

# Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*)

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## Keywords

Megachiroptera; phenology; foraging; behavior.

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## Abstract

Animal migrations offer a unique opportunity for developing and testing hypotheses about the ecological requirements of different species and the tradeoffs that they make between conflicting life-history demands. There has been relatively little research into the causes and consequences of migrations by fruit bats, despite their potential significance for pollination and seed dispersal. We assessed the causes of one of the most spectacular migrations of fruit bats known: the annual influx of an estimated 5–10 million *E. helvum* into Kasanka National Park in Zambia. We tested several predictions based on the hypothesis that *E. helvum* migrates to exploit seasonal variations in food supply opportunistically. Phenological data, feeding observations and monitoring of fruit bat movements provided the first quantitative evidence in support of the hypothesis that the migration of *E. helvum* in Zambia is driven by food supply. The *E. helvum* colony exhibited several surprising behaviors, including a tendency for migratory satellite colonies to aggregate, rather than to disperse, during the time of peak food production, and a tendency to fly well beyond the most immediate food sources when foraging. Alternative hypotheses to explain the *E. helvum* migration were not supported, but further research is needed to clarify the results of this preliminary study. Both the size of the colony and its potential for large-scale movements suggest that this bat may play an important economic and ecological role over a significant portion of sub-Saharan Africa. Information is still lacking about migration routes, food sources, habitat requirements and the role of migration in disease transmission between colonies of *E. helvum*.

## Introduction

Long-distance movements of animals offer an interesting opportunity to advance our understanding of their ecology and biogeography. Organisms that can exploit variability in complex environments can achieve substantial advantages, such as high reproductive success, that are unexplained by trophodynamics (Bakun & Broad, 2003). Changing habitats inevitably involves costs, such as increased energy expenditure, vulnerability to predation while travelling and time allocated to improving foraging efficiency in a new habitat. An understanding of the causes of animal migrations can yield valuable insights into the variables that determine their life histories, habitat requirements, and foraging strategies. The impacts of migratory species are also of interest; broad-scale movements of animals can have ecologically important local and landscape-level consequences (Polis, Anderson & Holt, 1997).

Most studies of migrations in terrestrial habitats have focused on birds and ungulates (Cox, 1985; Fryxell & Sinclair, 1988; Berthold & Terrill, 1991). There has been less research on bat migrations. In Australia and Africa, the Megachiroptera (fruit bats and flying foxes) may migrate as

far as 1500 km (Thomas, 1983; Eby, 1991; Palmer & Woinarski, 1999; Tidemann & Nelson, 2004). It is generally assumed that bats make these movements to take advantage of short, but high-volume, bursts in fruit and flower production that periodically make savanna habitats richer in food resources, on a per capita basis, than forest habitats (van Schaik, Terborgh & Wright, 1993; Hepburn & Radloff, 1995; Fleming & Eby, 2003).

In this paper, we focus on *Eidolon helvum* (Kerr, 1792), the straw-colored fruit bat, which is the most conspicuous migratory megachiropteran species in Africa. Uganda, Ivory Coast, Malawi, Nigeria, Angola, Zambia and Mauritania all report large, migratory *E. helvum* colonies (Mutere, 1967; Ansell, 1978; Thomas, 1983; DeFrees & Wilson, 1988; Bergmans, 1990; Cosson, Tranier & Colas, 1996). Synchronized seasonal roosting patterns at sites separated by hundreds of kilometers have led to the conjecture that *E. helvum* migrates long distances, but the actual migration paths and the drivers of its migrations have not been studied (Thomas, 1983; Kingdon, 1984; Cosson *et al.*, 1996).

It has been hypothesized that *E. helvum* is an opportunist, migrating to take advantage of variations in regional food supplies to increase its reproductive success (Jones, 1972;

Thomas, 1983; Kingdon, 1984; DeFrees & Wilson, 1988; Taylor & Kankam, 1999). There are at least eight other competing hypotheses that could explain migratory behavior (Table 1). Thomas (1982, 1983) provided strong arguments for the northern migration of *E. helvum* along a hypothesized food gradient, but data to test this hypothesis were not available. No studies in Africa have tracked individual fruit bats during migration.

In this paper, we quantify fruit resources to test the hypothesis that *E. helvum* migrates to exploit a seasonal increase in food availability. Although food availability is important at multiple scales, we focused explicitly on the role of local food availability during a stopover by a migratory colony.

Ecological theory makes a number of predictions about the timing of migration and the behavior of migratory bats upon arrival in a new location. If food availability is an important driver of migration in *E. helvum*, the colony should arrive at its new habitat when food abundance is high or increasing, and depart when food availability starts to decline (Katz, 1974; Charnov, 1976; Pyke, Pullman & Charnov, 1977). If food resources are limited, *E. helvum* should forage selectively and/or utilize feeding roosts to reduce competition with resident bat species (Thomas, 1982; Putman, 1994). To reduce commuting time and conserve energy, individuals from the colony should forage close to the roost and deplete nearby resources before exploiting more distant food resources (Hamilton & Watt, 1970; Morrison, 1978; Aronson & Givnish, 1983).

