Quantifying the ecological impact of the straw-coloured fruit bat (*Eidolon helvum)* in West Africa

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With immense gratitude to:

my parents and sisters;
my wife and children;
all others;
for helping make this possible through diverse ways.

The Lord God took man and put him in the Garden of Eden to work it and keep it.
Genesis 2:15, Holy Bible

When a man moves away from nature, his heart becomes hard.
Lakota Indian tribe, USA

Do not follow the path; go where there is no path to begin the trail.
Ashanti tribe, Ghana

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Summary

Ecosystems worldwide provide beneficial services to humans and other life-forms. Fruit-eating and flower-visiting animals play a particularly important role in the regeneration of numerous plant species through their dispersal of pollen and seeds, thereby ensuring the maintenance or restoration of these ecosystems especially in tropical Africa. However, the ability of ecosystems to function effectively and to provide these services is being compromised by many factors, including defaunation, such as through bushmeat, trophy and pet utilization; and habitat degradation, fragmentation and loss. Therefore, animals capable of long-distance seed dispersal are particularly important in fragmented landscapes for maintaining gene flow and colonizing new sites for plants. Volant seed dispersers such as birds and fruit bats capable of utilizing fragmented landscapes are thus receiving increasing attention to quantify their seed disperser services. However, many seed dispersers that eat fleshy fruit do not cover large distances and/or leave the forest cover; even those that do usually drop most seeds under the source tree, or quickly defecate ingested seeds after feeding. Thus, animal vectors, such as the straw-coloured fruit bat (*Eidolon helvum*), that are capable of covering large distances and retaining seeds for long periods are particularly important for maintaining connectivity among plant populations in fragmented landscapes. I expected that the seasonal migration of *E. helvum* over vast distances across the African continent, probably following seasonal bursts of resource availability, would cause enormous fluctuations in population size, which in turn may influence the bats' impact on local ecosystems.

I used a combination of state-of-the-art GPS/acceleration loggers and concurrent monitoring of the seasonal fluctuations in colony size, phenology of bat food resources and field-based feeding experiments to collect high spatio-temporal resolution data on the eco-physiological behaviour of fruit bats under different seasonal and landscape conditions. I quantified: 1) changes in foraging movements and colony population size in response to inter-seasonal environments; 2) changes in bat colony size, activity budgeting, movement ecology and body condition responses to intra-seasonal changes in food availability; and 3) dispersal distances for seeds of bat food resources.

I found that in the urban landscape in and around Accra, located in the forest ecosystem in southern Ghana, bats foraged locally (3.5 -36.7 km) and in urban areas with low tree cover during the wet season, when colony populations were low (~ 4000 individuals); major food sources during this period were fruits of introduced trees. This was in contrast to a tripling of foraging distances (24.1 - 87.9 km) during the dry season, with population peak (~ 150,000 individuals), which was not compensated for by reduced resting periods. Dry season foraging areas were random with regard to urban footprint and tree cover, and food consisted almost exclusively of nectar and pollen of native trees.

Fluctuations in food abundance potentially drive a variety of eco-physiological responses in frugivorous bats, including changes in body condition, activity budgets, diets and foraging areas. In view of earlier findings that pronounced inter-seasonal changes in *E. helvum* movement and foraging ecology, I next expected that if there were sufficiently strong environmental factors within a single season, the bats would exhibit distinct eco-physiological responses. In a savanna ecosystem in Ouagadougou, central Burkina Faso, I concurrently investigated intra-seasonal changes in food resource availability, colony size, bat activity budget and spatio-temporal movement patterns, and bat body condition during the mono-modal wet. I found that food availability was markedly different in the early (food high) and later (food low) stages of the wet season, with different composition of dominant food species during each period. The results indicate that *E. helvum* opportunistically shifted diets to capitalize on different food resources as they became dominant in the landscape within the same season. Colony size correlated positively with food availability, showing a two-fold decrease with increasing food scarcity. Body condition declined significantly during food scarcity. Although bats were equally active at night in both food periods, they spent more time foraging and commuting during food low. Travel time away from day roost was lower during food high, but travel distance was similar for the two food periods. The space use in core and foraging areas did not differ in the two periods. Overall, intra-seasonal fluctuations in food resources are markedly different and apparently caused significant changes in body condition and foraging time budgets but not in distance and area use. In addition, I report for the first time the ability of *E. helvum* to relocate to new day roosts as solitary individuals. Individual excursions last for 1 – 6 consecutive nights before returning to the main colony during periods of food scarcity. I report for the first time that the highly gregarious, central-foraging *E. helvum* can spend time as solitary individuals at day roosts in foraging areas far away from colonies, apparently in response to food scarcity.

Finally, I sought to translate the seasonal changes in *E. helvum* movements into a quantification of seed dispersal distances. By using a combination of high-resolution GPS-tracking of movements, field observations and gut retention time experiments, I modelled potential dispersal distances for small- and large-seeded fruits foraged by *E. helvum* during periods of colony population low (wet season) and high (dry season) in an urban and a rural landscape in the forest zone of Ghana. Nightly movements were generally longer in the urban than in the rural landscape and also longer in the dry than in the wet season. Gut passage time (mean 116 min; range 4-1143 min) was comparable to those of other fruit bats. Seed dispersal distances were similar for both large (median 42-67 m) and small (median 42-65 m) seeds, and reflected the fact that majority of seeds are dispersed only to feeding roosts through the foraging behaviour of shuttling between food trees and nearby feeding roosts. Estimated maximum seed dispersal kernel distance for small seeds was 75 km, four times further than previous maximum distance estimated for a frugivore. Furthermore, small seeds were dispersed over distances almost twice as long in the rural (49.7 km) compared to the urban (31.2 km) landscape. Maximum distances for small seeds in the urban landscape were three times longer during the dry season (75.4 km) versus the wet season (22.8 km); in contrast, distances in the rural landscape were three times longer in the wet season (67 km) compared to the dry season (24.4). For large seeds in the rural landscape, dispersal distance during the dry season (551 m) was almost twice that in the wet season (319 m). Phenology of food resources did not appear to influence seed dispersal distances. The maximum likelihood for seed dispersal beyond feeding roosts (99th percentile distance from food tree 263 m) was 4.7%. Small seeds were dispersed over even longer distances, > 500 and >1000 m, with a likelihood of 3.0 % and 2.3 % respectively.

I show that *E. helvum* retains ingested seeds for very long periods and traverses large distances, along which both long and short-distance seed dispersal occur. This probably makes *E. helvum* the most important animal seed disperser currently known, at least in tropical Africa. These findings suggest that *E. helvum* is a keystone species for ecosystem functioning and urge its conservation. This study suggests that straw-coloured fruit bats are likely to disperse seeds in the range of hundreds of meters up to dozens of kilometres, and to pollinate trees for up to 88 km. Straw-coloured fruit bats forage over much larger distances compared to most other Old World fruit bats, thus providing vital ecosystem services across extensive landscapes. I recommend increased efforts aimed at maintaining *E. helvum* populations throughout Africa, since their suspected keystone role in various ecosystems is likely to increase due to the escalating loss of other seed dispersers as well as continued urbanization and habitat fragmentation.

These findings provide additional evidence that (1) fruit bats may adapt their foraging movement patterns and diets within a single wet season in the savannah; similar changes were previously observed between seasons in the forest ecosystem; (2) the super-abundant production of shea and fig fruits in the savannah ecosystem may be an important factor in the annual northwards migration of *E. helvum* from the southern coastal forests in West Africa, thereby confirming the tight ecological inter-dependence of fruit trees and their seed dispersal via fruit bats.

Zusammenfassung

Ökosysteme bieten weltweit positive Leistungen für Menschen und andere Lebensformen. Früchte-essende und Blumen-besuchende Tiere spielen durch ihre Verbreitung von Pollen und Samen eine besondere Rolle in der Regeneration zahlreicher Pflanzenarten und stellen dadurch den Erhalt und die Wiederherstellung dieser Ökosysteme vor allem im tropischen Afrika sicher. Die Fähigkeit der Ökosysteme effektiv zu funktionieren und diese Leistungen anzubieten ist jedoch durch verschieden Faktoren eingeschränkt, inklusive Tierschwund wie beispielsweise durch den Missbrauch als Wildfleisch, Trophäen oder Haustiere, sowie Habitatverlust und -fragmentierung. Daher sind Tiere, die Samen über große Distanzen verbreiten können, besonders wichtig in fragmentierten Landschaften um den Genfluss aufrechtzuerhalten und neue Standorte für Pflanzen zu besiedeln. Fliegende Samenverbeiter wie Vögel und Flughund, die fähig sind fragmentierte Landschaften zu nutzen, erhalten daher eine zunehmende Aufmerksamkeit ihrer Leistung bei der Samenverbreitung. Viele der Samenverbreiter, die fleischige Früchte zu sich nehmen, überwinden jedoch keine großen Distanzen und/oder verlassen die Waldgebiete, und selbst die Arten, die dies tun, lassen die Samen in der Regel unter dem Nahrungsbaum fallen oder defäkieren die aufgenommen Samen rasch nach der Nahrungsaufnahme. Daher sind Tiervektoren wie der Palmenflughund (Eidolon helvum), die in der Lage sind große Distanzen zu überwinden und Samen für längere Zeiträume bei sich zu behalten, besonders wichtig um die Verbindung zwischen Pflanzenpopulationen in fragmentierten Landschaften aufrechtzuerhalten. In meiner Studie habe ich erwartet, dass die saisonale Migration von E. helvum über große Distanzen auf dem afrikanischen Kontinent vermutlich dem saisonalen Ausbruch an Ressourcenverfügbarkeit folgt und eine enorme Schwankung in der Populationsgröße verursachen wird, welche wiederum den Einfluss der Flughunde auf das lokale Ökosystem beeinflusst.

Ich habe eine Kombination von modernen GPS / Beschleunigungsloggern und der gleichzeitigen Überwachung der saisonalen Schwankungen der Koloniegröße, Phänologie der Nahrungsressource der Flughunde und feld-basierter Fütterungsexperimente benutzt, um hochauflösende zeitliche und räumliche Daten des ökophysiologischen Verhaltens der Flughunde in unterschiedlichen saisonalen und landschaftlichen Bedingungen zu sammeln. Ich quantifizierte: 1) Veränderungen in den Bewegungen zu Futtersuche und der Koloniegröße als Reaktion auf inter-saisonale Umgebungen; 2) Veränderungen in der Koloniegröße der Flughunde, Aktivitäten-Budgetierung, Bewegungsökologie und Reaktionen des Körperzustandes auf intra-saisonale Veränderungen in der Nahrungsverfügbarkeit; und 3) Verbreitungsdistanzen für Samen von Nahrungsressourcen von Flughunden.

Meine Ergebnisse zeigten, dass Flughunde in urbanen Landschaften in und um Accra, die im Waldgebiet in Südghana gelegen sind, sowie während der Regenzeit in urbanen Gegenden mit geringer Baumdeckung, wenn die Kolonien klein waren (~ 4000 Individuen) vor Ort auf Nahrungssuche gehen (3,5 – 36,7 km). Die Hauptnahrungsquelle in diesem Zeitraum waren Früchte eingeführter Bäume. Im Gegensatz dazu legten die Flughunde während der Trockenzeit eine dreifache Distanz (24,1 – 87,9 km) zur Nahrungssuche zurück, die nicht durch eine reduzierte Ruhezeiten kompensiert wurde. Die Gebiete zur Nahrungsaufnahme während der Trockenperiode waren zufällig in Bezug auf städtische Grundfläche und Baumbestand, und die Nahrung bestand fast ausschließlich aus Nektar und Pollen einheimischer Bäume.

Schwankungen in der Nahrungsverfügbarkeit könnte eine potentielle Vielfalt an ökophysiologischen Reaktionen in fruchtfressenden Flughunden hervorrufen, inklusive Veränderungen im Körperzustand, Aktivitätenbudget, Diäten und Nahrungsgebieten. Im Hinblick auf frühere Erkenntnisse zu ausgesprochenen inter-saisonalen Veränderungen in den Bewegungen und der Ernährungsökologie von E. helvum erwartetet ich daher, dass die Flughunde beim Vorhandensein ausreichend starker Umweltfaktoren innerhalb einer Saison ausgeprägte ökophysiologische Reaktionen zeigen würden. In einem Savannen-Ökosystem in Ouagadougou, Zentral-Burkina Faso, habe ich gleichzeitig intra-saisonale Veränderungen in der Nahrungsverfügbarkeit, der Koloniegröße, dem Flughund-Aktivitätsbudget und den räumlich-zeitlichen Bewegungsmustern, sowie dem Körperzustand der Flughunde während der monomodalen Regenperiode untersucht. Ich habe herausgefunden, dass sich die Nahrungsverfügbarkeit deutlich zwischen der Anfangs- (Nahrung hoch) und der späteren Phase (Nahrung niedrig) der Regenperiode unterschied, mit einer unterschiedlichen Zusammensetzung der dominanten Nahrungsarten während jeder Periode. Diese Ergebnisse deuten darauf hin, dass E. helvum seine Diät opportunistisch verschiebt, um so verschiedene Nahrungsquellen nutzen zu können in Abhängigkeit von ihrer Verfügbarkeit in der Landschaft innerhalb einer Saison. Die Koloniegröße korrelierte positiv mit der Nahrungsverfügbarkeit und zeigte eine zweifache Abnahme bei zunehmendem Nahrungsmangel. Der Körperzustand nahm signifikant während Nahrungsmangel ab. Obwohl die Flughunde in beiden Jahreszeiten gleich aktiv während der Nacht waren, verbrachten sie mehr Zeit mit Nahrungssuche und Pendeln während geringer Nahrungsverfügbarkeit. Die Flugzeit weg von der Schlafstelle war geringer während hoher Nahrungsverfügbarkeit, die Flugdistanz blieb jedoch während beider Zeiten ähnlich. Die räumliche Nutzung der Kerngebiete und der zur Nahrungssuche unterschied sich nicht zwischen den beiden Zeiten. Insgesamt sind die intra-saisonalen Schwankungen in der Nahrungsverfügbarkeit markant verschieden und verursachen scheinbar signifikanten Veränderungen im Körperzustand und dem Zeitbudget zur Nahrungssuche jedoch nicht in der Distanz und der Flächennutzung. Zusätzlich habe ich zum ersten Mal die Fähigkeit von E. helvum nachweisen, neue Schlafstellen als solitäre Individuen aufzusuchen. Individuelle Ausflüge während Nahrungsknappheit dauern 1 – 6 aufeinanderfolgende Nächte bevor sie zur Hauptkolonie zurückkehren. Ich berichte zum ersten Mal, dass die sehr geselligen, zentral Nahrungssuchende E. helvum auch Zeit als solitäre Individuen in Tages-Quartieren in Gegenden der Nahrungssuche weit entfernt ihrer Kolonie verbringen, offenbar als Reaktion auf Nahrungsknappheit.

Zu guter Letzt versuchte ich die saisonalen Veränderungen in den Bewegungen von E. helvum in eine Quantifizierung der Distanzen der Samenverbreitung zu übersetzen. Durch die Verwendung einer Kombination aus von hoch-auflösendem GPS-Tracking der Bewegungen, Feldbeobachtungen und Experimenten der Darmretentionszeit konnte ich potentielle Verbreitungsdistanzen für klein- und gross-samige Früchte modellieren, die während Zeiten geringer Populationsdichte (Regenzeit) und hoher Populationsdichte (Trockenzeit) in einer urbanen und einer ländlichen Landschaft durch E. helvum in einer Waldzone von Ghana verbreitet wurde. Die nächtlichen Bewegungen waren generell länger in der urbanen als in der ländlichen Gegend sowie in der Trockenzeit im Vergleich zur Regenzeit. Die Dauer der Darmpassage war vergleichbar mit anderen Flughunden (im Durchschnitt 116 min, von 4 – 1143 min). Auch die Distanz der Samenverbreitung war ähnlich für große (durchschnittlich 42-67 m) und kleine Samen (durchschnittlich 42-65 m) und reflektiert die Tatsache, dass ein Großteil der Samen nur bis zur Nahrungsstelle verteilt werden während dem Pendeln zwischen Schlaf- und nahegelegener Futterstelle bei der Nahrungssuche. Die geschätzte maximale Distanz der Samenausbreitung betrug für kleine Samen 75 km, viermal mehr als bisherige Schätzungen für Frugivore. Zudem wurden kleine Samen in ländlichen Gegenden über eine fast doppelt so große Distanz (49,7 km) verbreitet als in urbanen Gegenden (31,2 km). Die maximale Distanz, die kleine Samen in urbanen Landschaften verbreitet wurden, war in der Trockenzeit dreimal so groß (75,4 km) wie in der Regenzeit (22,8 km). Im Gegensatz dazu war die Distanz in ländlichen Gegenden während der Regenzeit dreimal so groß (67 km) wie in der Trockenzeit (24,4, km). Für große Samen war die Verbreitungsdistanz in ländlichen Gegenden in der Trockenzeit fast doppelt so hoch (551 m) wie während der Regenzeit (319 m). Die Phänologie der Nahrungsressource schien keinen Einfluss auf die Distanz der Samenverbreitung zu haben. Die größte Wahrscheinlichkeit der Samenausbreitung außerhalb der Nahrungsstelle lag bei 4,7 % (99. Perzentil Distanz vom Nahrungsbaum 263 m). Kleine Samen wurden mit einer Wahrscheinlichkeit von 3,0 % und 2,3 % sogar über größere Distanzen von > 500 m und >1000 m verbreitet.

Ich konnte nachweisen, dass E. helvum aufgenommene Samen für einen sehr langen Zeitraum behält und lange Distanzen zurücklegt, während derer die Samenverbreitung sowohl auf kurzen als auch auf langen Distanzen passiert. Dies macht E. helvum vermutlich nach dem derzeitigen Erkenntnisstand zu dem wichtigsten tierischen Samenverbeiter, zumindest im tropischen Afrika.

Diese Ergebnisse legen nahe, dass Palmenflughunde eine Schlüsselart für das Funktionieren des Ökosystems darstellen und fordern ihren Schutz. Diese Studie deutet darauf hin, dass Palmenflughunde Samen vermutlich über Distanzen von Hunderten von Metern bis hin zu zig Kilometern verbreiten und Bäume bis zu 88 km Entfernung bestäuben können. Palmenflughunde legen auf ihrer Nahrungssuche weitaus größere Distanzen zurück als die meisten anderen Flughunde der Alten Welt und erbringen damit lebenswichtige Ökosystemdienstleistungen über extensive Landschaften. Ich empfehle umfangreiche Anstrengungen zum Schutz der E. helvum Populationen über ganz Afrika, da ihre mutmaßliche Schlüsselrolle in verschiedensten Ökosystemen vermutlich mit dem enormen Verlust an anderen Samenverbreitern und der zunehmenden Urbanisierung und Lebensraumfragmentierung zunehmen wird.

Diese Ergebnisse liefern weitere Beweise, dass (1) Flughunde ihre Bewegungsmuster zur Nahrungssuche und Diäten innerhalb einer Regensaison in der Savanne anpassen können; ähnliche Veränderungen wurden zuvor schon zwischen den Jahreszeiten in Wald-Ökosystemen nachgewiesen; und dass (2) das überreiche Angebot von Sheanüssen und Feigen in Savannen-Ökosystemen ein wichtiger Faktor in der jährlichen Migration von E. helvum von den südlichen Wäldern der Küste in Westafrika Richtung Norden darstellt und damit die enge ökologische Verflechtung von Obstbäumen und die Verbreitung ihrer Samen durch Flughunde bestätigt.

CHAPTER 1

General Introduction

1.1 Background

Ecosystems provide numerous benefits to humans, such as food medicine, and regulation of vital environmental processes such as climate, nutrient cycling, water filtration, and erosion control(Kunz et al., 2011). Through their dispersal of pollen and seeds, fruit-eating and flower-visiting animals play a particularly important role in the regeneration of numerous plant species, thereby ensuring the maintenance or restoration of these ecosystems, including in tropical Africa (da Silva and Tabarelli, 2000; Jansen and Zuidema, 2001).

Uncontrolled bushmeat utilisation across Central and West Africa is causing the depletion of large mammals and birds, resulting in the reduction and even local extinction of seed and pollen dispersers such as hornbills, primates, antelopes and elephants (Bowen-Jones and Pendry, 1999; Wang et al., 2007; Gross-Camp et al., 2009; Harrison, 2011; Lenz et al., 2011). Extensive habitat degradation and losses from logging and agricultural activities translate these faunal depletions into a severe compromise or even loss of the regeneration ability of the ecosystems, thereby reducing their ability to provide their increasingly vital services (Andersen, 2000).

Fruit bats feature prominently in the frugivore communities of tropical ecosystems, and play a significant part in ecosystem function through their role in forest regeneration and maintenance via seed dispersal and pollination of a wide variety of ecologically and economically important plants (e.g. Muscarella and Fleming, 2007). However, only recently have these ecosystem services begun to be receive a more thorough evaluation (Kunz et al., 2011); even then, research attention has been dominated by New World Phyllostomidae, leaving the situation for Old World Pteropodidae largely unknown. Furthermore, the ecological and physiological responses of African fruit bats to seasonality is poorly understood. This severely constrains the development and implementation of policy and management actions that are crucial to the long-term survival of this taxon, especially in Africa.

I investigated the ecological impact of fruit bats in forest and savanna ecosystems in West Africa, using the straw-coloured fruit bat (*Eidolon helvum*) as a case study. *Eidolon helvum* is an Old World fruit bat that is gaining increasing recognition as a key species in bushmeat utilisation, human health threats and ecosystem function (Thomas, 1983; Thomas, 1991; Richter and Cumming, 2006; Richter and Cumming, 2008). It uses many different habitats from lowland rainforest to savannah, in an extremely wide distribution range spanningacross Africa; records from Yemen and Saudi Arabia extend its known distribution to the extreme southwest Arabian Peninsula (Harrison and Bates, 1991). Very little is known about migration behaviour on an individual level, but decreasing populations in the forest zone coincide with temporary colonies occurring increasingly North from the sedentary distribution range suggesting that it migrates annually into savannah regions along a north-south axis, over a range that extends from the northern parts sub-Saharan Africa to South Africa. It is presumed that the primary driver of the migratory pattern of *E. helvum* is the varying seasonal availability of fruit and flowers across its range (Thomas, 1983; Thomas, 1991; Richter and Cumming, 2006; Richter and Cumming, 2008; DeFrees and Wilson, 1988).

Eidolon helvum forms huge roosts within or close to human settlements, with colony sizes of up 10 million individuals recorded in Zambia (Richter and Cumming, 2006), and 300,000 - 1 million in West Africa, at population peaks (Jones, 1961; Rosevear, 1965; Norberg and Rayner, 1987; DeFrees and Wilson, 1988; Thomas, 1991). These huge aggregations exposes the species to severe hunting pressure (Kamins et al., 2011) and the potential for outbreak of zoonotic or potentially-zoonotic infections of public health importance to which it plays host is high (e.g. Hayman et al., 2008; Hayman et al., 2010; Baker et al., 2013). Without an adequate understanding of its ecology and contribution to human welfare, the negative perceptions associated with its zoonotic potential as well as the hunting pressure are likely to subject this species to large potential population declines in the near future.

Eidolon helvum is suspected to account for most long-distance genetic exchange of its food plants through the combination of huge aggregations, long-distance movements. This includes threatened, but high value timber species, such as Iroko (*Milicia excelsa*) ((Thomas, 1991); (Taylor et al., 2000)) and False Iroko (*Antiaris toxicaria)* (Kankam and Oduro, 2009), for which it might be the only significant disperser. It is likely that *E. helvum* plays a more significant role in ecosystem regeneration than any other single frugivore species in Africa. There is as yet no study specifically quantifying the ecosystem services of such fruit bats as *E. helvum*. The ecological and physiological responses of fruit bats to high fluctuations of food resources and weather within and between seasons are also unknown or poorly understood.

1.2 Goal and Objectives

The goal of this dissertation was to quantify the ecological impact of *E. helvum* in the forest and savannah biomes that mark the two ends of its annual migratory cycle in West Africa. Specifically, my objectives were to:

1) investigate the effect of seasonality on the movement ecology of *E. helvum,* a highly-gregarious central-place forager;

2) assess the eco-physiological response of *E. helvum* to a marked temporal fluctuation in food availability within the same season and landscape in Afro-tropical savanna ecosystems;

3) quantify the seed dispersal distances provided by *E. helvum* in fragmented Afro-tropical forest ecosystems.

I addressed these to quantify the seed dispersal services provided by *E. helvum* in fragmented Afro-tropical forest ecosystems objectives at a progressively increasing spatial-temporal scale (Fig 1.1), ranging from a single colony and landscape within a single season (in Ouagadougou, Burkina Faso), to multiple colonies and landscapes (Accra and Kibi, Ghana), as outlined in the chapter below.

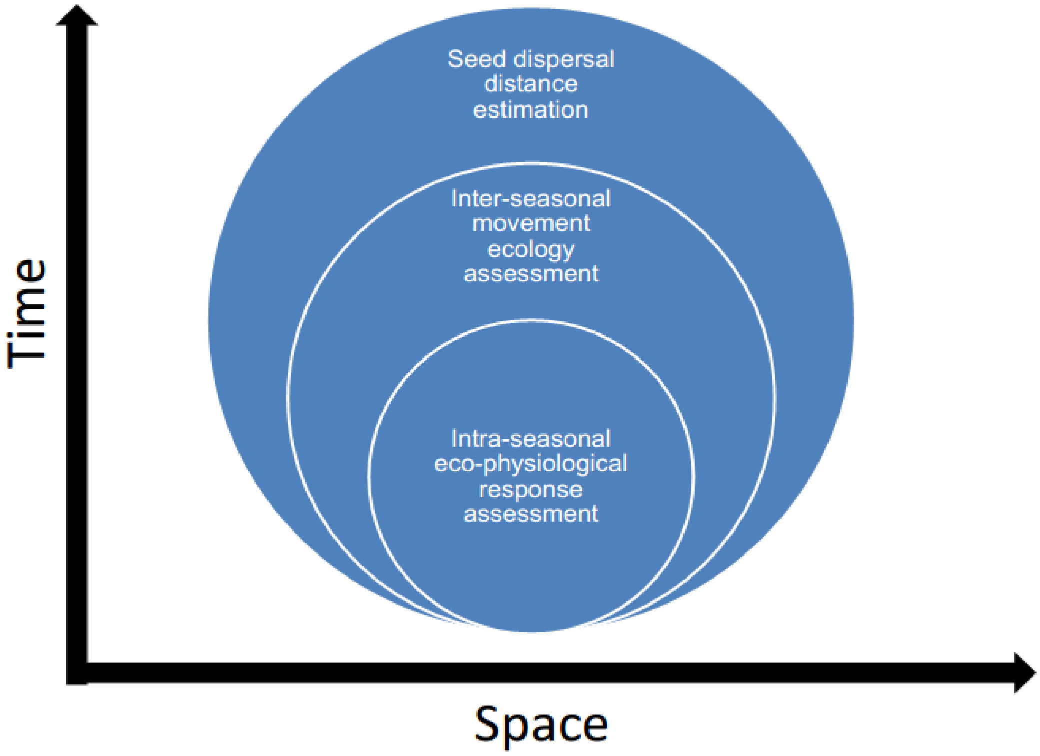

Fig 1.1. Spatio-temporal structure of study. Space axis represents increasing number of landscapes, while time scale represent increasing number of seasons.

I used a combination of state-of-the-art GPS/acceleration loggers to investigate *E. helvum* movement and activity budget, and concurrently monitored seasonal fluctuations in population, food availability and bat physiology at colonies in Ghana and Burkina Faso, West Africa (Fig. 1.2).

1.3 Chapter Outline

Chapter 2 focused on a single bat colony in an urban landscape located in a forest ecosystem. Here, I studied the foraging ecology of *E. helvum*, a highly gregarious central-place forager, under conditions of high seasonal fluctuations in population size of a colony located in an urban landscape in Accra, Ghana (published as Fahr et al., 2015). I investigated the variations in: the types, sizes and distances to foraging areas; and shifts in food sources by *E. helvum* during periods of pronounced fluctuation in colony size between the wet (population low) and dry (population peak) seasons. This chapter shows that fruit bats forage over much larger distances compared to most other Old World fruit bats. It also emphasizes the influence of some food plant species on the foraging movements of fruit bats.

Fig. 1.2. Location of study sites in the forest biome in southern Ghana (Accra and Kibi) and in the savanna biome (Ouagadougou) in central Burkina Faso.

Chapter 3 is an extension of Chapter 1, but investigated the intra-seasonal variations in bat movements, physiology and population. This time, the focus was an urban colony located in Ouagadougou, Burkina Faso, that foraged across a rural landscape in the savanna ecosystem. I sought to assess if intra-seasonal fluctuations in food resource availability strong enough to induce eco-physiological changes in fruit bats in the highly seasonal savanna environments. Specifically, I assessed changes in colony population size and food availability across the year and within the unimodal wet season; and estimated the ecological (activity budgets, diets and foraging areas) and physiological (body condition) of *E. helvum* to these changes. The findings show that intra-seasonal food availability is sufficiently marked to cause significantly responses in bat body condition, colony population size; and in foraging and roosting activity budgets.

In Chapter 4, I sought to translate the high fluctuations in seasonal movements and feeding behaviour of *E. helvum,* observed in Chapter 2, into a quantification of seed dispersal distances as a representation of the ecosystem services provided by fruit bats, especially relevant for the increasingly fragmented landscapes across Africa. The spatio-temporal context was colonies located in an urban landscape (Accra) and a rural landscape (Kibi) in the forest ecosystem in southern Ghana. Using a combination of high-resolution tracking of bat movements and feeding experiments I estimated the potential seed dispersal kernel distances for large- and small-seeded fruit species foraged by *E. helvum* in the dry and wet seasons. The results show that while large seeds that could not be ingested were potentially dispersed over a few hundred meters, small seeds could be dispersed over both short (< 1km) and extremely long ~ 75 km) distances. I also showed that both seasonal and landscapes differences appear to influence the extent of these dispersal distances.

Finally, in Chapter 5, I summarize the major findings in each chapter and highlight their significance for research and conservation action. I show that *E. helvum* is highly responsive to seasonal changes in its environment, and exhibits foraging behaviours that result in providing vital ecosystem services across extensive landscapes. Furthermore, by virtue of its vast distribution range, huge numbers, catholic in habitat use, ability to commute and especially migrate over long distances, *E. helvum* may thus fill many gaps left behind by other species of the seed disperser assemblage. I recommend that applied research and management efforts should be increased, aimed at maintaining *E. helvum* populations throughout Africa since their keystone role in various ecosystems is likely to increase due to the escalating loss of other seed dispersers as well as continued urbanization and habitat fragmentation.

CHAPTER 2

Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (*Eidolon helvum*)

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Abstract

Straw-coloured fruit bats (*Eidolon helvum*) migrate over vast distances across the African continent, probably following seasonal bursts of resource availability. This causes enormous fluctuations in population size, which in turn may influence the bats' impact on local ecosystems. We studied the movement ecology of this central-place forager with state-of-the-art GPS/acceleration loggers and concurrently monitored the seasonal fluctuation of the colony in Accra, Ghana. Habitat use on the landscape scale was assessed with remote sensing data as well as ground-truthing of foraging areas.

During the wet season population low (~ 4000 individuals), bats foraged locally (3.5 -36.7 km) and in urban areas with low tree cover. Major food sources during this period were fruits of introduced trees. Foraging distances almost tripled (24.1 - 87.9 km) during the dry season population peak (~ 150,000 individuals), but this was not compensated for by reduced resting periods. Dry season foraging areas were random with regard to urban footprint and tree cover, and food consisted almost exclusively of nectar and pollen of native trees.

Our study suggests that straw-coloured fruit bats are likely to disperse seeds in the range of hundreds of meters up to dozens of kilometres, and to pollinate trees for up to 88 km. Straw-coloured fruit bats forage over much larger distances compared to most other Old World fruit bats, thus providing vital ecosystem services across extensive landscapes. We recommend increased efforts aimed at maintaining *E. helvum* populations throughout Africa since their keystone role in various ecosystems is likely to increase due to the escalating loss of other seed dispersers as well as continued urbanization and habitat fragmentation.

Keywords: acceleration data; activity budgets; Africa; behaviour; body size; central-place foraging; Chiroptera; colony size; *Eidolon helvum*; foraging distance; Ghana; GPS tracking; movement ecology; Pteropodidae; remote sensing; seasonality; telemetry; utilization distribution.

2.1 Introduction

Old World fruit bats (Chiroptera: Pteropodidae) are important seed dispersers and pollinators of a wide range of economically important tree species, thereby providing crucial ecosystem services for the maintenance and regeneration of vegetation (Fujita and Tuttle, 1991; Muscarella and Fleming, 2007, Corlett, 2009; Kunz et al., 2011; Seltzer et al., 2013). Fruit bats that forage over large distances or migrate seasonally are expected to provide highly effective seed dispersal and pollination. However, wide-ranging and migratory species are especially vulnerable to anthropogenic changes because they depend on several ecosystems and are exposed to various threats when crossing ecosystems, country borders or even continents (Wilcove and Wikelski, 2008; Epstein et al., 2009). Given the beneficial effects of these animals as well as the potential threats they are facing, it is astonishing how little we still know about many fundamental aspects of their ecology. Hence it is crucial to understand how spatio-temporal movements and resource use by bats interact to determine the relevance of these bats for ecosystems on spatial scales of landscapes and larger.

Our study species, the straw-coloured fruit bat, *Eidolon helvum*, frequently gathers in enormous but patchily distributed colonies in many African cities such as Accra, Abidjan, Ibadan, Ife and Kampala (Rosevear, 1965; Funmilayo, 1979; Thomas and Henry, 2013). In the forest zone of West Africa, large numbers of bats congregate during the dry season in colonies for roughly six months (Huggel-Wolf and Huggel-Wolf, 1965; Thomas, 1983). With the onset of the wet season, these colonies are largely abandoned when most of the bats set out for their annual migration, and only a small fraction stays behind as residents. While the timing of migration varies locally, it appears linked to climatic factors and thus ultimately to seasonal changes in resource availability (Thomas, 1983 ; Fayenuwo and Halstead, 1974; Richter and Cumming, 2006).

In *E. helvum* as well as in other gregarious, tree-roosting Old World fruit bats, the ultimate causes for colonial aggregation are not well understood, but factors such as predator avoidance (‘selfish herd’, predator swamping) or information transfer within the colony are potential proximate explanations (Richter and Cumming, 2006; Tidemann et al., 1999; Welbergen, 2006). The tree roosts themselves seem unlikely to be sufficiently limited to explain such highly clumped aggregations because they will necessarily lead to intensive intraspecific competition for food resources (fruits and flowers) within the most profitable perimeter of the colony. Consequently, we should expect a density-dependent trade-off between the advantages offered by the colonies and increased resource depletion near the central place, which then requires longer travel distances to foraging areas (Wakefield et al., 2013).

Movement distances as well as selection of foraging areas are also key factors for effective seed dispersal and pollination, which *E. helvum* delivers for a large number of plants (Osmaston, 1965; Funmilayo, 1979; Thomas, 1982; Taylor et al., 2000; Richter and Cumming, 2006; Niamien et al., 2010). Indeed, straw-coloured fruit bats may account for much if not most long-distance genetic exchange of their food plants, many of which are economically important timber species (Bizoux et al., 2009; Kankam and Oduro, 2009; Daïnou et al., 2012).

Recent research further indicates that *E. helvum* is host of, and possible reservoir for, a variety of human-relevant diseases such as Lagos bat virus and paramyxoviruses (Boulger and Porterfield, 1958; Iehlé et al., 2007; Hayman et al., 2008; Tong et al., 2009; Dzikwi et al., 2010; Baker et al., 2012; Weiss et al., 2012; Pernet et al., 2014); however, actual transmission rates and pathways remain unknown. Urban bat colonies are in close contact with humans, which is exacerbated by massive hunting and consumption of bats as bushmeat in many parts of West and Central Africa (Mickleburgh et al., 2009; Kamins et al., 2011). Revealing movement patterns of these bats is thus an essential component to understand transmission of diseases for which they might be a reservoir.

We studied the foraging ecology of straw-coloured fruit bats and concurrently monitored the seasonal fluctuations of the colony in Accra, Ghana. Specifically, we hypothesized that travel distance to, and size of, foraging areas should increase during peak times of colony size when intraspecific competition for food resources should be highest. We further expected to find trade-offs between distances travelled and activity budgets. Habitat use should be more selective during low colony size if individual bats have more options to choose foraging areas under less crowded conditions. Finally, we predicted that central place foragers would commute greater distances when controlling for the predicted positive relationship between body size and travel distances of Old World fruit bats. We tested these hypotheses with high-resolution GPS and acceleration telemetry combined with remote sensing data, ground-truthing of utilized food resources as well as population monitoring of the focal colony.

2.2 Material and methods

2.2.1 Study site and animals

The study was conducted during two field seasons with straw-coloured fruit bats, Eidolon helvum, from a colony on the grounds of the 37 Military Hospital in Accra, Ghana (5°35'11''N, 0°11'02''W). The first bout of fieldwork took place in August 2009 during the wet season while the second bout of fieldwork was conducted in February 2011 during the dry season.

We caught bats when they returned from foraging in the early morning with canopy mist nets (Fahr and Kalko, 2011) and a 10 m high macro net (Rautenbach, 1986), and kept them individually in soft cloth bags until processing. Capture upon return in the morning ensured that the animals had fed before handling. We weighed all bats with Pesola spring balances and selected 30 adult males (10 in 2009, 20 in 2011; mean mass: 277 ± 26 g). We attached GPS loggers (e-obs, Munich, Germany, mass: 19.5 g in 2009, 20 g and 24 g in 2011; see also S1 Table) by clipping the dorsal fur below the shoulder blades and gluing on the loggers with Sauer Hautkleber (Manfred Sauer GmbH, Lobbach, Germany). Previous experience with other bat species showed that loggers are shed after a maximum of two weeks. Logger mass amounted to 6.8–8.8% of the bats' body mass, which is slightly above the recommended mass (Aldridge and Brigham, 1988a), but within the 5–10% range recommended through a meta-analysis of tracking studies (O'Mara et al., 2014). All animals were then hand fed *ad libitum* with banana. After release near the capture site all bats flew off without any apparent difficulty. Bats were named after the serial number of the logger they carried (Table 2.1).

