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



Michael Abedi-Lartey^{a,b,c}, Dina K.N. Dechmann^{a,b}, Martin Wikelski^{a,b,c,*},
Anne K. Scharf^{a,b,c}, Jakob Fahr^{a,b}

^a Department of Migration and Immuno-ecology, Max Planck Institute for Ornithology, Am Obstberg 1, 78315 Radolfzell, Germany

^b Department of Biology, University of Konstanz, Universitätsstr. 10, 78464 Konstanz, Germany

^c International Max Planck Research School (IMPRS) for Organismal Biology, Universitätsstr. 10, 78464 Konstanz, Germany

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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 the 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 the 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 maximum 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 distances for large seeds during the dry season (551 m) in the rural landscape were almost twice that in the wet season (319 m). We found no influence of food phenology 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 may traverse large distances, probably making it an important long

* Corresponding author at: Department of Migration and Immuno-ecology, Max Planck Institute for Ornithology, Am Obstberg 1, 78315 Radolfzell, Germany.

E-mail address: wikelski@orn.mpg.de (M. Wikelski).

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distance seed disperser in tropical Africa. We suggest *E. helvum* important for ecosystem functioning and urge its conservation.

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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. Seed dispersal 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 also 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 whereby the influence 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 metres 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., 2012a; Fahr et al., 2015). *Eidolon helvum* seasonally migrates for more than 2000 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. We used feeding trials with fruits offered to short-term captive *E. helvum* to assess their gut passage time (GPT) and monthly counts of an urban (Accra) and a rural (Kibi) colony in the forest zone of Ghana to determine the influence of season and land use on potential seed dispersal. We also monitored food phenology within each landscape as an indicator of seasonal trends in food availability. We used these data to model probability distributions of bat movements and GPT as to ultimately estimate differences in seed dispersal distance kernels and the probability of seed deposition at a given distance from the parent tree (Nathan et al., 2008) foraged by the bats.

Our study showed that *E. helvum* may potentially disperse 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). The estimates of seed dispersal distances 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 highly 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.

2. 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 A). The rural colony (Kibi; Appendix A) was composed of sub-colonies at the 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 to 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 1600 mm, which peaks in May–July and September–November. Average monthly temperature is 24–29 °C.

3. Methods

3.1. 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., 2012a; 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 A) 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 B.

3.2. Bat movement tracking

The movement behaviour of animal dispersers is a key component of the seed dispersal process (Westcot 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 (03:00–06:00 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 $8.6 \pm 1.0\%$ 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 C). Our animal handling protocols followed guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon and Sikes, 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 (GPS locations, 3-axial acceleration data, flight speed and altitude). Loggers were programmed according to regimes consecutively called Cohorts 1–4; logger IDs and settings are detailed in Appendix C. 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 $\geq 500 \text{ ms}^{-1}$, 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.

3.3. 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 focused 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 et al., 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 is available in the electronic appendix. 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 D).

3.4. 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 mucosa*, *F. sur*, *F. trichopoda*), *Milicia excelsa*, and *Anthocleista nobilis*. We housed bats individually in three cages (100 × 50 × 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 ([Clauss et al., 2008](#); [Wahaj et al., 1998](#)). Our initial observations further indicated that *E. helvum* would only consume fresh, fully ripe fruits. Thus, and in contrast to previous studies e.g. ([Kays et al., 2011](#); [Shilton et al., 1999](#); [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 trial for the same bat. Trials per bat ranged from 1 to 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 D). We then randomly drew 1000 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.

3.5. Seed dispersal kernel estimation

3.5.1. 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).

3.5.2. 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 1000 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 (Hodgkinson 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 three distance thresholds (100, 500 and 1,000 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. Results

4.1. Seasonality of colony size and food resources

The urban colony in Accra (Fig. 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 $57,594 \pm 67,624$, median 33,265, $n = 63$ months) were consistently larger than in Kibi (mean $14,174 \pm 11,303$, median 13,487, $n = 38$ months). While fruit and flower phenology also showed some fluctuation in both landscapes, overall food phenology (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 B.

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 returned to colonies at which we made download attempts during each fieldwork period. For a list of tracked individuals and logger settings see Appendix C. All tracking data are deposited on DOI available in the movebank data archive (<https://www.movebank.org/node/15294>).