We tested these predictions by monitoring local fruiting phenology, timing of *E. helvum* migration and foraging behavior of both migratory and resident fruit bat species at Kasanka National Park, in northern Zambia. We estimate the size of the migratory *E. helvum* colony at Kasanka to be between 5 and 10 million individuals, providing a strong test of migration hypotheses. Although our results provide the first quantitative support for the hypothesis that annual migration of *E. helvum* into Zambia is driven by food supply, we also observed some interesting and unexpected peculiarities in the nightly and seasonal foraging behavior of *E. helvum*.

## Methods

### Study species

*Eidolon helvum*, the straw-colored fruit bat, is the second largest fruit bat on the African continent. Adult *E. helvum* weigh 250–310 g, have an average wingspan of 80 cm and exhibit little sexual dimorphism (DeFrees & Wilson, 1988; Bergmans, 1990; Taylor, 2000). While the primary habitat for *E. helvum* is equatorial Africa, its migratory range extends from sub-Saharan Africa to South Africa (Kingdon, 1984). *E. helvum* is a strong flyer and is built for endurance rather than agility. Its body structure supports long migrations while restricting much of its foraging to the upper canopy layer, as a consequence of its relatively low manoeuvrability (Thomas, 1983; Norberg & Rayner, 1987).

**Table 1** Alternative hypotheses for *Eidolon helvum* migration

Hypothesis	Discussion
Unfavourable climate/food shortage avoidance (Cohen, 1967)	Less likely if the bats migrate from the equatorial rainforests in which they probably evolved (Bernard & Cumming, 1997)
Competition reduction (Thomas, 1982; Cox, 1985; Bergmans, 1990; Levey & Stiles, 1992)	Not tested, but the appearance of feeding roosts, coinciding with decreasing food availability, may indicate that competition for food resources is occurring. Removing fruits from focal trees and moving to feeding roosts may decrease interference competition (Morin, 1999).
Seek limiting nutrients (Thomas, 1984; Dumont, 2003; Nelson, 2003)	Analysis and comparison of the nutritional content of <i>E. helvum</i> food sources at Kasanka with other known food items are needed to exclude or support this hypothesis.
Optimize mate selection (Birkhead & Moller, 1998)	The capture of both adult males and pregnant females in 2000 (Stuart & Stuart, 2001), 2002 (P. Racey, pers. comm.) and 2003 clearly shows that the <i>E. helvum</i> colony at Kasanka is not composed of only young non-breeding individuals (Sorensen & Halberg, 2001). While mating has been observed at Kasanka, the hypothesis that it is primarily a mating aggregation is discredited by the range of ages and the different reproductive status of bats present in the colony. Mating aggregations would be expected to show a higher degree of reproductive synchrony.
Disease/parasite avoidance (Reeve, 1988; Loehle, 1995)	Bats should form smaller colonies that would reduce, rather than increase, probabilities of transmission. Interactions between African fruit bat colonies are an area of special concern as their roles in disease transmission, including Ebola, Lyssavirus and Nipah virus, are unclear.
Juvenile training (Kingdon, 1984)	The Miombo woodland at Kasanka has a simpler canopy structure than equatorial rainforest, and we would expect foraging to be easier there for clumsy juveniles. Some young were observed in the colony, but sightings were rare. Although juvenile survival may be higher as a consequence of the migration, we found no evidence to support this hypothesis.
Predator escape/predator swamping (Fryxell, Greever & Sinclair, 1988)	It has been suggested that predation on <i>E. helvum</i> in general is relatively infrequent and seems to pose no threat to the population (Jones, 1972; DeFrees & Wilson, 1988). When foraging, <i>E. helvum</i> did not exhibit common predator avoidance strategies such as lunarphobia. We observed eagles, snakes and crocodiles feeding on the bats, but none of these predators were present in particularly high abundances. It thus seems unlikely that <i>E. helvum</i> aggregates in such large numbers to swamp local predators.