2.2.2 Tracking loggers

The loggers are capable of recording several types of data (GPS bearing, flight speed and heading, altitude, and 3-axial acceleration data), and are flexibly programmable regarding sampling rates as well as onset and intermission of data collection. In addition, they contain a pinger which produces a signal equivalent to that of a radio transmitter, and can be turned on at specified times to facilitate localizing the animals and approach them to within downloading distance of the UHF radio link. We programmed the loggers according to data collecting regimes consecutively called cohorts 1–3 (see below and S1 Table).

The following parameters were the same for all loggers deployed in 2009: delayed start at 06:00 on the morning following release; acceleration data: data collection 15 s/min at a byte count of 1188 (56.23 Hz) on three axes (x = left-right, y = back-forward, z = up-down) during the entire data collection periods (day and night); GPS: off from 06:00–18:00 each day. The only difference was that cohort 1 (#1079–1083) was programmed to collect GPS fixes at a regular interval of 600 s during GPS on-times. Cohort 2 (#1084–1088) collected GPS fixes once every 900 s until an animal was moving at a speed of 5 m/s or more. At this point cohort 2 switched to a collecting interval of 300 s. Loggers deployed in 2011 (cohort 3) had the same settings but started data collection immediately after release of the animals. In addition, they collected GPS fixes once every 1800 s until the animal started flying. Then GPS fixes were collected every 300 s (acceleration informed, see (Brown et al., 2012). For data download we walked at least once during daytime through the colony with a base station connected to a directional high-gain antenna (e-obs). All data were subsequently uploaded to Movebank (www.movebank.org), a global repository of animal movement data.

Table 2.1. Size of core areas (50% UD) and foraging areas (home ranges; 90% UD, 95% UD) of bats tracked in wet vs. dry season. Kernel density estimation calculated with fixed smoothing and bandwidth (h) equalling mean distance between successive foraging points (wet: 124 m, dry: 187 m). LoCoH: local convex hulls, with *k* referring to the number of nearest neighbours used for constructing local hulls, and n° of points included at the respective UD bin.

Season	**Bat #**	**total n° points**	**50% UD**				**90% UD**				**95% UD**			
			kernel	**LoCoH**			**kernel**	**LoCoH**			**kernel**	**LoCoH**		
			area (ha)	**area (ha)**	**k**	**n° points**	**area (ha)**	**area (ha)**	**k**	**n° points**	**area (ha)**	**area (ha)**	**k**	**n° points**
Wet	1079	141	15.54	0.09	10	71	60.02	2.21	10	130	79.21	5.43	10	141
	1080	101	11.73	0.08	9	51	39.11	0.52	9	93	50.38	0.71	9	97
	1081	121	7.41	0.03	10	65	24.48	0.16	10	109	31.81	0.32	10	117
	1082	47	21.33	0.13	6	24	110.28	3.74	6	43	149.23	156.25	6	47
	1084	119	15.24	0.11	9	60	53.94	0.73	9	108	70.16	1.06	9	119
	1086	48	12.32	0.25	7	27	71.93	10.98	7	44	99.68	56.69	7	46
	1088	202	10.72	0.04	11	101	32.84	0.72	11	182	41.85	2.26	11	200
	Mean		13.47	0.11			56.09	2.72			74.62	31.82		
	Median		12.32	0.09			53.94	0.73			70.16	2.26		
Dry	1607	186	82.25	0.22	12	94	461.53	93.66	12	173	686.11	642.41	12	178
	1608	27	42.08	0.34	5	17	167.19	2.62	5	25	220.46	630.17	5	27
	1610	30	60.40	2.61	5	15	272.19	74.81	5	30	359.24	74.81	5	30
	1612	25	27.21	0.02	6	13	99.53	0.14	6	24	130.69	0.14	6	24
	1613	39	25.52	0.06	4	22	112.67	2.48	4	36	152.82	4.41	4	39
	1615	29	20.53	0.04	5	15	138.51	149.92	5	27	199.11	412.96	5	29
	1616	75	40.18	0.06	9	44	192.44	0.85	9	70	281.95	4.86	9	73
	1620	90	42.28	0.13	8	45	176.18	3.89	8	85	237.93	4.44	8	86
	1626	164	16.11	0.02	8	82	66.38	0.38	8	148	94.80	1.42	8	156
	Mean		39.62	0.39			187.40	36.53			262.57	197.29		
	Median		40.18	0.06			167.19	2.62			220.46	4.86		

2.2.3 Classification of acceleration data into discrete behaviours

To calibrate the acceleration data, we attached one logger to a captive E. helvum in a large flight cage of the Accra Zoo and observed the bat's behaviour for several hours. The pinger signal of the logger briefly speeds up before the 15 s-collection bout of the accelerometer, which allowed us to record the exact behaviour of the animal during this time. Acceleration data were then plotted with a visualization tool (Movebank acceleration viewer; http://www.3dyne.com/movebank-acceleration-viewer). We classified acceleration data into behaviours based on discrete patterns (see S1 Fig for examples). We distinguished between the categories "resting" (sleeping or otherwise immobile), "moving" (active but not flying), "flying" (bursts that were entirely composed of flying activity, which represented commuting flights between day roost and food trees or between food trees), "starting" (bursts where the animal started flying at some point during the 15 s), "landing" (where the animal was initially flying and then landed during the 15 s) and "short flight" (which started and ended within the 15 s and consisted just of a few wing beats). These last three categories of flights lasting one minute or less were summarized into "foraging flights" (i.e., short flights within food trees or between food trees and feeding perches). Our classification of flight data into commuting or foraging flights was verified by visual inspection of the GPS locations in Google Earth. More fine-grained classification of behaviours (see S1 Fig) would be possible, but were beyond the scope of our study.

2.2.4 Acceleration data analysis

We used data from full 24 h-cycles allowing missing 15 mins at each end and always starting at 18:00 hours UTC (= Ghana local time). We defined the beginning of "day" to be at 6:00 hours and the beginning of "night" at 18:00 hours, roughly corresponding to sunrise and sunset. We then calculated the percentage of time spent resting, moving, commuting and foraging separately per night and per day (commuting and foraging did not occur during the day). We tested for differences in the acceleration data with Mann-Whitney-U tests in InStat Version 3. Values are reported as means ± standard deviation unless otherwise noted. Significance level was 0.05 and all tests were two-tailed.

2.2.5 Spatial data analysis

GPS-points were classified into three behavioural categories: "roost" (all points in the immediate vicinity of the colony), "commute" (points connecting "roost" and "forage", i.e., when bats left and returned to the colony, and points connecting discrete foraging areas), and "forage" (clustered points around foraging trees). Points were initially classified into these categories based on their spatial context. We subsequently checked our classification with the acceleration data where "commute" included a consecutive row of acceleration bursts classified as "flying" (see above) either between the colony and the first or last foraging area visited in a night, or between discrete foraging areas. GPS-points classified as “forage” included all behavioural categories of the acceleration analysis.

Spatial data were analysed with ArcView 3.2a (ESRI, California, USA) in UTM coordinates (UTM zone 30N, WGS84). Utilization distributions (UDs) were calculated with two approaches (partly for comparability with other studies): kernel densities and local convex hulls (LoCoH). Kernel densities were estimated for each animal from foraging points with bivariate normal kernels and fixed smoothing. The smoothing factor h (bandwidth) was calculated as the mean distance between successive foraging points of all individuals within a tracking season (Laver, 2013). Kernel density estimations were computed with the “Home Range Extension for ArcView” (HRE, ver. 1.1c, (Rodgers AR, 2002) in percent volume, in 10%-contour steps plus the 95% contour, and with a 550550 m grid. X- and Y-bandwidths were not standardized.

We further estimated UDs with local convex hulls (ArcView extension LoCoH, ver. 2.1). The number of local neighbours (k) used for constructing local hulls was first evaluated by calculating a range of LoCoHs with k set to 3–15. We subsequently checked graphs where area was plotted as a function of k to identify jumps in area size. We visually inspected the gap-filling properties of the resulting local hulls around these area jumps and identified an optimized k for each individual by selecting 1) a value that avoided spurious holes in the core foraging area and 2) which was less than or equal to the square root of the number of foraging points (Getz and Wilmers, 2004; Getz et al., 2007). LoCoHs were then calculated with the selected k in 5%-density steps up to 100%. We defined core areas as those enclosed by a 50% UD and present foraging areas as both 90% and 95% UD isopleths (see Börger et al., (2006), who recommend the 90% rather than the commonly used 95% isopleth).

Cumulative distance flown per night and individual was calculated as straight lines connecting all points from 18:00 hours until 6:00 hours. Maximum foraging distance was calculated for each individual from the midpoint of the colony to the most distant GPS-point classified as foraging.

2.2.5.1 Habitat use

We used two land cover data sets derived from remote sensing to assess habitat use of E. helvum. Foraging in relation to tree cover was assessed with a regional MODIS-based data set corresponding to percent tree cover (“fractional cover”) and with a spatial resolution of 232 m (derived from MOD13Q1 and spanning from 15°25'N, 5°52'W to 4°40'N, 2°32'E, (Machwitz, 2011; Machwitz et al., 2015). Fruit and flower resources of *E. helvum* are woody plants, hence fractional tree cover should correspond to the density of woody plants within a grid cell potentially available to foraging bats. Use of urban habitat was evaluated with data of the radar satellite TerraSAR-X (Esch et al., 2010; Esch et al., 2012). This data set is a binary classification of built-up areas (grid value “1”) and areas without buildings (grid value “0”). The original data with a spatial grain of 4 m were additionally aggregated to 100 m and 232 m resolutions with the maximum value rule, i.e., larger grid cells containing at least one smaller grid cell classified as built-up were aggregated to “built-up”. We used this procedure to assess the bats’ use of urban habitat with the reasoning that even areas around a single building would have a human footprint.

Grid values of fractional tree cover (%) and built-up (0–1) were extracted for each GPS-point classified as “forage” (see above: Spatial data analysis). These values were compared to random points created within a circular buffer of 88 km around the colony, corresponding to the maximum foraging distance of the dry season. Excluded from this spatial buffer were inland water bodies and ocean as defined by the SWBD data set (SRTM Water Body Data, Shuttle Radar Topography Mission). Water bodies and areas beyond coastline were set to “no data” and excluded for the creation of random points. Fractional tree cover ranged between 8.1 and 80.1% within the extent of the 88 km-radius. Random points (10,000) were generated with Animal Movement (version 2.04; Hooge, P.N. Eichenlaub, 2000) and a distance-weighted function, i.e. with point density decreasing proportional to the distance from the colony (Rosenberg and McKelvey, 1999).

To balance the contribution of individuals to the habitat utilization analysis, we chose the lowest number of GPS locations of any individual in each season (wet: n = 51 foraging locations; dry: n = 25), and randomly sampled all individuals with a higher number of locations, thereby reducing them to the same number of bearings (Gschweng et al., 2012). We also calculated the mean land cover value for each individual and then tested for seasonal differences in habitat use.

2.2.5.2 Feeding behaviour

We visited most of the foraging areas of tracked bats by homing in on their GPS-coordinates. The high accuracy of the data allowed us to distinguish between trees used for gathering food and those used to consume food and/or rest (S2 Table). Food trees were identified by bearing either fruits or flowers during our visits while trees used as night roosts lacked food resources on the tree, but frequently showed feeding signs such as partially consumed fruits or ejecta pellets under the tree. Visited tree species were either identified in the field or by providing botanists with pictures of the food trees (see Acknowledgments).

2.2.5.3 Colony size estimation

We built on previous efforts monitoring the size of the bat colony in Accra (see Hayman et al., 2012). From January 2009 through January 2012, we strived to conduct visual counts on a monthly basis. For this, a single, trained observer walked through the colony during a single day and estimated the number of bats roosting in a cluster, then the number of clusters on each major branch, and continuing this way until all roost trees of the colony were covered. New observers initially estimated colony size in parallel with trained observers, thus ensuring that the same technique was followed and data remained comparable. For previous counts and a detailed description of methods to estimate colony size see Hayman et al., 2012.

2.2.5.4 Meta-analysis of foraging distances of pteropodid bats

We compiled literature data on linear distances between day roosts and foraging areas as well as on body mass of Old Wold fruit bats (S4 Table and S1 Appendix) to contextualize the foraging distances of *E. helvum* in our study, and to assess the scaling of foraging distances with body size. These data were log-transformed and the relationship analysed with a linear regression (SigmaPlot 12).

2.3 Results

2.3.1 Seasonal population fluctuations

Monitoring from January 2009 through January 2012 showed a cyclical fluctuation of colony size, with peak numbers during the dry season (October–March) and population minima during the wet season (April–September; Fig 2.1). Peak numbers (152,000–250,000 individuals) were ca. 50- up to 70-fold higher than the following minima (2,000–4,000 individuals).

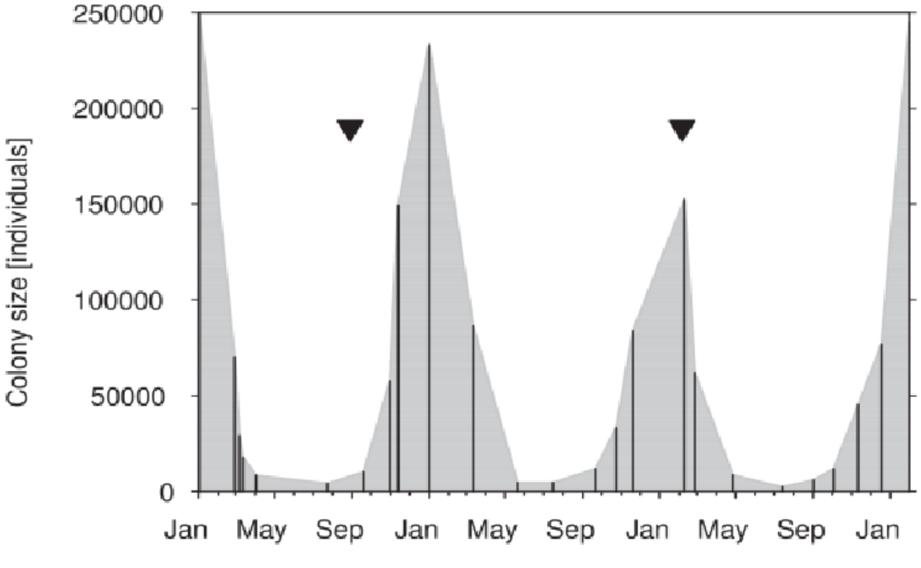

Fig 2.1. Seasonal colony fluctuations of *E. helvum* in Accra from January 2009 through January 2012. Triangles indicate tracking periods of the present study during population low (wet season 2009) and population high (dry season 2011); vertical lines represent colony counts.

2.3.2 Tracking data

We downloaded complete wet season data from six of the 10 loggers that returned to the colony within the lifetime of the batteries. This covered 2.0–3.4 nights of tracking data per individual. One additional logger (#1082) downloaded a partial dataset, but for unknown reasons the battery failed after the data for the first 23 hours 23 min had downloaded. During the dry season 2011 we downloaded data from nine out of 20 loggers, which covered 1.0–6.0 nights of tracking data per individual.

2.3.3 Seasonal differences in size of core and foraging areas as well as foraging distances

Both core and foraging areas as determined with kernel density estimation were significantly and on average about three-fold larger in the dry than in the wet season (Mann-Whitney U– 50% UD: $p = 0.002$; 90% UD: $p = 0.003$; 95% UD: $p = 0.003$; Table 2.1 and Fig 2.2). Although UDs of core and foraging areas calculated with the LoCoH-method showed the same trend (dry season areas were, on average, 4–13-fold larger), differences were not significant, which is probably explained by the large variance (Mann-Whitney U– 50% UD: $P = 0.916$; 90% UD: $P = 0.290$; 95% UD: $P = 0.290$; Table 2.1).

The mean cumulative distance covered per night as well as the maximum distance between the colony and the respective foraging areas were significantly larger in the dry than in the wet season (Mann-Whitney U—mean cumulative distance/night: $P = 0.003$; maximum distance to foraging site: $P = 0.006$; Table 1, Figs 2.2 and 2.3). On average, these distances tripled during the dry season compared to the wet season.

2.3.4 Habitat use in relation to season

Habitat use in relation to built-up areas (broadly corresponding to urban and suburban areas) revealed a parallel picture, with bats foraging 2–3 times more frequently in urban classes during the wet season while being found 1.5–5 times less frequently in these areas during the dry season compared to random expectations (see S2 Fig). This pattern held true irrespective of the spatial grain of the analysis.

These results were supported when based on mean values of each individual: in the wet season, bats used foraging areas with lower tree cover as well as urban space more frequently compared to the dry season (Mann-Whitney U—tree cover: $P = 0.004$; urban 4 m: $p = 0.005$, urban 100 m: $P = 0.033$; urban 232 m: $P = 0.010$; S3 Table).

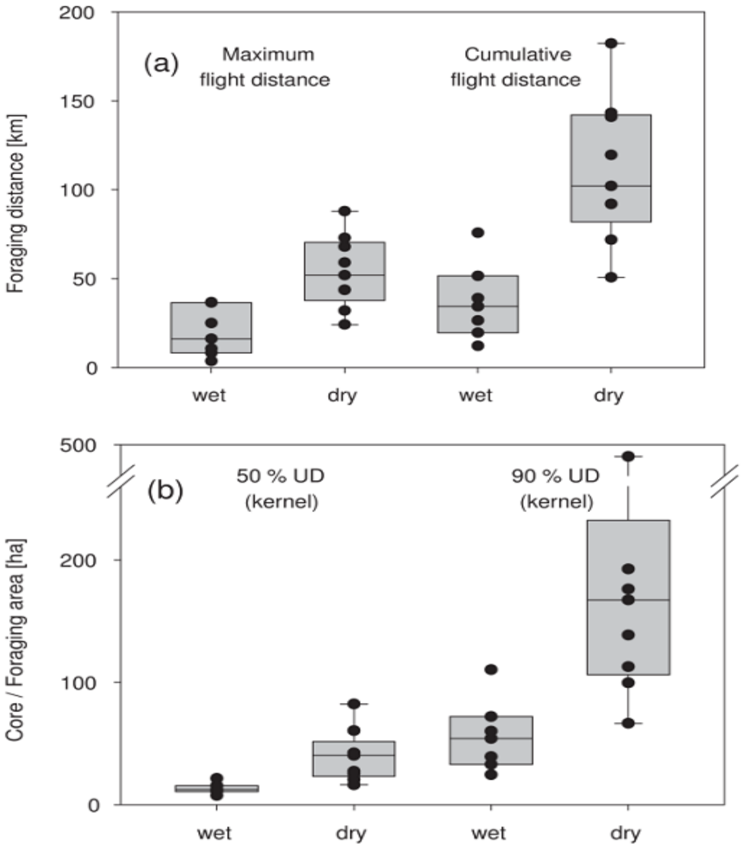

Fig 2.2. Seasonal changes of maximum and cumulative flight distances (a) and in size of core and foraging areas (b). Box plots show maximum flight distances from the colony to the most distant foraging area and the mean of daily cumulative flight distances. Box plots of core and foraging areas show the 50% and 90% kernel density UDs (Table 2.1). Dots represent raw data.

2.3.5 *Behavioural data*

We found no effect of foraging distance on activity budgets of the animals other than that of commuting flights (Table 2.2). Although cumulative and maximum foraging distances, and thus time spent flying, increased dramatically from wet to dry season, there was no significant difference between the seasons regarding time spent in foraging flight and/or resting/otherwise active. Bats spent more time moving (i.e., active but not flying) during the wet season (Table 2.2).

2.3.6 *Food types*

Wet season: We visited the foraging areas of all bats and identified most of their food trees (Table 2.3).

The most frequently used food tree was neem (*Azadirachta indica*), which was eaten by four of the seven bats.

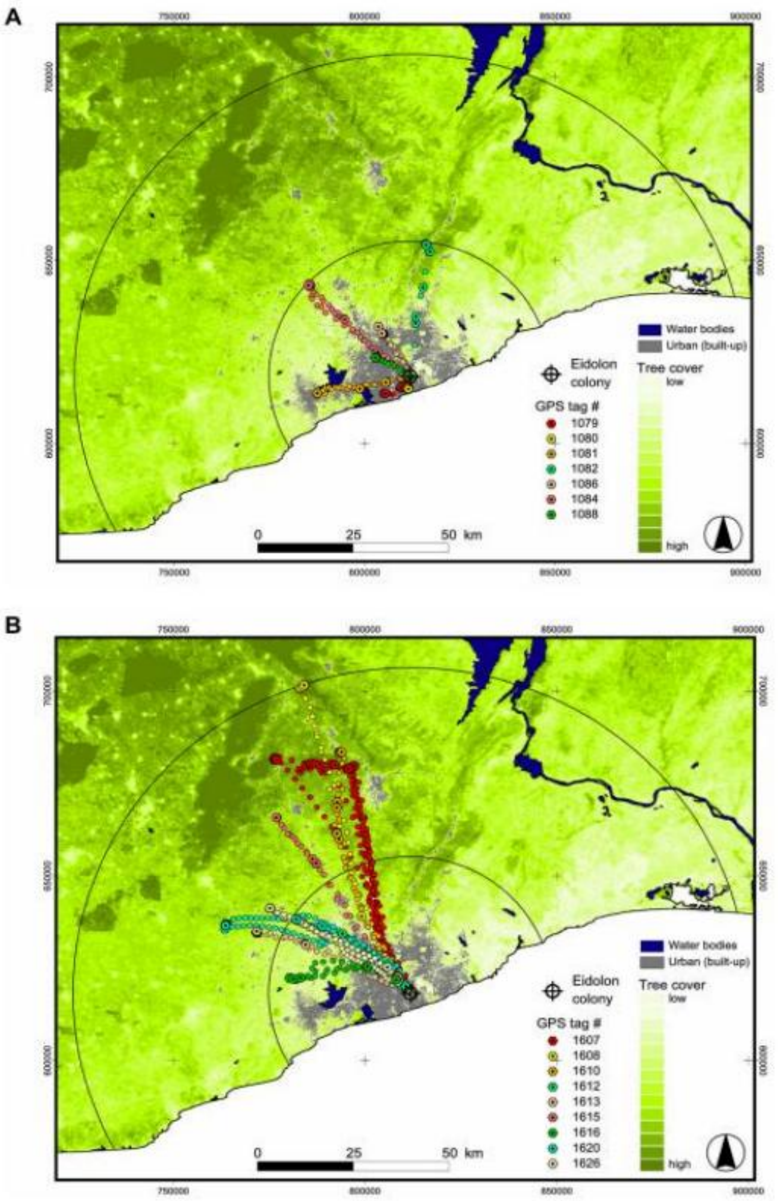

Fig 2.3. GPS tracks of *E. helvum* from wet (a) and dry season (b). Round dots represent commuting and roosting locations, and octagons foraging locations of *E. helvum*. Black circles indicate the maximum foraging distance of wet season (37 km) and dry season (88 km). Southern part of map corresponds to Atlantic Ocean. See Supporting Information (S3 Fig) for detailed maps of foraging areas of selected individuals.

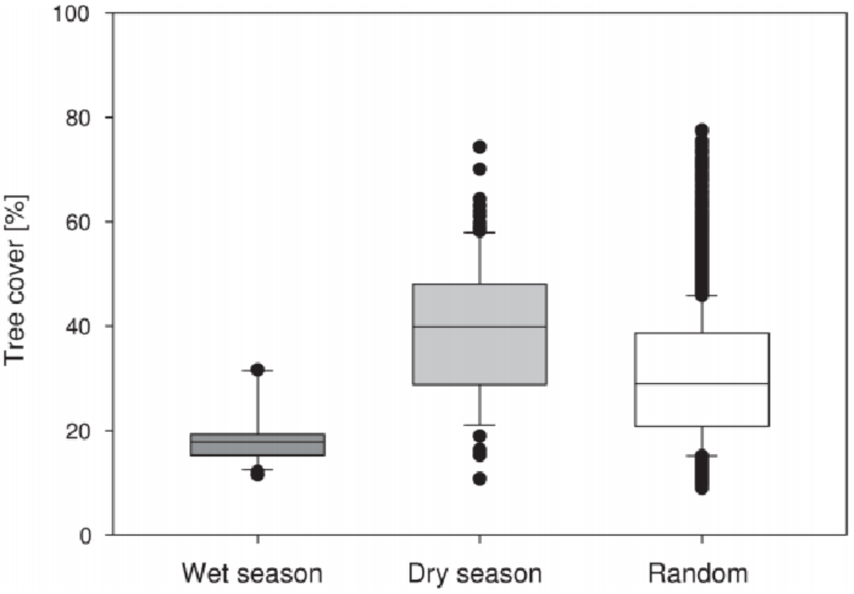

Fig 2.4. Habitat use of *E. helvum* with respect to tree cover. Box plot of foraging points during the wet (n = 306) and dry season (n = 225) compared to the frequency distribution of 10,000 random points within a radius of 88 km around the colony site. Black dots: outliers beyond the 5th / 95th percentiles.

Table 2. Summary of activity budgets of tracked E. helvum during the wet vs. dry season based on acceleration data (wet: n = 6 individuals, dry: n = 9 individuals).

		Wet season	**Dry season**	**Mann-Whitney U**	**U'**	***P***
Night	n° of acc. bursts	1587 ± 617	1505 ± 1281			
	range	780–2341	738–4729			
	% commuting flights	9.1 ± 6.1	26.1 ± 7.2	3	51	0.0028
	% foraging flights	3.7 ± 0.7	4.8 ± 2.5	12	42	0.0879
	% resting	34.0 ± 8.1	29.8 ± 13.5	24	30	0.7756
	% moving	52.0 ± 0.1	39.0 ± 0.1	10	53	0.0132
Day	n° of acc. bursts	1533 ± 655	1439 ± 1193			
	range	685–2876	694–4312			
	% resting	69.1 ± 12.1	71.7 ± 5.0			
24 h	% resting	51.0 ± 8.8	50.3 ± 6.6	26	28	0.9546

Table 2.3. Tracking nights, flight distances, foraging habitat and food types utilized by tracked E. helvum during wet vs. dry season. Food plants in italics = introduced and/or cultivated, bold = native, (+1) if consumption of additional food plant uncertain.

Season	Bat #	# nights tracked	Mean cumulative distance/night (km)	Max. distance to foraging site (km)	Foraging habitat	Food plant	Food type	# foraging trees
Wet	1079	2.9	19.5	8.2	urban	*mango* (**mahogany**)	fruit (leaves?)	2
			19.1–19.9 (n = 2)					
	1080	2.0	12.1	3.5	urban	*neem*	fruit	1 (+1)
			11.1–13.1 (n = 2)					
	1081	3.0	51.5	24.9	urban	*neem*	fruit	1 (+1)
			50.2–52.3 (n =)					
	1082	1.0	38.9 (n = 1)	36.5	urban	**fig1** (*papaya, banana*)	fruit	2
	1084	3.4	34.3	16.1	urban	*neem*, **fig2 (oil palm**, banana, papaya)	fruit	2
			33.9–35.0 (n = 3)					
	1086	2.0	75.7	36.7	plantation	papaya	fruit	1
			75.1–76.4 (n = 2)					
	1088	2.0	26.4	10.5	urban	*neem, sea almond*	fruit	3
			26.3–26.5 (n = 2)	19.5 ± 13.5				
	Mean ± SD		36.9 ± 21.4	16.1				
	Median		34.3	72.9				
Dry	1607	6.0	140.9	72.9	rural (2), urban	**kapok, African tulip**	flower	3
			128.1–165.2 (n = 6)					
	1608	1.0	182.3 (n = 1)	87.9	rural	n.d.	n.d	2
	1610	1.0	143.2 (n = 1)	67.9	rural	kapok (African tulip)	flower	2
	1612	1.0	50.6 (n = 1)	24.1	rural (2), urban	**kapok**	flower	3
	1613	1.0	92.0 (n = 1)	43.6	rural	*cassia*	flower?, leaves?	2
	1615	1.0	119.5 (n = 1)	59	rural	**kapok**	flower	1
	1616	2.0	71.8	31.9	rural	**kapok**	flower	2
			70.9–72.6 (n = 2)					
	1620	2.0	102.1	51.9	rural	n.d.	n.d	3
			75.0–129.3 (n = 2)					
	1626	2.0	91.9	43.5	rural	**kapok**	flower	1
			91.0–92.9 (n = 2)					
	Mean ± SD		110.5 ± 40.4	53.6 ± 20.4				
	Median		102.1	51.9				

Other food plants were mango (*Mangifera indica*), papaya (*Carica papaya*), sea almond (*Terminalia catappa*)–all introduced and/or cultivated plants except two fig species (*Ficus thonningii* and *F. vallis-choudae*). In two cases it was not possible to identify the exact food tree. Both of these bats were foraging in gardens where they may have fed on banana (*Musa sp.*) and/or papaya. All bats but one foraged in the city or the suburbs of Accra, or in the 36 km distant town of Akwapim-Mampong (#1082). Bat #1086 left the urban environment to forage in a papaya plantation. One of the fig trees (*F. vallis-choudae*, bat # 1084) was in a rural landscape near a quarry north of Accra; however this bat’s main foraging tree was a neem tree in the middle of an urban environment. In one case (#1079) we were not able to find a fruit tree; however, there was a row of largely defoliated mahogany trees at the site (*Khaya senegalensis*). Eidolon helvum has been reported to feed on various other leaves as well as bark (Malagnoux and Gautun, 1976; Kunz and Diaz, 1995), so this individual may have been eating mahogany leaves.

Dry season: Food resources were more uniform as most bats fed almost exclusively on flowers (Table 2.3), in particular those of kapok trees (*Ceiba pentandra*). Two individuals also visited flowering African tulip (*Spathodea campanulata*) while GPS locations of another individual clustered around a grove of *Cassia* (*Senna*) *siamea* trees. Flowers of the latter species are unlikely to provide nectar to fruit bats (Marazzi et al., 2007), and this species has not previously been reported in the diet of E. helvum; however, the leaves are eaten by humans as well as by fruit bats in Asia (Kunz and Diaz, 1995), from where the tree originates. Most of the kapok and African tulip trees were in small groves or even single individuals left in clear-cut areas or cacao plantations, and the bats flew past fruiting trees of species they consumed during the wet season, especially neem.

2.3.7 Scaling of foraging distances of Old World fruit bats in relation to body size

Body size and foraging distance of Old World fruit bats are positively correlated (y = 0.746x + 1.810, R2 = 0.384, $p < 0.0001$, Fig 2.5). Based on the 95% confidence interval of the linear regression, highly colonial fruit bats including *E. helvum*, *Rousettus aegyptiacus*, *R. madagascariensis*, *R. leschenaultii* and *Pteropus tonganus* forage farther from the colony than other pteropodid bats.

2.4 Discussion

The colony size of *Eidolon helvum* in Accra fluctuated dramatically and in a temporally consistent pattern over three years, with colony maxima of several hundred thousand individuals during the late dry season (January–February) and minima of a few thousand individuals during the wet season (May–September). The pattern agrees with the hypothesis that straw-coloured fruit bats reside in colonies along the West African coast during the dry season, and then migrate into northern savannas with the onset of the wet season, following concomitant resource flushes (Thomas, 1983).

Our tracking studies were scheduled to coincide with the seasonal population minima and maxima. The concurrent increase of commuting distances, cumulative flight distances, foraging areas and flight time with population size, and especially the magnitude of change in these parameters, is intriguing (Figs 2 and 3, Tables 1 and 3).

It is tempting to speculate that intraspecific competition increased strongly at peak population size during the dry season. According to optimal foraging theory, individuals should minimize travel distance, time and energy expenditure to locate food patches while maximizing food intake at these patches. In a central-place forager such as *E. helvum*, it is likely that exploitation of food resources in the immediate vicinity of the colony is intense, and that the density of foraging bats decreases with increasing distance from the colony. In consequence, a substantial proportion of the colony might be forced to forage at much larger distances during the population high, leading to the observed increase in movement parameters.

Similar patterns have been documented in central-place foraging seabirds where colony size was positively correlated with foraging distance and energy expenditure used for foraging (Ballance et al., 2009; Lewis et al., 2001; Wakefield et al., 2013). Interestingly and in contrast to expectations, the high-resolution activity budgets of tracked bats did not reflect a correlated increase of energetic costs incurred by longer commuting flights during the dry season. If commuting flights were very costly, we would have expected the bats to spend more time foraging at the feeding sites, and / or reduced activity in the colony during the day. Neither of these reactions was apparent (Table 2.2). Activity budgets may not be the right measure to reveal such potential trade-offs, but the high resolution of the acceleration data should at least indicate such a trend, if present, as other studies have shown (Wilson et al., 2006; Gleiss et al., 2011).

Alternatively or additionally, some of the differences between dry and wet season may be due to seasonal changes in the resource landscape, and potentially unrelated to colony size. Our diet data show a clear shift from introduced and cultivated fruit trees used during the wet season (in particular neem) to flower resources (mostly kapok trees) during the dry season. If kapok trees are, on average, found further from the colony than the wet season fruit resources, this could lead to the observed increase in foraging distances. However, neem as a steady-state fruiting tree was available also during the dry season but not used at all by our tracked individuals. Perhaps some types of fruit provide fall back staple food, but are less preferred in spite of greater spatial proximity and higher density, or other food sources become necessary as seasonal needs of the bats change. The latter effect, if true, should be more evident in females with increased energetic demands during reproduction (pregnancy during the dry season, see (Fayenuwo and Halstead, 1974), but this explanation seems unlikely as we only tracked males.

Currently, our data are temporal snapshots from the extremes in colony size. Critical tests to distinguish between these alternatives will require longer tracking periods, preferably covering an entire year. This should reveal whether movement parameters closely match the change in colony size and thus reflect competition, if they mirror the seasonal distribution of fruit and flower resources, or both. Given that bats showed rather stereotypic use of foraging areas over the course of several nights, medium- to long-term tracking of bats will reveal whether bats sequentially switch from one set of foraging areas to the next, both in terms of seasonal changes in resource availability but possibly also related to local depletions of resources over time. All of these avenues critically depend on the development of new solar-powered loggers that allow tracking of bats over longer time spans than in the present study.

The seasonal changes not only affected movement parameters but also habitat use. During the wet season, *E. helvum* foraged in patches characterized by comparatively low tree cover in (sub-) urban areas. Dry season foraging areas had higher tree cover and were mostly located beyond the (sub-) urban periphery (Figs 2.3 and 2.4). We cannot determine yet if this shift in habitat use is a consequence of the spatial distribution of these factors and correlated travel distance, *i.e.* tree cover increasing and urban areas decreasing with distance from the colony in the centre of Accra. Interestingly almost all of the plants consumed during the wet season were human-cultivated, introduced and/or invasive (see Table 2.3). It remains unclear if the observed partial migration is a recent phenomenon, but the urban landscape may offer predictable resource availability that the bats can fall back or even exclusively feed on to bridge periods of food paucity, which may become more severe with increased land use and climate change.

2.4.1 Foraging distances of Old World fruit bats in relation to body mass

The foraging distances covered by *E. helvum* during the dry season by far surpass any previously recorded flight distance of bats between day roosts and foraging sites (S4 Table). Theory would predict a positive relationship between body mass and daily travel distance (Garland T.Jr, 1983; Carbone et al., 2005). Indeed, currently available data on Old World fruit bats suggest such a relationship, though explaining a rather small amount of variation across species (R^2 = 0.38, Fig 2.5). Apparently factors other than body size are important in determining this aspect of space use in pteropodid bats. Interestingly, all species with exceptionally large foraging distances (*E. helvum, Rousettus aegyptiacus, R. madagascariensis, R. leschenaultii,* and *Pteropus tonganus*; S4 Table) are highly gregarious central-place foragers, and both *E. helvum* and the three Rousettus species also show high fidelity to their day roosts, exploiting the resource landscape over longer time periods rather than shifting colonies in a nomadic fashion. Disentangling the various factors that influence foraging distance of fruit bats will be a major step forward to predict their ecological role as seed dispersers and pollinators. Our data clearly show that compared to other Old World fruit bats, *E. helvum* is likely to provide exceptional long-distance services in this regard, especially for pollen carried on the fur and small seeds ingested and defecated during flight. These predictions are based on daily distances travelled and do not even include potential dispersal extremes that could be achieved during migration.

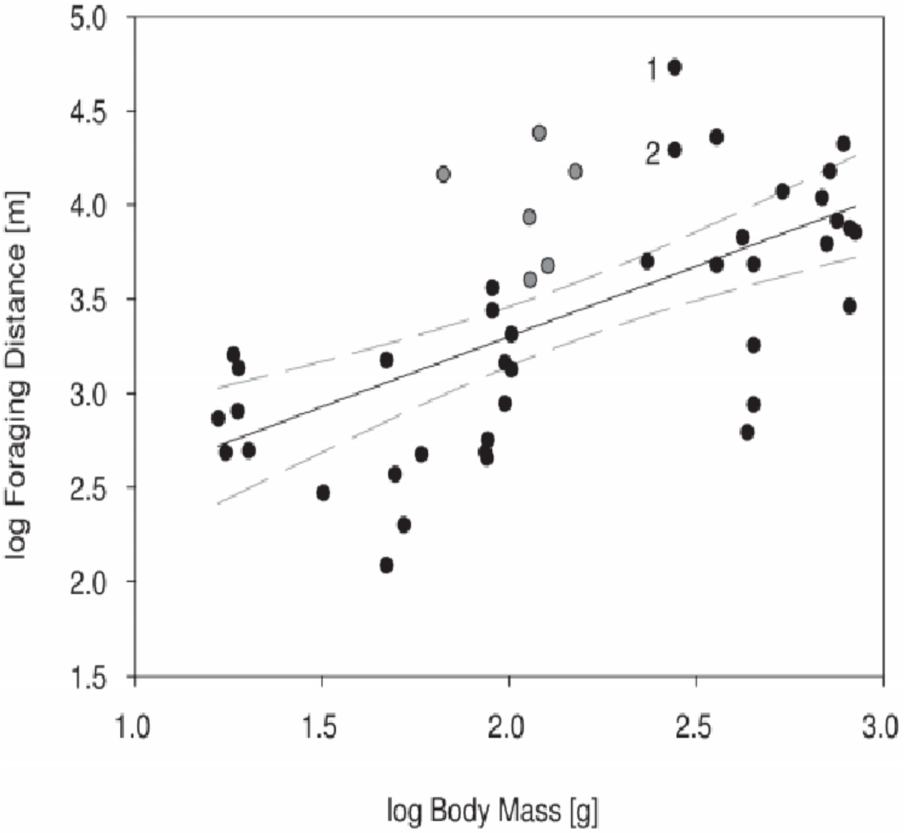

Fig 2.5. Foraging distances of Old World fruit bat species (Pteropodidae) in relation to body mass. 1: *E. helvum*, dry season, 2: *E. helvum*, wet season. Linear regression (y = 0.746x + 1.810, R2 = 0.384) with 95% confidence bands shown. Grey dots show cave-roosting Rousettus spp. See Supporting Information (S4 Table and S1 Appendix) for literature data.