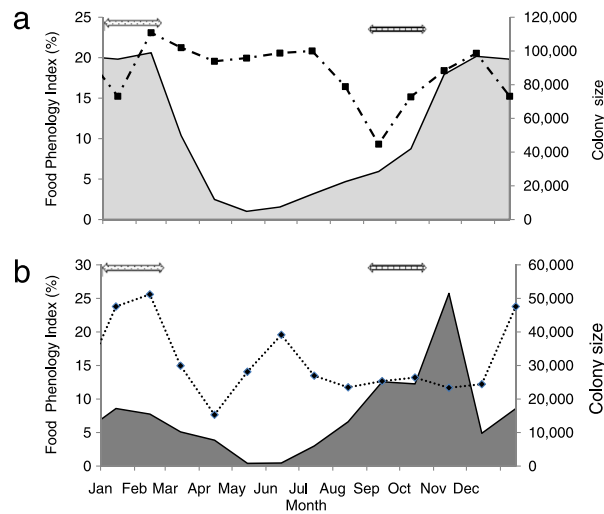


Fig. 1. Seasonal trends in food phenology (line plots) and bat colony size (shaded area plots) at the (a) urban and (b) rural landscapes in the forest zone of southern Ghana. Food phenology is indicated by Food Phenology Index, representing averaged proportion of fruiting plants known to be foraged by *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.

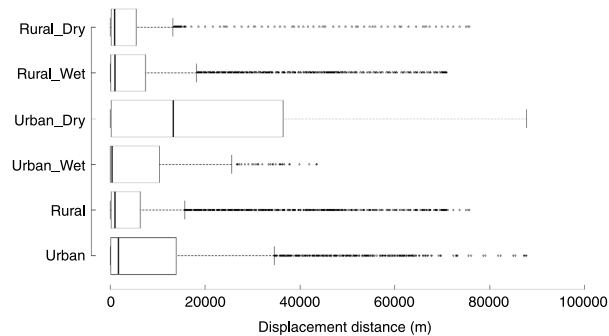


Fig. 2. Boxplots of estimated net displacement distances (metres) of GPS-tracked *E. helvum* after implied feeding during wet and dry seasons in urban and rural landscapes in the forest zone of southern Ghana. Boxplots represent, from left to right: one standard deviation (s.d.) below the mean, lower 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. Bat movement analyses

Net displacement distances of bats from food trees (Fig. 2) were higher in the urban (range 1–87,726 m, median 1678 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, $P < 0.001$).

4.4. Estimation of gut passage times

Mean GPT for small seeds was 116 ± 112 min (range 4–1143 min, median 72 min, $n = 112$ fruits). The probability distribution (Fig. 3) was best-fitted by a lognormal with $\mu = 4.3138853$ (meanlog) and $\sigma = 0.8674429$ (sdlog) (Appendix D).

4.5. Seed dispersal kernel estimation

4.5.1. Large seeds

Dispersal distance estimates for large seeds (Table 1, Fig. 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) landscape. 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).

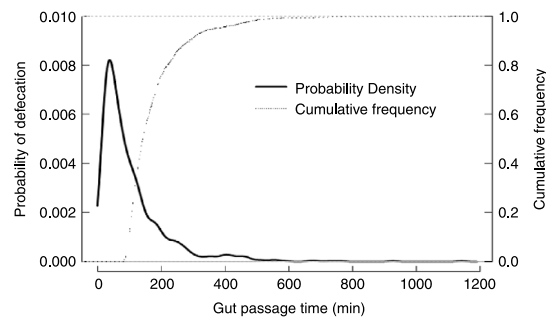


Fig. 3. Estimated probability (bold curve) and cumulative frequency (dotted curve) distribution of Gut Passage Times for small seeds ingested by captive *E. helvum*. Fruits were presented fresh and whole in field-based feeding experiments.

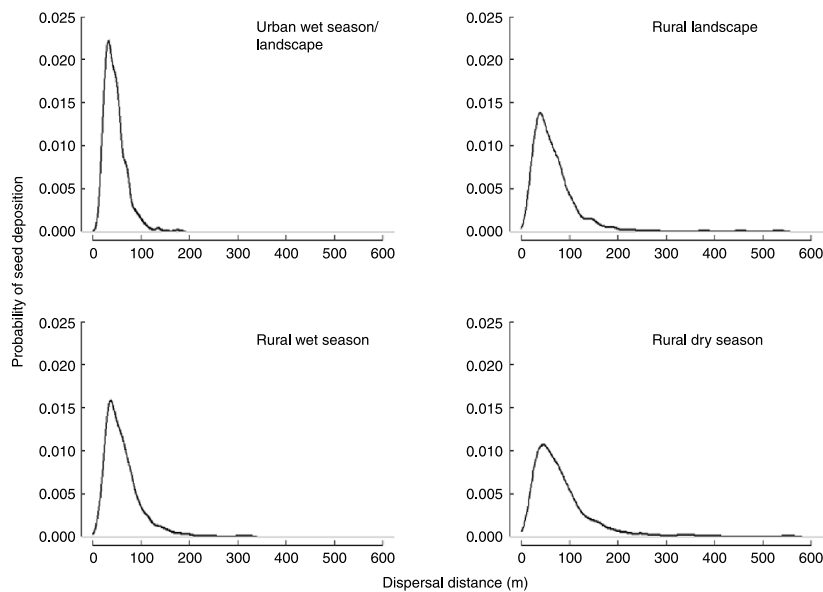


Fig. 4. Estimated dispersal distances of large seeds by *E. helvum* during the wet and dry seasons in an urban and a rural landscape in southern Ghana. X-axes are scaled for all plots to facilitate comparison.