**Study site**

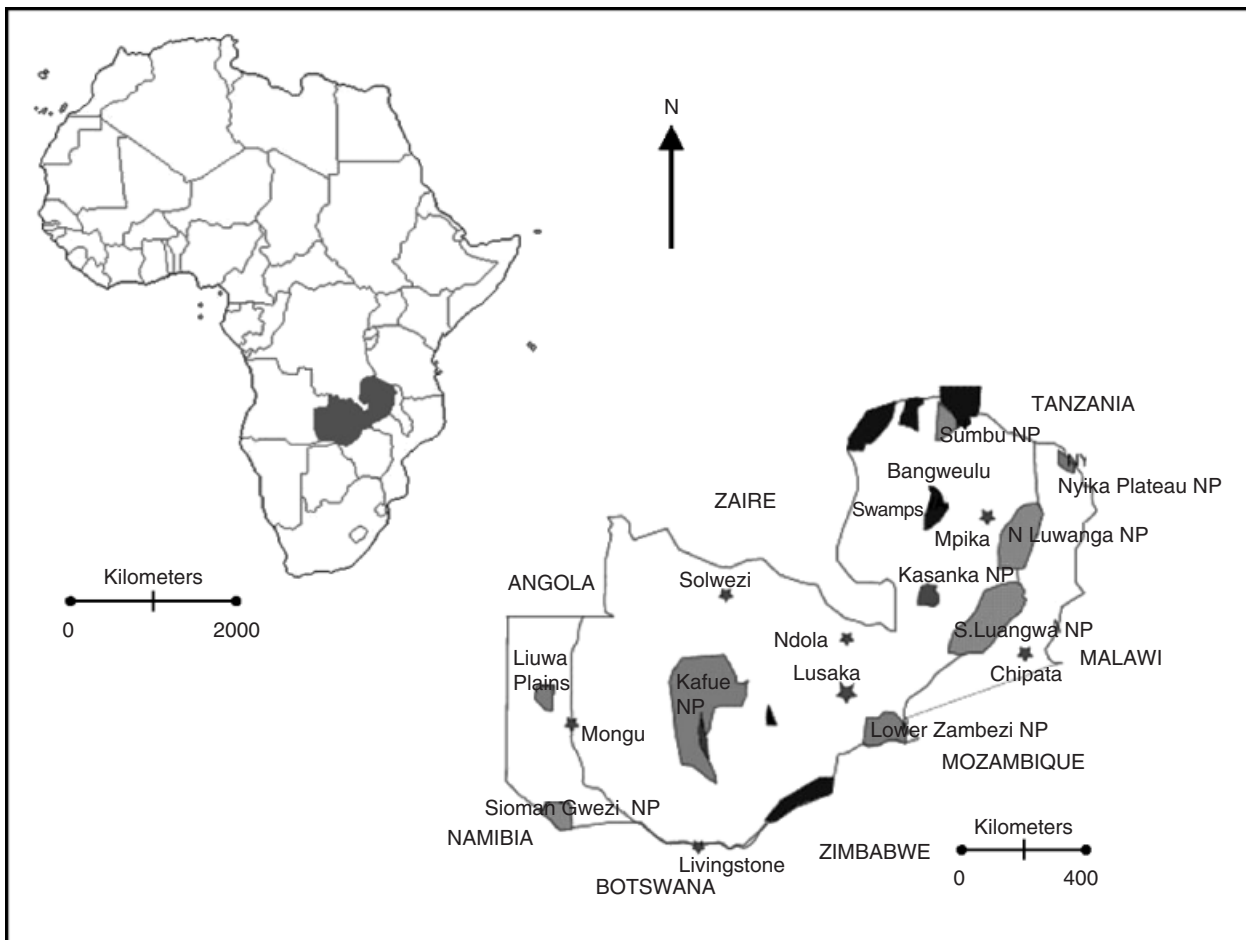
This study was conducted from August 2003 through January 2004 at Kasanka National Park (NP) in Central Zambia (12°30'S 30°14'E) (Fig. 1). Kasanka NP serves as a seasonal roost site, from October through January, for millions of migratory *E. helvum*. Kasanka is a 420 km<sup>2</sup>, privately managed NP, measuring c. 15 km north to south and 35 km east to west. The park has an average elevation of 1050 m, with the highest elevation measuring just under 1300 m. The region is dominated by Miombo woodland, and particularly the tree genera *Brachystegia*, *Isoberlinia* and *Julbernardia*. Miombo at Kasanka ranges from scrub to a tall woodland with canopy ≥20 m, and is interspersed with seasonally wet grasslands and rivers as well as some small patches of chipya, mushitu and mateshe forests (Smith & Fisher, 2001). Seasonal rainfall from November through April, totalling c. 1200 cm a year, supports a large seasonal fruit crop of food resources including *Uapaca* spp., *Syzygium* spp. and *Parinari curatellifolia*.

The two small patches of mushitu forest at Kasanka, which cover an area of about 0.4 km<sup>2</sup>, are the only known roost sites in the region for *E. helvum* colonies. Mushitu evergreen swamp

