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Seed Dispersal in the Dark: Shedding Light on the Role of Fruit Bats in Africa

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ABSTRACT

In spite of their recognized importance as seed dispersers in other parts of the tropics, seed dispersal by fruit bats has received scant research attention in Africa. To evaluate the role of African fruit bats in seed dispersal, we studied fruits and seeds below 480 bat feeding roosts in the East Usambara Mountains of Tanzania. We compared these findings to those reported in other African localities to place our results in a broader context. We found 49 plant species dispersed by bats: 28 species, 18 genera, and one family are novel reports of bat dispersal in Africa. Approximately 20 percent of the submontane tree flora of the East Usambaras is bat-dispersed, including both widespread and endemic trees. African fruit bats are important seed dispersers at our study site because they move seeds of dozens of species tens or hundreds of meters, even seeds that are too large to ingest (greater than 5 mm in length). Fruit bats are likely important seed dispersers in other Afrotropical forests, as bats elsewhere in Africa are known to consume 20 genera and 16 species of plants reported here. Insights from studying remains under bat feeding roosts offer a simple method to further document and substantially increase our understanding of the role of African fruit bats in seed dispersal.

Key words: Amani Nature Reserve; bat roosts; East Usambara Mountains; forest regeneration; frugivory; Pteropodidae; Tanzania.

Animals that disperse seeds are important drivers of forest regeneration, shaping community composition, structure, and functional dynamics. Animals are estimated to disperse seeds of over 95 percent of angiosperm plants in tropical forests (Terborgh *et al.* 2002), where species with fruits adapted for vertebrate seed dispersal comprise 75–92 percent of the flora (Jordano 2000). Among dispersers, some vertebrates, including African elephants (*Loxodonta africana*), Asian gibbons (*Hylobates* spp.), Neotropical howler monkeys (*Alouatta seniculus*), tamarins (*Saguinus mystax* and *S. fuscicollis*), and African hornbills (*Bycanistes* spp. and *Ceratogymna* spp.) disperse seeds of hundreds of plant species (McConkey 2000, Andresen 2002, Kitamura 2011, Campos-Arceiz & Blake 2011, Culot *et al.* 2011). While vertebrates broadcast seeds of numerous plant species, our knowledge and understanding of the contribution to seed dispersal and recruitment processes by different vertebrate taxa is geographically and taxonomically limited.

Here, we highlight the role of fruit bats as seed dispersers in Africa using new data and literature records. We focus on fruit bats for several reasons: (1) they are small-bodied, but capable of carrying large diaspores or fruits up to 25–250 percent of their body weight over 100 m (van der Pijl 1957); (2) they are important for secondary forest regeneration (Swaine & Hall 1983, Muscarella & Fleming 2007); (3) they have received less research effort than primates, birds, and large mammals; and (4) despite their nocturnal habits, sampling below feeding roosts can expand our knowledge of plant–bat interactions (Voigt *et al.* 2011). We suggest that the paucity of research on African fruit bats underestimates their role in seed dispersal, and seek to catalyze more interest in this important disperser guild.

Throughout the tropics, fruit bats disperse several hundred species of plants (Fujita & Tuttle 1991, Mickleburgh *et al.* 1992, Lobova *et al.* 2009) and facilitate forest regeneration (Banack 1998, Muscarella & Fleming 2007). Phyllostomid fruit bats of the Neotropics are incredibly diverse (approximately 142 species are at least partially frugivorous), dispersing at least 549 plant species in 191 genera from 62 families (Lobova *et al.* 2009). The 170 species of much larger pteropodid bats of Africa, Asia, southern Europe, Australia, and islands in the Indian and Pacific Oceans (Wilson & Reeder 2005) disperse seeds of at least 145 different plant genera (Marshall 1985), with long-distance seed dispersal estimated at 1–20 km for ingested seeds (Tsoar *et al.* 2010). Many studies of seed dispersal in Africa have been limited to daylight observations of frugivore behavior (*e.g.,* Gautier-Hion *et al.* 1985, Cordeiro *et al.* 2004, Gross-Camp *et al.* 2009), thus missing potential dispersal by fruit bats.

