilus* and two frugivores, *Epomophorus labiatus* and *E. wahlbergi*, and was associated with heavily disturbed sites.

### Discussion

This is the first study of species-specific and assemblage-wide responses of bats to rain-forest fragmentation in Kenya. Fragmentation negatively affected bat abundance and species richness, in agreement with fragmentation studies elsewhere (Meyer *et al.* 2016, Watling & Donnelly 2006). The larger, better protected forests had higher bat abundances and species richness and lower human impacts than the smaller, more degraded forest (Malava), which was inhabited by generalists. Additionally, the larger forests supported interior-forest specialists. Interior-forest insectivores appear more vulnerable to forest fragmentation (Farneda *et al.* 2015, Struebig *et al.* 2008).

### Impacts of forest fragmentation on bat abundance and species richness

At the assemblage level, bat abundance, species richness and diversity were all higher in the larger, less-disturbed Buyangu and Kisere forests than in Malava forest (Appendix 1). Previous studies have also demonstrated higher bat abundance and species richness in larger, more intact forests (Cosson *et al.* 1999, Struebig *et al.* 2011).

Increased canopy cover, tree density and basal area were all correlated with the higher bat abundance at Buyangu and Kisere forests. Malava forest was not only the smallest and most isolated of the three forests, but it was also the most disturbed. This forest had higher numbers of charcoal kilns, cut tree stumps and footpaths, and lower values of tree density, basal area and canopy cover than either Buyangu or Kisere forests (Figure 2). Highly degraded forests often have an open and simplified structure, more clearings, higher solar penetration and fewer food resources (Lagan *et al.* 2007), making them suboptimal for bats (Grindal & Brigham 1998). The lower tree density, canopy cover and basal area at Malava forest could limit food and/or roosting resources for bats (Kunz & Lumsden 2003), and these are often the basis for their vulnerability (Fenton 1997). Roost sites, particularly for tree-cavity and foliage-roosting species that depend directly on the forest itself, may be less common at the highly degraded Malava forest.

Although our study concurs with many previous studies finding negative effects of fragmentation on bats (Farneda *et al.* 2015, Meyer & Kalko 2008, Struebig *et al.* 2008), it contrasts with others that found little or no evidence of negative effects at the assemblage level (Faria 2006, García-García *et al.* 2014, Gorresen & Willig



conditions and dependence on the less-perturbed interiors of Kisere and Buyangu forests all suggest the vulnerability of these forest-interior specialists (Jones *et al.* 2003, Lane *et al.* 2006, Safi & Kerth 2004). Other studies have also demonstrated the greater response of forest-interior species to habitat fragmentation and degradation (Estrada-Villegas *et al.* 2010, Farneda *et al.* 2015, Meyer & Kalko 2008, Struebig *et al.* 2008, 2009).

### Edge effects

Edge effects were most pronounced at the small, highly disturbed Malava forest, where the edges and interiors differed modestly in canopy cover and tree density and had similar levels of disturbance. Only two species of frugivores (*E. labiatus*, *E. wahlbergi*) were present, and these generalists used forest edges and interiors indiscriminately. Generalist frugivores and forest-edge and open-space insectivores were typically absent from the interiors of less-disturbed forests, where forest-interior insectivores predominated. Like cavity-roosting species in Peninsular Malaysia (Struebig *et al.* 2008) and gleaning animalivorous bats in the Neotropics (Farneda *et al.* 2015, Gorresen & Willig 2004, Henry *et al.* 2010, Klingbeil & Willig 2009, 2010; Meyer & Kalko 2008, Pardini *et al.* 2009, Rocha *et al.* 2016), forest-interior insectivores appear highly susceptible to edge effects. Besides eliminating suitable roosting structures, edges cause tree mortality and open the canopy, increasing desiccation stress, windshear and wind turbulence (Laurance *et al.* 1997), ultimately modifying forest composition (Laurance *et al.* 2001, 2006).

