

Roost occupancy, roost site selection and diet of straw-coloured fruit bats (Pteropodidae: *Eidolon helvum*) in western Kenya: the need for continued public education

PAUL W. WEBALA¹, SIMON MUSILA², and ROGERS MAKAU²

¹Karatina University, School of Natural Resources and Environmental Studies, P.O. Box 1957-10101, Karatina-Kenya

²National Museums of Kenya, P.O. Box 40658, GPO 00100 Nairobi-Kenya

³Corresponding author: E-mail: paul.webala@gmail.com

Population fluctuations, roost site selection and diet of straw-coloured fruit bats, *Eidolon helvum* (Kerr, 1792) were studied for > one year in western Kenya. Total counts of bats at three identified roosts varied from 7,000 to 48,000 individuals. The bats moved between roosts within the same general area, probably reflecting seasonal variation in the availability of preferred foods and/or harassment and direct persecution at some roost sites by the rural community. Our study suggests that tree density and number of branches on trees were important factors in roost site selection for *E. helvum*, and the removal of roost trees has serious ramifications for their conservation in the region. Germination experiments and observations at roost sites indicated that *E. helvum* consumed fruits from 31 plant species of 16 families, potentially assisting in the dispersal of their seeds. Further monitoring is needed to provide a complete picture of the status and migration patterns of *E. helvum* in Kenya. Additionally, because the bats were viewed negatively and persecuted by roost tree clearance and direct eradication attempts, an education and community outreach programme in local schools and communities is proposed for the long-term conservation of viable populations of *E. helvum* in western Kenya.

Key words: population status, bat conservation, diet, education

INTRODUCTION

Fruit bats, or flying foxes, are keystone species for the maintenance and re-establishment of natural vegetation in the Old World tropics (Fujita and Tuttle, 1991). The role in seed dispersal and pollination is particularly important in tropical forest succession and vegetation dynamics (Fleming, 1982; Medellín and Gaona, 1999; Henry and Jouard, 2007). In general, fruit bats assist in maintaining genetic connectivity among fragmented patches in tropical rainforests and distant habitats because of their capability to fly over long distances (Richter and Cumming, 2008; Smith *et al.*, 2011; Tsoar *et al.*, 2011). A fruit bat species that forms large colonies, and plays a key role in seed dispersal and plant pollination, is the straw-coloured fruit bat, *Eidolon helvum* (Kerr, 1792). In West Africa, *E. helvum* is a critically important seed dispersal agent for the economically important and threatened timber tree, the African teak (*Milicia excelsa*) (Taylor *et al.*, 1999; Taylor, 2005; Dainou *et al.*, 2012). The ability of colony members to fly 59 km or more when foraging enhances seed dispersal and through their

long annual migrations, single colonies can disperse seeds even further (Richter and Cumming, 2008).

Colonies of *E. helvum* are rarely found in protected areas or in forests, but frequently near human habitations especially roosting on trees in the gardens of institutional houses such as government offices and in large towns (Mutere, 1967; Fayenuwo and Halstead, 1974; Baranga and Kiregyera, 1982; Racey, 2004), probably because there are fruit trees nearby. In Kenya, only a few colonies of *E. helvum* are known. One of the largest is in Vihiga County, ca. 30 km away from the rainforest at Kakamega. The role of *E. helvum* in the dispersal of seeds and pollination of flowers of many plants in western Kenya may be important but remains unstudied. Yet the species in Kenya is threatened by habitat loss and direct killing attempts at roosts (P. W. Webala, S. Musila, and R. Makau, unpublished data). Negative perceptions and traditional beliefs exert pressure on householders to destroy the bats and their roost sites. These threats are similar to those facing the species elsewhere (e.g., Mickleburgh *et al.*, 2008; Akite and Kityo, 2009). *Eidolon helvum* is listed as Near Threatened (NT) on the IUCN Red

List because of population declines and habitat losses (Mickleburgh *et al.*, 2008).

The main goal of this study was to provide baseline information for the maintenance of a viable population of *E. helvum* in Kenya, with the Vihiga colony as the focal point. Our study objectives were (1) to map roosts of *E. helvum* in western Kenya; (2) to monitor monthly population fluctuations at roost sites; (3) to analyse the diet to establish the potential importance of this species in plant regeneration and as potential consumer of the local fruit crop; (4) to investigate roost site selection by *E. helvum* and (5) document the nature of the threats faced by the bats and their habitats and to mitigate them.

MATERIALS AND METHODS

Study Area

This study was conducted near Mbale Town, Vihiga County (0°3'0"N, 34°43'30"E), in western Kenya (Fig. 1). Kuzmin *et al.* (2008) collected samples from some of these sites during their lyssavirus surveillance study.

With the highest human population density in rural Kenya at > 1000 persons per square km and a population growth rate of 3.3% (above the national average of 2.4%), the County has seen average farm sizes steadily decline to a current 0.5 ha (Government of Kenya, 2005). Vihiga County has a tropical climate

with annual mean precipitation between 1,800 mm and 2,000 mm and annual mean temperature of 24°C (Government of Kenya, 2005). Land use is mainly subsistence agriculture although tea plantations are common in a few areas. Common subsistence crops include maize, beans, vegetables, cassava, and millet for local consumption and an occasional dairy cow for milk production.

Mapping of Roost Sites and Bat Counts

We mapped five roost sites, three that were actively used by *E. helvum* and two that were abandoned (Fig. 1 and Table 1). The larger area of Vihiga County and adjoining areas were surveyed through interviews of local people and administrators, and through visits to, and interviews with, local wildlife, forestry and environmental agencies. The records of NGOs were examined for information on location of *E. helvum* roosts. Each roost site was mapped with a GPS. Bat counts were carried out at each active roost by counting the number of clusters for each branch and tree, and multiplying by the estimated mean number of bats in each cluster (50). This process was repeated at monthly intervals at each of the five roosts between October 2011 and July 2012.