As an alternative to observing bats directly, fruit bats leave behind abundant evidence of their foraging behavior directly below locations where they hang to process fruits ('feeding roosts', Voigt *et al.* 2011). The plant material under feeding roosts tends to be scattered in a small radius of ~1–2 m. While processing fruits, the flesh is eaten away from large seeds and the seed is dropped or spit out, sometimes without fruit pulp or with

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partially or fully masticated fruit pulp. Numerous terms, all of which are essentially synonymous, are used to describe these plant remains under bat feeding roosts, including ejecta (*e.g.,* Nyhagen *et al.* 2005), bolus (*e.g.,* Goveas *et al.* 2006), wads (*e.g.,* Corlett 1998), wadges (*e.g.,* Duncan & Chapman 1999), or spats (*e.g.,* Dumont 2003).

Feeding roosts may be far from the food source. African fruit bats typically process fruits and seeds at feeding roosts within 100 m from fruiting trees (*e.g.,* Kankam & Oduro 2009), similar to many fruit bats from other regions (Thomas *et al.* 1988, Melo *et al.* 2009). The fruits they carry can be quite heavy, enabling the dispersal of large seeds. Pteropodid bats, for example, can carry fruits weighing as much as 25 percent (Bonaccorso *et al.* 1980) to 68 percent (Marshall 1983) of their body mass, and in some cases, fruits 250 percent of their body mass can be carried up to 200 m (van der Pijl 1957). Through their feeding behavior, African fruit bats have the potential to move even large seeds among forest, fragments, and farms to facilitate gene flow and colonization for plants.

Our goal is to draw attention to bat frugivory and seed dispersal in Africa by placing our results from one forest into a broader context. We further suggest that fruit bats may be understudied relative to their contribution to seed dispersal, and ultimately encourage more research in Africa.

METHODS

Study site.—Bat feeding roosts were studied in and around the Amani Nature Reserve in the East Usambara Mountains (EUM) of Tanzania (5° 06′ 00″ S, 38° 38′ 00″ E), in the submontane forest from 700 to 1200 m asl. The EUM are part of the Eastern Arc mountain chain that stretches from southeastern Kenya to southern Tanzania. The EUM receive ~ 1900 mm of rain/yr with two rainy seasons and two mild dry seasons (Rodgers & Homewood 1982). Historically, the EUM supported more than 900 km^2 of forest, but today, only 263 km^2 of forest cover remains (Burgess *et al.* 2007). Amani Nature Reserve protects ~84 km^2 of lowland, submontane, and plantation forest in the southern region of these mountains (Doody *et al.* 2001). Non-forested lands are mainly tea plantations and subsistence farms. More than 150 native tree species (diameter at breast height [dbh] $\geq$10 cm) are found in the submontane forest of the EUM (Hamilton & Bensted-Smith 1989, Schulman *et al.* 1998). A preliminary study suggests that approximately 87 percent of submontane tree species have diaspores adapted for animal dispersal (Cordeiro *et al.* 2005). Many of these tree species are endemic or near endemic to the Eastern Arc Mountains (Lovett *et al.* 2006, Burgess *et al.* 2007), although several of the genera are widespread.

Fruit bats of the east usambaras.—Seven species of fruit bats are found in the EUM (nomenclature follows Nesi *et al.* 2012): *Rousettus aegyptiacus* (100–166 g), *Stenonycteris lanosus* (120–165 g), *Myonycteris angolensis* (65–91 g), *Eidolon helvum* (250–311 g), *Myonycteris relicta* (30+ g), *Epomophorus wahlbergi* (54–120 g), and *E. labiatus* (38–70 g) (Kingdon 1974, Bergmans 1980, Rodgers & Homewood 1982, Doggart *et al.* 1999, Doody *et al.* 2001). All of these species are recorded to primarily eat fruit, although most also visit flowers (Nowak 1994). In almost all cases, the genus or species of bat using the feeding roost was not observed, so most observations of frugivory and seed dispersal recorded herein are not attributed to a particular species of bat (except as noted in Table S2).