### Caveats

We used both ground-level mist nets and harp traps to sample Kakamega's diverse bat fauna. The absence of canopy-level mist nets may have caused us to overlook some high-flying species also found there (Meyer *et al.* 2011). In addition, many of the insectivorous bats inhabiting Kakamega forest commonly use their echolocation calls to evade capture and might be better sampled via acoustic monitoring (MacSwiney *et al.* 2008, O'Farrell & Gannon 1999). However, acoustic monitoring requires an exhaustive and corroborated call library. During the course of this fieldwork, we assembled a partial call library that can be used in future surveys (Webala *et al.* 2019). Even though we might have failed to capture some of Kakamega's bats, the method used is repeatable and would have introduced no systematic bias (Meyer *et al.* 2015).

We also focused sampling on the fragments themselves rather than on the bats' use of the surrounding matrix. There are virtually no data on the home ranges or foraging behaviour of the bat species documented by our work. Radio-tracking studies will be needed to elucidate matrix effects on the bats' space use and whether individual bats are able to treat the Kakamega fragments as foraging patches.

### Conclusions

Bat species and ensembles at Kakamega forest respond to fragmentation in predictable ways, likely determined by differences in their foraging ecology, wing morphology and movement behaviour (Klingbeil & Willig 2009). As expected, generalist frugivores and forest-edge and open-space insectivores predominated at degraded sites because of their tolerance of a range of habitats. Remarkably, these disturbance-tolerant species nevertheless preferred the edges of less-disturbed forests. Forest-interior insectivores, on the other hand, appear vulnerable to habitat fragmentation and degradation because they were confined to habitats within the interiors of less-disturbed

forests. Continued logging, charcoal production, livestock grazing or altered disturbance regimes that modify the quality of habitats within fragments at Kakamega Forest are likely to adversely impact forest-interior specialists. Clearly, the protection and maintenance of undisturbed forest interiors is crucial for these species (Andr n 1994, Metzger & D camps 1997, Meyer & Kalko 2008).

**Acknowledgements.** This project was conducted with Kenya Wildlife Service (KWS) and Kenya Forest Service (KFS) Permits KWS/4001 and RESEA/1/KFS/75, respectively. We thank Geoffrey M. Wambugu of Karatina University for digitizing the map of Kakamega Forest. Beryl Makori, Dedan Ngatia and Simon Masika (Karatina University), and Michael Bartonjo and Sospeter Kibiwot (National Museums of Kenya) provided invaluable help in the field. This study would not have been possible without the collaboration of staff of KWS and KFS. We especially thank Dr Samuel Kasiki and Mr James Mwang'ombe, from KWS and KFS, respectively, for facilitating access and research permits. The support and confidence of Bud and Onnolee Trapp and Walt and Ellen Newsom were instrumental to the effective execution of this work. PWW thanks Dr David Jacobs for funding his 3-month stay at the University of Cape Town for writing up the manuscript. We thank Ricardo Rocha and Adri n L pez Baucells for highly beneficial comments on an earlier version of this manuscript.

**Financial support.** Financial support was provided by grants from the British Ecological Society (BES 3571/4375), International Foundation of Science (IFS D/5278-1), Kenya's NACOSTI, and Field Museum's Council on Africa to PWW, the Barbara E. Brown Fund for Mammal Research to BDP, and the JRS Biodiversity Foundation to both lead and senior authors.