Tree Characteristics at Roost Sites

We measured tree and site parameters at active and abandoned roost sites and also at four random sites. Random sites were selected within the general area of Mbale town, not far from active roost sites. At each of the five sites used by bats, we

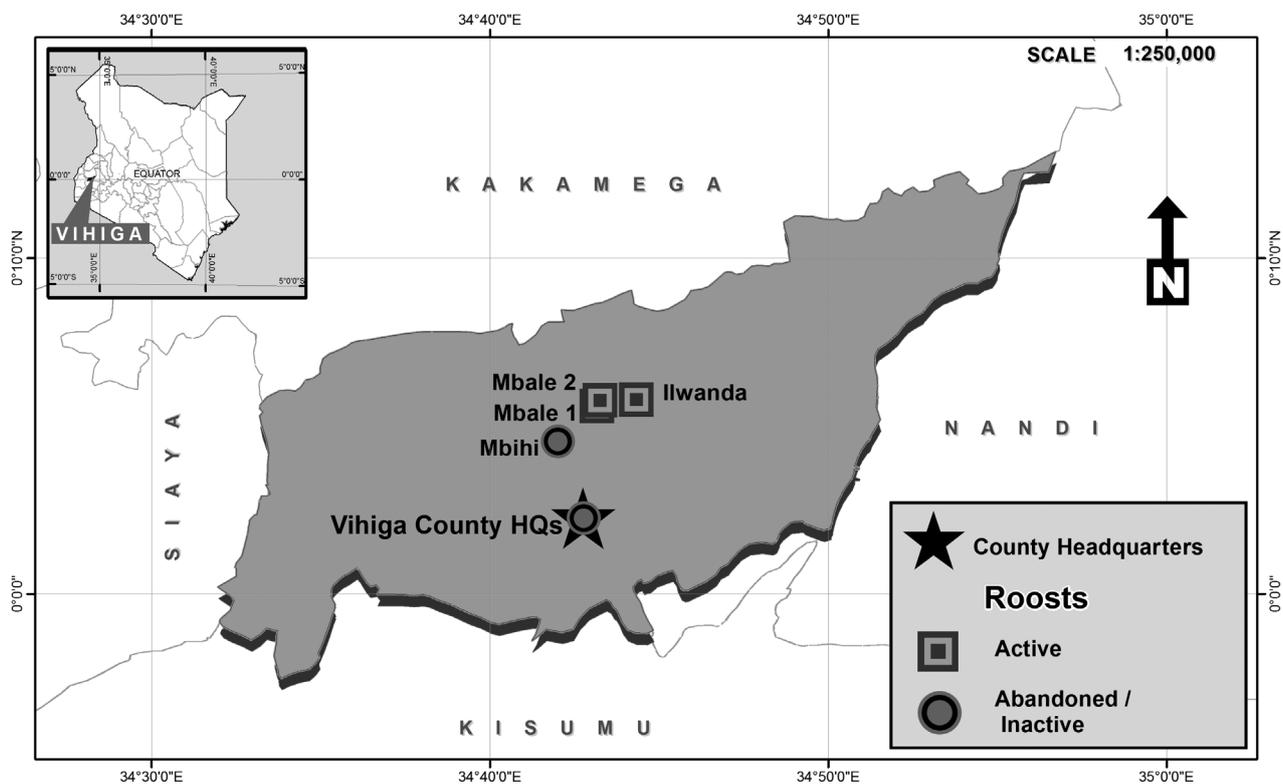


FIG. 1. Roost sites of *E. helvum* in Vihiga County, western Kenya. Inset shows the location of Vihiga County in Kenya

TABLE 1. Roost sites of *E. helvum* at Mbale, Vihiga County, Kenya, February 2013

Roost Site	Coordinates	Roost type	Roost status	Threat to bats and their roost
Mbihi	0°04'32"N, 34°42'01"E	Homestead	Oldest roost site but now abandoned after 80% of roost and non-roost trees were cut down for timber	Roost tree clearance — Farm owner too old with failing health and therefore unable to protect roost trees as before. Farm extensively cleared of trees to create farming land and for sale as timber to generate income. Remaining few trees were small and likely to be cut down as well.
Ilwanda	0°05'47"N, 34°44'21"E	Homestead	The ca. two ha farm, is owned by a single family, which practices mixed farming and agroforestry. Highest density of roost and non-roost trees planted and protected by owner. Bats tolerated despite torrents of negative myths from other villagers. Roost site least likely to be abandoned in the near future unless trees are cut down.	Limited tree regeneration — There was little evidence of regeneration on the farm since regular cultivation to eliminate weeds will also, inevitably, remove tree seedlings. Old and senescent trees were thus not replaced. Most of the <i>E. helvum</i> roost trees had been defoliated as result of huge weight of large numbers of roosting bats. Limited area to plant additional trees — Large family dependent on the farm for subsistence and sale of surplus to educate their children. Potentially, economic pressure may lead to tree clearance in the near future.
Mbale 1	0°05'35"N, 34°43'09"E	Homestead	Farm had few roost trees and these were found only in hedgerows as the small farms (<0.5 ha) were used for crop cultivation. The area had no capacity for planting more trees.	Tree clearance — Trees in hedgerows only source of timber or poles for constructing houses
Mbale 2	0°05'15"N, 34°42'46"E	Homestead	High density of suitable roost trees allowing past roosting by bats.	Chemical spraying of roosting bats — Farm owner tried driving bats away using an undisclosed chemical but this was ineffective and the bats returned after a while. Clearance of roost trees — In January 2012, main roost trees were felled to evict bats because (i) they were reportedly noisy; (ii) they dirtied the compound with large quantities of droppings; and (iii) the farm owner was under pressure from other villagers as the family was perceived to be practicing witchcraft that attracts bats
Vihiga County HQs	0°02'15"N, 34°42'46"E	Government offices	Compound had several tall trees. Bats evicted after preferred roost trees were cut down and through chemical poisoning. Site was abandoned by bats for years	Intolerance and tree clearance — Roost trees cut down to drive bats away

counted the trees actually used for roosting by bats and those with diameter at breast height ≥ 20 cm (large trees) in three 50 \times 50 m random plots. Roost tree density at each site was then estimated as the number of trees per hectare. For each large tree, DBH was measured using a tape at 1.3 m height and tree height was estimated using a Tree Vertex. The number of branches per tree was categorized on a scale of one to four as follows; 1 < 10; 2 = 10–19; 3 = 20–29; and 4 > 29. We considered both branches erupting from the trunk and from other branches since bats used both as roosts. Similarly, tree bark was assessed as 1 = smooth; 2 = intermediate; and 3 = rough. The trees were identified to species. In cases where this could not be done readily in the field, specimens were collected for later identification at the Herbarium of the National Museum of Kenya (NMK).