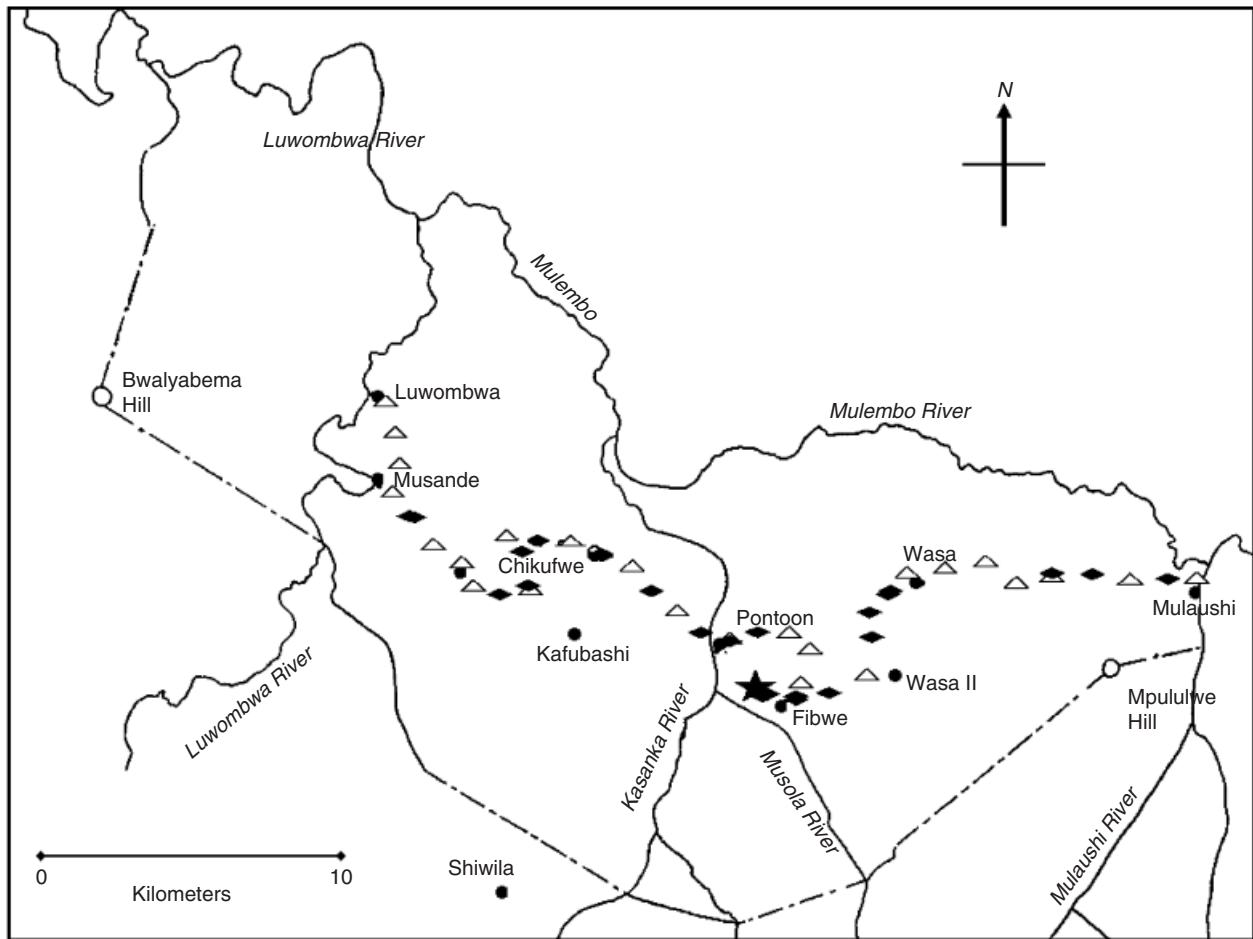
forests occur throughout the higher rainfall areas in Zambia. They are dominated by tree species that include *Khaya nyasica*, *Parkia filicoidea* and *Diospyros mespiliformis* (Storrs, 1995; Smith & Fisher, 2001). Mushitu has three canopy layers: a closed evergreen canopy up to 27 m, an understorey between 10 and 18 m and, below this, a dense thicket consisting mainly of ferns and climbers (Storrs, 1995; Smith & Fisher, 2001). Waterberry *Syzygium cordatum* and African mahogany *Khaya nyasica* dominate the taller canopy layer, while swamp fig *Ficus trichopoda* dominates the understorey.

**Vegetation monitoring**

Vegetation transects were established and monitored starting 7 September 2003. Transects were placed from the eastern park boundary to the western edge, where the Luwombwa river forms a natural boundary (Fig. 2). Transects were located about 1 km apart on primary dirt roads and crossed c. 45 km of park land. Every fifth transect was paired with an offset transect 100 m into the bush to test for the effects of roads on vegetation composition. Road transects were 100 m long and included 5 m on either side of the road. Off-road



**Figure 1** Location of the study site, Kasanka National Park, in Zambia. NP, National Park.



**Figure 2** Map of Kasanka National Park, Zambia. The Luwombwa and Mulembo Rivers form the northern boundary, the Mulaushi River forms the eastern boundary and the dotted lines delineate the southern and western park boundaries. The location of the *Eidolon helvum* roost (★) and vegetation transects where mist netting was (▲) and was not (◆) conducted are also marked.

transects were located perpendicular to the road, 100 m into the bush and were 10 m wide by 100 m long.

All fruiting trees and transect locations were marked with identification numbers using wire-mounted aluminium tags (Corstor Ltd, Johannesburg, South Africa). A fruiting tree was considered to be any tree whose fruit-bearing branches entered a transect. In each transect the location (using a Garmin GPS12 receiver, Garmin, Olathe, Kansas, USA), the diameter at breast height (DBH) and the species of each fruiting tree and shrub taller than 1 m were recorded.

The presence and availability of fruit in each transect were measured by assigning each tree an index of fruit availability, ranging from a score of 0 for trees with no fruit, to a score of 4 for trees with very abundant fruit (Chapman, Wrangham & Chapman, 1994). While scores are subjective fruit indices, the results were reliable and consistent across observers. After the disappearance of all fruits, the trees were monitored for 2 weeks to ensure that the first 0 did not reflect observer error. Evidence of feeding at fruiting trees was noted, and feeding roosts were marked and monitored.

Transects were monitored from 7 September 2003 until 5 January 2004. Each transect was checked every 7–10 days, for a total of 16 consecutive measures. In all, 350 trees were tagged and monitored for the presence of fruit in 45 transects. Trees and shrubs were identified by Zambian game scouts using local names, and identifications were confirmed using published field guides and Kasanka species records (Fanshawe, 1984; Storrs, 1995; Coates Palgrave, 2002).

Food sources for *E. helvum* were compiled from observations collected in 2000 and 2003. Game scouts noted where and when they saw fruit bats, how many bats there were and whether the bats were feeding or flying. If the bats were feeding, the scouts recorded which fruits the bats were feeding upon. These records were combined with observations of feeding bats, the presence of ejecta pellets under fruiting trees in the vegetation transects and seeds and ejecta pellets found under feeding roosts. Samples were collected from unidentified food sources in 2000 and were identified using reference samples at the University of Zambia herbarium.