Table 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 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

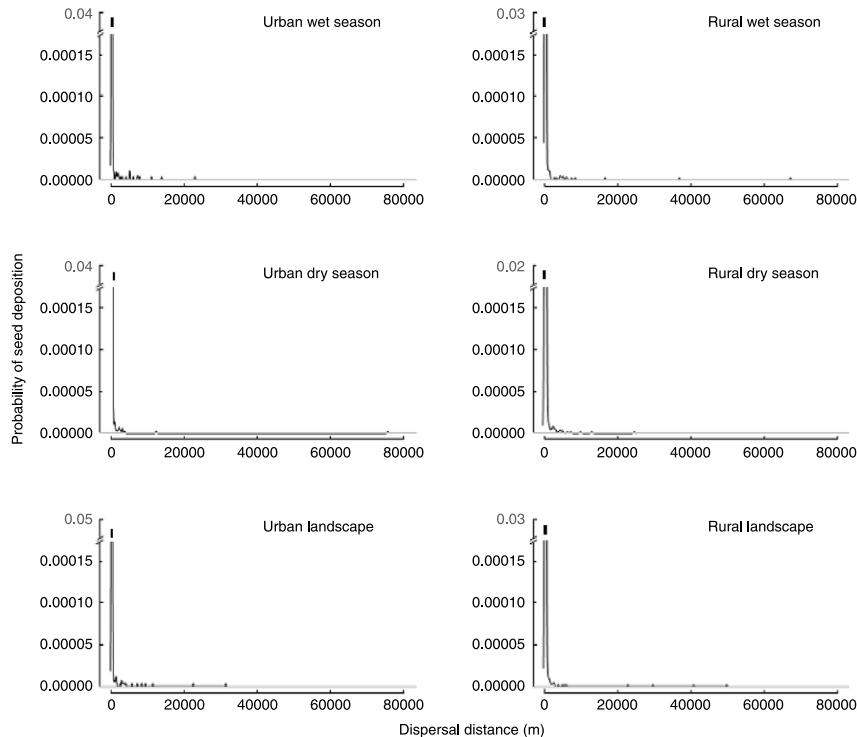
Pairwise comparisons of dispersal estimates showed that differences were significant (two-sample Kolmogorov–Smirnov tests, $P < 0.001$). The probability of large seeds being dispersed over long distances beyond 263 m (distance beyond the feeding roost), i.e., over 500 and 1000 m from a food tree was 0.1% and 0.0%, respectively.

4.5.2. Small seeds

Estimated dispersal distance kernels for small seeds (Table 2, Fig. 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

Table 2Estimated 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	> 1000
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. 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.

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 ($K-S = 0.155$, $P < 0.001$). Cumulative probabilities 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.

5. Discussion

Our results provide evidence for the longest estimates of potential seed dispersal distances by a mammalian frugivore investigated 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 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 important ecosystem functions 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 some of the 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 the ecological role of straw-coloured fruit bats: 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 2000 km seasonally covering several hundred kilometres in a given night (Richter and Cumming, 2008). A fruit consumed early in the night of such migratory flights may potentially be dispersed even 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. 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 a strong seasonal influence on bat movement, with a corresponding influence on potential dispersal distances.

We would like to emphasize that the distinction between small- and large-seeded fruits is important. 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). In this context it is important to note that *E. helvum* often crosses 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. Again, 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, the 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 found in the current study are modest, and could be performed by several other animal seed dispersal vectors. However, the maximal seed dispersal distance we found, 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). Nevertheless, species with higher GPT such as Asian elephants (> 72 h)

potentially transport large seeds over larger distances (> 100 km) (Blake et al., 2009). It is yet unclear whether very long seed dispersal distances also occur in other species and could 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 very valuable.

In summary, our results suggest that *E. helvum* may be one of the 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 and hornbills (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 several 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 58,000 individuals in Accra could potentially disperse some 58,000 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 that 150 million seeds of various sizes are dispersed throughout Africa by these bats per night. This underscores the urgent need to conserve the colonies and habitats of straw-coloured fruit bats to secure these 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 zoonotic diseases such as henipaviruses (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. Such a ground truthing could 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 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; while late succession species such as iroko would maintain established forests. The critical stages occur during (1) forest land conversion (e.g. farming, logging, mining) when suitable individual trees could be retained to proactively facilitate passive regeneration; and (2) during forest restoration initiatives, when suitable fruit trees and feeding roosts could be planted in spatio-temporal configurations that mimic the desired forest structure. Such forests 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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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.03.005>.

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