The tree and site characteristics were similarly measured at randomly selected sites and at sites considered to have been abandoned as roost trees by the bats.

Diet/Seed Rain Sampling

The total area beneath the crown of roost trees was sampled for seed rain by randomly placing twenty 1 m² seed traps (squares of plastic) on the ground under the crown of each tree. Trays were emptied every evening before the bats left roost sites for foraging bouts and the samples were collected the following morning after the bats had returned from foraging. Faecal samples were sealed in paper envelopes and labelled. Seeds were later separated for identification and germination in

the laboratory. Any seed that was not identified readily was planted in a greenhouse at the Botanic Gardens of NMK for subsequent identification of the seedling. We also identified plants growing beneath roost trees to species and categorized them as dispersed by bats or by other means based on information from the literature.

Statistical Analyses

Prior to analyses, all data were transformed [$\ln(x + 1)$] if they were not normally distributed. Nonparametric tests were applied when transformations were unsuccessful in rendering data normal and homoscedastic. All variables were continuous or rank ordered. To analyse relationships between tree diameter (DBH) and tree height, we used Spearman rank correlations, and the two variables were highly correlated at all sites ($r > 0.86$, $n = 492$, $P < 0.001$). However, both variables were retained for further analyses since we considered both height and DBH as important in the choice of roost sites for *E. helvum*. One-way ANOVAs were used to test for differences in tree diameter and height among active, random and abandoned roost sites, with height and DBH as dependent variables. Post hoc Tukey tests were performed to check for significant treatment differences (Day and Quinn, 1989). To test for differences in continuous and ordinal variables between active roost sites and random/ abandoned sites, Mann-Whitney *U*-tests were used because data were heteroscedastic (not normally distributed). All means are presented \pm SE. The analyses were carried out using Statistica 7.0 (Statsoft, Inc., Oklahoma, USA).

RESULTS

Roost Sites and Bat Counts

There were three sites actively used as roosts; Ilwanda, Mbale 1 and Mbale 2, the latter two situated near Mbale town (Fig. 1). The three roost sites were within three km of each other and the bats

appeared to move between them, as judged from the simultaneous changes in bat counts at the three roosts. Two other roost sites, Mbihi Village and Vihiga County Headquarters, were mapped but these were not used during the monitoring period and were probably permanently abandoned (Table 1). The site at Mbihi Village housed the largest colony of *E. helvum* in 2005 (ca. $> 50,000$ bats — P. W. Webala, personal observation) but reports indicate that it has been abandoned since 2006 after almost all roost trees were cut down. Similarly, anecdotal reports indicated that the roost site at Vihiga County headquarters hosted a large colony of *E. helvum* but the bats abandoned it after most trees were felled to ‘get rid of the bat menace’.

There were marked variations in the numbers of bats roosting at the three active sites. The colonies underwent considerable seasonal fluctuations in size during the monitoring period. Generally the total counts were lowest in November–January and highest in July–August (Fig. 2). Among the three roosts, the Ilwanda site had the highest bat count in July 2012, with the other sites recording no bats at all during the same month. Of all monthly counts, the lowest were in December 2011 and the highest in July 2012 (Table 2).

Roost Characteristics

The bats roosted mostly on cypress trees (*Cupressus lusitanica*; family Cupressaceae) and appeared to prefer this species to other trees available. However, to a smaller extent the bats also roosted in

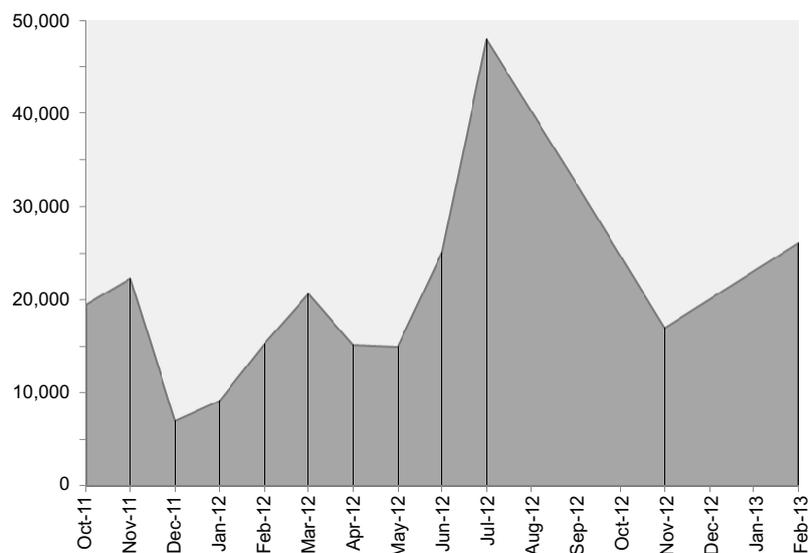


FIG. 2. Population fluctuations of *E. helvum* at three roost sites at Mbale and Ilwanda, Vihiga County, Kenya, from October 2011 to February 2013

TABLE 2. Population counts of *E. helvum* at three active roost sites in Vihiga County, Kenya