2.4.2 Conclusion and Outlook

Accra is one of the fastest growing cities in West Africa (Møller-Jensen et al., 2013). Currently both dry and wet season populations of straw-coloured bats seem to have sufficient food resources within accessible distances from the central colony in the downtown area of the city. In fact, the suburbs with plenty of introduced and cultivated fruit trees might provide an increased food supply, and seed dispersal of neem trees by the bats could have created a positive feed-back loop in this regard, i.e. bats planting their own food resources (Ayensu, 1974; Tsoar et al., 2010; Jordaan et al., 2011). Several *Pteropus* species in Australia and Japan seem to have likewise profited from introduced and cultivated food resources in (sub-) urban environments (Parry-Jones and Augee, 2001; Markus and Hall, 2004; Williams et al., 2006; Nakamoto et al., 2007b; Weber et al., 2015). In addition, the spatio-temporal resource availability might have significant implications for the migratory pattern of *E. helvum* because an increased year-round food supply could lead to a higher proportion of resident individuals, thus shifting the proportion of migratory vs. non-migratory bats. However, increasing agglomeration of buildings and infrastructure might eventually result in a decrease of food resources in distances energetically worthwhile. Unless the colony in Accra is persecuted with massive force, we do not expect *E. helvum* to disappear from this urban landscape, but it remains to be seen whether urban sprawl might eventually push resources so far from the colony that commuting flights are energetically too expensive to support the population sizes that are currently observed.

Supplementary material

S1 Appendix. Literature used to compile S4 Table.

Explanation of S4 Table BM: body mass [g]; mean distance: mean distance b/w roost and foraging site(s) [km]; error type: SD – standard deviation, SE – standard error; max distance: maximum distance b/w roost and foraging site(s) [km]; range distance: range of distances b/w roost and foraging site(s) [km]; midpoint range: arithmetic midpoint of range of distances [km]; long axis mean: mean distance of long axis of home range [km]; long axis range: range of distances of long axis of home range [km]; proxy: colour-coded value used in regression; sample size: number of tracked individuals; day roost inside / outside FA: whether day roosts were reported to be located inside or outside of foraging area(s).

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Figure S1: Examples of acceleration data.

Shown are four 15 s-bursts (recorded once a minute continuously). X-axis: time, y-axis: acceleration (m/s2). a) flying – magnified inset shows oscillating acceleration on z-axis, which corresponds to wing beats; b) resting; c) moving; d) moving, specifically scratching; note that orientation (i.e. which axis is shifted by 1 g) is different from a) because bat is hanging upside down as opposed to horizontally flying.

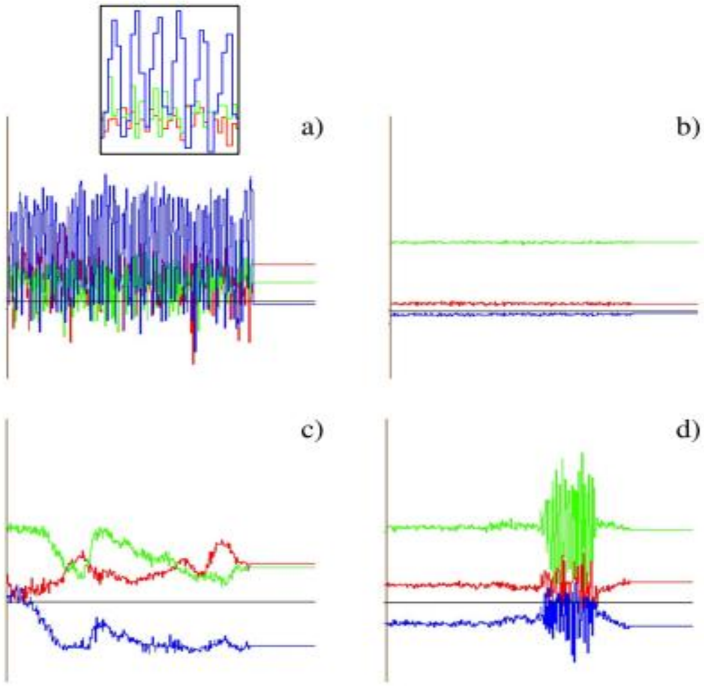


Figure S2: Habitat use of *Eidolon helvum* with respect to built-up areas. Frequency distribution of foraging points during the wet season (n=357) and the dry season (n=225) compared to the frequency distribution of 10,000 random points within a radius of 88 km radius around the colony site. Percent urban is the proportion of points classified as “built up” out of the entire pool of points at three spatial grains (see methods).

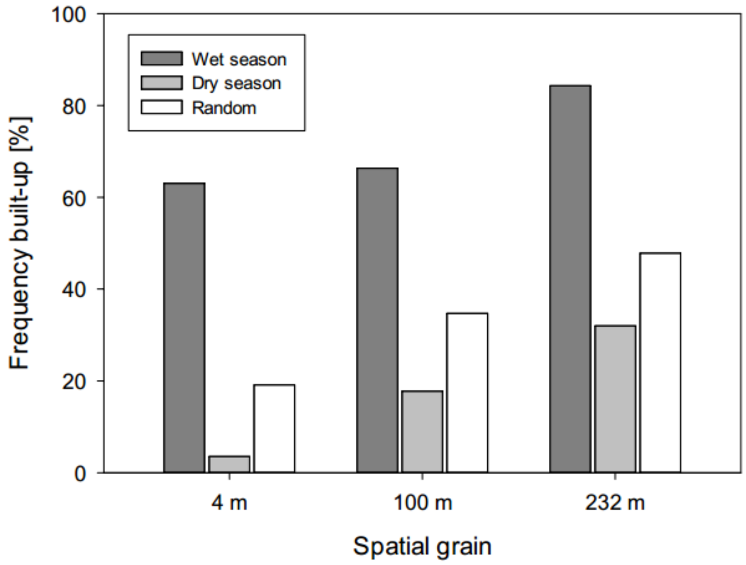
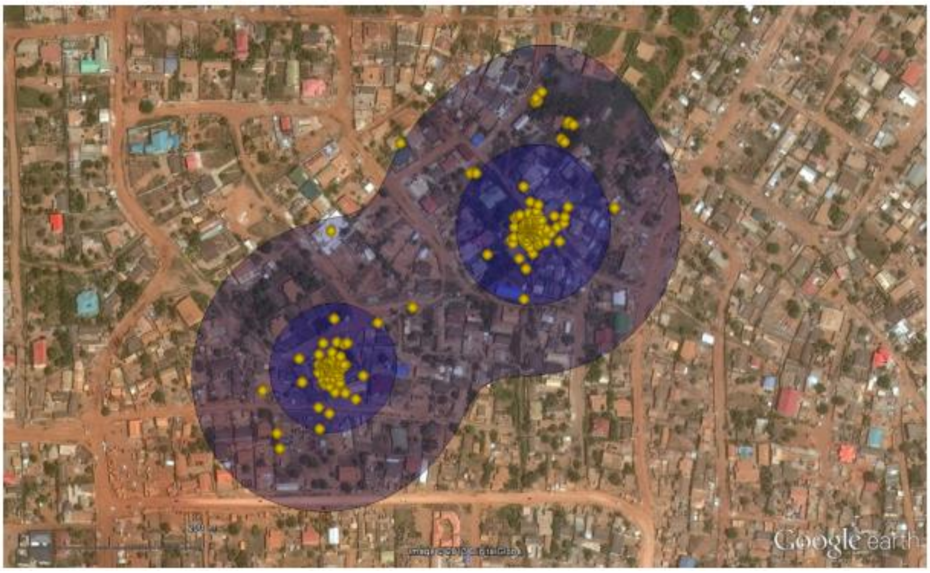


Figure S3: Examples of space use of *Eidolon helvum*.

Yellow dots: GPS-points, pale blue: foraging areas (95 % UD), dark blue: core areas (50 % UD). Map data © 2013 Google and DigitalGlobe / GeoEye.

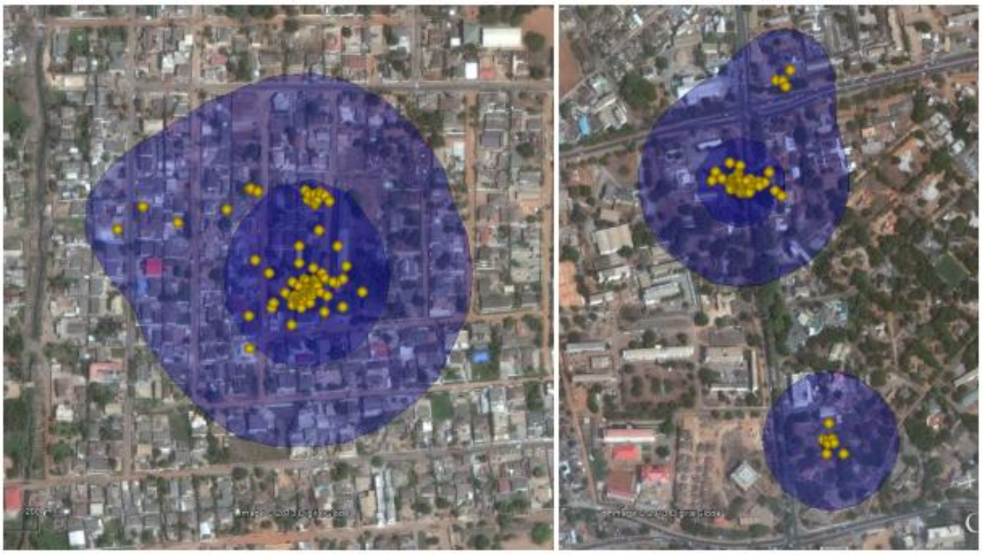
Wet season (note that foraging sites are mostly located in (sub-) urban areas)

Bat #1088:

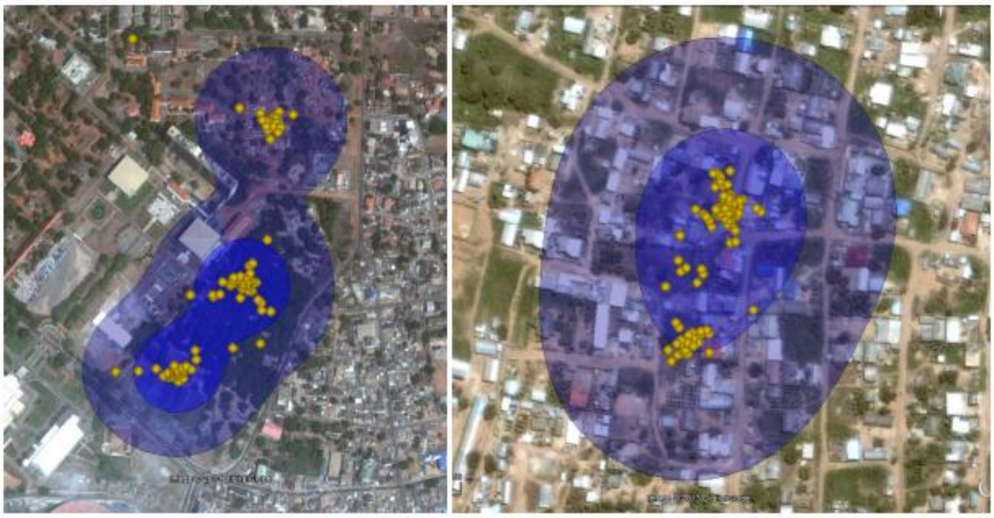


Bat #1078 overview:

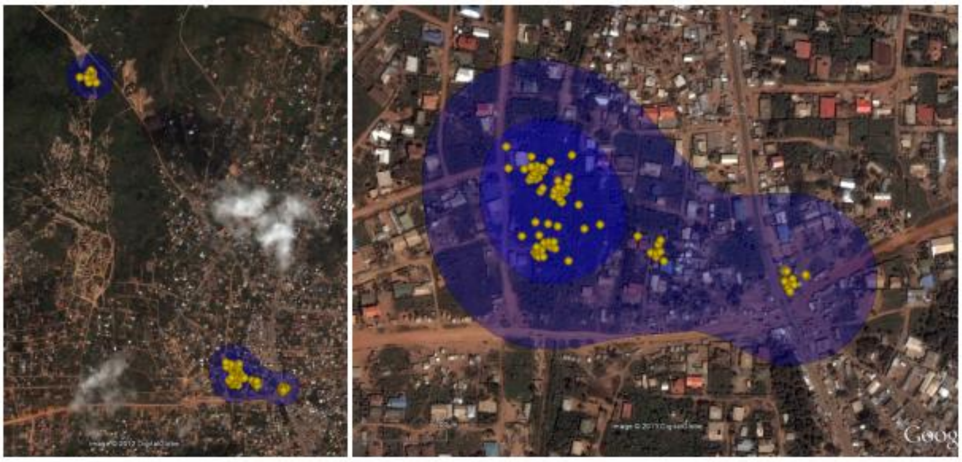
Bat #1078 detail:



Bat #1080 (left) and #1081 (right):

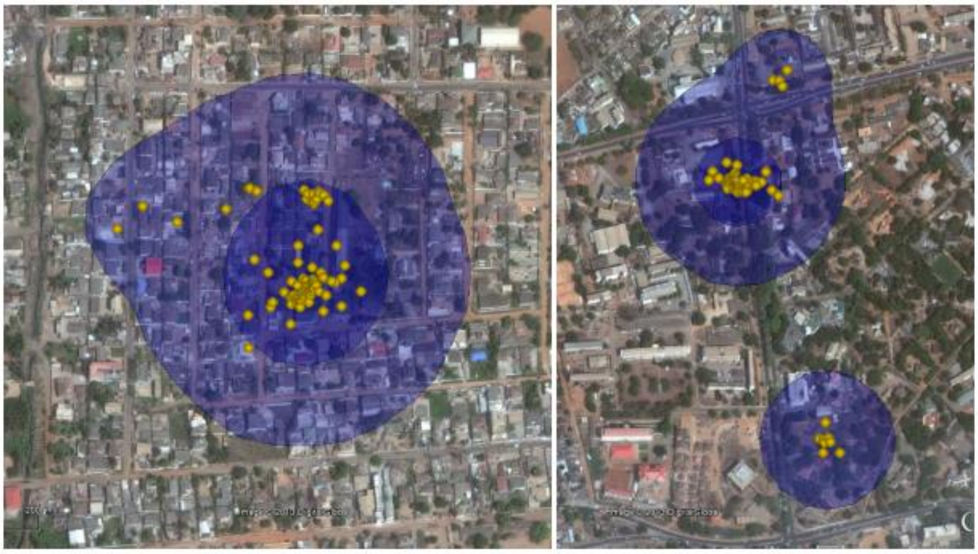


Bat #1084 overview (left) and detail (right):

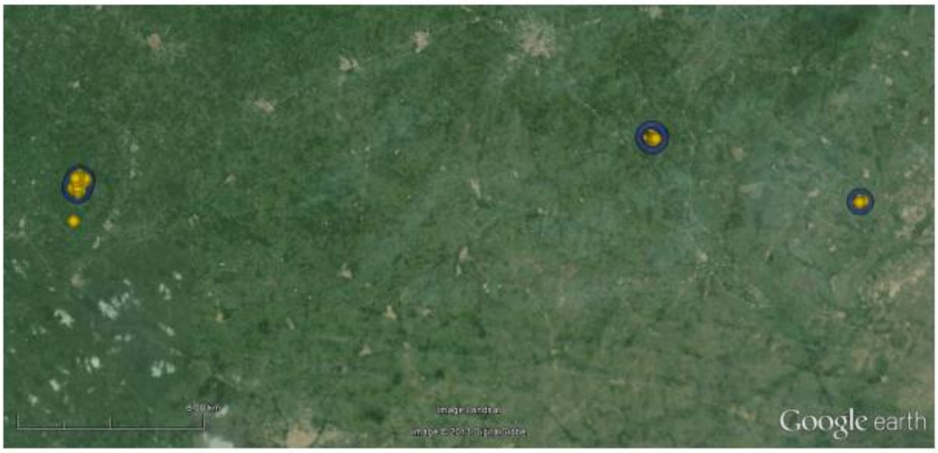


Bat #1078 overview:

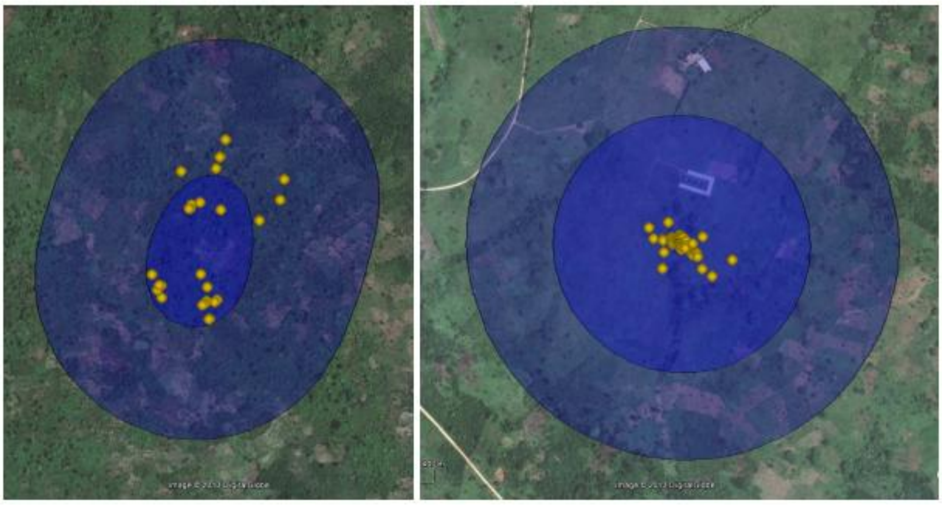
Bat #1078 detail:



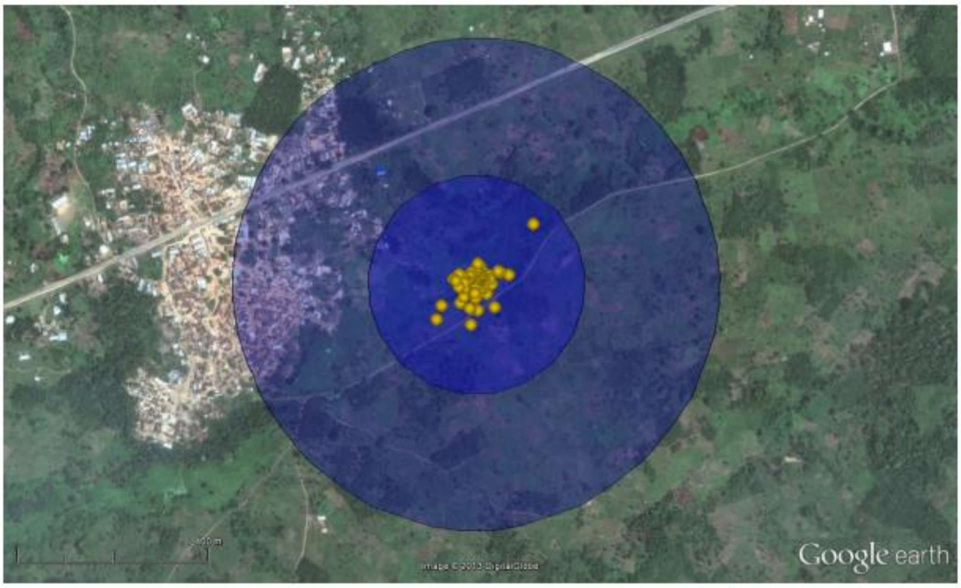
Bat #1620 overview:



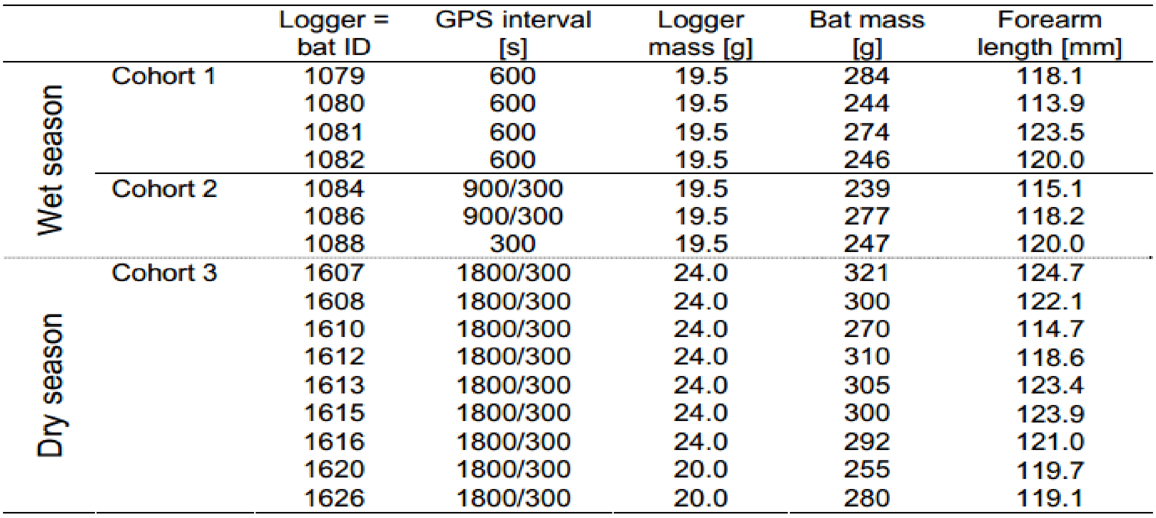
Bat #1620 detail (left: west, right: east):



Bat #1626:

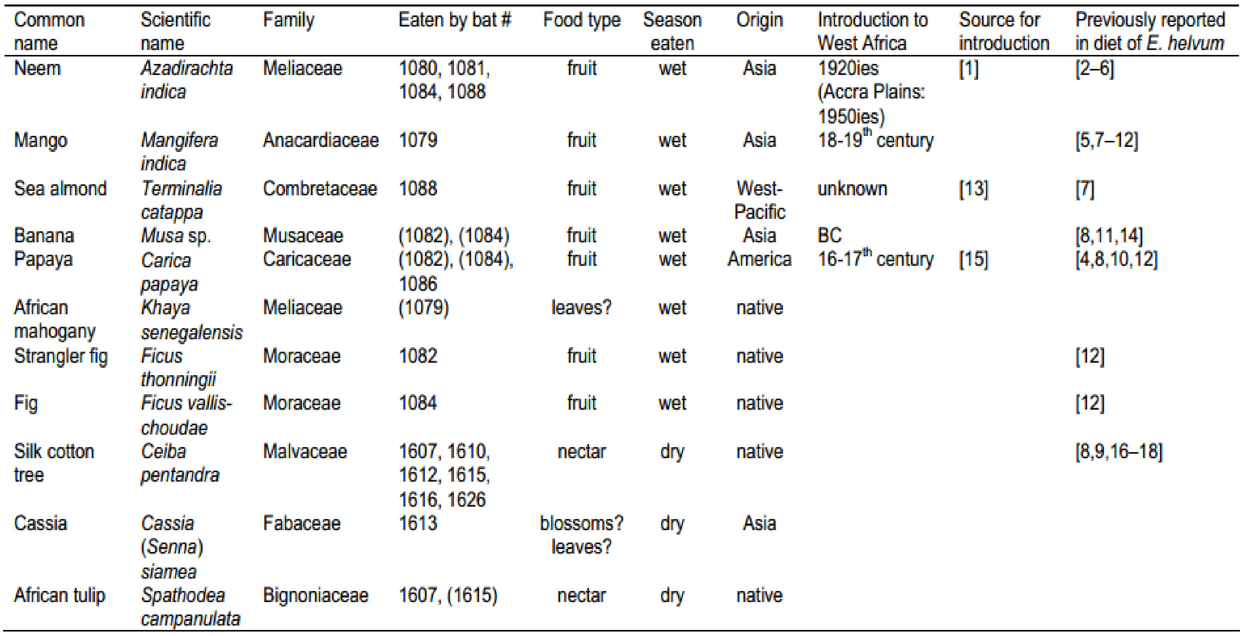


S1 Table. Logger programming and measurements of tracked individuals.



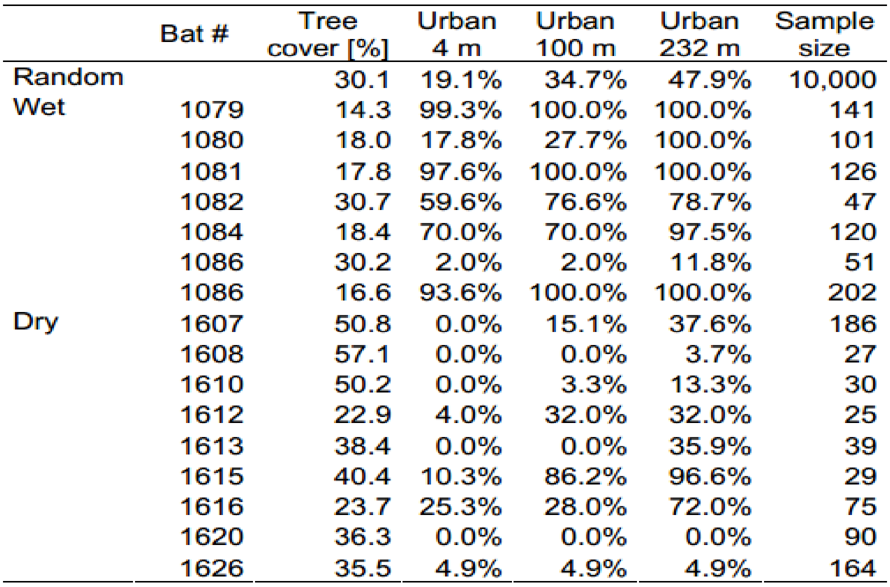
		Logger = bat ID	GPS interval [s]	Logger mass [g]	Bat mass [g]	Forearm length [mm]
Wet season	Cohort 1	1079	600	19.5	284	118.1
		1080	600	19.5	244	113.9
		1081	600	19.5	274	123.5
		1082	600	19.5	246	120.0
	Cohort 2	1084	900/300	19.5	239	115.1
		1086	900/300	19.5	277	118.2
		1088	300	19.5	247	120.0
Dry season	Cohort 3	1607	1800/300	24.0	321	124.7
		1608	1800/300	24.0	300	122.1
		1610	1800/300	24.0	270	114.7
		1612	1800/300	24.0	310	118.6
		1613	1800/300	24.0	305	123.4
		1615	1800/300	24.0	300	123.9
		1616	1800/300	24.0	292	121.0
		1620	1800/300	20.0	255	119.7
		1626	1800/300	20.0	280	119.1

S2 Table. Additional information on food trees utilized by Eidolon helvum.



Common name	Scientific name	Family	Eaten by bat #	Food type	Season eaten	Origin	Introduction to West Africa	Source for introduction	Previously reported in diet of *E. helvum*
Neem	*Azadirachta indica*	Meliaceae	1080, 1081, 1084, 1088	fruit	wet	Asia	1920ies (Accra Plains: 1950ies)	[1]	[2–6]
Mango	*Mangifera indica*	Anacardiaceae	1079	fruit	wet	Asia	18-19th century		[5,7–12]
Sea almond	*Terminalia catappa*	Combretaceae	1088	fruit	wet	West-Pacific	unknown	[13]	[7]
Banana	*Musa* sp.	Musaceae	(1082), (1084)	fruit	wet	Asia	BC		[8,11,14]
Papaya	*Carica papaya*	Caricaceae	(1082), (1084), 1086	fruit	wet	America	16-17th century	[15]	[4,8,10,12]
African mahogany	*Khaya senegalensis*	Meliaceae	(1079)	leaves?	wet	native			
Strangler fig	*Ficus thonningii*	Moraceae	1082	fruit	wet	native			[12]
Fig	*Ficus vallis-choudae*	Moraceae	1084	fruit	wet	native			[12]
Silk cotton tree	*Ceiba pentandra*	Malvaceae	1607, 1610, 1612, 1615, 1616, 1626	nectar	dry	native			[8,9,16–18]
Cassia	*Cassia* (*Senna*) *siamea*	Fabaceae	1613	blossoms? leaves?	dry	Asia			
African tulip	*Spathodea campanulata*	Bignoniaceae	1607, (1615)	nectar	dry	native			

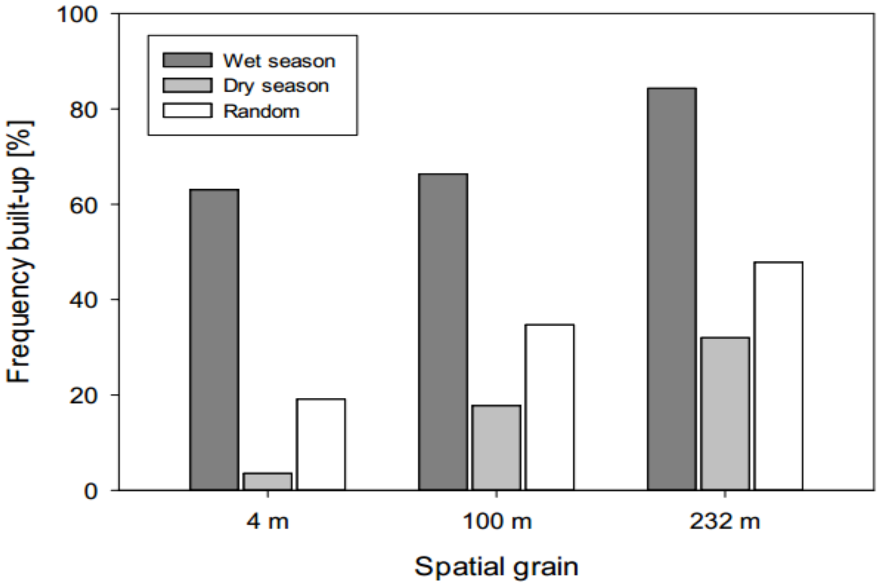
S3 Table: Habitat utilization of tracked *E. helvum* in relation to tree cover (mean grid values of foraging points) and built-up areas ('urban').



	Bat #	Tree cover [%]	Urban 4 m	Urban 100 m	Urban 232 m	Sample size
Random		30.1	19.1%	34.7%	47.9%	10,000
Wet	1079	14.3	99.3%	100.0%	100.0%	141
	1080	18.0	17.8%	27.7%	100.0%	101
	1081	17.8	97.6%	100.0%	100.0%	126
	1082	30.7	59.6%	76.6%	78.7%	47
	1084	18.4	70.0%	70.0%	97.5%	120
	1086	30.2	2.0%	2.0%	11.8%	51
	1086	16.6	93.6%	100.0%	100.0%	202
Dry	1607	50.8	0.0%	15.1%	37.6%	186
	1608	57.1	0.0%	0.0%	3.7%	27
	1610	50.2	0.0%	3.3%	13.3%	30
	1612	22.9	4.0%	32.0%	32.0%	25
	1613	38.4	0.0%	0.0%	35.9%	39
	1615	40.4	10.3%	86.2%	96.6%	29
	1616	23.7	25.3%	28.0%	72.0%	75
	1620	36.3	0.0%	0.0%	0.0%	90
	1626	35.5	4.9%	4.9%	4.9%	164

For urban, the percentage of foraging points in this class is given (binary data) while for tree cover the mean value of all grid cells is shown (continuous data). Also shown are the respective values for 10,000 random points.

Figure S2: Habitat use of *Eidolon helvum* with respect to built-up areas. Frequency distribution of foraging points during the wet season (n=357) and the dry season (n=225) compared to the frequency distribution of 10,000 random points within a radius of 88 km radius around the colony site. Percent urban is the proportion of points classified as "built up" out of the entire pool of points at three spatial grains (see Methods).



S4 Table. Literature data on foraging distance and body mass of Old World fruit bats used in Fig 5. (XLS).

Species	Country	BM [g]	mean distance	error	error type	max distance	range distance	midpoint range	long axis mean	error	error type	long axis range	proxy	sample size	day roost inside / outside FA	reference
Acerodon jubatus	Philippines	854	5.000	0.490	SE		0.44 – 12.6							5	O	Mildenstein et al. 2005
Acerodon jubatus	Philippines	841	7.117	2.722	SD		1.07 – 18.19						7.117	6	O	de Jong et al. 2013
Balionycteris maculata	Malaysia	14				1.000								6	O	Hodgkison et al. 2003
Cynopterus brachyotis	Malaysia	32	0.295	0.055	SD								0.295	7	I	Funakoshi & Zubaid 1997
Cynopterus horsfieldii	Malaysia	58	0.475	0.105	SD								0.475	6	I	Funakoshi & Zubaid 1997
Cynopterus sphinx	India	47	0.851			4.000	0.09 – 2.2							10	O	Nair et al. 1999
Cynopterus sphinx	India	47	1.500	0.825	SD	4.000	0.2 – 2.2						1.500	5	O	Nair et al. 1999: females
Cynopterus sphinx	India	47	0.122	0.045	SD		0.09 – 0.2						0.122	5	O	Nair et al. 1999: males
Dobsonia minor	New Guinea	88							0.566			0.150 – 1.150	0.566	8	I	Bonaccorso et al. 2002
Eidolon helvum	Ghana	277	53.600	20.400	SD		24.1 – 87.9						53.600	9	O	this study: dry season
Eidolon helvum	Ghana	277	19.500	13.400	SD		3.5 – 36.7						19.500	7	O	this study: wet season
Eidolon helvum	Zambia	304				59.000									O	Richter & Cumming 2008
Epomophorus crypturus	South Africa	90							2.739	0.584	SE	0.799 – 5.365	2.739	9	I	Bonnacorso et al. 2014: Shingwedzi
Epomophorus crypturus	South Africa	90							3.618	0.663	SE	1.066 – 5.998	3.618	7	I	Bonnacorso et al. 2014: Babalala
Epomophorus wahlbergi	South Africa	101					0.1 – 4.0	2.050					2.050	10	O	Fenton et al. 1985
Epomophorus wahlbergi	South Africa	97	0.880	0.080		1.300							0.880	10		Rollinson 2012: spring
Epomophorus wahlbergi	South Africa	97	1.450	0.200		2.000							1.450	10		Rollinson 2012: winter
Epomophorus wahlbergi	South Africa	101							1.334	0.184	SE	0.463 – 2.865	1.334	17	I	Bonnacorso et al. 2014
Hypsignathus monstrosus	Gabon	420	6.700			10.000							6.700	8	O	Bradbury 1977: from calling site to foraging area
Hypsignathus monstrosus	Gabon	234	5.000										5.000		O	Bradbury 1977: from day roost to foraging area
Macroglossus minimus	Malaysia	18	1.600	0.700		2.300							1.600	6	O	Watzke 2006
Macroglossus minimus	Malaysia	18													I	Watzke 2006
Macroglossus minimus	New Guinea	20							0.495	0.258		0.226 – 1.020	0.495	18	I	Winkelmann et al. 2003
Melonycteris melanops	New Guinea	50							0.371	0.090		0.229 – 0.549	0.371	10	I	Bonaccorso et al. 2005

Nyctimene robinsoni	Australia	52	0.200				0.06 – 1.01						0.200		I?	Spencer & Fleming 1989 (median: 0.506 km)
Ptenochirus jagori	Philippines	86	0.486	0.203					0.838	0.317		0.533 – 1.367	0.486	6	I	Reiter & Curio 2001: females
Ptenochirus jagori	Philippines	87	0.454	0.243					0.983	0.454		0.557 – 1.589	0.454	5	I	Reiter & Curio 2001: males
Pteropus alecto	Australia	812	7.500	0.600	SE		1.8 – 12.1						7.500	7	O	Markus & Hall 2004: Indooroopilly Island
Pteropus alecto	Australia	812	2.900	0.300	SE		1.8 – 12.1						2.900	5	O	Markus & Hall 2004: Norman Creek
Pteropus alecto	Australia	686	10.900			29.300	3.7 – 29.3						10.900	7	O	Palmer & Woinarski 1999: females
Pteropus alecto	Australia	706	6.200			22.900	1.6 – 22.9						6.200	9	O	Palmer & Woinarski 1999: males
Pteropus dasymallus	Japan	433	0.621	0.849	SD		0.0 – 6.88		1.200	1.200	SD		0.621	30	I	Nakamoto et al. 2012 (median: 0.277 km)
Pteropus lylei	Thailand	538	11.800	6.600	SD	23.600	2.2 – 23.6						11.800	19	O	Weber et al. 2015
Pteropus poliocephalus	Australia	782	21.000				17 – 25						21.000	2	O	Spencer et al. 1991
Pteropus poliocephalus	Australia	748				50.000								20	O	Eby 1991: females
Pteropus poliocephalus	Australia	970				50.000								2	O	Eby 1991: males
Pteropus rufus	Madagascar	720	15.080	2.310	SD								15.080	6	O	Oleksy et al. 2015: females
Pteropus rufus	Madagascar	751	8.210	7.920	SD								8.210	9	O	Oleksy et al. 2015: males
Pteropus tonganus	America Samoa	358	4.800	0.600	SE								4.800	18	O	Banack & Grant 2002: east side of island
Pteropus tonganus	America Samoa	358				46.700								1	O	Banack & Grant 2002: exploratory flight of imm. male within a single night
Pteropus tonganus	America Samoa	358	22.800	8.300	SE								22.800	18	O	Banack & Grant 2002: west side of island
Pteropus tonganus	America Samoa	450	1.800										1.800	20	O	Nelson 2002 (males: 1.5 km, females: 2.3 km)
Pteropus tonganus	America Samoa	450	4.840			16.000	2.4 – 9.0						4.840	5	O	Nelson 2002: east side of island
Pteropus tonganus	America Samoa	450	0.870			8.100	0.4 – 3.2						0.870	15	O	Nelson 2002: west side of island
Pteropus vampyrus	Philippines	807	5.000	0.490	SE		0.44 – 12.6							5	O	Mildenstein et al. 2005
Rousettus aegyptiacus	Israel	150	15.000	3.200	SD		7.1 – 20.6						15.000	15	O	Tsoar et al. 2011a
Rousettus aegyptiacus	South Africa	127					2.6 – 6.9	4.750					4.750	6	O	Barclay & Jacobs 2011: females

Rousettus aegyptiacus	South Africa	114					3.0 – 5.0	4.000			4.000	6	O	Barclay & Jacobs 2011: males
Rousettus aegyptiacus	South Africa	120	24.000								24.000	4	O	Jacobsen et al. 1986
Rousettus leschenaultii	China	113	8.570				6.6 – 10.5		10.180	7.5 – 11.7	8.570	3	O	Tang et al. 2010
Rousettus madagascariensis	Madagascar	67					14.2 – 14.8	14.500			14.500	2	O	Andrianaivoarivelo et al. 2011
Syconycteris australis	Australia	17	0.734				0.5 – 6.2				0.734	10	O	Law & Lean 1999
Syconycteris australis	Australia	19	1.360	0.190	SE	4.000	0.1 – 3.0				1.360	17	O	Law 1993: autumn & spring
Syconycteris australis	Australia	19	0.800	0.310	SE		0.1 – 3.6				0.800	13	O	Law 1993: winter
Syconycteris australis	New Guinea	18							0.484	0.263 – 0.725	0.484	11	I	Winkelmann et al. 2000

CHAPTER 3

Eco-physiological responses of fruit bats to intra-seasonal food resource fluctuations in African savanna ecosystems

Abstract

Strong fluctuations in resource availability in highly seasonal environments may induce behavioural changes in foragers, such as in fruit bats in savanna landscapes. Fluctuations in food abundance potentially drive a variety of eco-physiological responses in frugivorous bats, including changes in body condition, activity budgets, diets and foraging areas. However, most previous studies have focused on the Neo-tropics, and on inter-seasonal variations in food abundance; very little is known about frugivore response to food resource fluctuations within the same season, especially in Africa.