Plant sampling below bat feeding roosts.—Fruits and seeds were identified from under bat feeding roosts, which were identified by freshly dropped fruit, ejecta, or aggregations of large diaspores on the ground (see Figure S1 for photographs and additional explanation). In African forests, seeds left by fruit bats can easily be distinguished from those defaecated by Two-spotted palm civets (*Nandinia binotata*) and large forest hornbills (*Bycanistes* spp.). Palm civets defecate in conspicuous latrines and hornbills drop seeds at the base of mature trees in which they nest or spread seeds out over a wide area when in large communal roosts and rarely have diaspores larger than 3–4 cm in length (NJC & HJN, unpubl. data). Bat handling was confirmed by the presence of ejecta or fruit parts with teeth and/or claw marks. Identification of common or distinctive plant species was done by visual or olfactory inspection. Specimens that could not be identified in the field were assigned a morphospecies code and collected for a reference collection and/or germination. When possible, voucher specimens were collected for species identification of unknowns.

A total of 480 observations below feeding roosts at 35 different sites were made between February 2000 and October 2011. Each observation includes all of the plant species found in a discrete area below a feeding roost. Of these, 401 observations (80%) were from the ground below feeding roosts encountered in the forest during other fieldwork. The remaining 79 observations were from eight 1 × 1 m^2 seed traps placed below feeding roosts on farms where the daily records were pooled by month to equal one observation. One month is approximately the period of time that seeds are observable under feeding roosts without seed traps (C.E. Seltzer, pers. obs). To assess the completeness of our sampling, we plotted cumulative species richness on the number of observation areas below feeding roosts. Species rarefaction curves were generated using 500 randomizations of the sequence of observations added using EstimateS, v.8.2.0 (Colwell 2009).

Seed sizes.—Plant species were grouped according to length of longest seed dimension as small, medium, or large (Table S2). Small seeds can be swallowed by fruit bats, but medium and large sized seeds cannot, based on a maximum ingestible size of 5 mm for *Pteropus conspicillatus* (Australia, 400–1000 g) (Richards 1990).

Minimum dispersal distances.—Distance to the nearest mature conspecific tree (possible parent) from the feeding roost remains was measured in as many instances as possible. Lianas and vines were excluded from searches. We searched up to 50 m for the nearest adult conspecific in the forest and up to 325 m in

farmland where there are many fewer trees. Observations of species for which the nearest adult could not be located are not included in the minimum dispersal distances. In addition, plant remains found under a conspecific crown were considered as undispersed, and therefore not included in the calculations for minimum dispersal distances. The distance to the trunk was measured in the field, then the average crown radius for each species (or the average of all species for unmeasured species crowns) was subtracted to calculate the distance of dispersal beyond the crown edge.

RESULTS

Plant species found below feeding roosts.—Thirty-seven genera and 44 different species of trees, lianas, and vines dispersed by bats were identified to species, and two identified to genus only. Three morphospecies remain unidentified (Table S1). Four different species of *Ficus* were identified, and other *Ficus* specimens that could not be identified were lumped as *Ficus* spp. (included in the 'two identified to genus only'), which likely contains more than one additional species (at least four other *Ficus* spp. occur in the area). A species rarefaction curve shows that nearly 75 percent of bat-dispersed species were recorded after 150 observations, but new species continued to be added and, even by 480 observations, had not yet leveled off (Fig. 1).

We searched extensively for previous records of bat dispersal for all plant species reported in this study and found that 20 genera and 16 species are recorded from elsewhere in Africa (Tables S2 and S3). We identified 18 other genera not previously known to be dispersed by African bat species and/or in Africa and nearby islands (Tables S1 and S2). Including the newly reported species from previously reported genera, this study adds 28 more species dispersed by bats. Six of the bat-dispersed species are non-native (Table S1). Thirty-six species are trees (dbh $\geq$ 10 cm), six are lianas (woody vines), one is a non-woody vine, and the life form is unknown for five species.