### Literature cited

- Aldridge HDJN and Rautenbach IL (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology* **56**, 763–778.
- Andr n H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366.
- Anthony ELP (1988) Age determination in bats. Pp. 47–58 in Kunz TH (ed.), *Ecological and Behavioral Methods for the Study of Bats*. Washington, DC: Smithsonian Institution Press.
- Barlow J, Gardner TA, Araujo IS,  vila-Pires TC, Bonaldo AB, Costa JE, Eposito MC, Ferreira LV, Hawes J, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MBL, Mestre AM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, Da Silva MNF, Da Silva Motta C and Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences USA* **104**, 18555–18560.
- Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Nally RM, Thomson JR, Ferraz SFDB, Louzada J, Oliveira VHF, Parry L, Ribeiro De Castro Solar R, Vieira ICG, Arag o LEOC, Begotti RA, Braga RF, Cardoso TM, De Oliveira Jr RC, Souza Jr CM, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira JM, Vaz-De-Mello FZ, Veiga RCS, Venturieri A and Gardner TA (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**, 144–147.
- Clarke KR and Gorley RN (2001) *PRIMER v5: User Manual/Tutorial*. Plymouth: PRIMER-E, 91 pp.
- Cosson JF, Pons JM and Masson D (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology* **15**, 515–534.
- Cunto GC and Bernard E (2012) Neotropical bats as indicators of environmental disturbance: what is the emerging message? *Acta Chiropterologica* **14**, 143–151.
- Day RW and Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**, 433–463.
- Denzinger A and Schnitzler H-U (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology* **4**, 164. [10.3389/fphys.2013.00164](https://doi.org/10.3389/fphys.2013.00164).