Count date	Ilwanda	Mbale 1	Mbale 2	Total	Change in numbers	Percent change %
27/10/2011	17,000	2,500	0	19,500	0	0.0
19/11/2011	22,320	0	0	22,320	+2,820	+14.5
19/12/2011	1,215	0	5,805	7,020	-15,300	-68.5
19/01/2012	0	0	9,180	9,180	+2,160	+30.8
19/02/2012	15,250	0	0**	15,250	+6,070	+6.6
18/03/2012	15,795	4,860	0	20,655	+5,405	+35.4
19/04/2012	0	14,450	700	15,150	-5,505	-26.7
20/05/2012	0	14,300	650	14,950	-200	-1.3
26/06/2012	0	25,100	0	25,100	+10,150	+67.9
29/07/2012	47,950	0	0	47,950	+22,850	+91.0
29/09/2012	0	30,150	2,500	32,650	-15,300	-31.9
24/11/2012	17,000	0	0,0	17,000	-15,650	-47.9
15/02/2013	26,100	0	0,0	26,100	+9,100	+53.5

** — 80% of roost trees felled after January 2012 counts

croton trees (*Croton megalocarpus*; Euphorbiaceae), broadleaved croton (*C. macrostachyus*), kapok trees (*Ceiba pentandra*; Malvaceae), Nile tulip, Nile trumpet or siala trees (*Markhamia lutea*; Bignoniaceae), mango (*Mangifera indica*; Anacardiaceae), silky oak (*Grevillea robusta*; Proteaceae), and avocado (*Persea americana*; Lauraceae). Although the Sydney blue gum (*Eucalyptus saligna*; Myrtaceae) was abundant in the study area, bats generally avoided these trees.

The density of trees (DBH \geq 20 cm) differed significantly among the sites ($F_{8, 18} = 22.40$, $P < 0.001$). The Ilwanda roost had the highest tree density (42.7 ± 3.5 trees/ha), followed by Mbale 2 (33.7 ± 2.3 trees/ha) and each had greater densities than the Mbale 1 (20.0 ± 0.6 trees/ha), Mbihi (15.0 ± 1.7 trees/ha) and Vihiga sites (21.7 ± 2.8 trees/ha) (post-hoc Tukey test, $P < 0.05$). Overall there were no significant differences in DBH, tree height, and bark type between active roost sites and random/abandoned sites. However, active roost sites had significantly more branches on trees than random/abandoned sites (Table 4).

Nevertheless, tests of differences between individual sites in DBH showed significant differences ($F_{16, 864} = 8.74$, $P < 0.001$). For example, the abandoned roost site at Vihiga County Headquarters had highest DBHs (41.5 ± 2.5 cm), which differed significantly from the active roost sites at Mbale 1 (27.9 ± 2.2 cm), Mbale 2 (29.8 ± 0.8 cm) and Ilwanda (25.8 ± 0.5 cm) (post-hoc Tukey test, $P < 0.05$). However, the three active roost sites (Mbale 1, Mbale 2 and Ilwanda) showed no differences in DBH (post-hoc Tukey test, $P > 0.05$) and neither were they significantly different from the abandoned roost site at Mbihi (29.9 ± 1.8 cm) nor each of the four random sites (25.3 ± 2.2 cm; 27.4 ± 0.9 cm;

25.6 ± 1.5 cm; 27.8 ± 2.0 cm — post-hoc Tukey test, $P < 0.001$).

As with DBH, there were significant differences in tree height between sites ($F_{16, 964} = 8.74$, $P < 0.001$). Again, the abandoned roost site at Vihiga District Headquarters had the tallest trees (18.7 ± 0.5 m), which differed significantly from average tree heights at Mbale 1 (15.8 ± 0.4 m), Mbale 2 (14.6 ± 0.6 m) and Ilwanda (15.6 ± 0.4 m) (post-hoc Tukey test, $P < 0.05$). The three active roost sites (Mbale 1, Mbale 2 and Ilwanda) showed no differences in tree heights, and neither were they significantly different from the abandoned roost site at Mbihi nor any of the four random sites (in both cases $P > 0.05$, post-hoc Tukey test).

Diet

Germination experiments and direct observations at active roost sites revealed that *E. helvum* consumed fruits from at least 31 plant species belonging to 16 families (Table 3). Observations of germinating seedlings and saplings at roost sites and germinated seeds collected from faeces indicated that figs (*Ficus* spp.; Moraceae) were the dominant food items in the diet (Table 3). Germinated seeds also included fruits from locally-cultivated fruit trees (both indigenous and exotic) such as guava (*Psidium guajava*; Myrtaceae), papaya (*Carica papaya*; Caricaceae), loquat (*Eriobotrya japonica*; Rosaceae), as well as water berries (*Syzygium cordatum* and *S. guineense*; Myrtaceae).

DISCUSSION

Eidolon helvum forms large colonies in scattered locations across the tropical forest and woodland belt of Africa, and on some offshore islands

TABLE 3. Plant species whose fruits were fed on by *E. helvum* in Vihiga County, western Kenya. The species were identified from seeds in the bats' faecal material, after seed germination in the green house and through direct observations and identification of seedlings and saplings at bat roost sites. Plant nomenclature follows the International Plant Names Index (2005)