Using the straw-coloured fruit bat (*Eidolon helvum*) as a case study, we aimed to investigate if intra-seasonal fluctuations in food availability in a savanna ecosystem caused significant responses in the ecology and physiology of fruit bats. We concurrently studied food resource availability, colony size, bat activity budget and spatio-temporal movement patterns, and bat body condition during the mono-modal wet season in Ouagadougou, Burkina Faso.

Food availability was markedly different in the early (food high) and later (food low) stages of the wet season, with different composition of dominant food species during each period. Bats opportunistically shifted diets to capitalize on different food resources as they became dominant in the landscape within the same season. Colony size correlated positively with food availability, showing a two-fold decrease with increasing food scarcity.

Body condition declined significantly during periods of food scarcity. Overall, intra-seasonal fluctuations in food resources were markedly different, and appeared to cause significant changes in body condition and foraging time budgets, but not in distance and area use. Although bats were equally active at night in both food periods, they spent more time foraging and commuting during food low; however, night-time roosting duration was not different for the two periods. Travel time away from day roost was lower during food high, but travel distance was similar for the two food periods. The space use in core and foraging areas did not differ in the two periods.

We report for the first time the ability of *E. helvum* to relocate to new day roosts as solitary individuals. Individual excursions last for 1 – 6 consecutive nights before returning to the main colony during periods of food scarcity. We also report for the first time that the highly gregarious, central-foraging *E. helvum* can spend time as solitary individuals at day roosts in foraging areas far away from colonies, apparently in response to food scarcity.

These findings provide additional evidence that (1) fruit bats may adapt their foraging movement patterns and diets within a single wet season in the savannah; similar changes were previously observed between seasons in the forest ecosystem; (2) the super-abundant production of shea and fig fruits in the savannah ecosystem may be an important factor in the annual northwards migration of *E. helvum* from the southern coastal forests in West Africa, thereby confirming the tight ecological inter-dependence of fruit trees and their seed dispersal via fruit bats.

Keywords: *Eidolon helvum*; seasonality; food availability; foraging; activity budget; body condition; home range.

3.1 Introduction

The ability of animals to make eco-physiological responses to seasonal fluctuations in in their environments has been demonstrated across several taxa in seasonal ecosystems in the tropics, ranging from birds (Kitamura et al., 2002); bats (Heithaus et al., 1975); (Marshall and William, 2009; Thies and Kalko, 2004; Ramos Pereira et al., 2010); monkeys (Wallace, 2005) to elephants (Osborn, 2004; Campos-Arceiz and Blake, 2011).

Activity budgeting in animals, such as foraging behaviour, is believed to be influenced by factors such as climatic conditions, food resource availability, predation risk, and the animal's physical condition and reproductive status. These factors are considered major selective forces on decision-making by foraging animals (e.g. Lima and Dill, 1990; Suarez, 2014). Fluctuations in fruit availability in seasonal environments potentially drives eco-physiological responses in frugivorous bats, including activity rates (Aguiar and Marinho-Filho, 2004), body condition (Fleming, 1988), and diet (Bernard, 2002); (Bobrowiec and Cunha, 2010).

The Guinea and Sudan savannas of West Africa are characterized by a mono-modal rainfall pattern during which most fleshy fruit trees species utilized by bats produce huge amounts of fruits in the wet season (Devineau, 1999); (Oni et al., 2013). However, very little is known about food availability patterns for frugivores such as fruit bats within this wet season.

Despite strong indications that the annual migration of Africa's most abundant mammal species, the Straw-coloured fruit bat (*Eidolon helvum*) from the forest to savanna biome may be driven by a wet-season surplus of food resources in the savanna (Thomas, 1983; Richter and Cumming, 2006; Richter and Cumming, 2008; Fahr et al., 2015), no conclusive evidence has been documented yet. Even less is known about the fruiting patterns and consequent food availability, and the eco-physiological response of Old World fruit bats to environmental changes within the peak fruiting seasons in the savanna of Africa (see Richter and Cumming, 2008; Abedi-Lartey et al. 2016, in press). The distinct fluctuations in the fruit species and the abundance of fruit production in the wet season of a savannah ecosystem offered an opportunity to investigate the influence of food availability on fruit bat numbers, activity and physiology.

During the unimodal rainy season in the savannah belt of West Africa, our study species, the straw-coloured fruit bat, *Eidolon helvum*, migrate northwards in large numbers from their breeding grounds in the southern rainforests, apparently in response to climatic factors and seasonal changes in resource availability(Huggel-Wolf and Huggel-Wolf, 1965; Thomas, 1983; Richter and Cumming, 2008). It is suggested that a high amplitude of the seasonal fluctuations in fruit abundance in the savanna creates a wet-season rich surplus of food compared to the forest ecosystem (Thomas, 1983; Richter and Cumming, 2006; Richter and Cumming, 2008). However, the spatio-temporal pattern of food resources associated with a given bat colony in Africa has been documented only in a savanna ecosystem in Kasanka National Park in Zambia (Richter and Cumming, 2006) and forest ecosystem in Ghana (Abedi-Lartey et al, 2016, in press).

During the single wet season (June - September) in Burkina Faso there is a huge increase in fruiting of bat food, notably Shea (*Vitellaria paradoxa*) and figs (*Ficus* spp.) (Devineau, 1999). Previous studies (Fahr et al., 2015; Abedi-Lartey *et al*, 2016 in press) in Ghana showed that *E. helvum* exhibited marked differences in movement patterns during the wet and dry seasons within and between landscapes. Although these studies provided further evidence that African fruit bats track and respond to fluctuations in food levels between seasons and landscapes, the has been no conclusive evidence that a similar fluctuation in movement patterns occurred within the same season. Therefore, we expected that the foraging activity of *E. helvum* would vary with the two periods of high and low food levels within the same wet season of the savannah ecosystem as pertains in the landscape around Ouagadougou, Burkina Faso. If such intra-season movements could be confirmed, this would have important consequences for our understanding and assessment of the role of fruit bats for the distribution of seed and thus their role as ecosystem service agents. Whenever fruit bats change their movement patterns from a central-place roosting system to a roaming system, they will connect more different types of landscapes and thereby distribute seeds more widely across the African landscapes.

Our aim was to as assess the eco-physiological response of African fruit bats to a marked temporal fluctuation in food availability within the same season and landscape in an Afro-tropical savanna ecosystem. We sought to quantify for *E. helvum* during the single rainy season: (1) food resources levels; (2) response of bat body condition to food availability; (3) spatio-temporal patterns of movement and foraging activity and (4) home range sizes. We expected that *E. helvum* would (1) forage over cumulatively longer distances and times during period of food scarcity; (2) exploit different food types prevailing during each food abundance period; (3) utilize larger home ranges during period of food scarcity.

3.2 Methods

3.2.1 Study area

The study area was the landscape in and around the city of Ouagadougou, Burkina. The *E. helvum* colony (12°23'51.95"N, 1°29'21.36"W) was located within the Parc Urbain Bangr-Weoogo protected area in central Ouagadougou, capital of national Burkina Faso, West Africa. Ouagadougou is located in the dry Sudan savanna biome, at an altitude of around 300m above sea level. The climate is typical of the Sudan savanna zone, with both rain-fall and temperatures peaking once a year. Heavy rainfall (>1.3 mm min^{-1}) is frequent in June and July (Devineau, 1999), and annual precipitation is 600mm-1000mm, with evapotranspiration rates of 1700mm -2000mm. The wet season has an average of 66 rainy days in April-October, with peaks in August. The hottest month, April, records daily temperatures of >40° C, while December-February are the coldest months of the year with minimum temperatures down to 16° C at night (Virmani et al., 1980; INSD, 2006). From November to April, the climate is particularly dry and dusty and the wind regime is principally determined by the desert wind ('harmattan') blowing southwards from the Sahara. Windy days, when the average daily wind speed is >2 ms^{-1}, are particularly frequent in January and February; days with strong gusts of >16 $\text{ms}^{-1}$for short periods, occur from May-October and are particularly frequent in June and July (Devineau, 1999). The vegetation is an agro-pastoral ecosystem dominated *Poaceae, Fabaceae, Cyperaceae, Euphorbiaceae, Malvaceae, Mimosaceae, Asteraceae, Convolvulaceae, Rubiaceae* and *Caesalpiniaceae* (Madsen et al., 2003). The landscape is characterized by a steadily increasing agricultural land use involving a selective protection of trees in the field, such as *Bombax costatum, Parka biglobosa*, and *Vitellaria paradoxa* (Gijsbers et al., 1994).

3.2.2 Seasonality of food phenology and colony size

We defined food availability as an index (Food Phenology Index) of fruit bat food (flowers and fleshy-fruit) species that are flowering and/or fruiting in a given month, and that may be available for exploitation by *E. helvum*. Our method attempts to quantify food availability in terms of the relative proportion of fruiting trees of different species bearing ripe fruit that may be accessed by foraging bats. It is intended as an approximation of potential, rather than actual, abundance of bat food resources at a given time. The consistent use of the same method in space and time as well as the indices derived thereof allows for a comparison of relative food levels that the bats can potentially access. We calculated monthly FPI for all monitored tree species, and produced line plots and heat maps for visualisation of monthly patterns.

In order to assess the annual cycle of colony size, we monitored the size of *E. helvum* colony in Ouagadougou once a month from January 2013 - December 2014, as part of a long-term pan-African monitoring programme initiated in 2008 (Hayman et al., 2012a; Fahr et al., 2015). Trained observers estimated the number of bats roosting in a cluster, followed by the number of clusters on each major branch, until all roost trees of the colony were covered. Estimation methods are detailed in (Hayman et al., 2012a; Fahr et al., 2015). Monthly estimates were pooled for the two years to calculate the mean number of bats per month at the site. A colony of Gambian epauletted fruit bats (*Epomorphorus gambianus*) also shared the site, exhibiting similar day roosting habits but on roosting trees different from *E. helvum*.

Eidolon helvum foraged on fruit and flower resources of woody plants. We expected the fruiting and flowering of these food resources to fluctuate in accordance with the general phenological patterns of the seasonal savanna ecosystem. Therefore, we concurrently monitored the flowering and fruiting phenology of bat fruit trees species within Ouagadougou and its suburbs at the same times as the colony size monitoring, following methods detailed in Abedi-Lartey *et al*., (2016). We established four approximately 3 km long transects (two within and two outside) in Ouagadougou (Appendix 3A). We monitored trees reported in the literature (Ayensu, 1974; Marshall, 1985; Fahr et al., 2015; Abedi-Lartey et al, (2016).; J. Fahr unpublished data) and/or confirmed by local people, ground-truthing of our own tracking data to be foraged by fruit bats in the savanna landscape. We monitored 320 individual trees from 15 species and 10 families, located within approximately 50 m of transects. Fruiting and flowering phenology status of each tree was assessed on a scale of 0–5 (0: no flower/fruit, 5: > 50% drying or falling flowers/fruits) (see Devineau, 1999); the raw values were re-scaled to 0 = 0%, 1 = 5%, 2 = 30%, 3 = 75%, 4 = 100% and 5 = 25% to approximate the proportion of a tree crown bearing ripe fruits/flowers (Abedi-Lartey et al 2015). We estimated Food Phenology Index (FPI) (Abedi-Lartey et al 2016) for each month as a proxy for bat food resource availability. FPI was calculated as the ratio of the mean monthly score of all monitored tree species and the maximum score that could be theoretically reached in the landscape; monthly values were plotted as annual cycles of food phenology. We then plotted heatmaps of FPI to assess the monthly pattern each food tree species and to highlight the core plant species that may be potentially available for exploitation by the bats. Food phenology scores are detailed in Appendix 3B.

3.2.3 Bat capture and tracking

Our initial observations indicated that fleshy-fruited tree species foraged by bats fruited heavily during the wet season (June-October) in the Ouagadougou landscape. Generally, fruiting was particularly abundant in first half of the season, with a relative decline in the second half. We, therefore, carried out our fieldwork in August-September 2014 (“food low”) and June-July 2013 (“food high”) to coincide with these low and high fruiting periods, respectively.

Bats were captured with canopy mist nets (Fahr and Kalko, 2011; Ayensu, 1974; Marshall, 1985; Fahr et al., 2015; Abedi-Lartey et al, 2016). We captured bats as they returned from foraging at dawn

(03:00 h-06:00 h) or at dusk when flying out to forage (18:00 h-19:00 h). We measured bat body mass (g) with Pesola® spring balance, and forearm length (mm) with Vernier calipers. We tracked five bats over 24 nights in 2013, and eight bats over 28 nights in 2014 with GPS loggers (e-obs, Munich, Germany, mass: 24 g; (see Appendix 3C; original tracking data are available in www.movebank.org). We used only adult males with body mass >270 g and in good body condition to avoid the potential influence of loggers on immature, or pregnant/lactating females. Loggers were attached to bats by sewing onto Y-shaped collars made from soft goat leather, and closed with degradable suture thread (Safil® absorbable suture, B. Braun Melsungen AG, Germany), following Fahr et al, 2015, Abedi-Lartey et al, 2016.

The mean mass of logger and collar was 9.5 ± 0.5 g in 2013 and 9.3 ± 0.6 g, in 2014. Tracking data were acquired from five (body mass 266±11.9 g) and eight (body mass 275.6 ± 21.5 g) adult males in 2013 and 2014, respectively. The combined logger-and-collar mass of 9.3–9.5% of the bats' body mass, was slightly above the recommended mass (Aldridge and Brigham, 1988b) but falls within the 5–10% range recommended by (O'Mara et al., 2014). Animal handling protocols conformed with requirements of (Sikes and Gannon, 2011) and the Ghana Forestry Commission.

Bats were tracked between 18:00 – 06:00 with logger settings as in Fahr *et al*. 2015 and Abedi-Lartey et al. (2016). The GPS loggers were programmed to record locations, 3-axial acceleration data, flight speed and height (logger IDs and settings are detailed in Appendix 3B). Acceleration data were collected all day at intervals of 15 s per minute at a byte count of 1188 (56.23 Hz), on x-axis (left-right), y-axis (backward-forward) and z-axis (up-down). GPS-on times were 18:10-06:00 and 17:59 - 06:01, during which acceleration-informed fixes were taken: fixes every 1800 s until the bat started flying, then switched to fixes every 150 s. GPS- and associated acceleration data from deployed loggers were downloaded with e-obs basestations at day roosts for up to two weeks after tracking commenced.

3.2.4 Bat body condition and diet

Optimal body condition in bats should be a balance between nutritional needs and the mortality risks of flying with energy reserves. A low condition indicates an inability to maintain such optimal condition, and may affect a bat's eco-physiology (Smythe, 1986; Hamilton and Barclay, 1998; Charles-Dominique, 2009; Ramos Pereira et al., 2010).

To assess if the bats' body condition changed with the intra-seasonal fluctuations in food levels, we calculated a body condition index (BCI) as body mass divided by forearm length (Pearce et al., 2008; Reynolds et al., 2009; Ramos Pereira et al., 2010; Jonasson and Willis, 2011; Jonasson and Willis, 2011) as proxy for the bats' true body condition. To avoid statistical bias arising from immaturity, pregnancy or lactation (Ramos Pereira et al., 2010) we used only adult males in estimating bat body condition.

Fruit bats forage on the leaves, flowers and fruits of a wide variety of tree species (e.g. Marshall, 1985; Fleming and Heithaus, 1986; Wiles and Fujita, 1992; Richter and Cumming, 2006; Marshall and William, 2009; Nakamoto et al., 2007a; Kunz et al., 2011). From our initial literature search and personal observations, the Ouagadougou landscape exhibited marked spatio-temporal patterns of fruiting/flowering across the year and even within the wet season. We, therefore, expected a corresponding shift in diet and change in body condition during the two food periods. To assess this, we visited most bat foraging sites from the GPS-tracks to verify the species and fruiting phenology status of foraging trees. We further searched feeding roosts at or around fruiting food trees to verify fruit consumption by bats, evidenced by partly eaten fruit (bite marks) and ejecta pellets (bat palate imprints) (Fahr et al., 2015; Abedi-Lartey *et al.*, 2016).

3.2.5 Spatio-temporal bat activity

Bat activity budgets and movement patterns are essential to understanding the energy expenditure requirements to meet their physiological needs (Ramos Pereira et al., 2010). We expected travel distance to, and size of, foraging areas to increase during periods of food scarcity (see Fahr et al., 2015), when intraspecific competition should deplete food resources closer to the bat colony. We therefore quantified the spatio-temporal changes in *E. helvum* behaviour during the food availability periods as follows:

3.2.5.1 Activity budget estimation

Because flight in bats is an energetically-demanding activity (Speakman et al., 2003; Ramos Pereira et al., 2010), we expected foraging activity to reduce with food scarcity (Ramos Pereira et al., 2010; Fahr et al., 2015. In order to estimate bat activity budget, we first classified acceleration bursts from the GPG loggers (also see Section 2.3 above) during night-time (18:00 – 06:00 h; UTC = local time in Burkina Faso) into ‘flying’ and ‘non-flying’ bat movement categories, using an algorithm developed in R 3.2.2 (R Development Core Team, 2015), following Abedi-Lartey *et al.* (2016). We analysed separately for daytime (06:00 – 18:00 h), night-time, and over 24 hours per bat. Bat activity was estimated as the percentage of time bats were categorized as “flying”, and compared for the two food periods.

To assess spatio-temporal patterns of bat night-time behaviour between consecutive day roosts, we next classified (following (Fahr et al., 2015); Abedi-Lartey *et al.*, 2016) all GPS-points into three categories: ‘roosting’ (points in the immediate vicinity of day roosts, usually the bat colony), ‘foraging’ (clustered points around food trees), and ‘commuting’ (points connecting ‘day roost’ and ‘foraging’ areas). The duration of bat commuting, foraging and rooting each night, and the distances moved during these activities, were then calculated as the cumulative distance flown per night per bat as straight lines connecting all GPS points from the last point when a bat leaves a day roost at the beginning of the night, to the first point when it arrives at the subsequent day roost. The maximum foraging area used per night by a bat was calculated as the net distance and the time from day's roost to the most distant GPS point classified as foraging. To avoid potential biases, we excluded the first day of bat deployment from the time and distance estimates if deployment occurred after 18:00 h of that night. We then calculated the percentage of time and distances and compared their relative values for the two intra-seasonal food periods.

3.2.5.2 Home range estimation

We estimated bat space use as the home range covered per bat per night. We estimated utilization distributions (UDs) per bat per night. We used the dynamic Bivariate Gaussian Bridge (dBGB) model (Kranstauber et al., 2014), of the "move" package in R Version 3.2.3 (R Development Core Team, 2015), because it improves accuracy of estimated animal space use estimates in comparison with widely-adopted models such as the Brownian Bridge Movement Model (BBMM). We computed core area as 50% UD and foraging area as both 90% UD contour (Börger et al., 2006); (Fahr et al., 2015)) as well as the more commonly used 95% UD contour.

3.2.5.3 Day roosting behaviour

Preliminary observations indicated that bats could spend some day roosts at locations different from the previous day. We therefore identified the location of each day roost after bat deployment to determine if bats spent day roosts on consecutive days. Such day roosts were any of the following: (1) the same as the previous day roost, (2) at a different colony from the previous day, or (3) a solitary day roosting tree located in a foraging area.

3.2.6 Data analysis

All spatial and statistical analyses were done in R Version 3.2.3 (R Development Core Team, 2015). Data are reported as means ± standard deviation for the number of individuals (*n*), unless otherwise stated. The significance of differences was tested with two-tailed Mann-Whitney-U tests, with significance level set at 0.05. Spatial data were viewed in Google Earth Pro (Google Inc., Mountain View, CA, USA) version 7.1.1.1580 (beta) and analysed with R Version 3.2.3 (R Development Core Team, 2015), in UTM coordinates (UTM zone 30N, WGS84). All reported times are expressed as UTC. Box plots are represented as, from bottom to top: one standard deviation (s.d.) below the mean, lower quartile, median, upper quartile and one s.d. above the mean.

3.3 Results

3.3.1 Changes in food availability and colony size

Mean monthly range of the Food Phenology Index for pooled food resources (Fig. 3.1) showed bimodal peaks in January and September, with troughs in April and November. The species composition showed that the dominant bat food during high food period (June-July) were shea (*V. paradoxa),* marula *(Lannea microcarpa)* and neem *(A. indica).* In the low food period (August-September), distributions shifted to neem and figs *(Ficus iteophylla, Ficus platyphyla* and *Ficus gnaphalocarpa).* Colony size peaked at 67,177 individuals and 37,725 individuals at food high and food low, respectively.

The tracking data and public enquiries revealed three new colonies at outside Ouagadougou: (1) Rourè Sacred Grove (12° 12.041'N, 1° 54.237'W) village approx. 39 km to the southwest, Tenkodogo (11° 47.095'N, 0° 22.830'W) approx. 140 km to the southeast, and (3) Goudrin (11° 53.272'N, 1° 25.685'W), approx. 55 km to the south. Their population size and patterns of reported/observed bat movement interactions suggest that these may serve as satellites to the major colony in Ouagadougou.

Monthly colony size was positively correlated with rainfall ($r = 0.48, P = 0.12$) and food availability ($r = 0.14, P = 0.67$), but negatively with temperature ($r = -0.044, P = 0.90$). For food species availability, correlation with colony size was strongest with *V. paradoxa* ($r = 0.62, P = 0.03$) followed by *Ficus* spp. ($r = 0.50, P = 0.11$); on the contrary, availability of other food species was negatively correlated with colony size ($r = -0.24, P = 0.45$).

3.3.2 Changes in bat body condition and diet

Body Condition Indices (Fig. 3.2) were 2.31 ± 0.23 (range 1.74 - 2.83, median 2.32, n = 29 bats) and 1.81 ± 0.36 (range 1.19 - 2.67, median 1.75, n = 42 bats) for food high and food low, respectively. This represents about 30% drop in body condition over just a few weeks after depletion of *V. paradoxa*. The difference was significant (Mann–Whitney *U*: $P < 0.001$).

The dominant food species foraged by bats in both food periods (Table 3.1) was *V. paradoxa.* However, different other species were also consumed in each food period: *Lannea microcarpa* and Ficus *microcarpa* in food high and *Ficus gnaphalocarpa* in food low. Bats foraged in farms and forest patches dominated by the fruits on which they forage during each period of the wet season, although we did not quantify tree species composition and distribution at foraging site in this study. Even when feeding roosts were different, ejecta pellets and fruit remains were of the dominant fruit species in the vicinity.

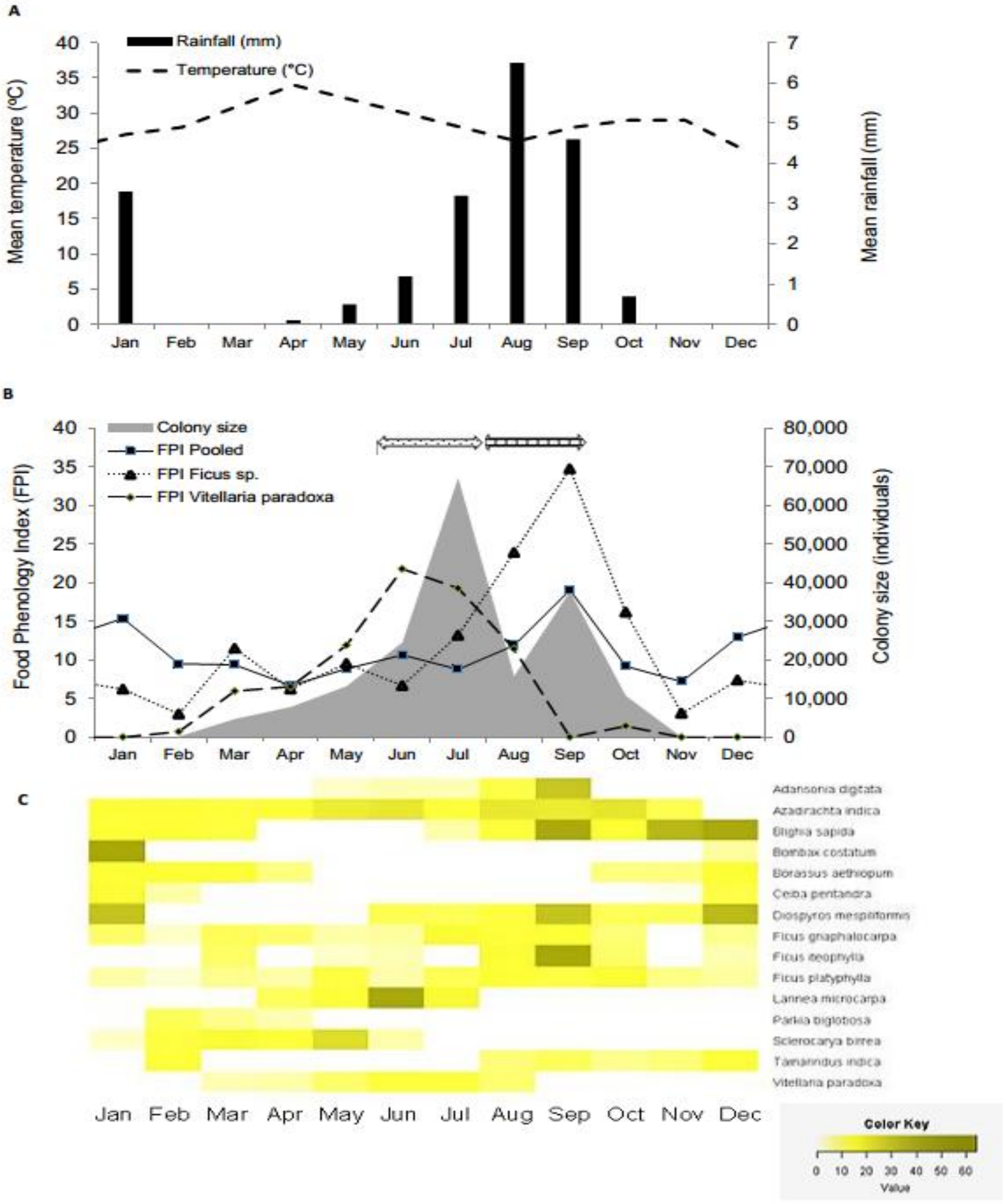


Fig. 3.1. Short-term monthly fluctuations in (A) weather, (B) food availability index (line plots) and colony size (area plot), and (C) heatmap of food availability for *E. helvum* from August 2013 to September 2014 in Ouagadougou, Burkina Faso. Weather is shown as mean monthly rainfall (line) and temperature (bars). Food availability is shown as Food Phenology Indices (line plots), with colony size represented by area plot. Heatmap represents monthly FPI values from low (white) to high (dark-grey).

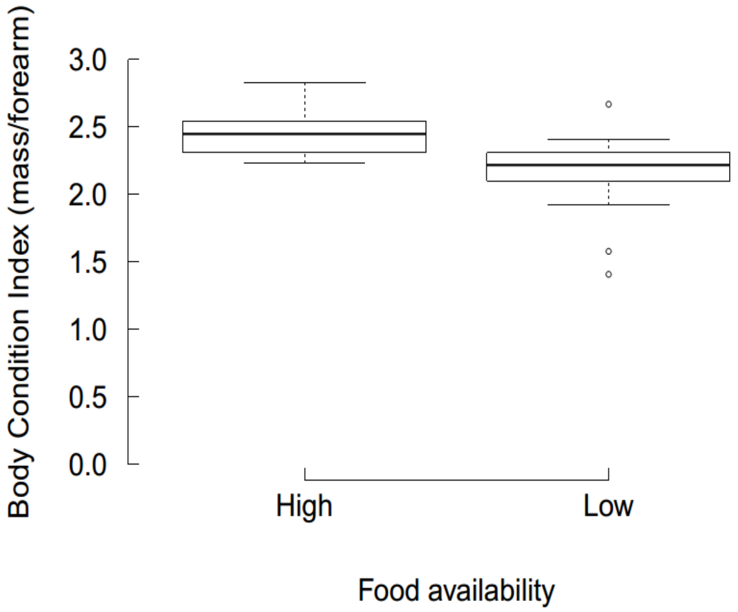


Fig. 3.2. Body Condition Index of adult male bats at high and low food levels. Asterisks represent outliers. Difference was significant (*P*<0.001).

Table 3.1 Summary of fruit species consumed by E. helvum in the food high and food low periods of the wet season in the landscape of Ouagadougou, Burkina Faso (food high: n = 9 bats; food low: n = 4 bats).

Food period	Food tree species	n° of trees	% diet
Food high	*V. paradoxa*	70	83.33
	L. microcarpa	11	13.10
	F. microcarpa	2	2.38
	A. indica	1	1.19
	Total	**84**	**100.00**
Food low	*V. paradoxa*	15	45.45
	F. gnaphalocarpa	9	27.27
	A. indica	6	18.18
	L. microcarpa	2	6.06
	S. birrea	1	3.03
	Total	**33**	**100.00**

3.3.3 Changes in bat activity

3.3.3.1 Bat activity budget

Bat activity budgets (Table 3.2) were 0.4 ± 0.4 % (range = 0-1.5, n = days = 21, bats = 6) in the daytime and 9.3 ± 6.3 % (range = 2.1-25.3, n = nights = 18, bats = 6) at night during food high. For food low, active periods were 0.4 ± 0.7 (range = 0-2.4, n = days = 22, bats = 5) in daytime and 11.8 ± 8.5 at night (range = 2.4-34.8, n = days = 18, bats = 5). Over a 24 h period, activity budgets were 4.2

± 3.4 % (range = 0-13, n = days = 21, bats = 5) and 5.1 ± 4.5 (range = 0-18.3, n = days = 22, bats = 5) for food high and food low, respectively. Only the daytime activity budgets were different (Mann–Whitney *U*: *P* < 0.05).

Table 3.2 Summary of activity budget of tracked *E. helvum* during the food high vs. food low periods in the wet season of Ouagadougou, Burkina Faso, based on GPS-logger acceleration data (food high: n = 6 bats; food low: n = 5 bats). Bold letter indicates significant difference.

	Activity	Food high	Food low	Mann-Whitney U	*P*
Daytime	n° of acc. bursts	719 ± 1	729 ± 46		
	average range	716-720	704-933		
	% active	0. 47 ± 0.44	0. 39 ± 0.70	307	**0.0355**
Night-time	n° of acc. bursts	714 ± 4	719 ± 1		
	average range	710-725	715-720		
	% active	9.28± 6.28	11.82 ± 8.52	131	0.3389
24 h	n° of acc. bursts	1331 ± 256	1318 ± 268		
	average range	717-1443	704-1452		
	% active	4.17 ± 3.40	5.12 ± 4.52	211	0.6354

3.3.3.2 Foraging time and distances

Overall, bats engaged in less foraging and roosting and more roosting activities in the high food period; commuting activity, however, was similar for in both periods (Fig. 3.3). Foraging activity budget were 43.7 ± 13.9 % (range = 20.0-73.0 %; median = 45.0 %; n = 27 nights) and 69.0 ± 19.5 % (range = 42.0-100 %; median = 68.5 %; n = 22 nights) for food high and food low, respectively. The difference in foraging activity was significant (Mann–Whitney *U*: *P* < 0.001). Commuting activity budget was 15.8 ± 8.1 % (range = 4.0-42.0 %; median = 14.0 %; n = 27 nights) food high and 34.0 ± 36.7 % (range = 6.0-100 %; median = 15.5 %; n = 22 nights) for food low. The difference in commuting activity was not significant (Mann–Whitney *U*: *P* = 0.5201). Roosting activity budget were 43.3 ± 15.5 % (range = 8.0-69.0 %; median = 43.0 %; n = 27 nights) and 39.6 ± 33.3 % (range = 10.0-100 %; median = 27.0 %; n = 22 nights) for food high and food low, respectively. The difference in roosting activity was significant (Mann–Whitney *U*: *P* < 0.05).

In both periods, foraging activity started soon after departure from day roosts, and rapidly rose to a peak around midnight, with a more gradual decline towards dawn. However, peak foraging during the high food period lagged behind that of low food period by about one hour.

Mean time of bat departure from day roosts (Fig. 3.4A) was 18:51 h (range 18:00 – 20:27 h, n = 18 nights) in the high food period and at 19:28 h (range 19:00 – 20:26 h, n = 18 nights) in the low food period each night. Departure time after sunset were 54.9 ± 24.1 min (range = 26.5-112.8 min) and 21.8 ± 26.6 min (range = -21.0-93.0 min) for food high and food low, respectively.

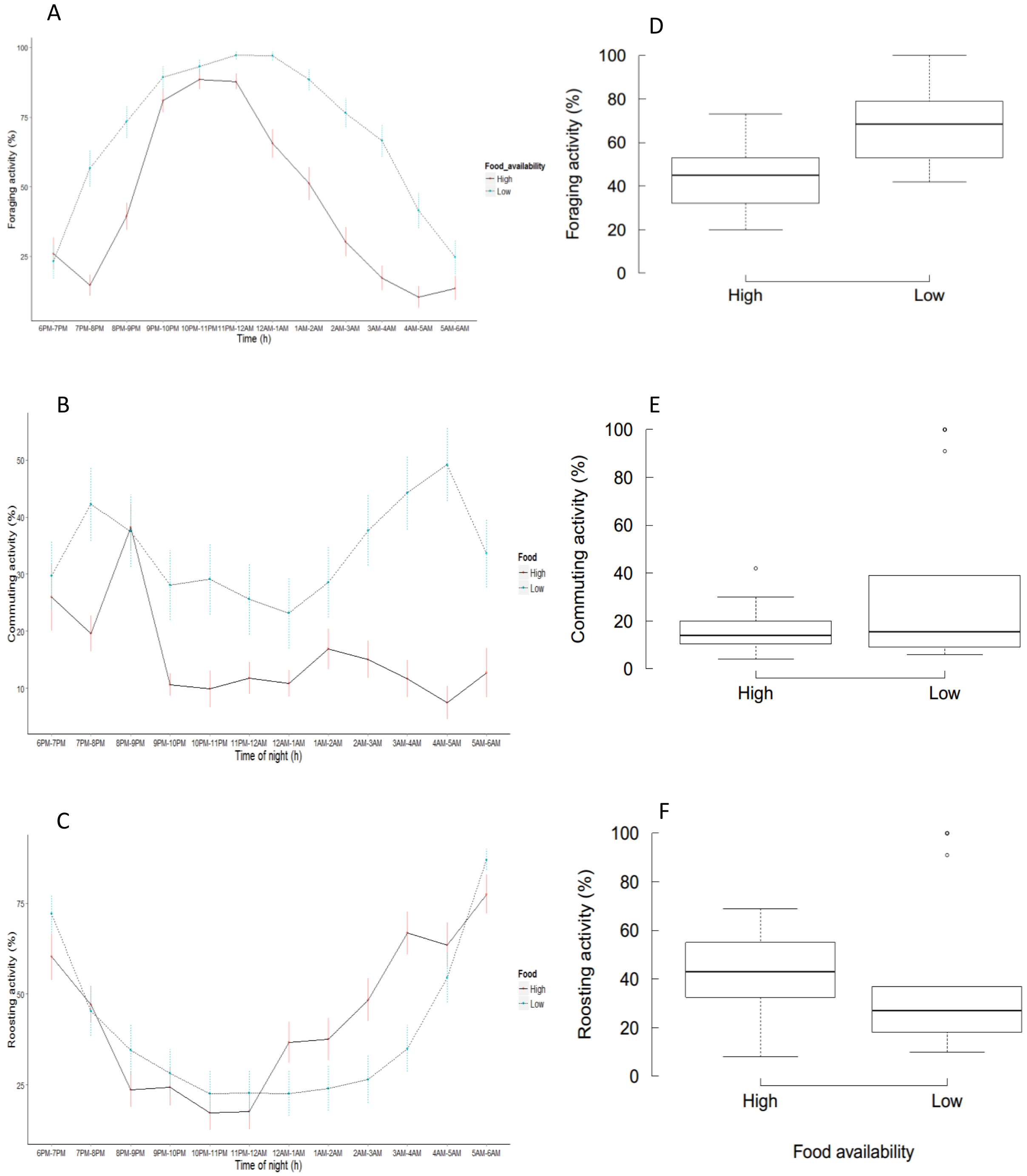


Fig. 3.3. Variation in nigh-time bat activity during high and low food levels in the rainy season in Ouagadougou, Burkina Faso. Line plots represent hourly variation (mean ± CI percentage time spent active per hour) in foraging (A), commuting (B) and roosting (C) activity. Boxplots represent night-time variations in foraging (D), commuting (E) and roosting (F) activity. The intra-seasonal differences were significant for foraging ($P < 0.001$) and roosting ($P < 0.05$).