## Mist-netting methods

Our dispersal and foraging data for *E. helvum* are observational because even though individual *E. helvum* could be easily grabbed by hand at the roost site, we did not capture any bats of this species in mist nets. The mist-netting data were collected from 4 November 2003 to 30 December 2003 at 26 sites throughout the park. Two types of 4-shelf mist nets were used: a 2.6 × 4 m, 110 denier/2-ply, 60 mm mesh and a 2.6 × 12 m, 50 denier/2-ply, 38 mm mesh (Avinet, Dryden, NY, USA). Bats were netted over 23 nights in the preset vegetation transects and at two camp sites: Wasa and Shiwila (Fig. 2). Sites were netted with some combination of one 2.6 × 12 m and two 2.6 × 4 m mist nets set at ground level. We did not use canopy nets because our original objective was to examine which fruit bat species were foraging within and under the canopy, rather than to catch bats that were commuting along natural corridors. Nets were placed within 5 m of a road, and at most sites, between one to three nets were placed across the road.

Nets were opened beginning around 18:15 h (dusk) and closed at about 04:45 h (sunrise). A site was netted for *c.* 3 h before nets were moved to a new location, and in this manner two to three sites were netted per night.

## Results

*Eidolon helvum* were first observed at Kasanka on 18 October 2003. All *E. helvum* had left the park by 24 December 2003. The first rainstorm occurred on 17 October, although the area did not receive significant precipitation again until mid-November. The arrival and departure dates of the colony conform to trends recorded in previous years, as documented by the Kasanka staff. In 1997, 1998, 1999 and 2001, a colony of *E. helvum* was first sighted on 21 October, while in 2000 the first bats were observed on 19 October. In the 2000–2001 season, the colony departed 9 January (2001), whereas in 2001 all of the bats had departed by 23 December. The colony did not arrive simultaneously; groups of bats arrived during multiple evenings, and colony size stabilized after *c.* 3 weeks. Departure also occurred in groups; however, the entire colony departed within one week of the first observation of declining numbers. Our observations were consistent with park records of arrival and departure behavior from previous years.

Of five *E. helvum* that were captured by hand in the roost site on 16 November 2003, two were pregnant females and three were adult males. In 2000, 10 female bats captured from the roost site were pregnant (Stuart & Stuart, 2001). In 2002, 18 female bats were captured by hand at the roost, of which 2 were lactating and 14 were pregnant (P. Racey, pers. comm.).

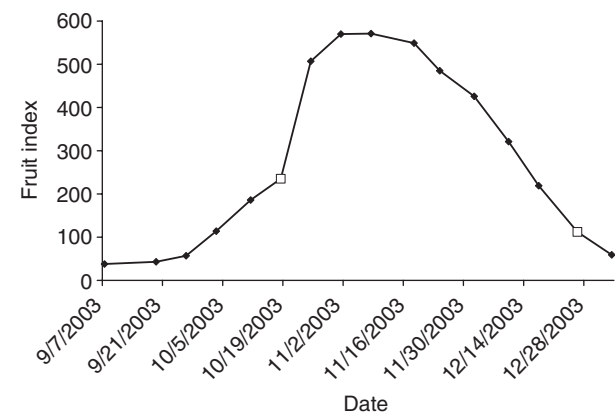
Mist netting at 24 sites on 23 nights, for a netting effort of 1970 net meter hours (one net meter hour equals 1 m<sup>2</sup> of net open for 1 h), yielded no *E. helvum* within 15 km of the roost. This result was unexpected since *E. helvum* was observed in large numbers flying over our net sites. We captured over 120 fruit bats of other species, including *Epomophorus*

*gambianus crypturus*, *Epomophorus minor*, *Epomophorus labiatus*, *Epomophorus wahlbergi* and *Micropteropus pusillus*.

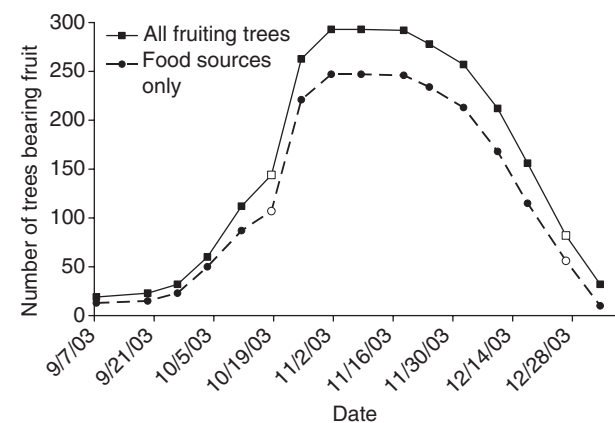
## Vegetation results

Comparison of by-road and off-road transects using the Wilcoxon rank sum test showed no significant influence of roads on the mean number of fruiting trees ( $n = 14$ ,  $Z = 0.261$ ,  $P = 0.795$ ). Fruit availability, whether measured using simple presence/absence data or the sum of scores for all trees, showed a similar response over time in all transects (Figs 3 and 4). For clarity, only the graphs illustrating the presence or absence of fruit on trees are discussed in the text.

Fruit availability began to increase from early October until it plateaued, remaining constant throughout most of



**Figure 3** Changes in the index of fruit availability over time. The fruit index equals the sum of scores for all fruiting trees at each time. Arrival (18 October 2003) and departure (23 December 2003) dates of the *Eidolon helvum* colony are indicated (□).