Family	Plant species	Exotic/Indigenous	Identification method
Anacardiaceae	<i>Mangifera indica</i>	Exotic	Direct observation
Apocynaceae	<i>Saba comorensis</i>	Indigenous	Seed germination
Canellaceae	<i>Warburgia ugandensis</i>	Indigenous	Direct observation
Caricaceae	<i>Carica papaya</i>	Exotic	Seed germination
Cucurbitaceae	<i>Momordica foetida</i>	Indigenous	Direct observation
Flacourtiaceae	<i>Flacourtia indica</i>	Indigenous	Seed germination
Clusiaceae	<i>Garcinia buchananii</i>	Indigenous	Seed germination
Lauraceae	<i>Persea americana</i>	Exotic	Direct observation
Meliaceae	<i>Melia azedarach</i>	Exotic	Direct observation
Moraceae	<i>Ficus amadiensis</i>	Indigenous	Direct observation
	<i>F. asperifolia</i>	Indigenous	Seed germination
	<i>F. lutea</i>	Indigenous	Seed germination
	<i>F. natalensis</i>	Indigenous	Seed germination
	<i>F. ovalifolia</i>	Indigenous	Seed germination
	<i>F. ovata</i>	Indigenous	Seed germination
	<i>F. sur</i>	Indigenous	Seed germination
	<i>F. sycomorus</i>	Indigenous	Germination/observation
	<i>F. thonningii</i>	Indigenous	Seed germination
	<i>F. vallis-choudae</i>	Indigenous	Seed germination
	<i>Morus alba</i>	Exotic	Seed germination
Myrtaceae	<i>Psidium guajava</i>	Exotic	Germination/observation
	<i>Syzygium cordatum</i>	Indigenous	Seed germination
	<i>S. guineense</i>	Indigenous	Germination/observation
Fabaceae	<i>Crotolaria lanchnocarpoides</i>	Indigenous	Seed germination
Rosaceae	<i>Eriobotrya japonica</i>	Exotic	Seed germination
	<i>Rubus apetalus</i>	Indigenous	Direct observation
Rubiaceae	<i>Vangueria apiculata</i>	Indigenous	Direct observation
Rutaceae	<i>Teclea nobilis</i>	Indigenous	Direct observation
	<i>T. trichocarpa</i>	Indigenous	Direct observation
	<i>Toddalia asiatica</i>	Indigenous	Seed germination
Sapindaceae	<i>Allophylus ferrugineus</i>	Indigenous	Direct observation

including the Gulf of Guinea and Zanzibar, Pemba and Mafia (off Tanzania) (Bergmans, 1990). The *E. helvum* colony in Vihiga County is one of the many others represented on continental Africa. Others are known at Jinja and Kampala in Uganda, Ile-Ife and Lagos in Nigeria, Accra and Wli Falls in Ghana, Abidjan in Côte d'Ivoire and Dar-es-Salaam in Tanzania (Bergmans and Sowler, 1992; Racey, 2004). Bat numbers in these roosts are thought to have declined in recent decades due to human hunting for food and the loss of habitat to expanding agriculture (Monadjem *et al.*, 2007; Mickleburgh *et al.*, 2008; 2009; Akite and Kityo, 2009). Furthermore, deforestation, widespread in almost all tropical areas of the world, has had several identifiable consequences for fruit bat population declines generally (US Fish and Wildlife Service and National Environmental Protection Board, 1989).

The Vihiga colony was monitored for over a year and fluctuated from as high as 48,000 to less than

8,000 individuals. However, although the monitoring period was short, our data demonstrate seasonal migrations as the numbers are initially high in November, show a decline in December to May and increase again in July to September. This is in agreement with Lang and Chapin (1917) who suggested that immense numbers of *E. helvum* move around irregularly and then become abundant in regions from which they were previously absent. Indeed, at the end of the project, our local surveys identified one additional roost site in Vihiga County near Luanda town, ca. 50 km NW of current roost sites at Mbale, a site that was unused during the monitoring period. It seems likely that other roost sites exist further afield. For instance, anecdotal reports suggest that another roost site exists in Kisii County, ca. 250 km east of Vihiga. According to Mickleburgh *et al.* (1992), population declines and altered population dynamics are a common phenomenon in many fruit bat species, and this could be a response to

TABLE 4. A comparison of continuous and ordinal variables of tree characteristics of active roost sites and abandoned /random sites in Vihiga County, western Kenya. Means (\pm SE) are presented

Variable	Roost sites	Abandoned/Random sites	Mann-Whitney <i>U</i> -tests	
	<i>n</i> = 3	<i>n</i> = 6	<i>Z</i> _{Adj}	<i>P</i> -value
DBH (cm)	27.2 \pm 0.5	30.8 \pm 0.9	-1.87	0.063
Tree height (m)	15.4 \pm 0.3	15.4 \pm 0.2	-0.52	0.602
Bark-cover class ^a	2.2 \pm 0.1	2.2 \pm 0.0	-1.43	0.213
Number of branches ^a	3.3 \pm 0.1	2.4 \pm 0.1	10.29	< 0.001

^a— Ordinal variables, all others are continuous

deforestation and other anthropogenic habitat changes (US Fish and Wildlife Service and National Environmental Protection Board, 1989) or, presumably, to variations in the distribution of the food supply. From our direct observations, some current roost sites were subjected to tree clearance. It is therefore possible that habitat destruction via loss of roost trees led to the break-up of the original bat colonies, causing the bats to find alternative roost sites. Loss of forest results not only in the loss of critical roost trees but also key food resources for *E. helvum*.

Fluctuations in the size of fruit bat colonies have also been attributed to annual migrations of part or most of the colony (Mutere, 1966, 1980; Thomas, 1983; Parry-Jones and Augee, 2001; Sørensen and Halberg, 2001; Richter and Cumming, 2006). We could not conclusively relate population fluctuations of the Vihiga colony to local shifts between roost sites, because of the short monitoring period. Clearly, further year-long, and inter-annual, regional monitoring network of roost sites is needed to provide a complete picture of the migration patterns of this species in Kenya. *Eidolon helvum* is a classic example of a species that needs a functional network of roosting and foraging sites (Poiani *et al.*, 2000), which probably means that it would require many roost sites for its survival. There is an urgent need to further survey and map roost sites in Vihiga County and adjacent areas in the region in order to assess their conditions and work with local people for the long-term protection and survival of this bat species in Kenya.

Like fruit bat colonies in some other African countries (e.g., Bergmans and Sowler, 1992), *E. helvum* in western Kenya roosted in areas near human habitations. The roost sites were located on private farms within busy villages near Mbale town. However, although these areas are densely populated with > 1000 people per km² (Government of Kenya, 2005), homesteads in some localities had a relatively high density of both indigenous and exotic trees.