- Estrada-Villegas S, Meyer CFJ and Kalko EKV** (2010) Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation* **143**, 597–608.
- Ewers RM and Didham RK** (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* **81**, 117–142.
- Fahrig L** (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* **34**, 487–515.
- Faria D** (2006) Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. *Journal of Tropical Ecology* **22**, 531–542.
- Farneda FZ, Rocha R, López-Baucells A, Groenenberg M, Silva I, Palmeirim JM, Bobrowiec PED and Meyer CFJ** (2015) Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology* **52**, 1381–1391.
- Fenton MB** (1997) Science and the conservation of bats. *Journal of Mammalogy* **78**, 1–14.
- García-García JL, Santos-Moreno A and Kraker-Castañeda C** (2014) Ecological traits of phyllostomid bats associated with sensitivity to tropical forest fragmentation in Los Chimalpas, Mexico. *Tropical Conservation Science* **7**, 457–474.
- Glenday J** (2006) Carbon storage and emissions offset potential in an East African tropical rainforest. *Forest Ecology and Management* **235**, 72–83.
- Gorresen PM and Willig MR** (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy* **85**, 688–697.
- Grindal SD and Brigham RM** (1998) Effects of small-scale habitat fragmentation on activity by insectivorous bats. *Journal of Wildlife Management* **62**, 996–1003.
- Guthiga P, Mburu J and Holm-Mueller K** (2008) Factors influencing local communities' satisfaction levels with different forest management approaches of Kakamega Forest, Kenya. *Environmental Management* **41**, 696–706.
- Handley CO Jr, Wilson DE and Gardner AL** (1991) Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panama. *Smithsonian Contributions to Zoology* **511**, 1–173.
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova S, Tyukavina A, Thau D, Stehman S, Goetz S and Loveland T** (2013) High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853.
- Harper KA, MacDonald SE, Burton PJ, Chen J, Brosfke KD, Saunders SC, Euskirchen ES, Roberts D, Jaitheh MS and Esseen PA** (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* **19**, 1–15.
- Henry M, Cosson JF and Pons JM** (2010) Modelling multi-scale spatial variation in species richness from abundance data in a complex Neotropical bat assemblage. *Ecological Modelling* **221**, 2018–2027.
- Hill JK and Hamer KC** (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* **41**, 744–754.
- Jones KE, Purvis A and Gittleman JL** (2003) Biological correlates of extinction risk in bats. *American Naturalist* **161**, 601–614.
- Jones G, Jacobs DS, Kunz TH, Willig MR and Racey PA** (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* **8**, 93–115.
- Kingston T, Francis CM, Zubaid A and Kunz TH** (2003) Species richness in an insectivorous bat assemblage from Malaysia. *Journal of Tropical Ecology* **19**, 67–79.
- Klingbeil BT and Willig MR** (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *Journal of Applied Ecology* **46**, 203–213.
- Klingbeil BT and Willig MR** (2010) Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos* **119**, 1654–1664.
- Kokwaro JO** (1988) Conservation status of the Kakamega Forest in Kenya: the easternmost relic of the equatorial rain forests of Africa. *Monographs in Systematic Botany of the Missouri Botanical Garden* **25**, 471–489.
- Kunz TH and Lumsden LF** (2003) Ecology of cavity and foliage-roosting bats. In Kunz TH and Fenton MB (eds), *Bat Ecology*. Chicago, IL: University of Chicago Press, pp. 3–90.
- Kunz TH and Pierson ED** (1994) Bats of the world: an introduction. In Nowak RM (ed.), *Walker's Bats of the World*. Baltimore, MD: Johns Hopkins University Press, pp. 1–46.
- Lagan P, Mannan S and Matsubayashi H** (2007) Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. *Ecological Research* **22**, 414–421.
- Lane DJW, Kingston T and Lee BPY-H** (2006) Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. *Biological Conservation* **131**, 584–593.
- Laurance WF, Laurance SG, Ferreira LV, Rankin-De Merona JM, Gascon C and Lovejoy TE** (1997) Biomass collapse in Amazonian forest fragments. *Science* **278**, 1117–1118.
- Laurance WF, Perez-Salicrup D, Delamonica P, Fearnside PM, D'Angelo S, Jerozolinski A, Pohl L and Lovejoy TE** (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**, 105–116.
- Laurance WF, Nascimento H, Laurance SG, Andrade A, Ribeiro J, Giraldo JP, Lovejoy TE, Condit R, Chave J and D'Angelo S** (2006) Rapid decay of tree community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences USA* **103**, 19010–19014.
- Laurance WF, Camargo JL, Luizão RC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benítez-Malvido J and Vasconcelos HL** (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* **144**, 56–67.
- Lepš J and Šmilauer P** (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Czech Republic: University of South Bohemia and Cambridge: Cambridge University Press.
- MacSwiney MC, Clarke FM and Racey PA** (2008) What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology* **45**, 1364–1371.
- Magurran AE** (2004) *Measuring Biological Diversity*. Oxford: Blackwell Publishing, 256 pp.
- Marinello MM and Bernard E** (2014) Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. *Canadian Journal of Zoology* **92**, 141–147.
- Metzger JP and Décamps H** (1997) The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Oecologica* **18**, 1–12.
- Meyer CFJ and Kalko EKV** (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography* **35**, 1711–1726.
- Meyer CFJ, Fründ J, Pineda W and Kalko EKV** (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology* **45**, 381–391.
- Meyer CFJ, Aguiar LMS, Aguirre LF, Baumgarten J, Clarke FM, Cosson J-F, Villegas SE, Fahr J, Faria D, Furey N, Henry M, Hodgkinson R, Jenkins RKB, Jung KG, Kingston T, Kunz TH, Gonzalez MCM, Moya I, Patterson BD, Pons J-M, Racey PA, Rex K, Sampaio EM, Solari S, Stoner KE, Voigt CC, Staden DV, Weise CD and Kalko EKV** (2011) Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology* **48**, 777–787.
- Meyer CFJ, Aguiar LMS, Aguirre LF, Baumgarten J, Clarke FM, Cosson J-F, Estrada-Villegas S, Fahr J, Faria D, Furey N, Henry M, Jenkins RKB, Kunz TH, MacSwiney Gonzalez MC, Moya I, Pons J-M, Racey PA, Rex K, Sampaio EM, Stoner KE, Voigt CC, Von Staden D, Weise CD and Kalko EKV** (2015) Species undersampling in tropical bat surveys: effects on emerging biodiversity patterns. *Journal of Animal Ecology* **84**, 113–123.
- Meyer CFJ, Struebig M and Willig MR** (2016) Responses of tropical bats to habitat fragmentation, logging, and deforestation. In Voigt CC and Kingston T (eds), *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Heidelberg: Springer, pp. 63–103.
- Mitchell N, Schaab G and Wägele W** (2009) Kakamega Forest ecosystem: an introduction to the natural history and the human context. *BIOTA East Africa Report 5. Karlsruher Geowissenschaftliche Schriften A* **17**, 1–56. Karlsruhe: Karlsruhe University of Applied Sciences, Faculty of Geomatics.
- Montiel S, Estrada A and Leon P** (2006) Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. *Journal of Tropical Ecology* **22**, 267–276.