Mean time of bat arrival at day roosts after a night out (Fig. 3.4B) was 04:44 h (range 03:10 – 05:38 h, n = 18 nights) in the high food period and at 02:31 h (range 0:01 – 05:01 h, n = 17 nights) in the low food period each night. Arrival time after sunset were 200.2 ± 107.3 min (range = 41.5-345.4 min) and 70.7 ± 42.8 min (range = 17.4-165.0 min) for food high and food low, respectively. Differences for both departure and arrival times were significant (Mann–Whitney *U*: *P* < 0.001).

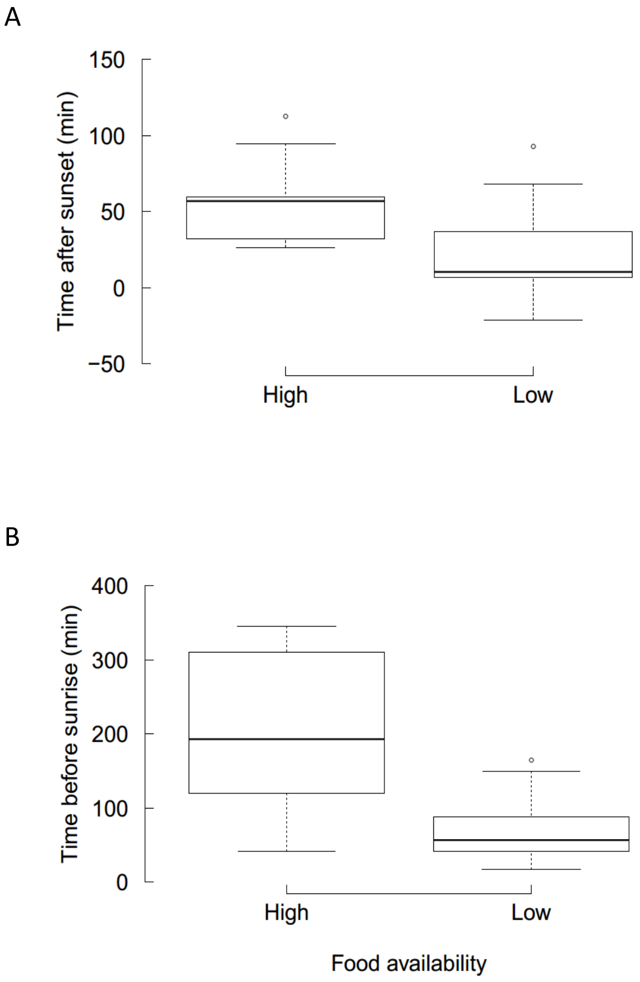


Fig. 3.4. Bat departure (A) and arrival (B) times from day roosts during high and low food levels in the rainy season in Ouagadougou, Burkina Faso.

Mean cumulative travel time spent each night away from a day roosts (Fig. 3.5A) were 6.9 ± 1.9 h (range 4.0 – 9.5 h, median = 7.1, n = 18 nights) and 9.9 ± 1.0 h (range 8.0 – 11.1 h, median = 10.1, n = 18 nights) for high and low food periods, respectively. The difference was significant (Mann–Whitney *U*: *P* < 0.001).

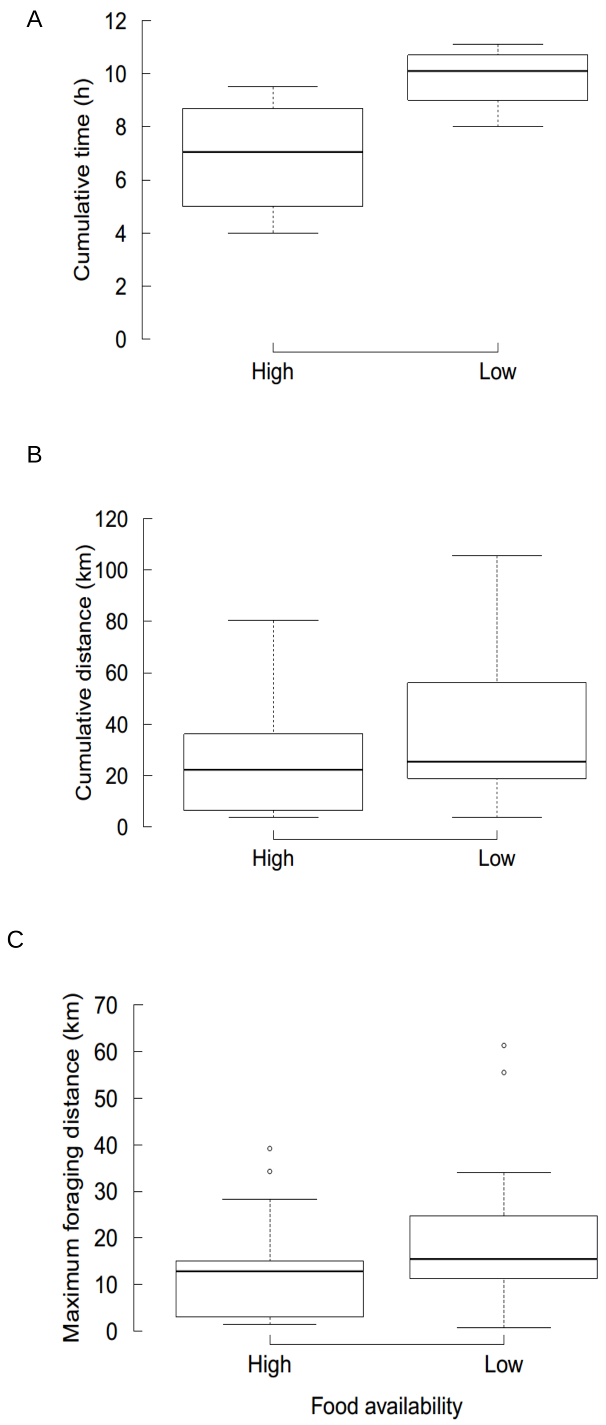


Fig. 3.5. Cumulative time (A) and distance (B), and maximum distance (C) to foraging sites travelled by *E. helvum* in the night between consecutive day roosts during periods of high and low food levels in the rainy season in Ouagadougou, Burkina Faso.

Mean cumulative travel distance away from a day roosts (Fig. 3.5B) were 26.63 ± 19.8 km (range 3.71 – 80.38 km, median = 22.3, n = 18 nights) and 35.84 ± 28.9 km (range 3.61 – 105.49 km, median = 25.5, n = 18 nights) for high and low food periods, respectively. The difference was not significant (Mann–Whitney *U*: *P* = 0.4572).

Mean maximum distances of foraging sites were 13.8 ± 10.9 km (range 1.4 – 39.2 km, median = 12.9, n = 18 nights) and 20.0 ± 16.6 km (range 0.8 – 61.3 km, median = 15.5, n = 18 nights) for high and low food periods, respectively. The difference was not significant (Mann–Whitney *U*: *P* = 0.3038).

3.3.4 Changes in space use

3.3.4.1 Foraging site area

During the high food period, bats exhibited a “star” foraging pattern each night, returning to the previous day’s roost at dawn. In contrast, bats tended to exhibit a higher tendency to use new day roosts on consecutive nights. Although they returned to the main colony after 1-6 days, they could spend daytimes as (probably) solitary individuals in small forest patches or large trees far away from the previous day’s roost. The maximum net distance bats moved from the main colony over several days during food low was 118 km, compared to 40 km during food high (Fig. 3.6)

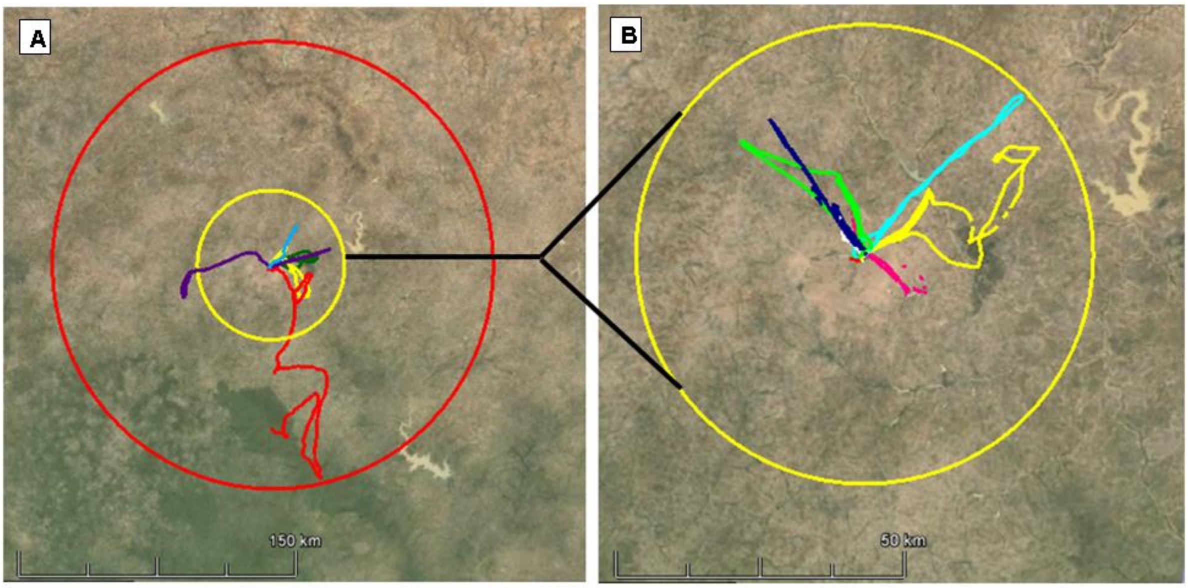


Fig. 6. GPS tracks of bat movement over at least one consecutive night from the *E. helvum* colony in Ouagadougou, Burkina Faso, during low (A) and high (B) levels of bat food availability. The red (radius = 118 km) and yellow (radius = 40 km) circles indicate maximum foraging extent from the colony at low and high food levels, respectively.

Mean of core area (50% UD) space use by bats each night (Fig. 7, Appendix 3D) were 0.63 ± 0.81 ha (range 0.01 - 3.39, median 0.31, n = 27 nights) and 0.76 ± 2.21 ha (range 0.01 - 10.68, median 0.10, n = 23 nights) during food high and food low periods, respectively. Mean foraging area (90% UD) was 5.54 ± 6.64 ha (range 0.03 - 27.85, median 2.17, n = 23 nights) for high food and 6.816 ± 12.28 ha (range 0.02 - 58.098, median 1.49, n = 23 nights) for low food periods. For the 95% UD, mean areas were 8.29±9.88 ha (range 0.05 - 40.65, median 3.13, n = 23 nights) and 10.07±17.17 ha (range 0.03 -

80.62, median 2.51, n = 23 nights) for high and low food periods, respectively. Differences were not significant (Mann-Whitney U– 50% UD: p = 0.062; 90% UD: p = 0.454; 95% UD: p = 0.579).

3.3.4.2 Day roosting sites

During periods of low food availability, bats spent 70% (n = 16 days), out of 23 day roosts, away from the colony at which they were deployed; 81% of these new day roosts were spent as solitary individuals. In high food availability, new day roosting sites were 19% (n = 5 days) out of 26 day roosts; 100% of these new days roosts were spent as solitary individuals.

3.4 Discussion

3.4.1 Intra-seasonal changes in food availability and colony size

This Chapter shows that although bat food (fruits/flowers) is generally available throughout the year, the major peaks occurred in the unimodal wet season, during the savanna phase of *E. helvum*'s migration cycle. In addition, there was a distinct intra-seasonal fluctuation in the levels and types of food available to fruit bats in the Ouagadougou landscape during this season. Different food types occur in each of these periods, with a general tendency for fruits that offered creamy pulp (shea, neem and marula) for ingestion by bats dominating in the high food period. In contrast, during the low food period fruits offered food mainly in liquid form (fig juice squeezed from ripe figs).

The results further show that bat food in the highly seasonal savannah ecosystem around Ouagadougou is ephemeral in time and space, with each species ripening massively over just a few weeks in the season. Besides, species composition and abundance of ripe fruits also fluctuate across the year and within the unimodal wet season when *E. helvum* colony is at its peak.

Fluctuations in colony size showed a positive correlation with food availability, especially with tree species dominant in fruit production during either food period. A two-fold reduction in colony size suggests that some bats might have dispersed to neighbouring colonies and/or spent more time at solitary day roosts with increasing food scarcity within the same season. This may be a behavioural response to intra-specific competition resulting from food scarcity.

3.4.2 Bat eco-physiological responses to food availability

As expected, I found bats spent longer time travelling each night during periods of food scarcity. However, food availability did not influence cumulative night travel distance. Bats were equally active over 24 h in both food availability periods. The difference in activity budget during daytime may be due to frequent disturbance from recreational activities accompanied by parties with loud music and hundreds of participants at the Ouagadougou colony site during the study period. Although I did not test for the relative nutritional values of food species, the temporal patterns of foraging activity show that *E. helvum* spent less time foraging and more time roosting during high food availability. This indicates that the bats might have acquired their nutritional needs faster with food offering more solid or creamy intake compared to the liquid intake gained from ripe figs, contributing to bats spending less time foraging during the season with high food availability (see Fig. 3.3). Similarly, it appears that a higher nutritional intake at high food level might have caused the significantly higher body condition in this food period. It is also possible, and eminently testable in the future, that figs are nutritionally sub-optimal to the shea/neem, leading to the differences in body condition. I suggest that this foraging behaviour within the same season may be considered as 'skimming off' super-abundant food sources during the period of high food availability; and 'scrounging' for depleted food sources during food scarcity.

The higher body condition in the food high period could also have benefited from bats foraging in earlier months. But both food resources and colony size were at the initial stages of increase (Fig. 3.1). Similarly, the significant body condition decline about a month after food and colony peaks suggests that bats readily respond to food increment and depletion, apparently via quality and/or quantity of nutritional intake. The absence of a difference in overall intra-seasonal activity budget suggests that the lower body condition during food scarcity could be due to lower nutritional values in the prevailing diet. The 30% drop in body condition over just a few weeks after depletion of *V. paradoxa* highlights the probable keystone role of this food species in the ecology of fruit bats. Incidentally, *V. paradoxa* is also of great socio-economic importance in the savanna, thereby making an additional case for its retention in the agro-ecosystem.

As expected, bats shifted diet between the two food availability periods, opportunistically exploiting the most abundant fleshy-fruited food types prevailing in each period within the season. The dominance of foraged trees species in the vicinity of food trees indicates that bats might target specific foraging grounds based on a combination of factors, such as memory from previous visits, information form conspecifics (e.g (Dechmann et al., 2013), (de Jong et al., 2013) .We did not explore factors related to foraging behaviour and landscape utilization, such as foraging site fidelity, possible group foraging (e.g.(de Jong et al., 2013)), characteristics of home range and foraging sites (e.g.(Weber et al., 2009), (Fahr et al., 2015), (Weber et al., 2015)). Nevertheless, while it is not yet known if *E. helvum* engages in group foraging, this study's result shows that as is typical for fruit bats, (Mickleburgh et al., 1992), its movements are not a random events, but are primarily driven by food resource availability, as also observed in the Golden-crowned flying fox (*Acerodon jubatus*) (Weber et al., 2015). Therefore, these and probably other factors to have also influenced the bats foraging behaviour in either food availability periods, and require further attention, The higher tendency for bats to shift day roosts (70%) during food low, as against 19% in food low suggest a behavioural adaptation to increased competition for depleted food resources from both cons-specifics and other frugivores. While all the solitary day roosting bats in the high food period retuned to the central colony at which they were deployed, , a relatively lower (81%) number of such solitary roosting occurred in the low food period (bats relocated to other colonies). Given that circumstances (e.g. weather, predation) at such foraging sites might be similar (not assessed under this study), this suggest that bats might have joined a colony in the remaining 19% to improve their chances of joining other bats at the colony to new food sites through foraging information-sharing (see (Dechmann et al., 2013)) during food scarcity. The solitary roosting indicate that once a food has been located at the end of the night foraging outing in periods of scarcity, it is intuitively more energy-efficient for the bat to stay in the vicinity than to risk a return flight back to the central colony. The lower body condition during food scarcity certainly supports an energy conservation scenario in such solitary roosting behaviour.

Bats departed day roosts earlier at dusk and retuned later at dawn when food resources were low. Since night-time activity budget was not different in the two food availability periods, the corresponding lower body condition in the low food period suggest that the net nutritional balance was lower during food scarcity, causing depletion of body fat reserves that had accumulated in the earlier food high.

Contrary to expectation, fluctuations in food availability within a single season did not affect *E. helvum* space use. Both core and foraging areas within the home range remained the same, as was the case in cumulative travel distance. In this context, the higher time budget during food scarcity, during which bats left day roosts earlier and arrive later, and also engaged in a higher foraging behaviour, suggests that bats adjusted their time budget to maximize their chances of meeting daily nutrition intake.

3.4.3 Management consideration

Considering the keystone role of *E. helvum* across different ecosystems in pan-African range (Fahr et al, 2015), it is imperative that management applications promote the food tree species dominating the periodic production of bat food across the year and within the wet season. Fortunately, the savanna ecosystem has been modified to meet anthropogenic land use needs (Madsen et al., 2003); (de Bie et al., 1998). What is urgently needed is to highlight and integrate the ecological needs of such useful species as fruit bats into agricultural and other land use policies and practices. I recommend that management practices that ensure the spatio-temporal diversity of fruit tree species (Lacki et al., 2007) must be encouraged and incorporated in the agro-pastoral practices of the savanna.

Acknowledgements

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3.5 Conclusions

The results show that although there is a general availability of bat food throughout the year, a few dominant fleshy fruit species that were available at temporally distinct periods during the wet season when *E. helvum* is present. Considering their role as main food sources during this time, these may be considered keystone food sources (see Wallace, 2004; Howe, 1993) during its migration into the savanna from the southern forests of West Africa. They therefore need to be promoted in the agro-pastoral land use system and in forested areas to enhance their contribution to the long-term survival of E. helvum and other fruit bats in the region. Because we tracked only males, we could not determine if the foraging behaviour is only limited to males or is representative also for the females of this species.

It appears that the eco-physiological response of *E. helvum* between wet and dry seasons is also mirrored within a single (wet) season in African landscapes. This study provides the strongest evidence to date, that similar to the situation in inter-seasonal resource fluctuations, intra-seasonal resource availability is also sufficiently marked to cause fruit bats such as *E. helvum* to make important eco-physiological adjustments. In addition, the type and abundance of food resources may be the ultimate driving forces in the spatio-temporal patterns of colony fluctuation during and between their annual migration cycle. We therefore recommend a concurrent investigation of the spatio-temporal pattern of food resource availability and colony size during the bi-directional migration between the forest and savanna biomes in Africa. Our study is limited to a single annual cycle, and therefore only offers a snap-shot of the potential influence of food availability on the eco-physiology of fruit bats. Longer-term studies are required to investigate how fruit bats respond eco-physiologically to environmental factors in different landscapes within forest and savanna ecosystems within their ranges. There is growing concerns about high variations and unpredictability of inter-annual weather patterns across Africa, as in there rest of the world, which is attributed to an evolving climate change. The spatio-temporal consequences for fruit bats, potentially via fluctuations in fruit production and weather, is unknown. Therefore, replicating this study concurrently in both the forest and savanna ecosystems, along the migration route of at least a single *E. helvum* population and over multiple years, would contribute to a better understanding of the potential effect of food resources and weather on bat migration and foraging patterns.

Supplementary material

Appendix 3A: Distribution of colony and phenology monitoring transects

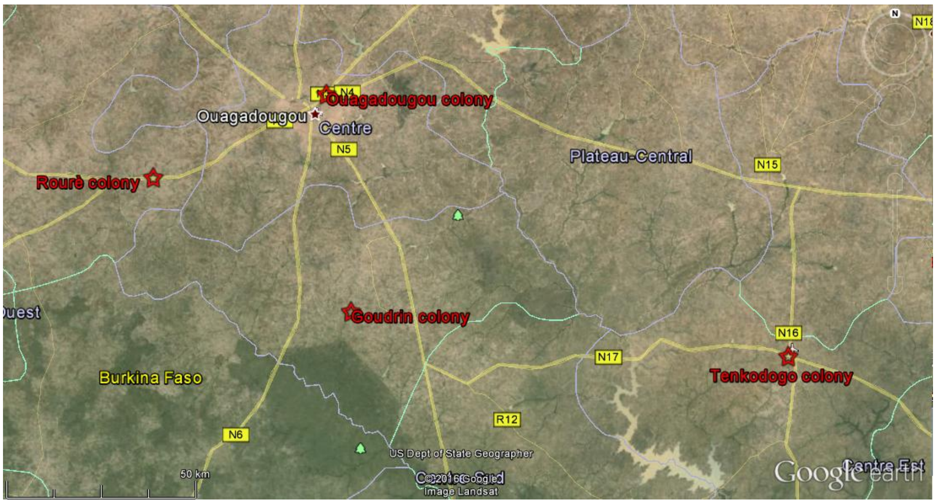

Fig. 3A.1 Distribution of *E. helvum* colonies used in population monitoring and GPS tracking (Ouagadougou) or identified (other) from tracked bats in Burkina Faso, West Africa.

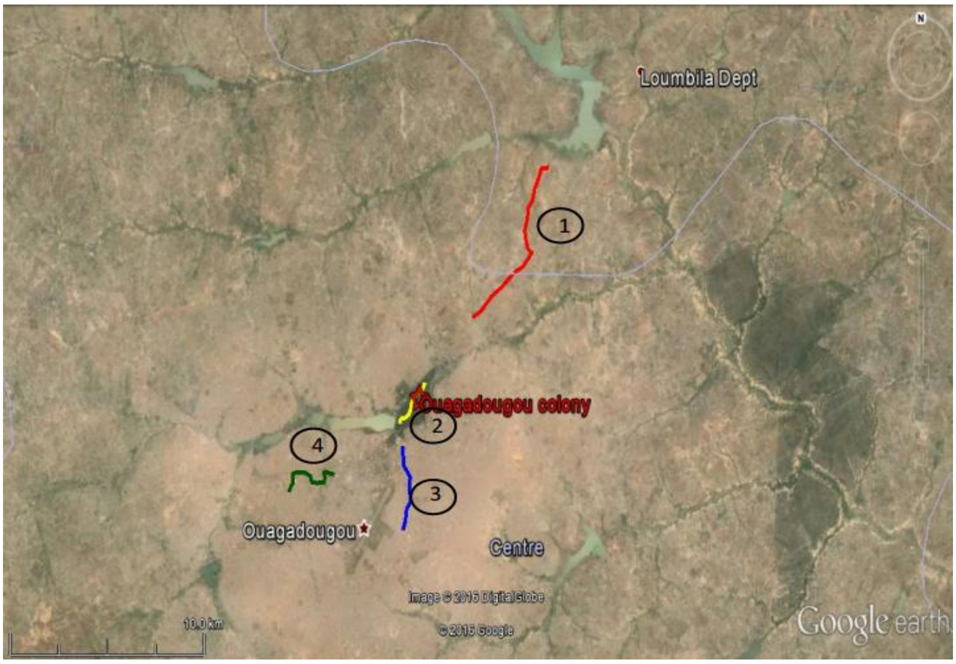

Fig. 3A.2 Distribution of transects used for monthly monitoring of food (fruiting and flowering) phenology in and around Ouagadougou, Burkina Faso, West Africa. Transect were located within the neighbourhoods of Loumbila (1), Parc Urbain (2), Zogona (3) and Stade du 4 Août (4).

Appendix 3B: Phenology monitoring species and scores

Table 3B.1 Fruit bat food species used in phenology monitoring in the landscape in and around Ouagadougou, Burkina Faso, West Africa.

No.	Plant species	Plant Family	Food type	Monitored in landscape				New record
				Loumbila	Parc Urbain	Zogona	Stade du 4 Août	
1	*Adansonia digitata*	Bombacaceae	flower	x	x		x	
2	*Azadirachta indica*	Meliaceae	flower/fruit	x	x	x	x	
3	*Blighia sapida*	Sapindaceae	fruit		x	x	x	x
4	*Bombax costatum*	Bombacaceae	flower	x	x			
5	*Borassus aethiopum*	Arecaceae	fruit		x		x	x
6	*Ceiba pentandra*	Bombacaceae	flower		x		x	
7	*Diospyros mespiliformis*	Ebenaceae	fruit	x	x			
8	*Ficus gnaphalocarpa*	Moraceae	fruit	x	x	x	x	
9	*Ficus iteophylla*	Moraceae	fruit	x		x		
10	*Ficus platyphylla*	Moraceae	fruit	x	x	x	x	
11	*Lannea microcarpa*	Anacardiaceae	fruit	x	x	x	x	x
12	*Parkia biglobosa*	Mimosaceae	flower	x		x	x	
13	*Sclerocarya birrea*	Anacardiaceae	fruit	x	x		x	x
14	*Tamarindus indica*	Fabaceae	fruit	x	x		x	x
15	*Vitellaria paradoxa*	Sapotaceae	flower/fruit	x	x	x		

Table 3B.2. Monthly Food Phenology Index (FPI) of fruit bat food species in the landscape in and around Ouagadougou, Burkina Faso, West Africa.

No.	**Plant species**	**No. individuals**	**Monthly FPI**												
			Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Species average FPI**
1	*Adansonia digitata*	5	0.00	0.00	0.00	0.00	5.00	6.00	6.00	15.00	40.00	0.00	0.00	0.00	***6.00***
2	*Azadirachta indica*	48	23.85	25.63	19.38	23.23	29.38	30.73	20.53	30.63	30.21	31.04	13.96	1.25	***23.32***
3	*Blighia sapida*	23	24.78	24.78	18.91	0.00	1.09	2.39	6.52	22.17	56.74	24.78	45.65	56.74	***23.71***
4	*Bombax costatum*	7	64.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.43	***5.98***
5	*Borassus aethiopum*	3	25.00	25.00	25.00	10.00	0.00	0.00	0.00	0.00	0.00	10.00	10.00	25.00	***10.83***
6	*Ceiba pentandra*	11	25.91	6.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.73	15.00	***4.20***
7	*Diospyros mespiliformis*	9	41.67	0.00	0.00	0.00	0.00	13.89	13.33	16.67	41.67	13.33	13.33	45.00	***16.57***
8	*Ficus gnaphalocarpa*	34	11.76	4.85	13.53	11.76	6.76	7.35	26.03	21.91	25.74	10.59	0.00	8.41	***12.39***
9	*Ficus iteophylla*	5	0.00	0.00	12.00	0.00	5.00	6.00	0.00	26.25	62.50	12.00	0.00	6.00	***10.81***
10	*Ficus platyphylla*	64	6.88	4.14	8.98	6.95	16.88	6.72	13.57	23.57	16.02	25.94	9.23	7.73	***12.22***
11	*Lannea microcarpa*	33	0.00	0.00	2.27	13.48	23.33	58.03	26.52	0.00	0.00	0.00	2.27	0.00	***10.49***
12	*Parkia biglobosa*	14	1.79	12.86	8.57	6.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***2.47***
13	*Sclerocarya birrea*	15	5.00	16.33	26.00	22.00	33.33	6.67	0.00	0.00	0.00	0.00	0.00	0.00	***9.11***
14	*Tamarindus indica*	7	0.00	21.43	0.00	0.00	0.00	0.00	0.00	10.71	12.86	8.57	10.71	21.43	***7.14***
15	*Vitellaria paradoxa*	42	0.00	0.71	5.95	6.55	11.90	21.79	19.29	11.43	0.00	1.43	0.00	0.00	***6.59***
	Monthly average FPI	***320***	***15.39***	***9.50***	***9.37***	***6.69***	***8.84***	***10.64***	***8.79***	***11.89***	***19.05***	***9.18***	***7.19***	***12.93***	

Table 3C1. GPS logger settings and body measurements of adult male *Eidolon helvum* tracked in 2013-2014 in Ouagadougou, Burkina Faso.

Tracking period	Bat #	Tracking year	# nights tracked	GPS-on time (day)	GPS fix intervals (s) [Acceleration-informed (resting vs. flying) initial/triggered]	Bat body mass (g)	Bat forearm length (mm)	Body Mass Index
Food Low	GPS 1617	2013	4	17:59-06:01	1800/150	265	118.3	2.24
	GPS1618	2013	5	17:59-06:01	1800/150	250	103.7	2.41
	GPS1619	2013	6	17:59-06:01	1800/150	275	118.9	2.31
	GPS 1624	2013	5	17:59-06:01	1800/150	280	124.8	2.24
	GPS 1621	2013	3	17:59-06:01	1800/150	260	124.0	2.10
Food High	GPS 1347	2014	1	17:59-06:01	1800/150	260	120.6	2.16
	GPS 1427	2014	1	17:59-06:01	1800/150	260	115.7	2.25
	GPS 3967	2014	3	17:59-06:01	1800/150	280	121.4	2.31
	GPS 3969	2014	4	17:59-06:01	1800/150	270	116.6	2.32
	GPS 3970	2014	4	17:59-06:01	1800/150	300	122.4	2.45
	GPS 3971	2014	6	17:59-06:01	1800/150	315	121.3	2.60
	GPS 3972	2014	2	17:59-06:01	1800/150	255	122.0	2.09
	GPS 3973	2014	5	17:59-06:01	1800/150	265	123.7	2.14

Table 3B.3. Food tree species confirmed to be consumed by GPS-tracked *E. helvum* at foraging sites in the landscape around Ouagadougou, Burkina Faso, West Africa.

Food period	Food tree species	n° of trees	% diet
Food high	*V.paradoxa*	70	83.33
	L.microcarpa	11	13.10
	F.microcarpa	2	2.38
	A. indica	1	1.19
	Total	**84**	**100.00**
Food low	*V.paradoxa*	15	45.45
	F.gnaphalocarpa	9	27.27
	A.indica	6	18.18
	L.microcarpa	2	6.06
	S.birrea	1	3.03
	Total	**33**	**100.00**

Size of core areas (50% UD) and foraging areas (home ranges; 90% UD, 95% UD) of bats tracked in periods of high vs. low food availability during the wet season. UD were estimated with dynamic Brownian Gaussian Bridge model.

Food period	Bat #	Night #	50% UD (ha)	90% UD (ha)	95% UD (ha)
High	OgT1347	1	0.01	0.37	1.76
	OgT1347	2	0.01	0.03	0.05
	OgT1427	1	0.02	0.21	0.29
	OgT3967	1	0.23	1.94	2.82
	OgT3967	2	0.20	1.08	1.62
	OgT3967	3	0.12	2.75	4.74
	OgT3969	1	0.05	0.21	0.30
	OgT3969	2	0.17	1.02	1.51
	OgT3969	3	0.55	17.78	28.35
	OgT3969	4	0.26	1.50	2.14
	OgT3970	1	0.18	1.14	1.72
	OgT3970	2	0.19	1.14	1.67
	OgT3970	3	0.57	3.37	4.72
	OgT3970	4	0.35	1.64	2.34

	OgT3971	1	1.06	5.63	7.70
	OgT3971	2	2.63	12.96	17.31
	OgT3971	3	0.77	9.36	13.85
	OgT3971	4	0.26	3.11	4.60
	OgT3971	5	1.26	10.30	15.04
	OgT3971	6	0.31	2.17	3.13
	OgT3972	1	0.11	1.75	2.86
	OgT3972	2	3.39	27.85	40.65
	OgT3973	1	1.35	8.07	11.55
	OgT3973	2	0.53	6.33	9.97
	OgT3973	3	0.31	2.11	3.13
	OgT3973	4	1.47	13.16	20.32
	OgT3973	5	0.67	12.54	19.81
n	8	27			
mean			0.63	5.54	8.29
median			0.31	2.17	3.13
Low	OgT1617	1	0.43	9.24	14.25
	OgT1617	2	0.29	10.54	17.26
	OgT1617	3	0.12	2.75	4.74
	OgT1617	4	0.14	13.76	21.39
	OgT1618	1	0.01	0.02	0.03
	OgT1618	2	1.06	14.38	20.93
	OgT1618	3	0.04	0.22	0.32
	OgT1618	4	0.05	0.24	0.36
	OgT1618	5	0.05	0.19	0.25
	OgT1619	1	0.09	1.49	2.51
	OgT1619	2	0.10	0.73	1.27
	OgT1619	3	0.06	0.40	0.70
	OgT1619	4	10.68	58.09	80.62
	OgT1619	5	0.06	0.31	0.58

	OgT1619	6	0.05	0.71	1.13
	OgT1621	1	0.04	0.22	0.37
	OgT1621	2	0.27	11.66	18.06
	OgT1621	3	0.44	10.59	16.20
	OgT1624	1	1.76	10.28	14.09
	OgT1624	2	1.28	6.80	9.18
	OgT1624	3	0.17	1.57	2.50
	OgT1624	4	0.09	1.36	3.10
	OgT1624	5	0.10	0.99	1.75
n	5	23			
mean			0.76	6.81	10.07
median			0.10	1.49	2.51

CHAPTER 4

Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape.

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Abstract

On-going fragmentation of tropical forest ecosystems and associated depletion of seed dispersers threatens the long-term survival of animal-dispersed plants. These threats do not only affect biodiversity and species abundance, but ultimately ecosystem functions and services. Thus, seed dispersers such as the straw-coloured fruit bat, *E. helvum*, which traverse long distances across fragmented landscapes, are particularly important for maintaining genetic connectivity and colonizing new sites for plant species. Using high-resolution GPS-tracking of movements, field observations and gut retention experiments, we quantify dispersal distances for small- and large-seeded fruits foraged by *E. helvum* during periods of colony population low (wet season) and high (dry season) in an urban and a rural landscape in the forest zone of Ghana. Gut passage time averaged 116 min (range 4-1143 min), comparable to other fruit bats. Movements were generally longer in the urban than in the rural landscape and also longer in the dry than in the wet season. As majority of seeds are dispersed only to feeding roosts, median dispersal distances were similar for both large (42-67 m) and small (42-65 m) seeds. However, small seeds were potentially dispersed up to 75.4 km, four times further than previous maximum distance estimated for a similar-sized frugivore. Maximum seed dispersal distances for small seeds were almost twice as long in the rural (49.7 km) compared to the urban (31.2 km) landscape. Within the urban landscape, estimated dispersal distances for small seeds were three times longer during the dry season (75.4 km) compared to the wet season (22.8 km); in contrast, distances in the rural landscape were three times longer in the wet season (67 km) compared to the dry season (24.4). Dispersal distance during the dry season (551 m) was almost twice that in the wet season (319 m). We found no influence of food availability patterns on dispersal distances. The maximum likelihood for seed dispersal beyond feeding roosts (mean distance from food tree 263 m) was 4.7%. Small seeds were dispersed over even longer distances, > 500 and >1000 m, with a likelihood of 3.0 % and 2.3 % respectively. Our data show that *E. helvum* retains ingested seeds for very long periods and traverses large distances, probably making it the most important currently known animal seed disperser in tropical Africa. We suggest *E. helvum* is important for ecosystem functioning and urge its conservation.

Keywords: *Eidolon;* fragmentation; foraging; gut passage; seasonality

4.1 Introduction

Seed dispersal affects many key aspects of plant biology, including vegetation structure and composition as well as the diversity and dynamics of plant communities and meta-populations. It influences spatial structure and dynamics of plant populations because it establishes the initial spatial template of offspring dispersion (Cain et al., 2000; Russo et al., 2006)]. Seed dispersal offers plants a chance to (1) escape from density- or distance-dependent seed and seedling mortality to sites with a relatively high probability of survival, and (2) colonize suitable sites unpredictable in space and time (Wenny, 2001). In linking the reproductive cycle of adult plants with the establishment of their offspring, seed dispersal is also the main vector of gene flow among patches in fragmented landscapes apart from pollination (Bacles et al., 2006; Ozawa et al., 2013). Animals that feed on fleshy-fruited plants play a pivotal role in the dispersal of such plant species: through their movement and foraging behaviour by influencing dispersal quantity, distance, direction, and quality (Schupp, 1993; Wang and Smith, 2002; Westcott et al., 2005).

On-going fragmentation, degradation and loss of tropical forest ecosystems impede plants and animals in their ability to move among habitat patches (Foley et al., 2005; Mayaux et al., 2005; Bacles et al., 2006). Effective seed dispersal by zoochorous vectors in fragmented landscapes requires that the dispersers traverse relatively long distances, often across matrix habitat, to favourable sites for seed establishment (Roberts et al., 2012). However, many seed dispersers throughout the tropics, including birds, mammals and reptiles, are facing local extinction from hunting and habitat loss. These threats do not only cause the loss and reduction in abundance of these animal species, but also affect the plants they disperse (Roberts et al., 2012). Therefore, animals capable of long-distance seed dispersal are particularly important in fragmented landscapes for maintaining gene flow and colonizing new sites for plants. Volant seed dispersers, such as birds and fruit bats, capable of utilizing fragmented landscapes are thus receiving increasing attention to quantify their seed disperser services (e.g. Westcott et al., 2005; Tsoar et al., 2010; Kays et al., 2011). However, many seed dispersers that eat fleshy fruit do not cover large distances and/or leave the forest cover; even those that do usually drop most seeds under the source tree, or quickly defecate ingested seeds after feeding (Alcantara et al., 2000; Taylor et al., 2000; Van Houtan et al., 2007). Thus, animal vectors covering large distances and retaining seeds for long periods are particularly important for maintaining connectivity among plant populations in fragmented landscapes (Nathan, 2006; Damschen et al., 2008). Fruit bats are prime candidates in this regard, as their ability to fly over long distances during foraging makes them particularly suited for this role (Shilton et al., 1999; Richter and Cumming, 2006; Tsoar et al., 2010). In addition, they are important pollinators and seed dispersers for a large number of plants of high ecological and economic value (Fujita and Tuttle, 1991; Muscarella and Fleming, 2007; Kunz et al., 2011; Seltzer et al., 2013; Scanlon et al., 2014).