Our study revealed that tree density and number of branches per tree were key factors in the choice of roost sites. Indeed, active roost sites were located in areas with relatively high tree density compared to abandoned and random sites. For instance, the roost site at Ilwanda Village was located on a 2.0-ha private agroforestry farm with more than 100 indigenous and exotic trees interspersed within crops such as coffee, bananas, and maize. This site recorded the highest number of roosting bats during the monitoring period (Table 2).

DeFrees and Wilson (1988) suggest that *E. helvum* selects day roosts in tall trees that are large with spreading branches. Our study suggests that tree size and height were not important factors for the choice of roost sites. However, the defunct roost site at Vihiga County Headquarters had the tallest and largest diameter trees of all sites, but the roost site was unused during the monitoring period and had reportedly been abandoned for a couple of years due to persistent persecution via chemical spraying. The *E. helvum* colony in this study was large (with a maximum number of > 47,000 individuals), conspicuous and thus vulnerable to human persecution. Therefore, other than tree density, *E. helvum* presumably selected roost sites on the basis of persecution levels, which have included targeted eradication efforts such as chemical poisoning, and regular disturbances (e.g., stones being thrown at them). Indeed, information from local people indicated that eradication programs have been attempted in the area. For instance, after failed attempts to kill and evict the bats through chemical poisoning at Mbale 2, most roost trees were felled in February 2012 to get rid of the bats (P. W. Webala, S. Musila, and R. Makau, unpublished data).

The loss of roost trees at currently active roost sites appears to be a major threat to *E. helvum* in western Kenya, making the future of this bat colony uncertain in the region. The precarious situation is aggravated by the fact that the colony occurs on private land with no formal protection. While high

numbers of bats roosting on trees may result in tree destruction through defoliation (Happold, 1987; Ayoade *et al.*, 2012), roost sites can also potentially be altered through extraction of trees for timber, poles, firewood, or creation of space for human settlement and crop cultivation. With high human densities in Vihiga County, existing roost sites are likely to be affected, as local people are forced to exploit existing resources for survival. Although *Eucalyptus* trees were abundant at most of the active and abandoned roost sites in Vihiga County, *E. helvum* did not use them as roosts. However, *E. helvum* roosted on the Sydney blue gum (*E. saligna*) in Kampala, Uganda, rather than on other tree species such as mango (*M. indica*), candlenut (*Aleurites moluccana*; Euphorbiaceae), Nile tulip, Nile trumpet or siala tree (*Markhamia lutea* = *M. platycalyx*) and *Ficus* spp. (Baranga and Kiregyera, 1982). It is unclear why *Eucalyptus* trees were not utilized as roost sites in this study.

Frugivorous bats are effective seed dispersers over large distances (Hall, 1983). They can enhance seed interchange between different forest patches and the re-vegetation of large open areas (Boon and Corlett, 1989; Mickleburgh and Carroll, 1994). In fragmented landscapes they transfer seeds and pollen between isolated sites (Bollen *et al.*, 2004). Marshall (1985) reports that *E. helvum* diet includes flowers, fruits and leaves. Our study revealed that *E. helvum* consumed fruits from ca. 31 plant species of 16 families, including economically important fruit trees and many fig species (*Ficus* spp.) and, by feeding on fruits, *E. helvum* potentially assisted in the dispersal of these and many other plants in the region (Table 3). This species has the ability to forage as far as 59 km or more from the roost site in a single night (Richter and Cumming, 2008), suggesting that it is a long-distance seed disperser. Furthermore, because *E. helvum* spends at least half of each year on a long distance migration, probably to take advantage of seasonal fluctuations in different fruit and flower resources (Thomas, 1983; Richter and Cumming, 2006, 2008), its impact can be enormous in facilitating tropical forest regeneration and succession (Fleming, 1982).

According to Hodgkison *et al.* (2004), the abundance and predictability of food sources may determine the density of fruit bats that an environment can support. It was not possible to attribute the existence and constant shifting of *E. helvum* bats at different roost sites in this study to the presence and seasonal fluctuation of wild and domestic fruiting trees throughout the year or to persecution of the

bats and disturbance at roost sites. However, fruiting trees were abundant in the region and could have played a part in the back and forth movements exhibited by *E. helvum*. Although agricultural fruits may be less nutritionally beneficial than wild fruits for bats (Nelson *et al.*, 2000), the presence of large amounts of such fruits could allow a higher density to be supported than by primary forest (Dallimer *et al.*, 2006). Indeed, Juste and Ibáñez (1994) suggested that populations of fruit bats on the islands of the Gulf of Guinea increased when soft fruit trees were introduced after the islands were discovered and colonized since the late 15th century. Roost sites of *E. helvum* in western Kenya occur in an area with high rainfall, and the existence of indigenous and exotic fruit trees throughout the year could be the reason that these bats may not migrate far away in search of fruiting plants.

According to DeFrees and Wilson (1988), the guano of *E. helvum* may create an unpleasant smell and pose health risks in the villages where they roost. Interviews with farmers and villagers in Vihiga County indicated that farm owners were under immense pressure from neighbours to drive the fruit bats away. Generally, the bats were regarded as a public nuisance because they were reportedly noisy and roosted on trees, and defecated on compounds, lawns and farms. Furthermore, fellow villagers viewed households 'hosting' bats as harbouring witchcraft or using evil spirits for purposes of attracting or accumulating wealth. The consequence of this social pressure led to continued tree clearance to evict the bats at some roost sites because family members could not bear the negative view from neighbours. Superstition and ignorance by the general public have led to direct killing of the bats or roost site destructions elsewhere in Africa (Altringham, 1996; Taylor, 2000). In Vihiga County, roost trees were also cleared as a source of income through timber sales.