- Morris RJ** (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3709–3718.
- Mueller-Dombois D and Ellenberg H** (1974) *Aims and Methods of Vegetation Ecology*. New York, NY: John Wiley and Sons. 547 pp.
- Müller D and Mburu J** (2009) Forecasting hotspots of forest clearing in Kakamega Forest, Western Kenya. *Forest Ecology and Management* **257**, 968–977.
- Neuweiler G** (1984) Foraging, echolocation and audition in bats. *Naturwissenschaften* **71**, 446–455.
- Norberg UM and Rayner JMV** (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences* **316**, 335–427.
- O'Farrell M and Gannon W** (1999) A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* **80**, 24–30.
- Pardini R, Faria D, Accacio GM, Laps RR, Mariano E, Paciencia MLB, Dixo M and Baumgarten J** (2009) The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* **142**, 1178–1190.
- Patterson BD and Webala PW** (2012) Keys to the bats (Mammalia: Chiroptera) of East Africa. *Fieldiana: Life and Earth Sciences* **6**, 1–63.
- Pielou EC** (1975) *Ecological Diversity*. New York, NY: Wiley InterScience. 165 pp.
- Presley SJ, Willig MR, Wunderle JM and Saldanha LN** (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology* **45**, 14–25.
- Rocha R, López-Baucells A, Farneda FZ, Groenberger M, Bobrowiec PED, Cabeza M, Palmeirim JM and Meyer CFJ** (2016) Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology* **32**, 31–45.
- Safi K and Kerth G** (2004) A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology* **18**, 1293–1303.
- Saldana-Vázquez RA and Munguía-Rosas MA** (2013) Lunar phobia in bats and its ecological correlates: a meta-analysis. *Mammalian Biology* **78**, 216–219.
- Schnitzler H-U and Kalko KMV** (2001) Echolocation by insect-eating bats. *BioScience* **51**, 557–569.
- Schnitzler HU, Moss CF and Denzinger A** (2003) From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology and Evolution* **18**, 386–394.
- Sherwin HA, Montgomery WI and Lundy MG** (2013) The impact and implications of climate change for bats. *Mammal Review* **43**, 171–182.
- Simpson EH** (1949) Measurement of diversity. *Nature* **163**, 688.
- Sokal RR and Rohlf FJ** (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, Third edition. New York, NY: W.H. Freeman. 887 pp.
- Struebig MJ, Kingston T, Zubaid A, Adnan AM, Nichols RA and Rossiter SJ** (2008) Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation* **141**, 2112–2126.
- Struebig MJ, Kingston T, Zubaid A, Lecomber SC, Adnan A, Turner A, Kelly J, Bozek MS and Rossiter SJ** (2009) Conservation importance of limestone karst outcrops to Palaeotropical bats in a fragmented landscape. *Biological Conservation* **142**, 2089–2096.
- Struebig MJ, Kingston T, Petit EJ, Le Comber SC, Zubaid A, Mohd-Adnan A and Rossiter SJ** (2011) Parallel declines in species and genetic diversity in tropical forest fragments. *Ecology Letters* **14**, 582–590.
- Thies W, Kalko EKV and Schnitzler H** (1998) The roles of echolocation and olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on *Piper*. *Behavioral Ecology and Sociobiology* **42**, 397–409.
- Wagner P, Kohler J, Schmitz A and Bohme W** (2008) The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. *Journal of Biogeography* **35**, 1349–1361.
- Watling JI and Donnelly MA** (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conservation Biology* **20**, 1016–1025.
- Webala PW, Rydell J, Dick CW, Musila S and Patterson BD** (2019) Echolocation calls of some high duty-cycle bats from Kenya. *Journal of Bat Research and Conservation* **12**, 10–20.
- World Bank** (2008) *World Development Indicators 2008*. Washington, DC: World Bank.