**Figure 4** Changes in the total number of fruiting trees in the vegetation transects over time. Solid line indicates the total number of fruiting trees and the dotted line includes only those trees known as food sources for *Eidolon helvum*. Arrival (18 October 2003) and departure (23 December 2003) dates of the *E. helvum* colony are indicated (□, ○).

**Table 2** Records of feeding observations and ejecta pellets at fruiting trees

Tree species	Scout				Ejecta		Obs	
	2000		2003		2003		2000	2003
	# Obs	%	# Obs	%	# Obs	%		
<i>Ficus</i> spp.	0	0.0	1	2.0	0	0.0	×	×
<i>Magnistipula butayeei</i>	15	10.0	7	16.0	0	0.0		
<i>Mangifera indica</i>	1	<1.0	0	0.0	0	0.0		
<i>Musa</i> spp.	0	0.0	2	5.0	0	0.0	×	
<i>Parinari curatellifolia</i>	18	12.0	3	7.0	0	0.0	×	
<i>Syzygium cordatum</i>	0	0.0	0	0.0	4	4.0		×
<i>Syzygium guineense guineense</i>	4	3.0	6	14.0	59	59.0		×
<i>Syzygium guineense huillense</i>	1	<1.0	15	34.0	13	13.0	×	×
<i>Uapaca kirkiana</i>	40	26.0	9	20.0	1	1.0		
<i>Uapaca banguelensis</i>	32	21.0	1	2.0	18	18.0		
<i>Uapaca sansibarica</i>	42	27.0	0	0.0	5	5.0		×

Data are from feeding records collected by game scouts (Scout), the presence of ejecta pellets under fruiting trees and at feeding roosts (Ejecta), or from personal observation of bats feeding at trees (Obs). Data include the number of observations of bats at each tree species (# Obs), as well as the per cent of all feeding records for the tree species each year (%).

November. Food availability rapidly decreased throughout December and almost no trees were observed with fruit at the beginning of January. The colony arrived immediately before the peak of fruit production, and left when fruit availability was low, but before it was exhausted (Figs 3 and 4).

Observations of feeding bats and ejecta pellets at fruiting trees yielded 297 records of local food sources for *E. helvum* (Table 2). These included *Ficus* spp., *Musa* spp., *Magnistipula butayeei*, *Parinari curatellifolia*, *Syzygium* spp. and *Uapaca* spp. *E. helvum* feeds on most species that fruit from October to December (Fig. 4). These trees cover a wide range of sizes, from the shorter 4 m *Syzygium* to taller *Parinari* that were, on average, 11 m in height (Table 3).

Four *E. helvum* food sources were relatively abundant while the colony was at Kasanka: *Syzygium guineense guineense*, *Syzygium guineense huillense*, *Uapaca kirkiana* and *Uapaca banguelensis*. *Uapaca* and *Syzygium* species exhibited a strong seasonal presence, and the departure of the colony coincided with a marked decrease in the availability of fruit from these trees (Fig. 5).

While ejecta pellets were found at many fruiting trees beginning in October, the first feeding roosts were not found until 24 November 2003, coinciding with the initial decrease in food availability in the area (Fig. 4). Eight feeding roosts were found in the vegetation transects, and seeds and ejecta pellets were found from *U. kirkiana*, *U. banguelensis* and *Syzygium guineense guineense* under these trees. Feeding roosts were located in *Brachystegia spiciformis*, *Isoblerlinia angolensis* and *Julbernardia paniculata* trees.

*E. helvum* exhibits refuging behavior at Kasanka, and disperses from a central place along radial lines to its feeding grounds. If *E. helvum* selectively forages to minimize travel time and maximize energy gain, resources close to the roost site should be depleted before the bats travel farther to feed (Pyke *et al.*, 1977; Morrison, 1978; Aronson & Givnish, 1983). At the distances measured in this study, transects

closer to the roost did not show earlier decreases in fruit availability (Fig. 6). Most *E. helvum* continued to disperse radially at distances greater than 15 km from the roost site throughout the residence period of the colony. We found no evidence that *E. helvum* at Kasanka minimized travel time by foraging close to the roost before commuting longer distances.

Many other *E. helvum* colonies disperse to form smaller colonies during the wet season; however, the timing of the arrival of *E. helvum* in Central Zambia does not coincide with the dispersal of other large, well-known colonies (Fig. 7). The annual disappearance of an *E. helvum* colony in Mauritania closely precedes the arrival of the Kasanka colony (Cosson *et al.*, 1996), but because of the distance from Mauritania to Zambia, it is unlikely that this is the same colony.