To address some threats facing the *E. helvum* colony in western Kenya, we conducted a robust and comprehensive bat education and community programme. We held six workshops with village elders, local leaders and church leaders in attendance to sensitize them to the importance on protecting *Eidolon* roost sites in Vihiga County. Further, as future custodians of natural resources, schoolchildren were the focus of our educational campaigns. Students were encouraged and facilitated to join Wildlife Clubs of Kenya (a local non-governmental organisation dedicated to promoting environmental conservation through schools). Seminars were

conducted in more than 50 schools in Vihiga County to improve understanding about bats and dispel myths and traditional beliefs. In addition, we organised awareness events and activities like tree planting, cultural days and football match competitions, which are common in western Kenya, through which the conservation message of bats and other local fauna was delivered. We also carried out livelihood analyses and identified income generating activities (e.g., agroforestry, poultry farming, bee keeping, dairy farming, handicrafts). Consequently, self-sustaining income-generating activities were initiated to enable farmers to buy into the conservation of bats. Finally, we also explored bat-friendly ecotourism opportunities as an additional motivation for the conservation of *E. helvum* and other bat species in Vihiga County. Local people were educated about establishing controlled visitation to selected roost sites. Through this, visitors and local people learn about the importance of bats and how to protect them and this advances long-term protection of *E. helvum* because locals derive direct income from bat-based ecotourism. These efforts should be sustained into the future to ensure the protection and survival of *E. helvum* and their roost sites in Kenya.

ACKNOWLEDGEMENTS

The authors thank the Eidolon Monitoring Network, and in particular Dr. Jakob Fahr, TU Braunschweig and Max-Planck Institute for Ornithology, Germany, for his conceptual input and for sharing his experience on *Eidolon* research in the rest of Africa. The project was supported by a generous grant from Rufford Small Grant for Nature Conservation, UK (Grant number 10078-1). The authors also like to acknowledge the partial support from Bat Conservation International (USA). The article is dedicated to the farmers hosting the colony of straw-coloured fruit bats on their farms in Vihiga County, Kenya. This is publication # 1 from the Eidolon Monitoring Network.

LITERATURE CITED

- AKITE, P., and R. M. KITYO. 2009. Populations of *Eidolon helvum* in Kampala over 40 years. *Tanzania Journal of Forestry and Nature Conservation*, 79(2): 1–7.
- ALTRINGHAM, J. D. 1996. *Bats: biology and behaviour*. Oxford University Press, Oxford, UK, 262 pp.
- AYOADE, O. J., S. O. OKE, and E. O. OMISORE. 2012. The impact of bats on the greens (landscape features): a case study of Obafemi Awolowo University Campus, Ile-Ife, Nigeria. *Agricultural Science Research Journals*, 2: 405–411.
- BARANGA, J., and B. KIREGYERA. 1982. Estimation of the fruit bat population in the Kampala Bat Valley, Uganda. *African Journal of Ecology*, 20: 223–229.
- BERGMANS, W. 1990. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 3. The genera *Scotonycteris* Matschie, 1894, *Casinycteris* Thomas, 1910, *Pteropus* Brisson, 1762, and *Eidolon* Rafinesque, 1815. *Beaufortia*, 40: 111–177.
- BERGMANS, W., and S. SOWLER. 1992. *Eidolon helvum*. Pp. 56–59, in *Old World fruit bats. An action plan for their conservation* (S. P. MICKLEBURGH, A. M. HUTSON, and P. A. RACEY, comp.). IUCN, Gland, Switzerland, viii + 252 pp.
- BOLLEN, A., L. VAN ELSACKER, and J. U. GANZHORN. 2004. Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. *Journal of Tropical Ecology*, 20: 599–612.
- BOON, P. P., and R. T. CORLETT. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). *Malayan Nature Journal*, 42: 251–256.
- DAÏNOU, K., E. LAURENTY, G. MAHY, O. J. HARDY, Y. BROSTAU, N. TAGG, and J.-L. DOUCET. 2012. Phenological patterns in a natural population of a tropical timber tree species, *Milicia excelsa* (Moraceae): evidence of isolation by time and its interaction with feeding strategies of dispersers. *American Journal of Botany*, 99: 1453–1463.
- DALLIMER, M., T. KING, D. COPE, and M. B. JIANA. 2006. Estimation of population density of *Eidolon helvum* on the island of Príncipe, Gulf of Guinea. *Mammalia*, 70: 48–51.
- DAY, R. W., and G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, 59: 433–463.
- DEFREES, S. L., and D. E. WILSON. 1988. *Eidolon helvum*. *Mammalian Species*, 312: 1–5.
- FAYENUWO, J. O., and L. B. HALSTEAD. 1974. Breeding cycle of straw-coloured fruit bat, *Eidolon helvum*, at Ile-Ife, Nigeria. *Journal of Mammalogy*, 55: 453–454.
- FLEMING, T. H. 1982. Foraging strategies of plant-visiting bats. Pp. 287–325, in *Ecology of bats* (T. H. KUNZ, ed.). Plenum Press, New York, 425 pp.
- FUJITA, M. S., and M. D. TUTTLE. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology*, 5: 455–463.
- GOVERNMENT OF KENYA. 2005. Vihiga District Strategic Plan 2005–2010 for implementation of the national population policy for sustainable development. National Coordination Agency for Population and Development, Ministry of Planning and National Development, Nairobi, 560 pp.
- HALL, L. S. 1983. Black flying-fox. Pp. 280–281, in *Complete book of Australian mammals* (R. STRAHAN, ed.). Angus and Robertson Publishers, Sydney, 530 pp.
- HAPPOLD, D. C. D. 1987. *The mammals of Nigeria*. Clarendon Press, Oxford, UK, 402 pp.
- HENRY, M., and S. JOUARD. 2007. Effect of bat exclusion on patterns of seed rain in tropical rain forest in French Guiana. *Biotropica*, 39: 510–518.
- HODGKISON, R., S. T. BALDING, A. ZUBAID, and T. H. KUNZ. 2004. Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. *Biotropica*, 36: 522–533.
- JUSTE, B. J., and C. IBÁÑEZ. 1994. Bats of the Gulf of Guinea islands: faunal composition and origins. *Biodiversity and Conservation*, 3: 837–850.
- KUZMIN, I. V., M. NIEZGODA, R. FRANKA, B. AGWANDA, W. MARKOTTER, J. C. BEAGLEY, O. Y. URAZOVA, R. F. BREIMAN, and C. E. RUPPRECHT. 2008. Lagos bat virus in Kenya. *Journal of Clinical Microbiology*, 46: 1451–1461.
- LANG, H., and J. P. CHAPIN. 1917. Part III. Field notes, in *The American Museum Congo Expedition collection of bats*