## Appendix 1.

Bat captures, species richness, evenness and diversity at Kakamega Forest, western Kenya. For ensembles: F, frugivore; FI, forest interior; FE, forest edge; OS, open space

Family	Species	Ensemble	Buyangu forest (3950 ha)		Malava forest (100 ha)		Kisere forest (400 ha)		Total	
			edge	interior	edge	interior	edge	interior		
Pteropodidae	<i>Eidolon helvum</i> (Kerr, 1792)	F	13	0	0	0	2	0	15	
	<i>Epomophorus labiatus</i> (Temminck, 1837)	F	627	5	101	42	382	1	1158	
	<i>E. wahlbergi</i> (Sundevall, 1846)	F	592	2	121	32	432	6	1185	
	<i>Hypsignathus monstrosus</i> H. Allen, 1861	F	54	2	0	0	45	5	106	
	<i>Micropteropus pusillus</i> (Peters, 1868)	F	8	1	0	0	10	2	21	
	<i>Myonycteris angolensis</i> (Bocage, 1898)	F	81	2	0	0	32	1	116	
Hipposideridae	<i>Doryrhina camerunensis</i> Eisentraut, 1956	FI	0	35	0	1	0	15	51	
	<i>Hipposideros beatus</i> K. Andersen, 1906	FI	6	412	0	0	0	35	453	
	<i>H. ruber</i> (Noack, 1893)	FI	12	82	0	6	1	35	136	
Megadermatidae	<i>Lavia frons</i> (É. Geoffroy, 1810)	E	3	0	0	0	0	0	3	
Emballonuridae	<i>Taphozous mauritanus</i> (É. Geoffroy, 1818)	OS	2	0	0	0	0	0	2	
Nycteridae	<i>Nycteris arge</i> Thomas, 1903	FI	3	58	0	0	3	28	92	
	<i>N. thebaica</i> É. Geoffroy, 1818	FE	25	1	6	0	12	1	45	
Molossidae	<i>Chaerephon major</i> (Trouessart, 1897)	OS	28	0	0	0	0	0	28	
	<i>C. pumilus</i> (Cretzschmar, 1830)	OS	32	0	36	0	42	0	110	
Miniopteridae	<i>Miniopterus cf. inflatus</i> Thomas, 1903	FE	122	8	0	0	100	8	238	
Vespertilionidae	<i>Glauconycteris argentata</i> (Dobson, 1875)	FE	2	0	0	0	8	0	10	
	<i>Glauconycteris humeralis</i> J. A. Allen, 1917	FI	0	1	0	0	0	0	1	
	<i>Hypsugo crassulus</i> (Thomas, 1904)	FI	1	32	0	0	0	18	51	
	<i>Kerivoula cuprosa</i> Thomas, 1912	FI	1	424	0	0	0	79	504	
	<i>Myotis bocagii</i> (Peters, 1870)	FE	18	0	0	0	15	0	33	
	<i>M. welwitschii</i> (Gray, 1866)	FE	7	0	0	0	5	0	12	
	<i>Neoromicia capensis</i> (A. Smith, 1829)	FE	321	21	31	2	134	1	510	
	<i>N. nana</i> (Peters, 1852)	FE	34	1	5	2	18	2	62	
	<i>Scotophilus dinganii</i> (A. Smith, 1833)	FE	23	0	0	0	12	0	35	
	<i>S. nux</i> Thomas, 1904	FE	3	0	0	0	3	0	6	
	Bat captures ( <i>N</i> )			2018	1087	300	85	1256	237	
	Species richness ( <i>S</i> )			24	16	6	6	18	15	
	Evenness ( <i>J'</i> )			0.63	0.60	0.75	0.81	0.66	0.80	
Simpson ( <i>D</i> )			0.79	0.69	0.70	0.61	0.77	0.82		