## Discussion

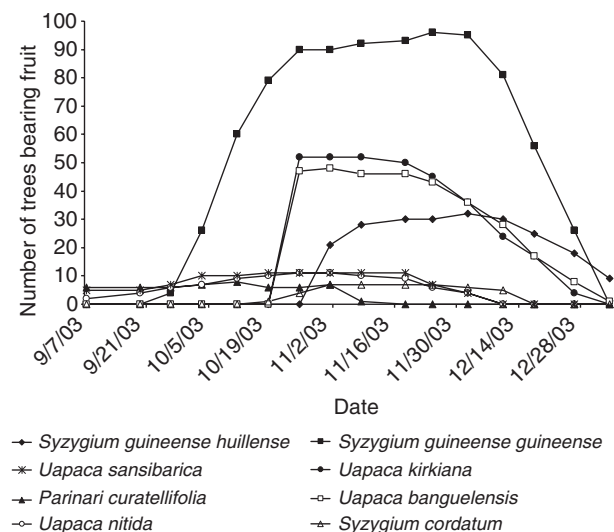
Our results suggest, as expected, that migratory *E. helvum* arrive at Kasanka when fruit abundance is increasing and depart when fruit abundance is decreasing. We found no direct evidence to support competing hypotheses, but some alternative hypotheses could not be excluded (Table 1). The arrival of the colony at Kasanka coincided with a marked increase in the number of fruiting *Syzygium* and *Uapaca* species; these trees accounted for greater than 80% of all fruit-bearing trees at that time. The colony departed immediately before the *Syzygium* and *Uapaca* fruit crops were depleted. *Syzygium* is a known food source for *E. helvum* in Sub-Saharan Africa (Marshall, 1985); however, foraging on *Uapaca* may be a new example of diet switching in the region.

The arrival of the *E. helvum* colony at Kasanka is historically more predictable than the onset of the rains and the associated rise in indices of fruit availability. The departure of the *E. helvum* colony on 23 December 2003

**Table 3** *Eidolon helvum* food sources, their fruiting times, mean species diameter at breast height (DBH) and height (HT) in 2003

Tree species	Local name	Begin fruiting	End fruiting	DBH (cm)	HT (m)
<i>Parinari curatellifolia</i>	Mupundu	August	Early November	64.4 ± 32.0	11 ± 5
<i>Uapaca kirkiana</i>	Masuku	Late August	Early to mid-January	10.5 ± 4.0	6 ± 1
<i>Uapaca nitida</i>	Nsokolobe	Late August	Early December	10.7 ± 3.0	6 ± 1
<i>Uapaca banguelensis</i>	Makonko	Late August	Late December	9.5 ± 3.1	6 ± 1
<i>Uapaca sansibarica</i>	Swebya	Late August	Early to mid-December	16.2 ± 7.4	7 ± 2
<i>Syzygium cordatum</i>	Mufinsa	Mid-October	Early to mid-December	22.9 ± 7.9	10 ± 2
<i>Syzygium guineense guineense</i>	Insafwa	Late September	Late December	7.2 ± 3.1	4 ± 1
<i>Syzygium guineense huillense</i>	Mufinsa	Mid-October	Early to mid-January	18.1 ± 11.7	5 ± 1

Values given are the mean ± 1 sd.



**Figure 5** Availability of known food sources for *Eidolon helvum* during the study period. The *Uapaca kirkiana* and *Uapaca banguelensis* lines exclude trees bearing unripe fruits.

coincided with decreasing trends in local fruit indices, but in previous years the colony has left as late as the second week of January. This range in departure dates may reflect the principle that predicting fruit abundance from a remote location is more challenging (and consequently more 'hard-wired') than assessing when local fruit abundance is low. It may also be a function of varying resource depletion rates, depending upon the year's fruit crop quantity and quality. There are no phenological data available for previous years that would have allowed this hypothesis to be tested.

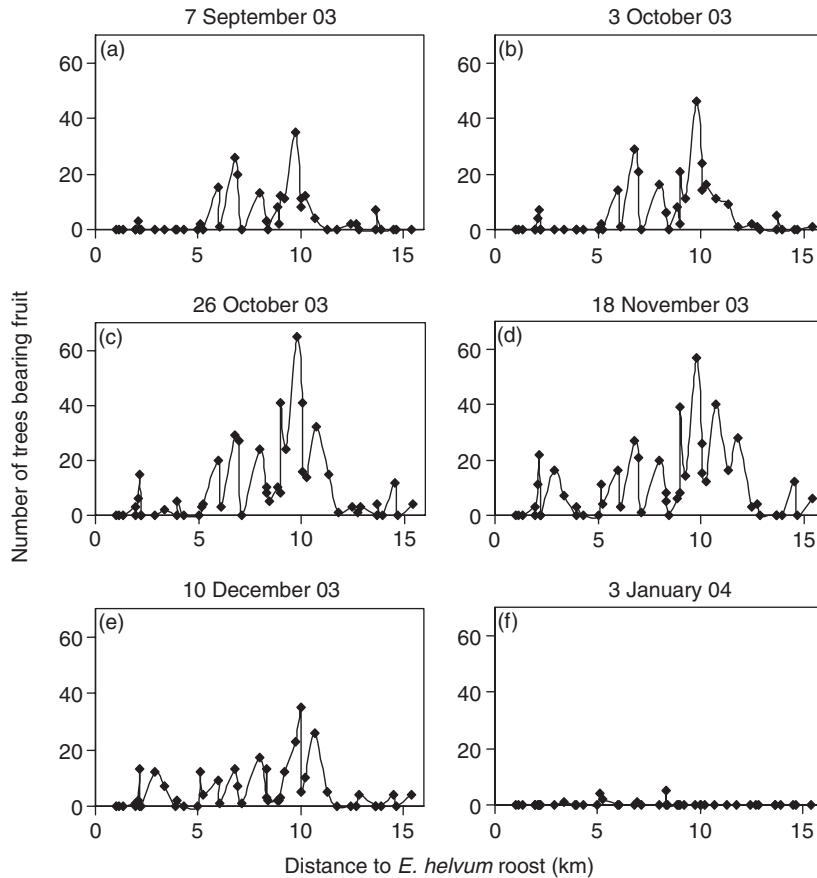
Although the relationships between fruit production and migration in *E. helvum* were consistent with our original predictions, the local foraging behavior of *E. helvum* was unexpected. With over 5 million *E. helvum* roosting within 2–15 km of our mist-netting sites, it is remarkable that not a single *E. helvum* was captured in a mist net. There are three possible explanations for this result. First, the bats may fly farther than 15 km before descending to feed. Colonially roosting bats may make long commuting flights to reduce competition with conspecifics (Bonaccorso *et al.*, 2002), and