Currently, estimated seed dispersal distances by animals vary from a few meters to approximately 20 km (Willson, 1993; Cain et al., 2000; Russo et al., 2006; Nathan et al., 2008; Kays et al., 2011). Nathan *et al* (2008) recommend the use of a question-specific distance threshold to distinguish between seeds dispersed close to a parent tree (Short-Distance Dispersal, SDD) and those dispersed farther away (Long-Distance Dispersal, LDD), the latter usually defined as distances of more than 100 – 500 m (Foley et al., 2005; Russo et al., 2006; Nathan et al., 2008; Kays et al., 2011). Growing interest in LDD has been stimulated by recognition of its critical importance for nature and humankind. Effectively quantifying LDD promises an improved, quantitatively derived understanding of seed dispersal. However, quantifying seed dispersal has proven to be challenging largely because it is difficult to track individual seeds, and especially in the context of LDD, which often involves rare events driven by complex and highly stochastic processes that are hard to measure. Fortunately, growing improvements in telemetry, analytical methods and the incorporation of animal behaviour in the seed dispersal process offer opportunities to improve estimates of dispersal distance (e.g. Russo et al., 2006; Tsoar et al., 2010 ; Kays et al., 2011; Lenz et al., 2011).

Eidolon helvum (Kerr, 1792), the straw-coloured fruit bat, is a prime example of an animal disperser that could be particularly effective for seed dispersal and pollination of plants, especially in fragmented landscapes. This species congregates across tropical Africa in sometimes huge colonies such as the one in Kasanka National Park in Zambia, which seasonally hosts roughly ten million individuals (Richter and Cumming, 2006). Colonies in West Africa range from a few thousand to one million bats (Thomas, 1983; Hayman et al., 2012; Fahr et al., 2015). *Eidolon helvum* seasonally migrates for more than 2,000 km between forest and savanna biomes, likely in response to seasonal fluctuations in food availability (Thomas, 1983; Richter and Cumming, 2008; Ossa et al., 2012). On a daily basis, *E. helvum* flies up to 88 km from its colony to foraging areas (Fahr et al., 2015) and in the process potentially disperses seeds and pollen over both short and long distances. However, it is unknown how variations in movement patterns influence seed dispersal distances in different landscapes and seasons.

Our overall aim was the assessment of seed dispersal services provided by straw-coloured fruit bats in fragmented Afrotropical forest ecosystems. We chose *E. helvum* as a particularly mobile species, and because previous knowledge about foraging movements already indicated long but variable foraging distances (Fahr et al., 2015). In order to elucidate the role of *E. helvum* as an ecosystem service provider, we tested the influence of three variables on dispersal distances: 1) seed size: *E. helvum* feeds on a wide variety of fruit (e.g. Richter and Cumming, 2006; Webala et al., 2014), and large-seeded fruits are probably mainly shuttled to feeding perches near food trees, whereas small seeds can be ingested and dispersed much farther, potentially over the entire daily range of the disperser. 2) season: colonies fluctuate substantially in size over the course of a year (Richter and Cumming, 2006; Webala et al., 2014), and movement patterns have been shown to differ in parallel with large and small colony sizes (Fahr et al., 2015). We thus expected season to influence dispersal distances. 3) human land use: heavily deforested urban landscapes should offer a different spectrum (introduced and cultivated vs. native) and density of available food plants compared to rural landscapes, thus affecting foraging behaviours and resulting seed dispersal. We used high-resolution GPS-tracking of *E. helvum* movements combined with ground-truthing to determine food trees; feeding trials with fruits offered to short-term captive *E. helvum* to asses gut passage time (GPT); and monthly counts of an urban (Accra) and a rural (Kibi) colony in the forest zone of Ghana. We also monitored food phenology within each landscape to establish seasonal trends. We used these data to model probability distributions of bat movements and GPT as to ultimately estimate differences in seed dispersal distance kernels, the probability of seed deposition at a given distance from parent tree (Nathan et al., 2008) foraged by the bats.

Our study showed that *E. helvum* potentially dispersed seeds over a modest median of 42-67 m, and up to a maximum of 75.4 km, which is four times farther than the previously highest maximum distance of 20 km estimated for the Egyptian fruit bat (*Rousettus aegyptiacus*) (Tsoar et al., 2010). Overall seed dispersal distances estimates varied by season and landscape.. We provide evidence that a combination of long gut retention times with the ability to traverse large open spaces and the large diversity of food plants multiplied by the sheer numbers of this bat species presents *E. helvum* as probably one of the most important seed dispersers in tropical Africa. This disperser role is especially relevant in landscapes heavily influenced by humans through habitat fragmentation and/or frugivore decimation.

4.1.1 Study sites

We collected all data between August 2009 and October 2014 around two colonies of *Eidolon helvum* in the forest zone of southern Ghana. The urban colony was located on the grounds of the 37 Military Hospital in Accra (5°35'11''N, 0°11'02''W; see also Appendix 4A). The rural colony (Kibi; Appendix 4A) was composed of sub-colonies at the local Royal Mausoleum at Kibi (6°09'54''N, 0°33'19''W), at the local sacred grove in Old Tafo-Akim (6°14'05''N, 0°23'38''W), and a raffia palm (*Raphia* spp.) swamp on the outskirts of Anyinam (6°23'38''N, 0°32'36''W).

The urban study area entails the city of Accra and surrounding settlements, forming a landscape from the Atlantic coastal plains northwards to the Akwapim Range (30 – 60 m a.s.l, with isolated hills up to 400 m). The bimodal climate has average monthly temperature ranges from 25 °C in March to 28 °C in August; annual rainfall averages 810 mm with major wet season from March-June, a minor wet season in September-October and a dry season July-August. Remnant patches (e.g. *Ceiba pentandra, Bombax* spp., *Antiaris* spp., and *Ficus* spp.) of previously more extensive coastal savanna forest (Hilton, 1966; Jenik and Hall, 1976) and closed-canopy forest (Hall and Swaine, 1976) are scattered in a landscape currently dominated by introduced trees, including *Azadirachta indica*, *Mangifera indica*, *Cassia* spp., *Carica papaya, Khaya anthotheca* and *Tectona grandis* (Campbell, 2004).

The rural study site at Kibi is part of the moist semi-deciduous forest zone of Ghana (Hall and Swaine, 1976), interspersed with various levels of degraded forests and farmlands, including plantations of *Theobroma cacao*. Emergent tree species include *Triplochiton scleroxylon*, *Milicia excelsa*, *Cola gigantea*, *Ceiba pentandra* and *Khaya ivorensis*. A prominent feature of the Kibi landscape is the Atewa mountain range, which peaks at 842 m a.s.l. and is characterized by closed forest cover, mostly within the Atewa Forest Reserve (McCullough et al., 2007). The climate shows the same bimodal patterns as in the Accra landscape, but with a higher annual rainfall of up to 1,600 mm, which peaks in May-July and September-November. Average monthly temperature is 24-29°C.

4.2 Methods

4.2.1 Seasonality of colony size and food resources

We monitored the size of both colonies once a month and during a single day. For this, trained observers walked through a colony and estimated the number of bats roosting in a cluster, then the number of clusters on each major branch, and continuing this way until all roost trees of the colony were covered. For a detailed description of methods see (Hayman et al., 2012; Fahr et al., 2015). We pooled monthly estimates for each colony across years and calculated the mean number of bats per month and site.

In addition, we monitored the flowering and fruiting phenology of tree species in the two landscapes. We monitored 807 individual trees from 33 species in the urban, and 173 individual trees from 27 species in the rural landscape. We established 3.5–4.5 km long transects (nine in urban and seven in rural) in representative land cover types across each landscape (Appendix 4A) to minimize the influence of local conditions on landscape-scale phenology. Monitored trees were located within 50 m of transects, and individuals of the same tree species along each transect were spaced at least 50 m apart. We confirmed bat usage of monitored tree species through local people, ground-truthing of our own tracking data and/or the literature (Ayensu, 1974; Rosevear, 1965; Marshall, 1985; Fahr et al., 2015; J. Fahr, unpublished data). We visited marked trees once each month to assess fruiting and flowering on a scale of 0–5 (0: no flower/fruit, 5: > 50% drying or falling flowers/fruits) (see Devineau, 1999; Roberts et al., 2012). These raw values were rescaled to 0 = 0%, 1 = 5%, 2 = 30%, 3 = 75%, 4 = 100% and 5 = 25% as a rough approximation of the proportion of a tree crown bearing ripe fruits/flowers. We calculated each month's Food Phenology Index (FPI) as the ratio between the mean monthly score of all monitored tree species and the maximum score that could be theoretically reached in each landscape; monthly values were then plotted as annual cycles of food phenology. Food phenology protocols and scores are detailed in Appendix 4B.

4.2.2 Bat movement tracking

The movement behaviour of animal dispersers is a key component of the seed dispersal process (Westcott et al., 2006; Nathan et al., 2008; Tsoar et al., 2010) as it influences how far a seed will be carried. We tracked bats in the urban landscape from 2009 to 2013, and in the rural landscape from 2011 to 2013 to quantify bat movements. We tracked bats between the dry season (January–March; period of high bat colony size) and wet season (August–October; period of low bat colony size) in both landscapes to assess the effect of seasonal variation in movement patterns on seed dispersal distances (see also Fahr et al., 2015. We captured bats with canopy mist nets (Fahr and Kalko, 2011) and a 10 m-high macro net (Rautenbach, 1986) as they returned from foraging at dawn (03:00 h-06:00 h), and kept them in soft cloth bags until processing. We fitted 54 and 37 adult male bats with GPS loggers (e-obs, Munich, Germany) at the Accra and Kibi colonies, respectively. However, we were able to retrieve suitable tracking data from 27 of these in Accra (body mass 272.9 ± 24.3 g) and 14 at Kibi (body mass 268.4 ± 14.1 g). The mean mass of logger plus collar was 21.0 ± 1.8 g and 24.8 ± 1.8 g, for Accra and Kibi. Logger mass was 8.6 ± 1.0% of the bats' body mass, above the recommended mass of 5% (Devineau, 1999) but less than the 10% threshold recommendation (see Amelon et al., 2009; O'Mara et al., 2014; see also Appendix 4C). Our animal handling protocols followed guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al., 2007); and requirements of the Ghana Wildlife Division, Forestry Commission (P.O. Box M239, Accra, Ghana; permit numbers FCWD/GH-01 24/08/09 and 02/02/11). We conducted these experiments despite surpassing the 5% weight rule because our previous captive and wild tests on logger attachment and size had not indicated negative effects on the flight and foraging performance of the large, male bats we investigated. We therefore felt that the benefit of knowing the ecosystem service function of fruit bats outweighs potential risks to individual bats.

We tracked bat movements during 18:00 – 06:00 with logger settings as in Fahr *et al*. (2015). The GPS loggers are capable of recording several types of data (e.g. GPS locations, 3-axial acceleration data and flight speed). Loggers were programmed according to regimes consecutively called Cohorts 1-4; logger IDs and settings are detailed in Appendix 4C.

Acceleration data were collected all day at intervals of 15 s per minute at a byte count of 1188 (56.23 Hz). Acceleration axes for all loggers were X = left-right, Y = backward-forward, and Z = up-down. Cohort 1 and 2 (2009) were programmed for delayed start at 06:00 on the morning following release. Cohort 1 collected GPS-fixes at a regular interval of 600 s during GPS on-times. Cohort 2 collected GPS-fixes at the same rate until the animal was moving at a speed of ≥ 500 ms^{-1}, after which they switched to a GPS-interval of 300 s. Cohort 3 (2011) and Cohort 4 (2012-2013) started data collection immediately at release of the animal; GPS-on times were 18:10-06:00 and 17:59-06:01. In addition, GPS-fixes for Cohort 3 and Cohort 4 were acceleration-informed. They collected fixes every 1800 s until the bat started flying, then switched to fixes every 300 s (Cohort 3) and 150 s (Cohort 4).

In 2009–2011, we attached loggers to bats by gluing (Sauer Hautkleber, Manfred Sauer GmbH, Lobbach, Germany) them to clipped dorsal fur below the shoulder blades (Fahr et al., 2015). Since many bats quickly lost their glued-on loggers, we switched to sewing the loggers onto Y-shaped collars made from soft goat leather, which were closed with degradable suture thread (Safil® absorbable suture, B. Braun Melsungen AG, Germany). This ensured that collars shed off without harming the bats (O’Mara et al., 2014). With both attachment methods, bats flew off without any apparent difficulty, and variation in flight distances and activity times showed no correlation with relative logger mass (data not shown). We downloaded GPS- and associated acceleration data from deployed loggers with e-obs basestations at day roosts for up to two weeks after tracking commenced.

4.2.3 Bat movement analyses

We estimated seed dispersal from a tree’s perspective and, therefore, used bat displacement distances from parent trees as starting points for modelling dispersal kernels. In our analyses, we focussed on seed dispersal by *E. helvum* beyond the crown of parent trees. Seeds small enough to be swallowed (‘small seeds’) are dispersed in two ways: Firstly, a fruit may be taken from a parent tree and its seeds deposited at feeding roosts in the form of *ejecta* (masticated and spat out) and/or *rejecta* (non-masticated fruit parts dropped during eating), and/or defecated at the feeding roost leading to short-distance dispersal (SDD) from a parent tree to a feeding roost. Secondly, seeds may be ingested at a parent tree or at a nearby feeding roost, and then defecated somewhere along the bat’s trajectory depending on the gut passage time. This would result in long-distance dispersal (LDD). The dispersal kernel for small seeds should incorporate both dispersal types. Seeds that are too large to be swallowed (‘large seeds’) will be only deposited as *ejecta* and *rejecta*, and thus not dispersed beyond feeding roosts.

We, therefore, distinguished between bat movements involving the displacement of (1) large seeds from food trees to nearby feeding roosts; and (2) small seeds carried to nearby feeding roosts and either ejected and deposited there, or ingested and deposited later. We first dissected bat behaviours related to SDD, i.e. movements between food trees and feeding roosts. For this, we classified all GPS-points into three categories based on their spatial context: ‘day roost’ (all points in the immediate vicinity of a colony), ‘foraging’ (clustered points around food trees), and ‘commuting’ (points connecting ‘day roost’ and ‘foraging’, that is when bats left and returned to the colony, and points connecting discrete foraging areas).

In a second step, we quantified dispersal distances between food trees and feeding roosts from GPS-points categorized as ‘foraging’. Since fruit bats are known to process and drop the vast majority of large as well as uningested small seeds under feeding roosts (e.g. (Hodgkison and Balding, 2003; Richter and Cumming, 2006; Tsoar et al., 2010), we reasoned that GPS-points in flight should be largely irrelevant for short-distance dispersal. We used the temporally corresponding acceleration bursts to assign the category ‘flying’ or ‘non-flying’ to each GPS-point. Given that the variance in ‘flying’ acceleration bursts was much higher than during other activities, we identified these categories by clustering the variances of the Y- and Z-axes of the acceleration bursts into two groups, corresponding to flying and non-flying. These analyses were done in R 3.1.2 (R Development Core Team, 2015; R-script will be made available upon publication of this manuscript). By subsequently excluding all points classified as flying, we maintained GPS-points within foraging areas where bats were either stationary or moving but not flying.

We used the GPS-tracks to visit most foraging clusters to identify food trees and their phenological status (bearing ripe fruits or flowering). We further searched these areas for feeding roosts, which were spotted by looking for partly eaten fruits (usually with bite marks) and ejecta pellets (usually with imprints of the palate). Where ground-truthing was impossible, e.g. due to inaccessible areas, we inferred food trees within foraging areas as the midpoint of those clusters of GPS-points that were first approached by bats after commuting flights. Next, we used a circular buffer with a radius of 22 m around the midpoint of both visited and inferred food trees (corresponding to the mean positional error of e-obs-loggers in forest areas; see (Kays et al., 2011), and filtered out all GPS-points except for each midpoint.

Ground-truthing data showed that 99% of feeding roosts were located ≤ 263 m from food trees. Short distance dispersal (SDD) was then determined by calculating linear distances between a food tree and each maintained GPS-point within a circular buffer of 263 m radius around this food tree.

We next tested observed displacement data for each season and in each landscape with probability distributions (normal, logistic, Cauchy, lognormal, exponential, Weibull, and gamma) using the “*fitdistrplus*” package Ver. 1.0-3 (Delignette-Muller and Dutang, 2015) in R (R Development Core Team, 2015) to derive their univariate distribution parameters based on the maximum-likelihood stochastic optimization. The model with the lowest Akaike Information Criterion (AIC) value was considered the best fit (details in Appendix 4D).

4.2.4 Estimation of gut passage times

Gut Passage Time (GPT) is usually determined by feeding experiments (Shilton et al., 1999; Westcott et al., 2005; Tsoar et al., 2010; Kays et al., 2011; Lenz et al., 2011) and then used to derive probability distributions of when ingested seeds are likely to be defecated. We determined GPT for small seeds by feeding 20 bats in February-March 2014 with figs (*Ficus mucoso, F. sur*, *F. trichopoda*), *Milicia excelsa*, and *Anthocleista nobilis*. We housed bats individually in three cages (100 x 50 x 200 cm) for on-site observations in the field. Our visual observations were assisted by time-lapse photographs of a Bushnell X-8 camera inserted at the top of each cage; a 5 min-photo interval was chosen for compatibility with the GPS-interval of the tracking data.

We expected GPT to be influenced by the medium in which seeds are consumed (Wahaj et al., 1998; Clauss et al., 2008). Our initial observations also indicated that *E. helvum* would only consume fresh, fully ripe fruits. Thus, and in contrast to previous studies e.g. (Shilton et al., 1999; Kays et al., 2011; Lenz et al., 2011), we used only fully ripe fruits collected from the field shortly before trials started. Captive bats were fed each night from 18:00 h to around 04:00 h when they appeared satiated and ceased eating. We then continued to observe them until the beginning of the next experiment at 18:00 the following evening.

We defined a feeding trial as the period during which at least three whole fruits were presented to a bat, at least one of which was eaten until feeding clearly stopped from apparent satiation. Thus each bat went through at least one trial per night, and trials were separated by intervals of at least one hour when they were engaged in other activities. Fruits in each feeding trial were coated and dyed with red, green or chartreuse fluorescent food dye (*Radiant Color NV, Houthalen, Belgium*). We observed the sequence of a bat’s interaction with a fruit by tracking the colour fruit, faeces, ejecta and uneaten fruit remains (rejecta) on the ground sheet from the series of photos. Ground sheets were removed after all fruits were eaten after each trial or at 6:00 the next morning. We then took additional photographs (Panasonic Lumix DMC-FZ47) to supplement the time-lapse photographs of the cage floor. Each morning after a feeding experiment, we visually cross-linked the ground-sheets and the photographs to match locations, colours and timing of faeces, ejecta and fruit remains as the location of fruit remains and ejecta was sometimes disturbed during removal of the sheet, but visual inspection was more reliable than photographs.

We subsequently estimated the amount of fruit consumed by subtracting the weight of its remains and ejecta from the original fruit weight. From the time-lapse photos, we defined GPT start time as the mid-point of the 5 min interval when a bat picked up a fruit to the 5 min interval during which all ejecta and/or rejecta for that fruit were detected on the ground sheet. GPT was then calculated as the time between this mid-point and the mid-point of the time band in which each defecation event associated with the fruit by colour was observed. After each trial, we fed bats with slices of papaya (*C. papaya)* or banana (*Musa* spp.) to serve as a marker for the end of defecation from that trial before starting the next trail for the same bat. Trials per bat ranged from 1-3 per night.

We next fitted the observed GPT data with probability distribution families, as in the displacement distance analysis above, choosing the model with the lowest AIC value (details in Appendix 4D). We then randomly drew 1,000 times from the best-fitted frequency distribution to draw GPT probability values according to the modelled frequency function, which was subsequently used in the modelling small seeds dispersal estimates below.

4.2.5 Seed dispersal kernel estimation

4.2.5.1 Large seeds

We use the best-fitting parametric distribution models (see above) of bat net displacement distances between food trees and their surrounding feeding roosts as the dispersal kernel distance models for large seeds by season and landscape. Dispersal estimates for the urban landscape were only for the wet season (which was also used as proxy for the urban landscape) because *E. helvum* foraged almost exclusively on the flowers of kapok (*Ceiba pentandra)* trees during the dry season there (see Fahr et al., 2015).

4.2.5.2 Small seeds

Small seeds were either dropped at feeding roosts (SDD) or ingested and defecated farther away (LDD) (Nathan et al., 2008; Tsoar et al., 2010). In order to derive a composite kernel density distribution for small-seeded fruits, we needed to combine the separate modelled distributions for ingested seeds and ejected seeds. We therefore used a mixed modelling approach to incorporate the two probability distribution (SDD and LDD) model components into a joint distribution model of small-seed dispersal for each landscape and season. The SDD distribution model component used was the same as described for the large-seed model above (i.e., a distribution model of non-ingested seeds deposited between the parent tree and nearby feeding trees). For the LDD model component, we estimated the probability distribution of distances at which an ingested seed was potentially deposited from a parent tree by: 1) randomly drawing 1,000 times *t* from the fitted GPT distribution above, and 2) selecting the distance *d* from the corresponding *t* from the distribution model of bat post-feeding net displacement distances. Our observation of faeces in the feeding trials, supported by literature (Hodgkison et al., 2003; Heer et al., 2010; McConkey et al., 2012) indicated that fruit bats selectively ingested about 5% of fig seeds and discarded the rest as ejecta/rejecta at feeding roosts. We therefore assigned weighting of 0.05 and 0.95 to the LDD and SDD distribution components, respectively. We then combined the separate SDD and LDD component distributions, with these weights, to estimate a mixed distribution for dispersal kernel distance of small seeds per landscape and season, using the *UnivarMixingDistribution* function of the *distr* package in R Ver. 3.2.3 (Ruckdeschel and Kohl, 2014).

We used 263 m (the 99th percentile of feeding roost distances from food trees; see displacement distance analysis above) to define LDD of small seeds, and therefore estimated the proportion of seeds dispersed beyond this distance. To make our finding comparable with seed dispersal estimates for bats and birds (e.g. Tsoar et al., 2010; Kays et al., 2011; Lenz et al., 2011), we additionally estimated the proportions of seeds dispersed beyond two distances (100 and 500 m). Differences between study sites and between seasons at each study site were tested for significance at 0.05 with two-sample Kolmogorov-Smirnov test (K-S). All statistical analyses were done with R Ver. 3.2.3 (R Development Core Team, 2015).

4.3 Results

4.3.1 Seasonality of colony size and food resources

The urban colony in Accra (Fig. 4.1) peaked during November-February (dry season) with 119,300 individuals (Nov. 2013), and had lowest numbers in June-July (wet season) with 3991 individuals (Jun. 2013). In the rural landscape of Kibi, peak numbers were reached in November 2013 (51,500) and lowest in June 2013 (523). Monthly colony sizes in Accra (mean 57,594 ± 67,624, median 33,265, n = 63 months) were consistently larger than in Kibi (mean 14,174 ± 11,303, median 13,487, n = 38 months). While fruit and flower phenology also showed some fluctuation in both landscapes, overall Food Phenology Index (FPI) did not seem to be correlated with colony cycles (Fig. 1). Corresponding heatmaps of FPI showing periods of relative occurrence of food plant species are provided in Appendix 4B.

4.2. Bat movement tracking

We downloaded useful tracking and acceleration data from about 50% of deployed loggers over 2-6 nights per individual bat. Successful loggers were from bats that retuned to colonies at which we made download attempts during each fieldwork period. For a list of tracked individuals and logger settings see Appendix 4C. All tracking data are deposited on Movebank.org (DOI available upon publication of the manuscript).

4.3.2 *Bat movement analyses*

Net displacement distances of bats from food trees (Fig. 4.2) were higher in the urban (range 1-87,726 m, median 1,678 m) than in the rural (range 1-75,751 m, median 954 m) landscape. Dry season distances were longer (urban landscape: range 1-87,726 m, median 13,252 m; rural landscape: range 1-75,751 m, median 933 m) than during wet seasons (urban landscape: range 1-43,589 m, median 330 m; rural landscape: range 1-70,924 m, median 979 m). All pairwise comparison of differences between sites and seasons were significant (two-sample Kolmogorov-Smirnov test, *P* < 0.001).

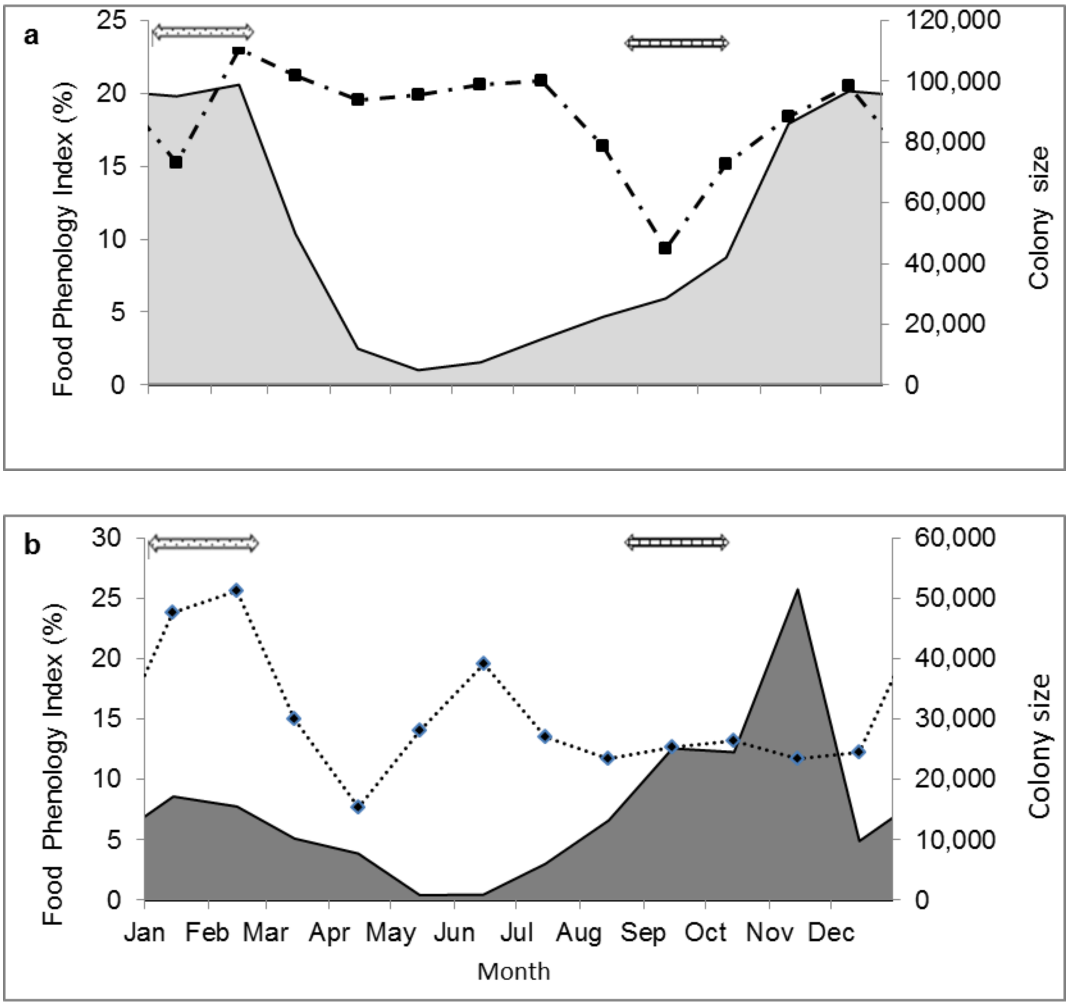

Fig. 4.1 Seasonal trends in bat food (line plots) and colony size (shaded area plots) at the (a) urban and (b) rural landscapes in the forest zone of southern Ghana. Food availability is indicated by Food Phenology Index, representing averaged proportion of fruiting plants known to be foraged by *E. helvum*. Fieldwork covered colony peaks to commencement of decline (⟺) and commencement of colony increase (⟺) to reflect colony size and landscape conditions that may influence bat movement patterns and ultimately seed dispersal potential.

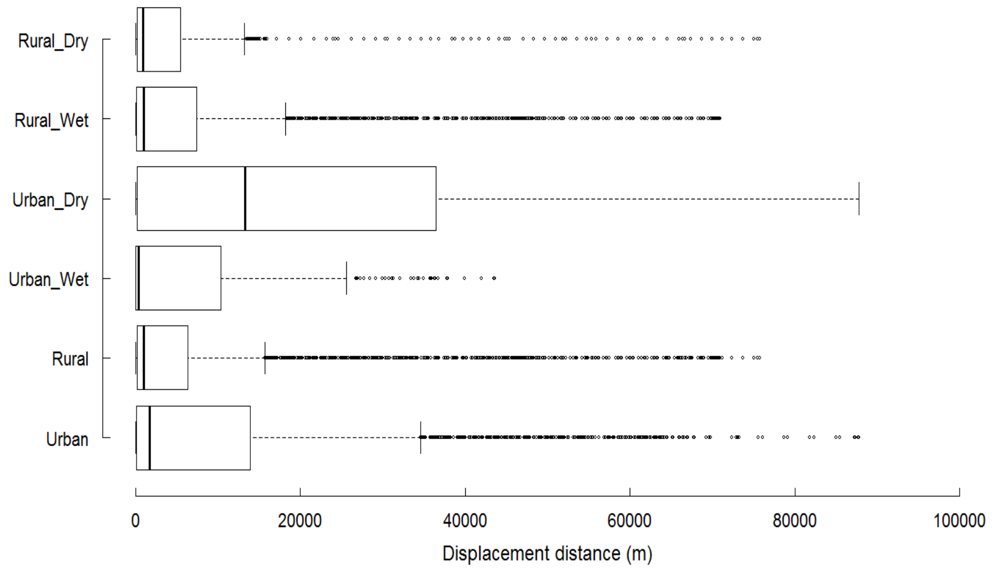

Fig. 4.2. Boxplots of estimated net displacement distances (meters) of GPS-tracked *E. helvum* after implied feeding during wet and dry seasons in urban and rural landscapes in the forest zone of southern Ghana. Boxplots represent, from left to right: one standard deviation (s.d.) below the mean, lower quartile, median, upper quartile and one standard deviation (s.d) above the mean; circles represent outliers. The maximum values represent bat's position at day roost subsequent to a night's outing, at which bats stayed until subsequent evening emergence.

4.3.3 Estimation of gut passage times

Mean GPT for small seeds was 116 ± 112 min (range 4 – 1,143 min, median 72 min, n = 112 fruits). The probability distribution (Fig. 4.3) was best-fitted by a lognormal with μ = 4.3138853 (meanlog) and σ = 0.8674429 (sdlog) (Appendix 4D).

4.3.4 Seed dispersal kernel estimation

4.3.4.1 Large seeds

Dispersal distance estimates for large seeds (Table 4.1, Fig. 4.4) were longer in the rural (range 9-532 m, median 56 m, n = 11 bats) than in the urban (range 8-179 m, median 42 m, n= 8 bats). In the rural landscape, distances were longer in the dry season (range 9-551 m, median 67 m, n = 4 bats) than in the wet (range 8-319 m, median 53 m, n = 7 bats). Pairwise comparisons of dispersal estimates showed that differences were significant (two-sample Kolmogorov-Smirnov tests, *P* < 0.001. The probability of large seeds being dispersed over long distances beyond 263 m (i.e. distance to feeding roost), 500 m, and 1,000 m from a food tree was 1.7%, 0.1% and 0.0%, respectively.

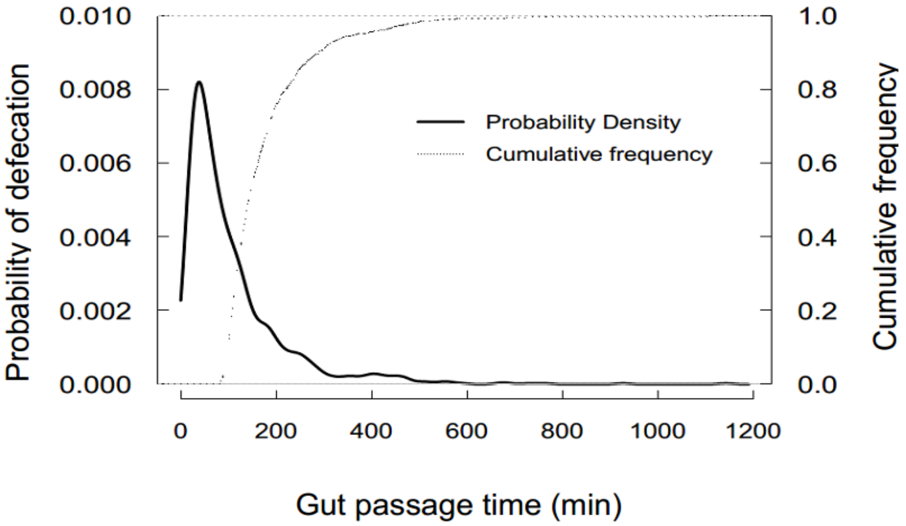

Fig. 4.3. Estimated probability (bold curve) and cumulative frequency (dotted curve) distribution of Gut Passage Times for small seeds ingested by captive *E. helvum*. Fruits were presented fresh and whole in field-based feeding experiments.

4.3.4.2 Small seeds

Estimated dispersal distance kernels for small seeds (Table 4.2, Fig. 4.5) was longer in the rural (range 7-49,650 m, median 55 m, n = 11 bats) than in the urban landscape (range 1-31,235 m, median 43 m, n = 16 bats) landscape. The difference was significant (K-S = 0.215, *P* < 0.001). In the urban landscape, distance was longer in the dry (range 0-75,443 m, median 42 m, n = 8 bats) than in the wet (range 4-22,779 m, median 43 m, n = 8 bats) season; the difference was, however, not significant (K-S = 0.031, *P* = 0.7226). The seasonal trend was reversed in the rural landscape, where dispersal distances were longer in the wet (range 9-67,044 m, median 52 m, n = 7 bats) than in the dry (range 3-24,374 m, median 65 m, n = 4 bats) season; the difference was significant (K-S = 0.155, *P* < 0.001). Probability of LDD for small seeds beyond 263, 500 and 1000 m from a food tree in the rural landscape were 4.7%, 3.0% and 2.3%, respectively; corresponding estimates for the urban landscape were 2.6%, 2.2% and 2.0%, respectively.

Table 4.1. Estimated distances for large-seed dispersal by *E. helvum* during wet and dry seasons in an urban and rural landscape in southern Ghana. The 263 m distance threshold was the 99th percentile of feeding roost distances from food source trees. No seed dispersal distances were estimated for the dry season in the urban landscape because bats foraged almost exclusively on flowers (*Ceiba pentandra*) during that period.

Site	Season	Seed dispersal distance (m)			Probability of seed dispersal (%)			
		Minimum	Median	Maximum	> 100	> 263	> 500	> 1000
Urban	Wet	8	42	179	2.5	0.0	0.0	0.0
	Dry	NA	NA	NA	NA	NA	NA	NA
Rural	Wet	8	53	319	11.3	0.2	0.0	0.0
	Dry	9	67	551	25.4	1.7	0.1	0.0
	Pooled	9	56	532	15.2	0.5	0.1	0.0

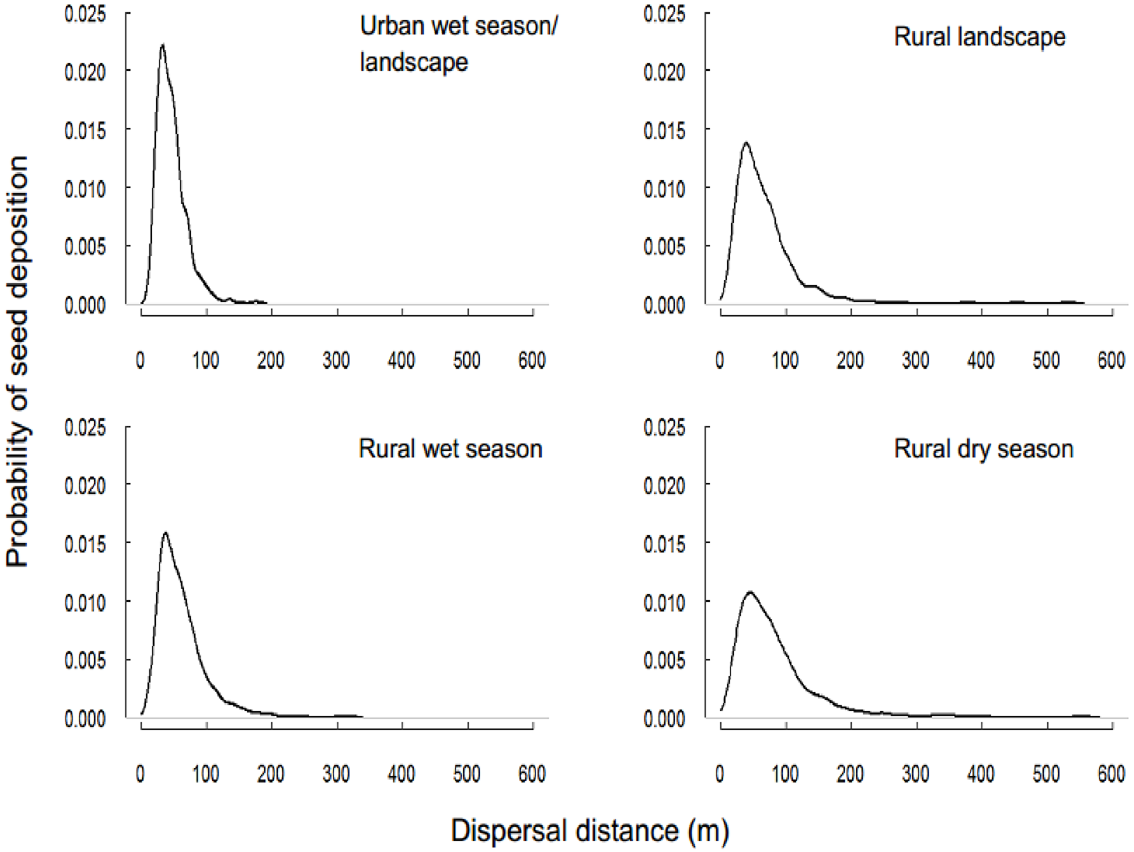

Fig. 4.4 Estimated dispersal distances of large seeds by *E. helvum* during the wet and dry seasons in an urban and a rural landscape in southern Ghana. X-axes are scaled for all plots to facilitate comparison.

Table 4.2. Estimated distances for small seed dispersal by *E. helvum* during wet and dry seasons in an urban and rural landscape in southern Ghana.