- (J. A. ALLEN, H. LANG, and J. P. CHAPIN, eds.). *Bulletin of the American Museum of Natural History*, 37(18): 497–563.
- MARSHALL, A. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society*, 83: 351–369.
- MEDELLÍN, R. A., and O. GAONA. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 3: 478–485.
- MICKLEBURGH, S. P., and J. B. CARROLL. 1994. The role of captive breeding in the conservation of Old World fruit bats. Pp. 352–364, in *Creative conservation: interactive management of wild and captive animals* (P. J. S. OLNEY, G. M. MACE, and A. T. C. FEISTNER, eds.). Chapman and Hall, London, xxxiv + 517 pp.
- MICKLEBURGH, S. P., A. M. HUTSON, and P. A. RACEY (comp.). 1992. *Old World fruit bats. An action plan for their conservation*. IUCN, Gland, Switzerland, viii + 252 pp.
- MICKLEBURGH, S. P., A. M. HUTSON, W. BERGMANS, J. FAHR, and P. A. RACEY. 2008. *Eidolon helvum*, in IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 8 April 2013.
- MICKLEBURGH, S. P., K. WAYLEN, and P. A. RACEY. 2009. Bats as bushmeat — a global review. *Oryx*, 43: 217–234.
- MONADJEM, A., P. J. TAYLOR, F. P. D. COTTERILL, R. M. KITYO, and J. FAHR. 2007. Conservation status of bats in sub-saharan Africa. *Bat Research News*, 48: 267.
- MUTERE, F. A. 1966. On the bats of Uganda. *Uganda Journal*, 30(1): 75–79.
- MUTERE, F. A. 1967. The breeding biology of equatorial vertebrates: reproduction in the fruit bat, *Eidolon helvum*, at latitude 0°20'N. *Journal of Zoology (London)*, 153: 153–161.
- MUTERE, F. A. 1980. *Eidolon helvum* revisited. Pp. 145–150, in *Proceedings of the Fifth International Bat Research Conference* (D. E. WILSON and A. L. GARDNER, eds.). Texas Tech Press, Lubbock, 434 pp.
- NELSON, S. L., M. A. MILLER, E. J. HESKE, and G. C. FAHEY, JR. 2000. Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. *Ecography*, 23: 393–401.
- PARRY-JONES, K. A., and M. L. AUGEE. 2001. Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology*, 26: 47–55.
- POIANI, K. A., B. D. RICHTER, M. G. ANDERSON, and H. E. RICHTER. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *Bioscience*, 50: 133–146.
- RACEY, P. A. 2004. 8,000,000 fruits bats, Africa's best-kept wildlife secret. *Bats*, 22(1): 1–5
- RICHTER, H. V., and G. S. CUMMING. 2006. Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology (London)*, 268: 35–44.
- RICHTER, H. V., and G. S. CUMMING. 2008. First application of satellite telemetry to track African straw-coloured fruit bat migration. *Journal of Zoology (London)*, 275: 172–176.
- SMITH, C. S., J. H. EPSTEIN, A. C. BREED, R. K. PLOWRIGHT, K. J. OLIVAL, C. DE JONG, P. DASZAK, and H. E. FIELD. 2011. Satellite telemetry and long-range bat movements. *PLoS ONE*, 6: e14969.
- SØRENSEN, U. G., and K. HALBERG. 2001. Mammoth roost of nonbreeding straw-coloured fruit bat *Eidolon helvum* (Kerr, 1792) in Zambia. *African Journal of Ecology*, 39: 213–215.
- TAYLOR, D. A. R. 2005. The straw-colored fruit bat, *Eidolon helvum*, and *Milicia excelsa* seed dispersal, survival, and germination. M.Sci. Thesis, Northern Arizona University, Flagstaff, 102 pp.
- TAYLOR, D. A. R., B. O. KANKAM, and M. R. WAGNER. 1999. The role of the fruit bat, *Eidolon helvum*, in seed dispersal, survival, and germination in *Milicia excelsa*, a threatened West African hardwood. Available at <http://nau.edu/cefns/forestry/research/ghana/seed-dispersal>.
- TAYLOR, P. J. 2000. *Bats of Southern Africa: guide to biology, identification and conservation*. University of Natal Press, Pietermaritzburg, RSA, 206 pp.
- THOMAS, D. W. 1983. The annual migrations of three species of West-African fruit bats (Chiroptera, Pteropodidae). *Canadian Journal of Zoology*, 61: 2266–2272.
- TSOAR, A., R. NATHAN, Y. BARTAN, A. VYSSOTSKI, G. DELL'OMO, and N. ULANOVSKY. 2011. Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences of the USA*, 108: e718–e724.
- US FISH, WILDLIFE SERVICE AND NATIONAL ENVIRONMENTAL PROTECTION BOARD (STATENS NATURVARDSSVERK [SNV]). 1989. Amendments to Appendices i and ii of CITES. Transfer of *Pteropus insularis*, *P. mariannus*, *P. molossinus*, *P. phaeocephalus*, *P. pilosus*, *P. sameoensis*, *P. tokudae* and *P. tonganus* (dead specimens and parts only) from Appendix ii to Appendix i (with annotation of *P. pilosus* and *P. tokudae* as P. E.) and inclusion of *Pteropus* spp. in Appendix ii for reasons of similarity of appearance. Available at http://www.cites.org/eng/cop/07/prop/e07-prop-02_&_04-11_pteropu.

Received 21 August 2013, accepted 27 February 2014