since the relative energetic costs of flight are low for large bats, they can afford to fly further away to forage (Horner, Fleming & Sahley, 1998). However, reducing competition with conspecifics by increasing commuting time should not necessarily decrease competition from the other fruit bat species that are relatively abundant in the area. Second, *E. helvum* may only feed in the upper canopy near their roost. Examples of *E. helvum* feeding primarily in the upper canopy have been observed in other African regions (Thomas, 1982). Based on observations made while mist netting, this possibility seems less likely to us as an explanation of our results. *E. helvum* is a large bat that can normally be observed feeding at night without much difficulty, and we saw very few feeding *E. helvum* in the transects. A third possibility is that fruit abundance is considerably higher in the chitemene agricultural systems outside Kasanka, and the bats simply fly to the area of highest fruit abundance to forage. Further investigation of bat activity outside the park would help to resolve this question.

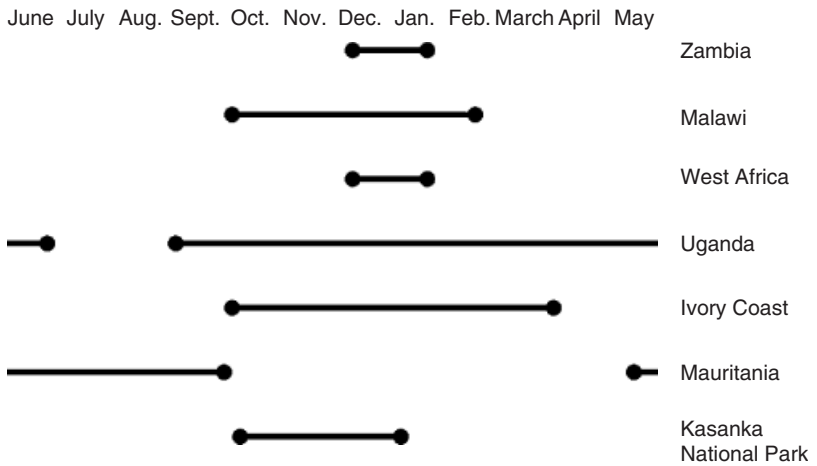
The arrival of straw-colored fruit bats at Kasanka cannot easily be explained by the vacating of other breeding colonies (Sorensen & Halberg, 2001) because its timing does not coincide with the dispersal of other large colonies in West or East Africa. The only colony that reportedly migrates at this time is in Mauritania, about 6000 km away, and is composed of only a few hundred individuals (Cosson *et al.*, 1996). The migratory colony at Kasanka may have simply been undetected until now on the rest of its migration route, although a second explanation is more likely. The degree of asynchrony in reproductive timing is evidence that the colony at Kasanka may be composed of smaller satellite colonies from other African populations. *E. helvum* frequently disperses when rains arrive in an area (Kingdon, 1984), and if multiple satellite colonies are congregating at Kasanka the explanation for this behavior is unclear.

## Synthesis

Taken as a whole, our results suggest that *E. helvum* migrate to Kasanka to exploit seasonal fruit resources, fulfil the energetic demands of pregnancy and lactation and support the growth of juveniles that may be weaned at that time (Thomas & Marshall, 1984; Cumming & Bernard, 1997; Fleming & Eby, 2003). The survival of neonatal bats may be an important factor in the timing of migration, with



**Figure 6** Spatial and temporal trends in fruit availability. Dates range from 7 September 2003 to 3 January 2004 (a–f). x-axis represents km from the *Eidolon helvum* roost; y-axis represents the number of fruiting trees of known food sources. Date is midpoint of the sampling period.



**Figure 7** Known *Eidolon helvum* colonies in Africa and dates in residence at each site (Mutere, 1967; Ansell, 1978; Thomas, 1983; DeFrees & Wilson, 1988; Bergmans, 1990; Cosson *et al.*, 1996).

weaning coinciding with the period of highest food availability (Fayenuwo & Halstead, 1974; Cumming & Bernard, 1997), but at present we lack sufficient data to test this hypothesis for *E. helvum* at Kasanka. Adults may also exploit the period of high food availability in a habitat that is structurally simpler than equatorial rainforest to teach any young bats in the colony how to forage and find food more effectively (Kingdon, 1984).

In addition to the primary hypotheses discussed here, we note that large aggregations of bats may confer other advantages, including provision of an ‘information centre’ where animals congregate to transfer information about feeding sites (Ward & Zahavi, 1973), group defence against predators, group defence of feeding areas and more efficient exploitation of resources (Brown & Orians, 1970). These possibilities have yet to be tested for any fruit bat species.

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