Site	**Season**	**Seed dispersal distance (m)**			**Probability of seed dispersal (%)**			
		Minimum	**Median**	**Maximum**	**> 100**	**> 263**	**> 500**	**> 1,000**
Urban	Wet	4	43	22,779	6.1	2.6	2.2	2.0
	Dry	0	42	75,443	5.3	2.4	1.7	1.2
	Pooled	1	43	31,235	5.3	2.6	2.1	1.8
Rural	Wet	9	52	67,044	14.1	3.2	2.5	1.8
	Dry	3	65	24,374	26.3	4.7	3.0	2.3
	Pooled	7	55	49,654	16.9	3.4	2.3	1.6

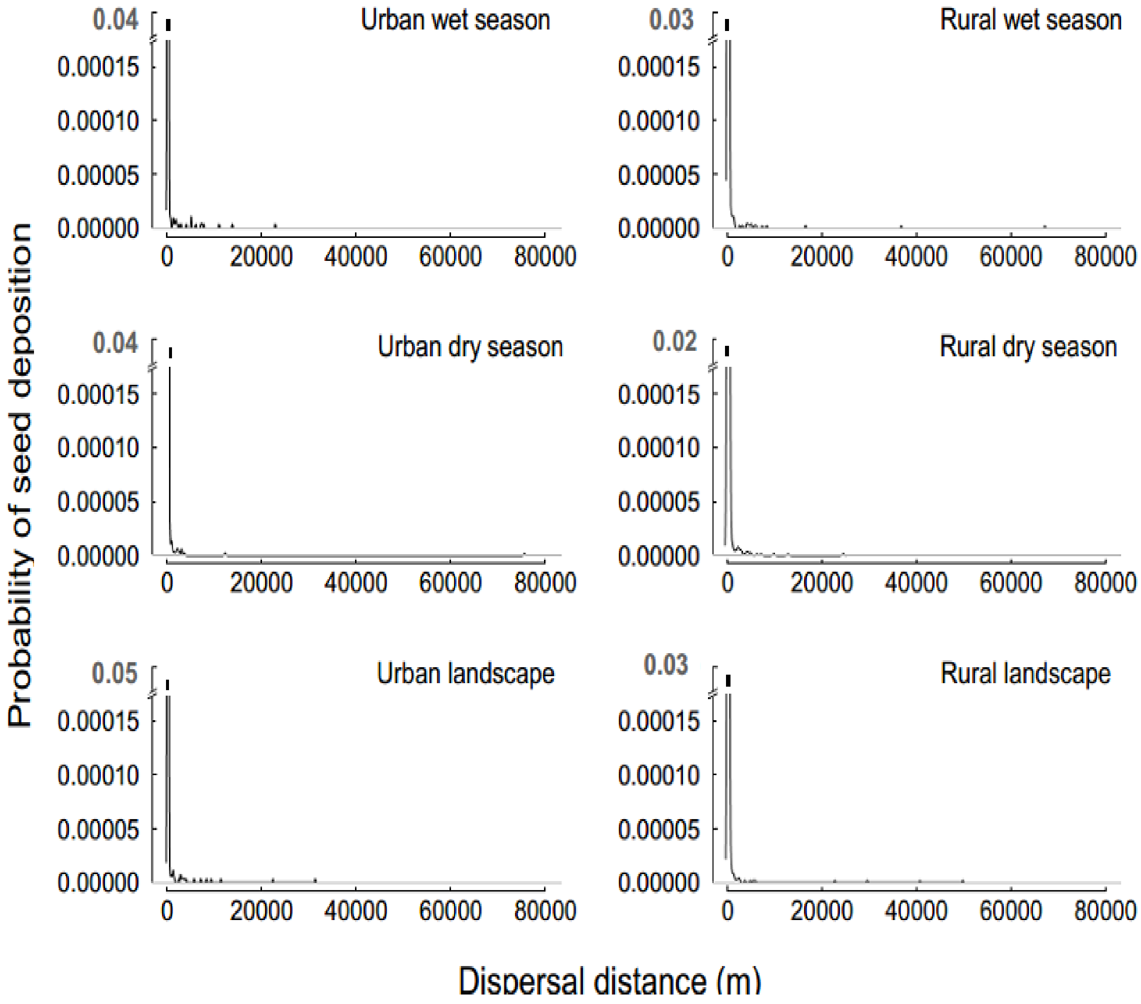

Fig. 4.5 Estimated dispersal distances of small seeds by *E. helvum* during the wet and dry seasons in an urban and a rural landscape in southern Ghana. X-axes are scaled for all plots to facilitate comparison.

4.4 Discussion

Our results provide evidence for the longest estimates of potential seed dispersal distances by a mammalian frugivore estimated to date. Frugivore-mediated seed dispersal is of great importance for the persistence of species and plant gene flow across fragmented landscapes and thus of great ecological and economical value (Hamilton, 1999; McConkey et al., 2012). Despite immense challenges in measuring and extrapolating seed dispersal (e.g. Clark et al., 2003; Nathan et al., 2003), ecologists have been making considerable progress in recent decades, especially by incorporating animal vector behaviour in dispersal kernels estimates (e.g. Russo et al., 2006; Tsoar et al., 2010; Kays et al., 2011). Nathan *et. al.* (2008) emphasized the identification of vectors responsible for long distance dispersal, as different vectors might be of varying importance for predicting and understanding large-scale dynamics of plant distribution. We now add to this knowledge by demonstrating that our study species, *E. helvum*, is capable of performing both short- and extraordinarily long-distance dispersal of seeds of fleshy fruits, including potential distances of up to almost 80 km in highly fragmented landscapes.

The behaviour of the bats in our study regarding distances covered, diet consumed, and number of trees visited varied strongly among seasons and sites. For example, *E. helvum* visited almost exclusively flowering trees in Accra during the dry season at colony peak size, especially *Ceiba pentandra*, thus providing no seed dispersal, but important pollination services (not assessed here) for these trees, which remain only in isolated patches or even as single trees in the landscape (see also Fahr et al., 2015). In the corresponding rural Kibi dry season, the bats' diet was more varied and bats visited more trees per night on average. In Kibi the bats also used more native fruits than in the urban landscape, which in combination with the high potential for large dispersal distances enhances the important role of these bats for landscapes in sub-Saharan Africa where they are ubiquitous.

These sub-Saharan African landscapes are often densely populated by humans and consequently highly fragmented. Even though the literature agrees that zoochory is the most important dispersal mechanism for large fleshy fruits that are typical for the trees of the forest zones (Nathan, 2006; McConkey et al., 2012), the efficiency of animals as dispersers varies greatly. Many species are reluctant to leave the protective forest cover and/or defecate rapidly to reduce weight before undertaking long-distance movement and especially flight, hence resulting in low probabilities for seed dispersal over greater distances.

Fruit bats in general, and *E. helvum* in particular, are increasingly assuming keystone species status for the effective seed dispersal of a large number of plants (Marshall, 1985; Hodgkison et al., 2003; Muscarella and Fleming, 2007; Seltzer et al., 2013; Fahr et al., 2015) in the increasingly fragmented Afro-tropical landscape. Due to *E. helvum*'s unique combination of long-distance movements (this study; Fahr et al., 2015), long seed retention in the gut (this study; Huggel-Wolf and Huggel-Wolf, 1965; Shilton et al., 1999), and defecation during flight, these bats may account for most if not all long-distance genetic exchange of their food plants, many of which are economically important timber or fruit species (Kunz et al., 2011; Fahr et al., 2015). Straw-coloured fruit bats also carry large numbers of seeds into degraded or deforested areas, thus fostering the natural regeneration of vegetation (Taylor et al., 2000; Kunz et al., 2011; Thomas, 1983), which is crucial for the functional connectivity of fragmented landscapes (Mueller et al., 2014).

Several factors are important modulators of this keystone role: on the one hand *E. helvum* is a central-place forager (Fahr et al., 2015). That reduces the diversity of landscapes into which seed may be carried at any given time. However, defecation may still occur during the emergence of the following night (personal experience) and during flight. On the other hand, depending on the foraging area and season *E. helvum* may use several day roosts and visit a number of foraging areas and trees (this study, Fahr et al., 2015), mitigating this effect. In addition, *E. helvum* famously migrates over distances of up to 2,000 km seasonally covering several hundred kilometres in a given night (Richter and Cumming, 2008). Any fruit consumed early in the night of such migratory flights may potentially be dispersed far beyond the distances we record here.

While we found no influence of season on short distance dispersal (SDD) in our dataset, season had the strongest effect on foraging behaviour and thus long-distance dispersal (LDD) distances of small seeds. The longest distance covered occurred in the dry season of the urban study site Accra. However, the longest estimated dispersal kernels (but not maximum) occurred in the rural study site Kibi during the wet season. In contrast to our expectations based on a previous study (Fahr et al., 2015), we did not find an effect of colony size on dispersal distance, suggesting that the resource landscape around a given colony has a major influence on movements and thus dispersal distance. We also did not find a correlation between food phenology, i.e. the fruiting status of potential food plants, on foraging and seed dispersal distance. This may mean that longer foraging and correlated seed dispersal distances are not an effect of individuals avoiding competition with colony members in seasonally larger colonies, but rather an effect of current food availability and choice, a subject that warrants further exploration including much larger sized colonies such as the one in the Kasanka National Park of Zambia with colony sizes numbering up to several millions seasonally (Richter and Cumming, 2006). Whilst fruit bats may forage on over 450 plant species (reviewed in Kunz et al., 2011), a few food species in a given landscape, in our study notably Moraceae (figs and *Milicia excelsa*) and *C. pentandra*, appear to have strong seasonal influence on bat movement, with a corresponding influence on dispersal distances.

Important here is the distinction between small- and large-seeded fruits. Large fruits are typically shuttled to feeding roosts where the seeds are then dropped. The 99th percentile distance of feeding roosts from food source trees was 263 m, and the estimated maximum distance 561 m, which is a considerable movement away from the parent tree and well within the range of the bulk of dispersal distances provided by many frugivorous species (Kays et al., 2011 and citations therein). Most importantly, *E. helvum* often crossed open landscapes between single-standing food trees and feeding roosts (see also Fahr et al., 2015). For small-seeded fruits however, estimated maximum dispersal distances are much larger. Here, too, most seeds are deposited under the feeding roost both through ejecta and rejecta, but ingested seeds could potentially travel much farther distances.

One factor that importantly influences dispersal distances is gut passage time. Most studies in the past have estimated these using natural seeds inserted into slices of highly preferred food, particularly papaya (Kays et al., 2011; Tsoar et al., 2010; Oleksy et al., 2015). While this may often be more feasible and also may lead to standardized and comparable values, accumulating evidence indicates that the species and ripeness of consumed fruits may have a great influence on gut passage times, especially due to the content of secondary plant compounds, which may speed up gut passage and also influence food preference by the bats (Baldwin and Whitehead, 2015; Whitehead et al., 2015). We thus used only food naturally consumed by *E. helvum* and found GPTs that were generally comparable to those of the similar-sized greater short-nosed fruit bat (>12 h, Shilton et al., 1999); Egyptian fruit bat (mean = 53 min, range = 16-114 min, Tsoar et al., 2010); trumpeter hornbills (median = 57 min, maximum 155 min, Lenz et al., 2011); toucans (mean 26 min, range: 4-98 min , Kays et al., 2011); or palm civets (mean 2.6 h, Nakashima and Sukor, 2010).

The median dispersal distance estimates of under 100 m are modest, and could be performed by several other animal seed dispersal vectors. However, the maximal seed dispersal distance of 75.4 km for SSF by *E. helvum* is much higher than documented for any other frugivore such as elephants (6 km, Campos-Arceiz and Blake, 2011); primates (494 m, Tsuji et al., 2009), hornbills (14.8 km (Mueller et al., 2014)); fish (2.1 km, Anderson et al., 2011); and other fruit bats (Tsoar et al., 2010; Oleksy et al., 2015). Even despite higher GPT and displacement distances e.g. >72 h and >100 km for Asian elephants (Blake et al., 2009), resulting estimates of the currently reported longest maximum dispersal distances (20 km) are far less than our estimates for *E. helvum*. Fruit size, numbers of dispersed fruits of a given species and the diversity of fruits dispersed by these dispersers may be different from our system, and result in different forest composition and structure as well as dispersal efficiencies. Our f very long distance estimates of small-seed deposition may not occur in other species, and could also have been missed in previous studies (Cain et al., 2000, but see (Shilton et al., 1999) due to data filtering or an experimental setup that did not follow defecation long enough after feeding.

Our weighting of the ingesta (LDD) and ejecta/rejecta (SDD) components of the small seed analysis by 0.05 and 0.95 respectively may have conservatively biased distance estimates towards SDD. Nevertheless, we believe that from the tree's perspective, the relatively few viable seeds (Hodgkison et al., 2003; Heer et al., 2010; Munin et al., 2011) that are transported further are still extremely valuable.

In summary, our results clearly show that *E. helvum* may be one of the most important seed dispersers of sub-Saharan Africa. Many landscapes face the near complete to complete loss of large but important seed-dispersers (Blake et al., 2009), especially elephants, hornbills and (Russo et al., 2006; Blake et al., 2009; Fritz and Purvis, 2010; Mueller et al., 2014; Campos-Arceiz and Blake, 2011). *Eidolon helvum* is highly abundant and catholic in its habitat use, occupies a vast distribution range, commutes and especially migrates over long distances, and may thus fill many gaps left behind by other species of the seed disperser assemblage.

Assuming only one seed is effectively dispersed by a bat per night, a mean colony of 57,594 ± 67,624 individuals in Accra could potentially disperse up to an upper limit of 125,218 seeds each night over up to 80 km radius from a colony. A rough guess of up to 150 million *E. helvum* across its range suggests up to that much seeds of various sizes dispersed per night. It is unlikely that this could be matched by any other frugivore taxa. This underscores the urgent need to conserve its colonies and habitats to secure the ecological services. The location of huge colonies and foraging areas of *E. helvum* in close proximity to human populations probably make it the most high-profile bat in African landscapes, as observed in our study sites. This poses both positive and negative consequences for its long-term survival. In addition to a high hunting pressure for the bushmeat industry (Kamins et al., 2011), its recent but unconfirmed implication as a reservoir and vector in the spread of in zoonotic diseases such as henipaviruses and Ebola (Hayman et al., 2012b; Baker et al., 2013; Peel et al., 2013) require proactive interventions from research, policy, management, to awareness creation. Thus, a critical step would be to map and secure all *E. helvum* colony sites and to strengthen and enforce policies and management practices from local to international levels, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS), to which most countries within the species' range are signatory.

Another foremost management consideration would be the field validation of our dispersal estimates to assess the accuracy of the spatial distribution of ejecta/rejecta and seedlings around fruiting individuals of key *E. helvum*'s food trees (e.g. figs and Iroko, *Milicia excelsa*) in our study sites or in similar landscapes. This will provide the necessary input for the spatial configuration of trees for restoration efforts and for proactive measures in forest conversion that ensure the maintenance of ecological functions.

Additionally, identifying, retaining and even increasing suitable keystone and generalist fruit plant species at various forest succession stages will help secure their seed dispersal services (Muscarella and Fleming, 2007; McConkey et al., 2012). Fruit bats are important introducers of pioneer species into clearcut areas (Thomas, 1983; Taylor et al., 2000; de la Peña-Domene et al., 2014). Fruit tree species that are predominantly foraged by *E. helvum* (e.g. figs, umbrella tree (*Musanga cercropioides*)) would promote forest regeneration; whilst late succession species such as iroko would maintain established forests. The critical stages are during (1) forest land conversion (e.g. farming, logging, mining) when suitable individual trees could be retained to proactively facilitate passive regeneration; and (2) forest restoration initiatives, when suitable fruit trees and feeding roosts could be planted in spatio-temporal configurations that mimic the desired forest structure, and also provide food and movement opportunities for animals. Selected exotic fruit trees (e.g. papaya (*Carica papaya*) and neem (*Azadirachta indica*) Fahr et al., 2015), which have already integrated into the West African landscape, appear to be important buffer food sources during periods of general food scarcity for fruit bats, and should be considered for restoration and land use practices.

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Supplementary material

Appendix 4A. Locations of colonies and phenology monitoring sites

Table A.1. Distribution of *E. helvum* colony sites, transects and trees used for monthly monitoring of food (fruiting and flowering) phenology in an urban (Accra) and rural (Kibi) landscape in

Ghana, West Africa. Transect lengths are approximate values. *Total number of species per landscape refer to distinct species monitored across that landscape.

Site	Colony sites	Transect sites	Transect coordinates	Transect Length (km)	nº food tree species*	nº individual food trees
Urban Landscape (Accra)	37 Military Hospital (5°35'11"N, 0°11'02"W)	Accra Ministries	5°32'47.26"N, 0°11'47.45"W	3.5	8	99
			5°33'23.13"N, 0°11'55.00"W	3.5		
		Accra Legon Campus	5°38'15.34"N, 0°10'55.60"W	3.8	27	326
			5°39'30.14"N, 0°11'8.99"W	4.4		
		Accra Achimota	5°37'1.80"N, 0°13'2.97"W	3.5	12	136
			5°37'19.60"N, 0°12'59.59"W	3.5		
			5°37'29.53"N, 0°13'18.24"W	4.1		
		Aburi Gardens	5°51'7.27"N, 0°10'23.58"W	3.5	27	157
		Aburi Gyankama	5°48'58.35"N, 0°11'13.56"W	4.5	10	89
Urban Totals	**1**	**5**			**33**	**807**
Rural Landscape (Kibi)	Kibi (6°09'54"N, 0°33'19"W) Old Tafo (6°14'05"N, 0°23'38"W) Anyinam (6°23'38"N, 0°32'36"W)	Kibi	6° 9'23.68"N , 0°33'24.01"W	3.5	16	92
			6° 9'37.57"N, 0°33'15.47"W	3.5		
			6° 9'58.12"N, 0°33'12.41"W	3.7		
			6°10'4.76"N, 0°32'17.76"W	3.8		
		Sagyimase	6°14'9.87"N, 0°30'35.38"W	4.5	22	61
			6°13'51.76"N, 0°31'11.36"W	4.2		
		Bunso	6°15'57.04"N, 0°27'46.03"W	3.6	10	20
Rural Totals	**3**	**3**		**26.8**	**27**	**173**

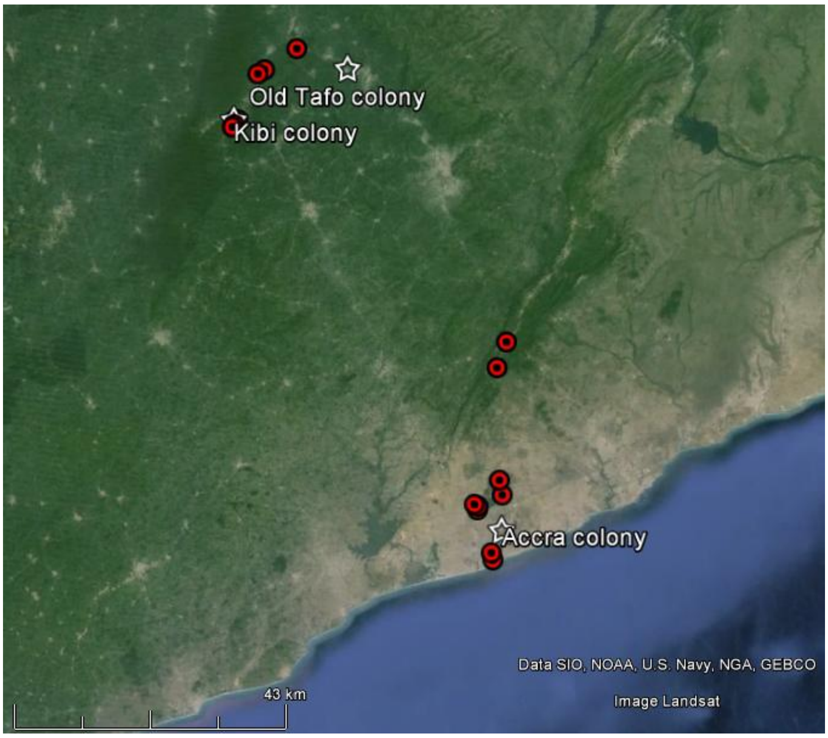

Fig. 4A.1. Distribution map of *E. helvum* colony sites and transects used for monthly monitoring of food (fruiting and flowering) phenology in the landscapes around urban (Accra) and rural (Kibi and Old Tafo) colonies in southern Ghana, West Africa.

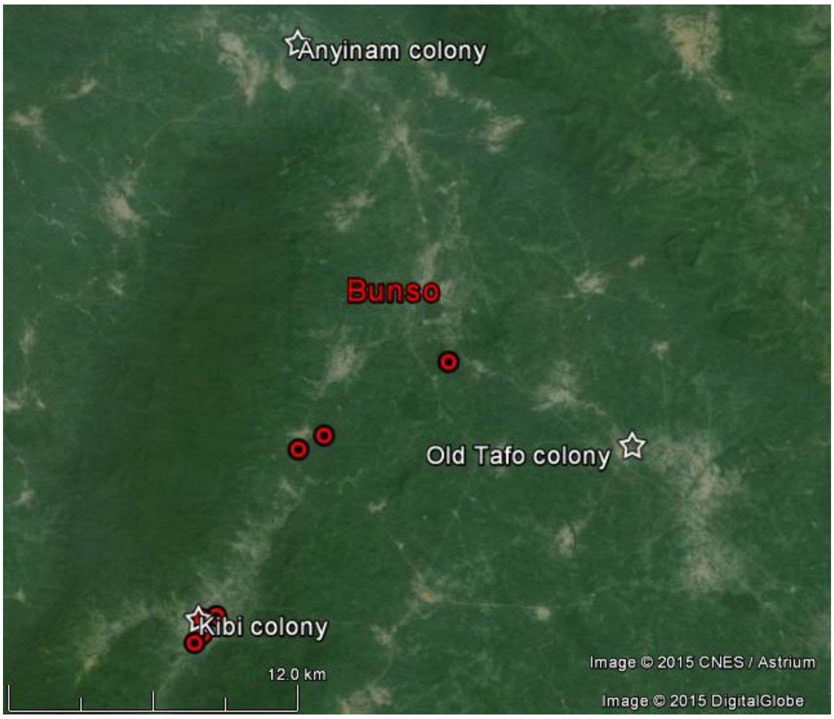

Fig. 4A.2. Distribution map of *E. helvum* colony sites and transects used for monthly monitoring of food (fruiting and flowering) phenology in the rural landscape of Kibi in Ghana, West Africa.

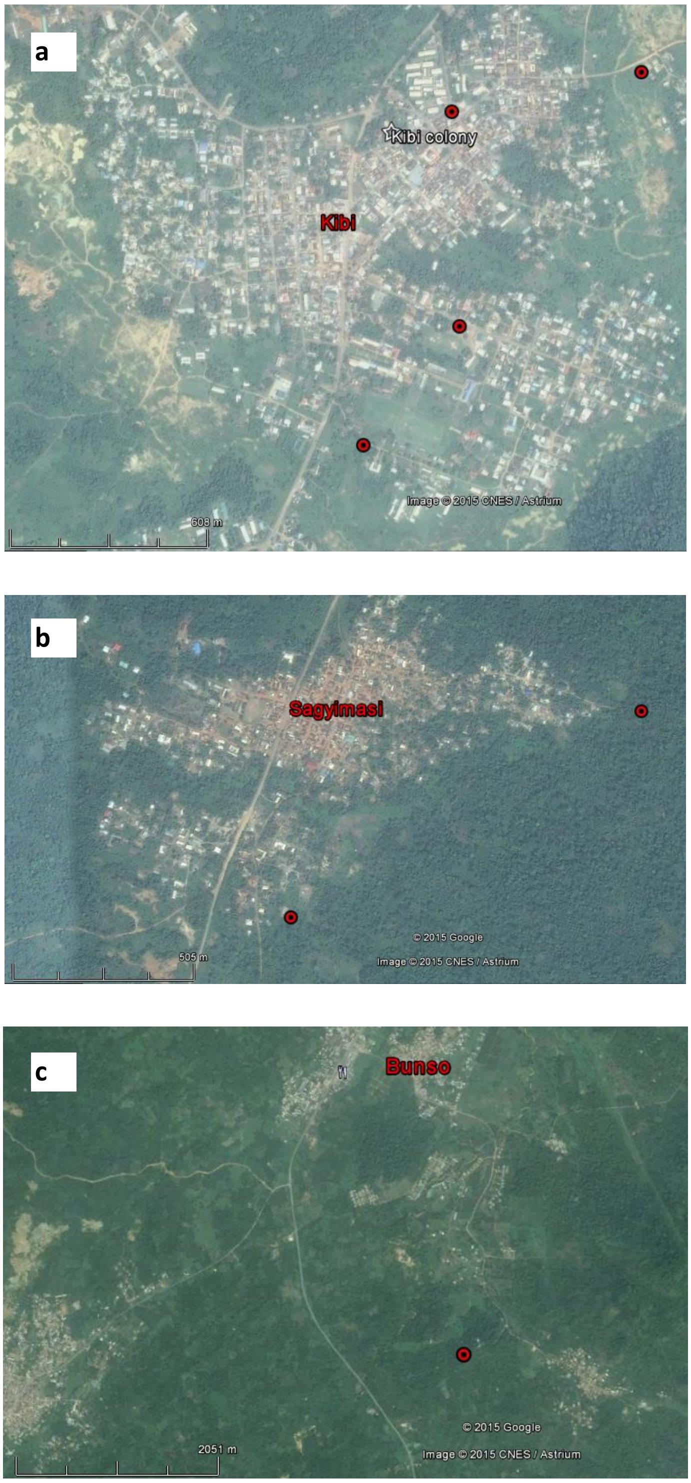

Fig. 4A.3. Large scale distribution map of *E. helvum* colony sites and transects used for monthly monitoring of food (fruiting and flowering) phenology in the townships of (a) Kibi, (b) Sagyimasi and (c) Bunso in the rural landscape at Kibi in Ghana, West Africa.

Fig. 4A.4. Distribution map of *E. helvum* colony sites and transects used for monthly monitoring of food (fruiting and flowering) phenology in the urban landscape of Accra, Ghana, West Africa.

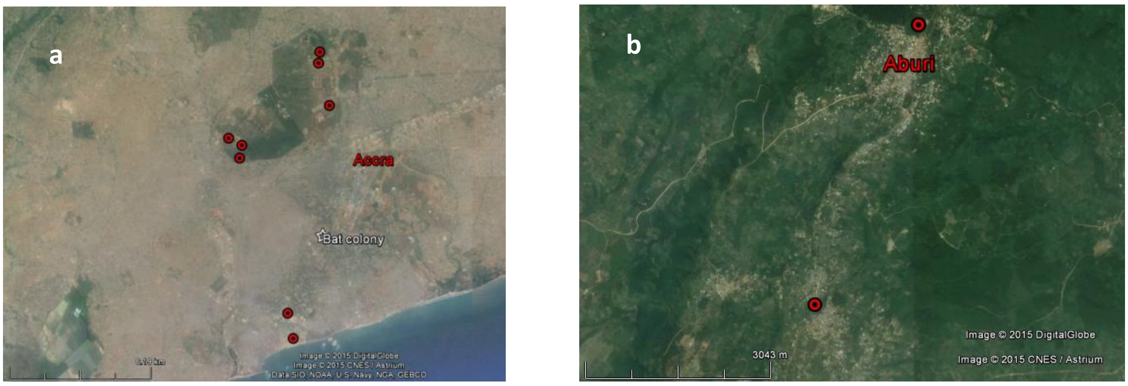

Fig. 4A.5 Large scale distribution map of *E. helvum* colony sites and transects used for monthly monitoring of food (fruiting and flowering) phenology at the core (a) and suburb (b) of urban landscape, Accra, Ghana, West Africa.

Appendix 4B. Phenology monitoring scores, species and heatmaps

Table 4B.1. Score scheme for monitoring phenology of fruit bats food plants in the forest zone of southern Ghana.

Flowering status	Fruiting status	Phenology Field Score	Phenology Score re-scaling (%)	Rescaling rational
No flower	No fruit	0	0	0
Flower buds with less than 10% of open flowers	Early fruit setting with less than 10% of mature size fruits	1	5	(0-10)/2
Flower buds present and 10 - 50% of open flowers	10 - 50% of mature size fruits	2	30	(10-50)/2
Height of flower boom	Peak of fruit maturity	3	75	All mature, but bat can identify ripe ones not visually detectable by humans
Full-blown flowers, but 10 – 50% turning dry	Mature fruit present; and beginning of fruit fall and seed scattering	4	100	All fruits/flowers ripe, many overripe.
More than 50% of flowers dry and the fall of flowers clearly occurring	More than 50% of fruit dry and/or fallen	5	25	Ripe stock nearly exhausted

Table 4B.2. Fruit bats food species used in phenology monitoring in the urban (Accra) and rural (Kibi) landscapes in the forest zone of southern Ghana.

Plant species	Plant Family	Food type	Urban landscape	Rural landscape	New Record
Adansonia digitata	Bombacaceae	flower	x		
Albizia zygia	Mimosaceae	flower	x		
Anacardium occidentale	Anacardiaceae	fruit	x	x	
Anthocleista nobilis	Loganiaceae	fruit	x		
Antiaris toxicaria	Moraceae	fruit	x	x	
Azadirachta indica	Meliaceae	fruit	x	x	
Blighia sapida	Meliaceae	fruit	x	x	x
Carica papaya	Caricaceae	fruit	x	x	
Caryodendron orinocense	Euphorbiaceae	fruit		x	x
Ceiba pentandra	Bombacaceae	flower	x	x	
Coccoloba uvifera	Polygonaceae	fruit	x		x
Cola acuminata	Sterculiaceae	fruit	x		x
Cola gigantea	Sterculiaceae	fruit	x	x	
Cola nitida	Sterculiaceae	fruit	x		x
Diospyros mespiliformis	Ebenaceae	fruit	x		
Ficus ardisioides	Moraceae	fruit		x	?
Ficus benjamina	Moraceae	fruit	x		?
Ficus elasticoides	Moraceae	fruit	x	x	?
Ficus exasperata	Moraceae	fruit	x	x	
Ficus mucuso	Moraceae	fruit		x	?
Ficus platyphyla	Moraceae	fruit	x		?
Ficus polita	Moraceae	fruit		x	
Ficus sur	Moraceae	fruit	x	x	

Ficus tessellata	Moraceae	fruit	x	x	?
Ficus trichopoda	Moraceae	fruit	x		?
Ficus umbellata	Moraceae	fruit	x		
Glyphaea brevis	Tiliaceae	flower?		x	x
Macaranga barteri	Euphorbiaceae	fruit		x	x
Mangifera indica	Anacardiaceae	fruit	x	x	
Milicia excelsa	Moraceae	fruit	x	x	
Milicia regia	Moraceae	fruit	x		x
Musa sp.	Musaceae	fruit	x	x	
Musanga cercropioides	Moraceae	fruit		x	
Panda oleosa	Pandaceae	fruit		x	x
Peltophorum pterocarpum	Fabaceae	flower?	x		x
Persea americana	Lauraceae	fruit	x	x	x
Psidium guajava	Myrtaceae	fruit	x		x
Pycnanthus angolensis	Myristicaceae	fruit		x	
Spathodea campanulata	Bignoniaceae	flower	x	x	
Spondias mombin	Anacardiaceae	fruit	x	x	
Terminalia catappa	Combretaceae	fruit	x	x	
Vitellaria paradoxa	Sapotaceae	fruit	x		

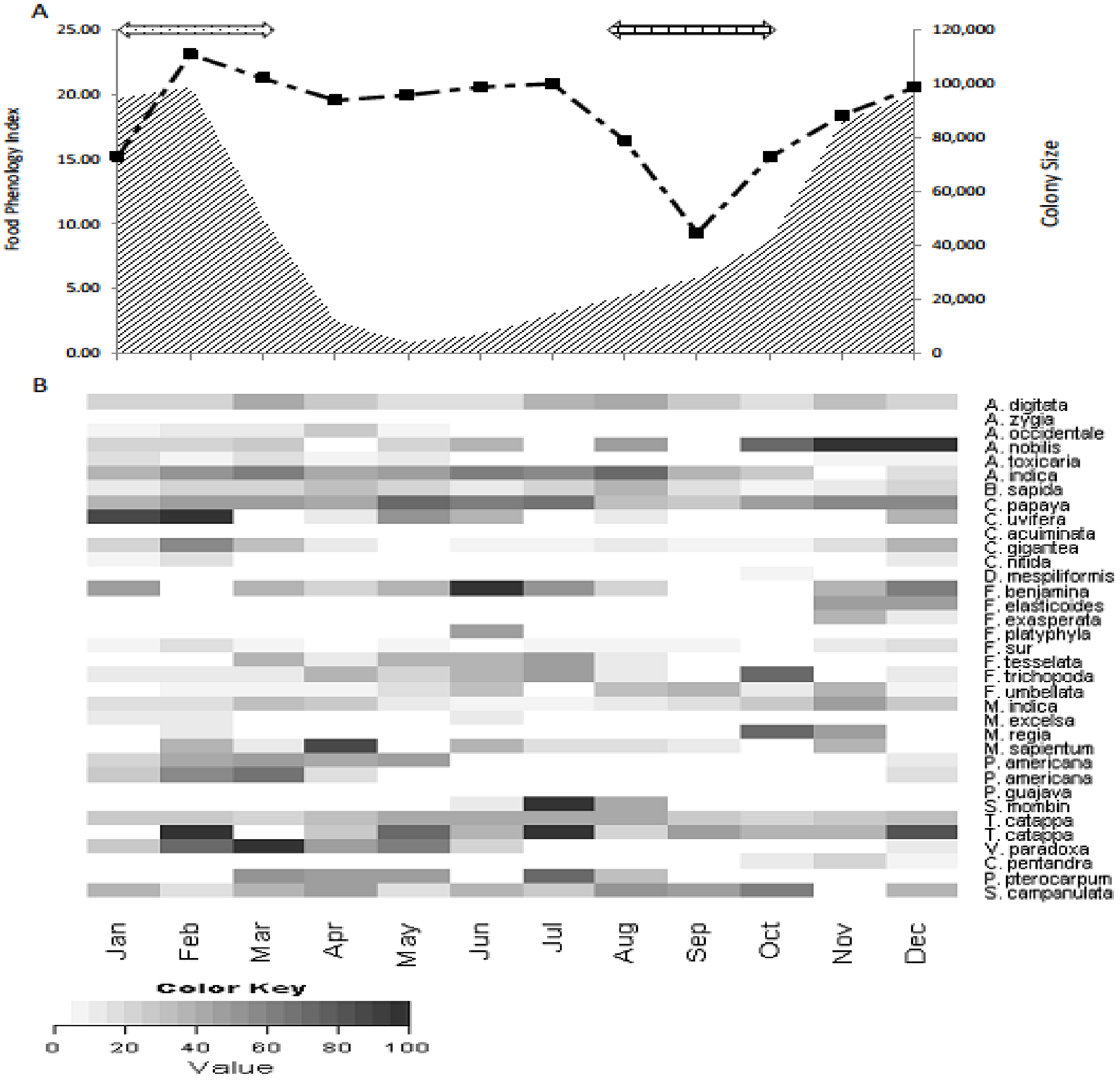

Fig. 4B.1. Temporal fluctuation of (A) *Eidolon* colony size (▨) and phenology of food resources (··◆···◆··) in the urban landscape in and around Accra in the forest biome of southern Ghana. Fieldwork was carried out at periods of the commencement of colony decline (⇔) and colony increase (⇔) to reflect colony size and landscape conditions that may influnece bat movement patterns and ultimately seed dispersal potential. Corresponding heatmap of food phenology index (FPI) (B) shows periods of relative occurrence of food resources.

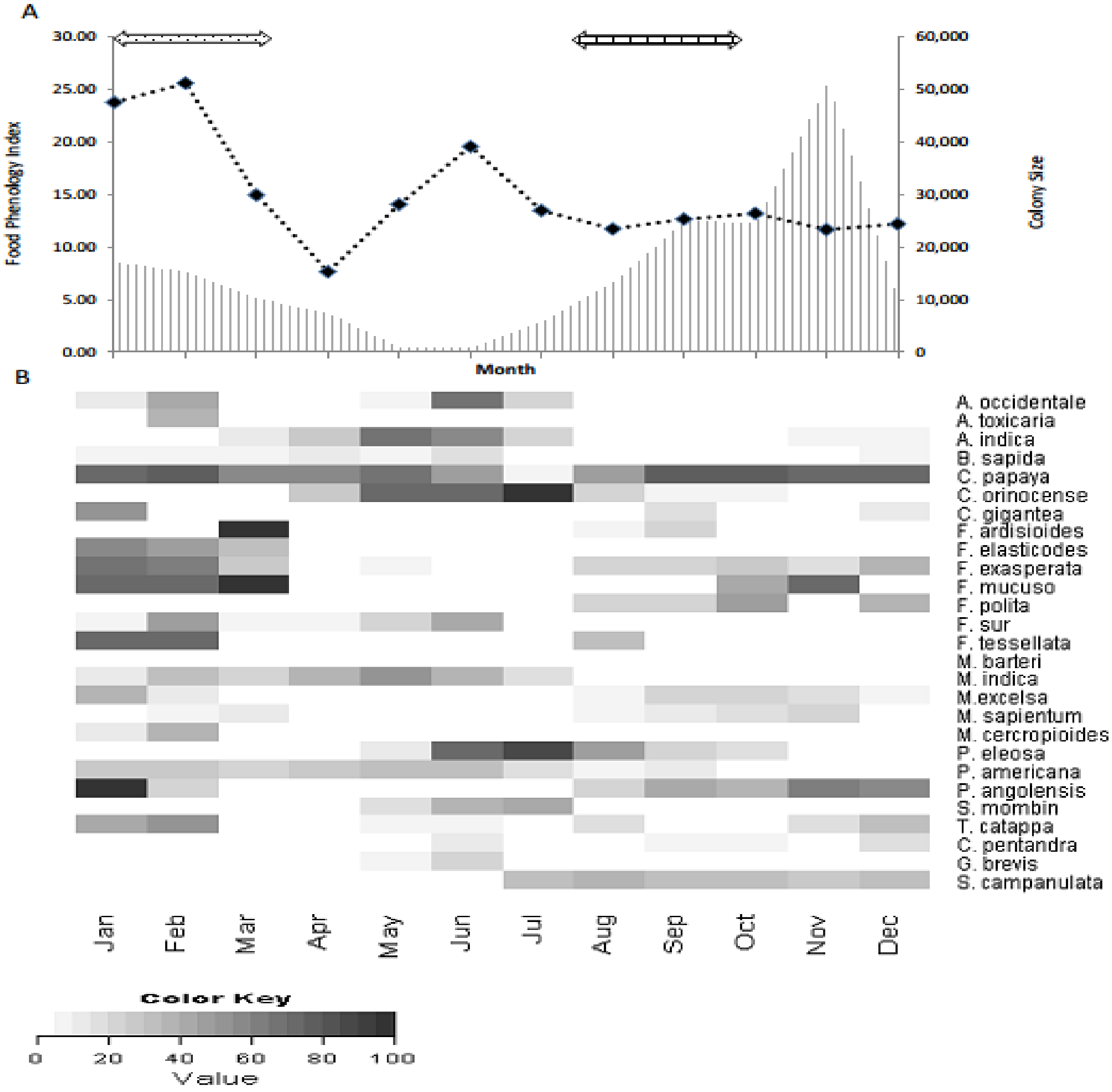

Fig. 4B.2. Temporal fluctuation of (A) *Eidolon* colony size (▥) and phenology of food resources (··◆···◆··) in the rural landscape in and around Kibi in the forest biome of southern Ghana. Fieldwork was carried out at commencement of colony decline (⇔) and colony increase (⇔) to reflect colony size and landscape conditions that may influnece bat movement patterns and ultimately seed dispersal potential. Corresponding heatmap of food phenology index (B) shows periods of relative occurrence of food resources.

