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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 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) compare 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

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

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