Appendix 4 C. GPS logger settings and bat body measurements

Table 4C. e-obs GPS logger settings and body measurements of adult male *Eidolon helvum* tracked in 2009-2013 in southern Ghana.

Cohort #	Bat #	Landscape	Tracking Year	Tracking Season	# nights tracked	GPS-on time (day)	GPS fix intervals (s)			Bat body mass (g)	Bat forearm length (mm)
							Speed-informed (≥ 500 ms-1 threshold); initial/triggered	Acceleration-informed (resting vs. flying) initial/triggered	Other intervals		
1	Tag1079	Urban	2009	Wet	3	18:10-06:00			600	284	118.1
1	Tag1080	Urban	2009	Wet	2	18:10-06:00			600	244	113.9
1	Tag1081	Urban	2009	Wet	3	18:10-06:00			600	274	123.5
1	Tag1082	Urban	2009	Wet	1	18:10-06:00			600	246	120.0
2	Tag1084	Urban	2009	Wet	4	18:10-06:00	600/300			239	115.1
2	Tag1086	Urban	2009	Wet	2	18:10-06:00	600/300			277	118.2
2	Tag1088	Urban	2009	Wet	2	18:10-06:00	600/300			247	120.0
3	Tag1607	Urban	2011	Dry	6	18:10-06:00		1800/300		321	124.7
3	Tag1608	Urban	2011	Dry	1	18:10-06:00		1800/300		300	122.1

3	Tag1610	Urban	2011	Dry	1	18:10-06:00	1800/300	270	114.7
3	Tag1612	Urban	2011	Dry	1.0	18:10-06:00	1800/300	310	118.6
3	Tag1613	Urban	2011	Dry	1	18:10-06:00	1800/300	305	123.4
3	Tag1615	Urban	2011	Dry	1	18:10-06:00	1800/300	300	123.9
3	Tag1616	Urban	2011	Dry	2	18:10-06:00	1800/300	292	121.0
3	Tag1620	Urban	2011	Dry	2	18:10-06:00	1800/300	255	119.7
3	Tag1626	Urban	2011	Dry	2	18:10-06:00	1800/300	280	119.1
3	Tag697	Urban	2012	Wet	1	17:59-06:01	1800/300	252	123.5
3	Tag1870	Rural	2011	Wet	3	18:10-06:00	1800/300	275	117.5
3	Tag1875	Rural	2011	Wet	4	18:10-06:00	1800/300	280	119.1
4	Tag2394	Rural	2012	Wet	2	17:59-06:01	1800/150	275	118.8
4	Tag2396	Rural	2012	Wet	5.5	17:59-06:01	1800/150	270	121.6
4	Tag2402	Rural	2012	Wet	6	17:59-06:01	1800/150	272	120.3
4	Tag2404	Rural	2012	Wet	4.5	17:59-06:01	1800/150	270	121.9
4	Tag2608	Rural	2013	Dry	3.5	17:59-06:01	1800/150	275	117.9

4	Tag2612	Rural	2013	Dry	5.5	17:59-06:01	1800/150	250	125.6
4	Tag2770	Rural	2013	Dry	4	17:59-06:01	1800/150	250	113.2
4	Tag2772	Rural	2013	Dry	3	17:59-06:01	1800/150	245	122.0

Appendix 4D. Parameters for GPT and seed dispersal distribution models

Table 4D.1. Parameters for best-fit distribution function for Gut Passage Time of small seeds from *Ficus* spp., *Milicia excelsa* and *Anthocleista nobilis* fruits consumed by *Eidolon helvum* during field-based feeding experiments.

Best-fit distribution	Distribution parameters (± s.e)	Log-likelihood
lognormal	meanlog = 4.305 (0.009), sdlog = 0.867 (.006)	-55814.75

Table 4D.2. Best-fit distribution function for large seeds dispersed by *Eidolon helvum* during the dry and wet seasons in an urban and rural forest landscape in Ghana, West Africa.

Site / landscape	Season	Best-fit distribution	Distribution parameters (± s.e)	Log-likelihood	AIC
Urban	Wet	lognormal	meanlog = 3.729 (0.014) sdlog = 0.454 (0.0102))	-4359.2	8722.3
	Dry	-	-		
	Combined	lognormal	meanlog = 3.729 (0.014) sdlog = 0.454 (0.0102))	-4359.2	8722.3
Rural	Wet	lognormal	meanlog = 3.9551 (0.017) sdlog = 0.548 (0.012))	-4773.1	9550.1
	Dry	lognormal	meanlog = 4.174 (0.021) sdlog = 0.648 (0.0145)	-5159.6	10323.2
	Combined	lognormal	meanlog = 4.000 (0.019) sdlog = 0.6001495 (0.01)	-4908.25	9820.5

Table 4D.3. Best-fit distribution functions for small seeds dispersed by *Eidolon helvum* during the dry and wet seasons in an urban and rural forest landscape in Ghana, West Africa.

Site	Season	Best-fit distribution	Distribution parameters (± s.e)	Log-likelihood	AIC
Urban	Wet	cauchy	location = 40.673 (±0.596) shape = 11.832 (±0.4878)	-4840.7	9685.5
	Dry	cauchy	location = 40.142 (±0.6078) scale = 12.048 (±0.495)	-4800.3	9604.7
	Combined	cauchy	location = 40.506 (±0.655) scale =12.577 (±0.511)	-4868.4	9740.8
Rural	Wet	cauchy	location = 47.996 (±0.881) scale = 17.637 (±0.738)	-5264.7	10533.4
	Dry	lognormal	meanlog = 4.243 (0.029) sdlog = 0.917 (0.021)	-5574.8	11153.6
	Combined	cauchy	location = 51.099 (±0.964) scale = 19.256 (±0.812)	-5321.5	10647

CHAPTER 5

General discussion

The goal of this doctoral study was to quantify the ecological impact of fruit bats, represented by the straw-coloured fruit bats (*E. helvum*) in African forest and savanna landscapes. Using state-of-the-art GPS/acceleration loggers and concurrent monitoring of the seasonal fluctuations in colony size, phenology of bat food resources and field-based feeding experiments, I collected data, at high spatio-temporal resolution, on the eco-physiological behaviour of fruit bats under different seasonal and landscape conditions. I used these data to quantify: 1) changes in foraging movements and colony population size in response to inter-seasonal environments; 2) changes in bat colony size, activity budgeting, movement ecology and body condition responses to intra-seasonal changes in food availability; and 3) dispersal distances for seeds of bat food resources. The data collected were snapshots in time and space, and covered only one fruit bat. But high spatio-temporal resolution gained from GPS tracking and concurrent monitoring of climatic, demographic and food resource variables provide a wealth of information previously unknown or poorly understood about fruit bats and their roles in ecosystem function. The following are major findings that contribute to our knowledge of fruit bats in general and *E. helvum* in particular:

Seasonality of colony size and food resources availability

Bat colony size clearly showed a cyclical fluctuation between and within seasons in the two ecosystems. Although not covered under this study, fluctuations in the size and timing of colonies across the year strongly support the hypothesis of a northward migration from the forest ecosystem into the savanna with the onset of the rains around April, and a reverse migration around October. A partial migration in which zero (in the southern forests) to a few thousands (northern savanna) individuals may remain seem to support the food resource driven hypothesis (Thomas, 1983). The exact spatio-temporal patterns of this migration, however, still remain unknown, and call for urgent redress.

Likewise, bat food was generally available throughout the year in both the forest ecosystem in southern Ghana (Chapter 2 and 4) and the savanna ecosystem in Burkina Faso (Chapter 3). However, there were periods of marked fluctuations in the abundance and species composition of food resources between and within seasons in these ecosystems. This is particularly the case for figs (*Ficus* spp.) and Iroko (*M. excelsa*) in the forest ecosystem, and figs and Shea fruit (*V. paradoxa*) in the savanna. Thus, food resources for fruit bats in West Africa could be considered spatio-temporarily ephemeral, to which *E. helvum* appears to respond with corresponding eco-physiological changes during the wet and dry seasons at each of the migration phases in West Africa.

Changes in bat movement ecology, activity budgeting, diet and body condition

Colony size fluctuations correlated positively with the ephemeral food availability, especially with tree species dominant in fruit production during either food period. If optimal foraging theory applies to a central-place forager such as *E. helvum* in this study situation, we should expect individuals to minimize travel distance, time and energy expenditure to locate food patches while maximizing food intake at these patches (Munin et al., 2011). Indeed, during the dry season colony high in the forest ecosystem, I observed a significantly longer travel time and a larger mean cumulative distance covered per night as well as a maximum distance between the colony and the respective foraging areas. In contrast, during colony peak/food high season in the savanna ecosystem, intra-seasonal travel movements and mean nightly travel times were significantly shorter, but I found no difference in travel distances or the core area or overall area of foraging.

Thus, I would like to hypothesize that intraspecific competition in a central-place forager such as *E. helvum* increased strongly at peak population size during the dry season, leading to an intense exploitation of food resources in the immediate vicinity of the colony, and that the density of foraging bats decreases with increasing distance from the colony in the southern forests. However, in the northern savanna, it appears that the driving force behind foraging movement parameters may be both the abundance and type of prevailing food species in the landscape. Bats generally spent longer time at the same locations or type of foraging area to maximize dwindling food resources during low food periods. Furthermore, the expectation that a substantial proportion of the colony might be forced to forage at much larger distances during the population and/or food high was upheld for the forest ecosystem, but did not necessarily show up in the savanna.

Similarly, an expectation that the high-resolution activity budgets of tracked bats would reflect a correlated increase of energetic costs during colony peaks/food abundance was not met in either ecosystem under study. A higher daytime increase in activity in the savanna high-food period could be attributed to higher incidence of recreational activity at the central colony site in the Ouagadougou city centre. Thus, the higher foraging/travel time during food scarcity and /or colony highs might have been spent searching for food within or close to food trees with no extra expenditure of movement effort. It could also have been spent consuming a greater amount of food with sub-optimal energetic content in comparison with food types in the food high period. A study on the chemical composition and nightly energy needs intake should help clarify this in a future study.

A two-fold reduction in colony size within the single wet season in the savanna suggests that some bats might have dispersed to neighbouring colonies and/or spent more time at solitary day roosts with increasing food scarcity within the same season. Such solitary roosting may be a behavioural response to intra-specific competition resulting from food scarcity

It is quite likely that some of inter- and intra-seasonal movement and foraging differences may be due to changes in the resource landscape, rather than primarily to colony size. In the forest ecosystem, bats clearly shifted from introduced and cultivated fruit trees used during the population low wet season (in particular neem) to flower resources (mostly kapok trees), figs and Iroko during the population high dry season. In my study I did not investigate whether the bats were simply exploiting food resources (perhaps opportunistically) on the basis of their spatial proximity and density, or for specific nutritional needs in a given season. Irrespective of a (potential) seasonal shift in nutritional needs, the spatio-temporal pattern in the food resource landscape could greatly influence bat movements. Improvements in logger design and weights would allow tracking of both sexes and to assess the impact of energetic demands on movements.

I report for the first time the ability of *E. helvum* to roost as solitary individuals during the daytime away from the usual gregarious colonies. During periods of food scarcity, bats showed a higher (70% of the time) tendency to roost over at least one day at the last foraging site of a night; this is in contrast to 19% solitary day roosting in food abundance periods, during which time bats generally travelled overnight in a loop pattern between the central colony and foraging sites. Such solitary day roosts may be at the same or different locations over consecutive days. Over a period of up to six days during food scarcity in the savanna ecosystem, an individual bat ranged up to 118 km away from the colony at which it was initially caught; this was in comparison to a generally shorter (40 km) overnight flight distance during food abundance. This difference in movements may indicate that bats opted for the advantage of remaining in a foraging area at which they found food resources, even if already scarce, rather than making an energetically costly round trip back to the central colony or previous day roost.

As expected, bats were in better body condition when food availability was high, dropping by about 30% just a few weeks later in the season when food resources reduced. It should be noted that the observed higher body condition might have resulted from intensive foraging in months prior to the study period, as bats had already migrated to the area from the southern forests from as far back as April. Nonetheless, the significant decline in body condition in a short time shows that bat physiology was responding quickly to food resource availability. This study also highlights *V. paradoxa* as a keystone food species for the ecology of fruit bats and for the socio-economic welfare of the savanna agro-ecosystem.

Quantification of seed dispersal distances for bat food resources

My study adds to the growing wealth of knowledge on the role of frugivores in seed dispersal by demonstrating the longest estimates of seed dispersal kernel distances to date. I show that *E. helvum*, Africa's second largest fruit bat and the most populous mammal on the continent, with perhaps 100 million individuals, is capable of performing both short- and extraordinary long-distance dispersal of seeds of 10s of fleshy-fruit species over distances of up to almost 80 km in highly fragmented landscapes. Large seeds are potentially dispersed over a few 100s of meters (8 – 551 m). Through a combination of long post feeding distances of bats from food (range 1-87,726 m) and long gut retention times (range 4 – 1,143 min), small seeds could be dispersed over 10s of kilometres (0 – 75.4 km). Although the bulk of dispersed seeds fell within a 263 m radius of food trees (threshold for long-and short-distance dispersal kernels derived from feeding roost distribution around food trees), a very small percentage were transported over exceptionally long distances: 0 – 0.5 % for large seeds and 2.4 – 4.7 % for small seeds.

Dispersal distances vary by season and by landscape. For large seeds, estimated maximum kernel distance was about five times longer in the rural (532 m) compared to the urban (179 m) landscape. Within the rural landscape, maximum distance was twice (551 m) longer in the dry season than in the wet season (319 m). For small seeds, a maximum kernel distance of 49,650 m in the rural landscape showed a 150% increase over the 31,235 m estimated for the urban landscapes. Estimates of inter-seasonal seed dispersal kernel distances showed contrasting results. In the urban forest landscape, estimates of dry season maximum dispersal distance (75,443 m), as against the wet season 22,779 m; although theses maximum values were about 300% different, overall distance estimates were not significantly different. This was reversed in the rural landscape, where maximum dispersal distance was about 260% longer in the wet (67,044 m) than the dry (24,374 m) season.

Management implications

These findings contribute a wealth of knowledge for making informed decisions on the management of fruit bats, especially *E. helvum*, and fragmented landscapes. Firstly, locations of huge *E. helvum* colonies and foraging areas in close proximity to human populations probably make it the most high-profile bat in African landscapes, with both positive and negative consequences for its long-term survival, such as hunting pressure (Kamins et al., 2011), presumed implication as a reservoir and vector in the spread of zoonotic diseases such as henipaviruses and Ebola (Hayman et al., 2012b; Baker et al., 2013; Peel et al., 2013). These challenges to the species' long-term survival require proactive interventions from research, policy and management and call for awareness creation. I suggest that the most immediate action would be the mapping and protection of all *E. helvum* colony sites and the strengthening and enforcing of policies and management practices from local to international levels, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS), to which most countries within the species' range are signatory.

Secondly, time, financial and logistics constraints did not permit assessing the accuracy of these dispersal kernel estimates through field validation of the spatial distribution of ejecta/rejecta and seedlings around fruiting individuals of key *E. helvum*'s food trees (e.g. figs and Iroko) in our study sites or in similar landscapes. Habitat restoration efforts and proactive measures in forest conversion will benefit greatly from information on the spatial configuration of trees that could be derived from such validation efforts.

Finally, pioneer (e.g. figs, umbrella tree (*Musanga cercropioides*)) succession species such as Iroko (*Milicia excelsa*) fruit species are predominantly foraged by *E. helvum* bats. They are subsequently dispersed into various habitats, from clear-cuts (Thomas, 1983; Taylor et al., 2000; de la Peña-Domene et al., 2014) to intact forest cover in both the forest and savanna ecosystems. Managers could promote the integration of the fruit bat's seed dispersal services into the landscape by identifying, retaining and increasing suitable keystone and generalist fruit plant species at various forest succession stages. Such a management strategy will help secure their seed dispersal services (Muscarella and Fleming, 2007; McConkey et al., 2012). The critical stages for management actions are during:

1) forest land conversion (e.g. farming, logging, mining) when suitable individual trees could be retained to proactively facilitate passive regeneration; and

2) forest restoration initiatives, when suitable fruit trees and feeding roosts could be planted in spatio-temporal configurations that mimic the desired forest structure, and also provide food and movement opportunities for animals. Selected exotic fruit trees (e.g. papaya (*Carica papaya*) and neem (*Azadirachta indica*) (Fahr et al., 2015), which have already integrated into the West African landscape, appear to be important buffer food sources during periods of general food scarcity for fruit bats, and should be considered for restoration and land use practices.

Concluding remarks

These results show that *E. helvum* is arguably one of the most important seed dispersers of sub-Saharan Africa. This could be attributed to the highly abundant population and wide distribution, very long nightly commuting and seasonal migration distances, and conservative tastes in fruit species as well as habitats. Thus, it fills many gaps left by the loss or depletion of other species of the seed disperser assemblage, especially elephants, hornbills and primates.

Considering their role as critical food sources for fruit bats and other frugivores during different periods of the year, some food species should be considered and promoted as keystone food sources (see also Howe, 1993; Wallace, 2005) in the forest belt (e.g. *Ficus* spp. *M. excelsa*, *M. cercropioides* and *C. pentandra*) and savanna (*V. paradoxa*, *Ficus* spp. *C. pentandra*, *S. birrea*, and *Lannea microcarpa)* ecosystems in West Africa. Since these species already provide concurrent socio-economic services to human societies, enhancing their integration should offer few, if any challenges from the acceptance perspective.

This study further highlights the high eco-physiological adaptability of *E. helvum* to life in the different ecosystems across its annual migration route. It provides a better understanding of the ecological considerations needed to design and implement effective conservation strategies. Above all, the study emphasizes the keystone role of fruit bats in general (and of *E. helvum* in particular) in the regeneration and maintenance of fragmented landscapes across Africa. This makes it imperative that host countries and relevant global conservation bodies take urgent steps to maintain *E. helvum* populations.

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Permits and Animal Ethics Statement

Animal capture, handling and logger attachments protocols during fieldwork adhered best current practices, particularly guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al., 2007). Our use of only adult male in good body condition was designed to avoid negative impact on reproductive females or immature individuals. To the best of my knowledge, no animal was harmed in this study.

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Back in 2011, I certainly did not expect to find it easy to transition from an eleven-year career in protected areas management and project management to academic-based research. I had faced very tough mental and physical challenges which I thought were adequate preparation; after all, I was going to work on wildlife in the same West Africa as before. But from hindsight, I had grossly underestimated the challenges that would face over the next four years as an old doctoral candidate, splitting my life between field-based scientific research and family life in two continents.

My foremost thanks, therefore, go to the Creator, whom I acknowledge as Jehovah, for granting me life, health, and everything else. I subscribe to the school of those who know that human science is but an extension of the Creator’s omniscience. And to my family, words cannot express my gratitude for all the support you have given me at your expense during this period. To my father, Macauley, and mother, Georgina, and sisters Hannah and Barbara, thank you for being parents I could never replace for anyone else. To my wife, Juliana, yours is an unquestionable labour of love. To our children, Felix, Maxwell, Michael, Manuella, Michelle and Madeline, I am sorry for the frequent emotional separations, but deeply grateful for the love and laughter you show me every day. Surely, this study has provided the best foundation for my guidance in your current and future studies.

I am indebted to many persons and institutions for their contributions in various ways to the success of this study. IMPRS Coordinators Dr. Daniel Piechowski, Dr. Mäggi Hieber Ruiz, and their support team Elvi and others, were very patient with advice and much laughter from the first to the very last day of my study. My PhD Advisory Committee (PAC) provided me with immense constructive guidance. Firstly, Dr. Dina Dechmann (MPIO / University of Konstanz) and Dr. Jakob Fahr (MPIO / University of Braunschweig) introduced to what has turned out to be a satisfying field of nature conservation. They exposed me to all the necessary guidance in the theory, fieldwork, writing skills and intellectual reasoning needed to produce this dissertation, resulting publications, and for a future involving bat conservation/ecosystem management. Other members of the PAC, Prof. Dr. Roland Kays (North Carolina State University and Museum of Natural Sciences), Dr. Wolfgang Fiedler (MPIO) and Prof. Dr. Martin Wilkelski (MPIO / University of Konstanz), also provided me with unequalled guidance in the overall execution of this study. Above all, Prof. Wikelski greatly encouraged me to trust in my abilities and to never give up; I simply cannot thank you enough.

I have had the honour of meeting many great people, of all ages and backgrounds, from across the world. My fellow students provided me with a stimulating social and academic environment. The Dechmann/Safi group showed me that studies could also be fun in many innovative ways. To my lab mates, especially Yann, Javier, Marion, ….thanks for your great inspiration. The LaPoint and O’Mara families brought their American side into many lively interactions: thanks, Yankees. So did the entire staff of the Max Planck Institute for Ornithology, especially in Radolfzell. You are partly to blame for my failure to learn Deutsch because of the many times you practiced your English on me. The IT and Workshop teams, the Maximum Guest House team, Elke, Jennifer, Elvi, Silvi, Heidi, Kumar, Teresia, Shovar, all the Monikas,……..space will not allow me to do justice to your friendship by mentioning all your names here. Know that I treasure every bit of our interactions over the past years, and hope that we keep our support network alive *ad infinitum*.

Dr. David Santos and Ing. Bernd Vorneweg, and the University of Konstanz workshop team introduced me to the challenges of GPS logger assembly and settings. Although some of their results were not directly applied in the Chapters above, lessons learnt will be useful for the rest of my career.

Möggingen will be prominent in the numerous places I have called home in a long life. The Baron and people of this peaceful village kindly hosted me at different times over the past four years. I couldn't have had a better place for learning and enjoying nature at a pace different from what I am used to in Africa. During my last few months, Fnu Sherub showed me the rudiments of heathy cooking and smart quips, and accompanied me on several nature walks that I will remember forever.

I met some great Africans right in the Konstanz area: my extended family member Diana and her husband Andreas; and Joyce and the entire fellowship of Jesus Is Alive Ministries in Radolfzell. It is unfortunate we met so late.

Finally, I am highly indebted to International Max Planck Research School (IMPRS) for Organismal Biology, the joint programme between Max Planck Institute for Ornithology and the Department of Biology at the University of Konstanz, for funding my PhD study. This opportunity has provided me with a first-class scientific training that I doubt could be matched anywhere else.

To any person or institution not acknowledged here, please pardon the oversight; your contribution is deeply appreciated. I hope I could repay you in some way, some day, somewhere.

Record of Achievement

Except for stipulations listed below, I designed the overall study structure, executed data collection, analysis and presentation, and report writing of this dissertation, under the joint supervision of Dr. Dina Dechmann, Dr. Jakob Fahr and Prof. Dr. Martin Wikelski, who collectively conceived the original idea and facilitated my recruitment for a PhD study.

Chapter 2

Drs. Fahr and Dechmann designed the experiments. I participated in fieldwork (bat tracking and groundtruthing in 2011) with Drs. Fahr, Dechmann, Wikelski and Richard Suu-Ire (Wildlife Division, Forestry Commission, Ghana). Drs. Fahr and Dechmann did data analysis and paper writing.

Chapter 3

I designed and implemented the experiments, with guidance from Drs. Fahr, Dechmann and Wikelski. I carried out all bat tracking, groundtruthing, colony and food phenology monitoring, as well as data analysis. I wrote the manuscript, under supervision of Dr. Wikelski, and review by Drs. Dechmann and Fahr.

Chapter 4

I designed and implemented the experiments, with guidance from Drs. Fahr, Dechmann and Wikelski. Drs. Fahr, Dechmann, Wikelski and I did bat tracking and groundtruthing in 2009-2011. I carried out all fieldwork and data analysis. I wrote the paper with Drs. Fahr, Dechmann and Wikelski and Ms. Anne K. Scharf.

Several people helped during field- and lab-work, and are acknowledged at the end of each chapter. Dr. Fränzi Körner provided invaluable suggestions for statistical analyses (Chapter 4).

Publications

Peer-reviewed:

Fahr, J., **Abedi-Lartey, M.**, Esch, T., Machwitz, M., Suu-Ire, R., Wikelski, M. and Dechmann, D.K., 2015. Pronounced Seasonal Changes in the Movement Ecology of a Highly Gregarious Central-Place Forager, the African Straw-Coloured Fruit Bat (Eidolon helvum). *PloS one*, *10*(10), p.e0138985.

Accepted:

Abedi-Lartey, M., Dechmann, D.K.N., Wikelski, M., Fahr, J., Scharf, A.K. 2016. Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Global Ecology and Conservation.*

Curriculum Vitae

Michael Abedi-Lartey

(Project Management / Conservation & Environmental Systems Management)

CONTACT & PERSONAL DETAILS

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Nationality: Ghanaian.

EDUCATION

Feb. 2012 – Present **PhD Candidate**

Institution: International Max Planck Research School for Organismal Biology, University of Konstanz, Konstanz, Germany.

Degree: PhD Organismal Biology.

2002 – 2004:

Institution: International Institute for Geo-Information Science and Earth Observation (ITC), Enschede, The Netherlands.

Degree: M.Sc. Geo-Information Science and Earth Observation (*Environmental Systems Analysis and Management* specialization).

1991 – 1994

Institution: Institute of Renewable National Resources (IRNR)
University of Science and Technology, Kumasi, Ghana.

Degree: B.Sc. (Hons) Natural Resources Management (*Wildlife and Range Management*).

KEY PUBLICATIONS

Fahr, J., ***Abedi-Lartey, M.***, Esch, T., Machwitz, M., Suu-Ire, R., Wikelski, M. and Dechmann, D.K., 2015. Pronounced Seasonal Changes in the Movement Ecology of a Highly Gregarious Central-

Place Forager, the African Straw-Coloured Fruit Bat (Eidolon helvum). *PloS one*, *10*(10), e0138985. doi:10.1371/journal. pone.0138985

Tranquilli, S, ***Abedi-Lartey***,***M***., Abernethy, K., Amsini, E., Asamoah, A., Balangtaa, C Blake, S. *et al*. "Protected Areas in Tropical Africa: Assessing Threats and Conservation Activities. "*PloS One* 9, no. 12 (2014): e114154.

Tranquilli, Sandra, ***Michael Abedi-Lartey***, Fidele Amsini, Luis Arranz, Augustus Asamoah, Ogunjemite Babafemi, Nsengiyunva Barakabuye et al. "Lack of conservation effort rapidly increases African great ape extinction risk."*Conservation Letters* 5, no. 1 (2012): 48-55.

Bene, Jean-Claude Koffi, Eloi Anderson Bitty, Kouakou Hilaire Bohoussou, ***Michael Abedilartey***, Joel Gamys, and Prince Aj Soribah. 2013. "Current conservation status of large mammals in Sime Darby oil palm concession in Liberia." G.J.B.A.H.S.,Vol.2(3):93-102.

Abedi-Lartey, M 2004. "*Bushmeat hunters do better: Indigenous vs. Conventional Habitat Evaluation Techniques*". MSc Thesis. International Institute for Geo-Information Science and Earth Observation, Enschede, The Netherlands.

Decher, J, Kadjo B., ***Abedi-Lartey, M***, Tounkara, E. O, and Kante. S. "Une étude rapide des petits mammifères (musaraignes, rongeurs et chiroptères) des Forêts Classées de la Haute Dodo et du Cavally, Côte d'Ivoire." *Une Évaluation Biologique de Deux Forêts Classées du Sud-ouest de la Côte d'Ivoire A Rapid Biological Assessment of Two Classified Forests in* (2005): 91.

Oates, J. F., ***M. Abedi***-Lartey, W. S. McGraw, T. T. Struhsaker, G. H. Whitesides. 2000. *Extinction of a West African Red Colobus Monkey. Conservation Biology*.Vol. 14, No. 5. Pp. 1526-1532.

Abedi-Lartey, M. and Amponsah, J. 1999. *Preliminary survey of anthropoid primates in Krokosua Hills Forest Reserve.*Unpublished report, Protected Areas Development Program and Wildlife Division of the Forestry Commission, Accra, Ghana.

McGraw, W. S., I. T. Monah and ***M. Abedi-Lartey***. 1999. *Survey of endangered primates in the forest reserves of eastern Côte d'Ivoire. African Primates*. 3: 22-25.

Abedi-Lartey, M. 1994. "*Comparative Study of some aspects of reproduction in Maxwell's duiker (*Cephalophus maxwelli*) and Black Duiker (*C. niger*)*". *BSc. Thesis*. Institute of Renewable National Resources, University of Science and Technology, Kumasi, Ghana.

<u>INTERNATIONAL COURSES / WOKSHOPS / CONFERENCES</u>

March 13th –15th 2015	***4th International Berlin Bat Meeting: Movement Ecology of Bats. Berlin, Germany.*** Awarded “Rising Star” prize for most promising research work.
February 9th –15th 2013	***African Bat Conservation Summit: Establishing a Bat Conservation Network - 2013***. Kenya Wildlife Service Training Institute, Naivasha, Kenya.
June 5th –11th 2010	***Community-based Carbon Stock Assessment for Reducing Emissions from Deforestation and Forest Degradation (REDD).*** Dormaa, Ghana.
Nov. 16th –19th 2009	***Bushmeat and Sustainable Livelihoods Workshop: Lessons from Guinea, Liberia and Sierra Leone.*** Tiwai Island, Sierra Leone.
Nov. 18th –20th 2008	***Mano River Union Trans-border Technical Forestry Conference***. Mano River Union States on Trans-boundary Biodiversity Management. Sérédou, Republic of Guinea.
Jun. 9th –21st 2008	***Mobile Seminar on Protected Area Planning and Management.*** Multiple locations nationwide, Costa Rica. Conservation International.
Aug. 6th – 10th 2007	***International Workshop to Prepare a Strategic Plan For the Protected Forest Area Network of Liberia***, Ganta, Liberia.
Apr. 2nd – 6th 2006	***International Conference on the Management of National /Natural Parks and Biodiversity Conservation in Africa.*** Accra, Ghana.
Feb. 11th –11th Mar. 2006	***Refresher Course in GIS and Remote Sensing for Bio-Conservation,*** International Institute for Geo-Information Science and Earth Observation (ITC), Enschede, The Netherlands.
Nov. 28th –Dec. 9th 2005	***The Use of Geo-information as a Tool for Combating Bushfires in West Africa.*** UNU-ITC programme on Capacity Building for Disaster Geo-Information Management; Kumasi, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana.
Oct. 3rd –24th 2004	***Strengthening Capacity for Biodiversity Conservation in West Africa:*** Training of Trainers in Tropical Biodiversity survey and Identification. Kakum and Ankasa, Ghana. BirdLife International and Darwin Initiative.

Sept. 6th -10th , 2004 ***Biodiversity and Management of the West African Rainforests:*** ecological synthesis of knowledge on biodiversity and forests of Upper Guinea. Abidjan, Côte d'Ivoire. Organizers: Ecosyn International.

PROFESSIONAL EXPERIENCE

June 27th 2011 – January 26th 2012.

Project Coordinator

Fauna & Flora International. Liberia Country Office

"Environmental and Social Assessment of Sime Darby Liberia Plantation Project".

- Coordinated a comprehensive environmental and social assessment of a 300,000 ha oil palm concession in western Liberia; included personnel recruitment, project reporting, and lead contribution to the development of an HCV assessment and national interpretation toolkit development.

June 5th – July 5th 2011.

Short Term Consultant (STC)

World Bank -GEF. Liberia Country Office

"Field Verification for Review of Forest Assessments in Liberia".

- Conducted field surveys in Liberia for land cover and land use, as part of GIS-based review of forest assessment practices in Liberia.

August – November 2010.

Chief Technical Advisor/ Project Manager

Fauna & Flora International. Liberia Country Office

"Establishing the Basis for Biodiversity Conservation at Sapo National Park and In South-east Liberia" Project.

- As in Position immediately below, with additional responsibilities for development of Protected Management Plans and management effectiveness assessment.

July 2006 – July 2010.

Chief Technical Advisor/ Project Manager;

Fauna & Flora International, United Kingdom (Liberia country Office)

“Establishing the Basis For Biodiversity Conservation At Sapo National Park and In South-east Liberia” Project.

- Provided strategic direction to Forestry Development Authority efforts to revive Protected Areas management after the civil war, using Sapo NP as the flagship;
- Represented the project and institutional interests at domestic and international fora;
- Nurtured and strengthened FFI’s relations with in-country and international partners;
- Led capacity building of local and international project staff, with emphasis on progressively transferring implementation responsibilities to Liberians;
- Produced draft of first comprehensive park management plan for Sapo National Park, including a management effectiveness assessment framework based on IUCN standards.

May 2005 – June 2006

Protected Areas Planning Manager

Planning Unit, Wildlife Division Headquarters, Accra., Ghana

- National counterpart to IUCN consultancy on PA management planning.
- Coordinated integration of GIS-based decision support systems in protected area management planning;
- Co-authored the development of new, and review of existing management plans for Ghana’s protected areas;
- Coordinated implementation of protected area management plans;
- Coordinated network of inter-sectorial/ministerial contacts in forest conservation sector;
- Coordinated Environmental Impact Assessment programmes in Pas;
- Provided technical assistance on biodiversity conservation inside and outside PAs;
- Coordinated a monitoring and evaluation scheme for protected area management effectiveness.

December, 2000 – May 2005.

Bio-monitoring Unit Manager

Biological Monitoring Unit, National Office, Goaso, Brong-Ahafo Region, Ghana Wildlife Department (now Wildlife Division of Forestry Commission), Ghana

- Established and managed the first Bio-monitoring Unit for Ghana’s Wildlife Department;
- Provided GIS-based decision support for PA planning and management;
- Conducted the first nation-wide wildlife inventory in Forest Reserves in Ghana;
- Developed and integrated a biodiversity monitoring system into PAs and their surrounding landscapes;

- Conducted training programmes for technical and professional personnel in environmental monitoring techniques, problem-animal management, human-wildlife conflict resolution.

September, 1996 – November 2000.

Protected Area Manager (Park Warden)

Nini-Suhien National Park and Ankasa Resource Reserve, Western Region, Wildlife Department

- Co-managed a 4.5 million Euro, EU-funded conservation and development project in two contiguous Protected Areas (Ghana's highest biodiversity hotspot).

Lead responsibilities for:

- Park management, law enforcement, personnel administration, prosecution in court;
- Design and implementation of biological and socio-economic research and monitoring programmes;
- Coordinating park infrastructural development and maintenance (roads and buildings);
- Coordinating the development and implementation of Ghana's first holistic community participation and conservation education programmes: the Community Resource Management (CREMA) programme;
- Supervising the development and implementation of conservation education and eco-tourism development programmes.
- Personnel administration (45 key staff, plus 60-70 variable auxiliary community personnel).
- Conducted field surveys for endangered primates in Ghana and Cote d'Ivoire that led to confirmation of the extinction of the Waldron's red colobus.

November 1994– August 1996.

Assistant Wildlife Officer / Deputy Zoo Manager

Kumasi Zoological Gardens, Ghana Wildlife Department

- Supervised the construction and maintenance of zoo facilities and grounds;
- Conducted research on zoo exhibits, (emphasis on primate and antelope ecology);
- Managed Zoo's Conservation Education Centre (CEC).

SKILLS

Technical/Management

- 21+ years' experience in natural resources planning and management centred on in Ghana, Liberia, and with brief experience in Togo, Burkina Faso, Sierra Leone, Guinea and Cote d'Ivoire.
- Analysis and communication of environmental systems.
- Remote Sensing /GIS applications in natural resources management.
- National-scale natural resource surveys, and in managing and sharing the resulting data obtained.
- Natural resource governance initiatives, such aincluding FLEGT and REDD$^+$ processes, as well as in-depth knowledge of general forestry/wildlife issues in Ghana and Liberia.
- Facilitating collaborative approaches to management of shared natural resources (e.g. trans-boundary protected areas, community participation in protected areas).
- Training-of-trainers in wildlife conservation, law enforcement and community resource management.
- Workshop facilitation, with focus on sustainable use and protection of natural resources.

Communication & Computer skills

- Verbal and written communication, including a computer literacy (Windows Office suite), statistics (XLstat, Minitab, R Statistics), Remote Sensing / GIS (QGIS, ILWIS, OpenJUMP).

LANGUAGE SKILLS

(*Spoken/Written, on a scale of 0-5 for competence where 5 is the highest*)

International:	English: (5/5).	German: (0.5/1).	French: (1/1).
Liberian:	Sapo/Kru: (1/0).		
Ghanaian:	Twi: (5/5).	Ga: (2/1).	Nzema: (1/0).

MEMBERSHIP OF PROFESSIONAL BODIES

- Max Planck Society, Germany
- British Ecological Society
- Fauna & Flora international (FFI)
- World Commission on Protected Areas (WCPA), IUCN.
- Wildlife Conservation Society, Bronx, NY (WCS).
- International Primatological Society (IPS)
- Ghana Association for the Conservation of Nature (GACON).
- Ghana Wildlife Society (GWS).

REFEREES

Academic

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Professional

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   Country Manager
   Fauna & Flora International
   P. O. Box 10-3010, Monrovia, Liberia
   e-mail: *jens.lund17@gmail.com*

2. Mr. Phi Marshall (*Supervisor, Ghana*)
   GFA Consulting Group GmbH
   Namibia.
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