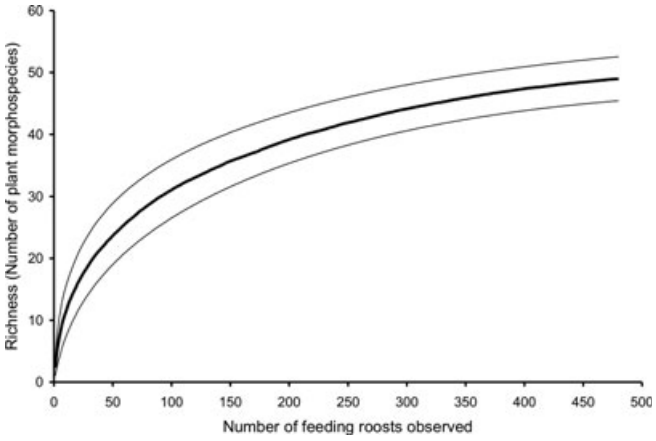


FIGURE 1. Plant species rarefaction curve (bold line) and 95% CI (thin lines) of bat-dispersed species with respect to the number of feeding roosts observed. Curves were smoothed by 500 random reorderings.

Twenty-four and 22 species have also been observed to be dispersed by large birds and primates, respectively (Table S2).

Seed sizes.—Twelve species had small, ingestible seeds (length <5 mm), 31 had medium-sized seeds (5< length <30 mm), and six had large seeds (length >30 mm) (Table S1). Fruit types, colors, and seed dimensions can be found online (Table S2).

Dispersal distances.—Minimum dispersal distances were measured from below feeding roosts to 127 mature trees of 18 different species; the mean minimum dispersal distance was 55.7 m (median = 30.2, range 0.2–320.5 m). The median distances for six tree species with at least seven minimum dispersal distance measures are displayed in Fig. 2. Species for which we searched unsuccessfully for the nearest adult tree are not included in the calculations. The longest recorded distance was 320.5 m for *Cephalosphaera usambarensis* (Myristicaceae) in a farmland setting.

DISCUSSION

Evidence from a single area of Tanzania revealed 49 bat-dispersed plant species, of which 28 species, 18 genera, and one family are novel reports of bat dispersal in Africa. This comprises about 20 percent of the submontane tree flora in the East Usambara Mountains (Ruffo *et al.* 1989, Lovett *et al.* 2006), which is notably more than the six percent of bat-dispersed tree flora found in central French Guiana (Lobova *et al.* 2009) where fruit bats are more widely recognized for their role as seed dispersers in the Neotropics. Furthermore, bat dispersal of 16 species and 20 genera is confirmed in other parts of tropical Africa, underscoring the widespread contribution of fruit bats to seed dispersal and regeneration across the continent.

Not only do bats disperse seeds of several plant species in and around the Amani Nature Reserve, they also disperse species with a wide range of seed sizes. Seed size has been shown to be an important influence on how seeds are handled and dispersed (Wheelwright 1985). Because bats can swallow small seeds while ingesting fleshy pulp (Utzurrum & Heideman 1991), it is likely that our estimates of the number of small-seeded species are conservative as small seeds could be defecated in flight, hidden by leaf litter, or rot quickly. Many species of bats, especially in the Paleotropics, are known to disperse seeds much larger than they are capable of ingesting (Muscarella & Fleming 2007). It is noteworthy that most plant species recorded in our study (37 of 49) have seeds that are too large to be swallowed by bats. Bats appear to play an important role in the dispersal of large-seeded species, and in many instances, these non-ingested seeds are often dispersed far from the nearest possible parent.

In our study, distances to the nearest possible parent ranged from 0.2 to 320.5 m (median = 30.2, mean = 55.7), and distances exceeding 100 m were not uncommon (20.5 percent of 127), especially for bat roosts in farmland (Fig. 2). Three reasons suggest that these are conservative estimates of dispersal distances: (1) these represent the minimum possible dispersal distances in each case, as the nearest conspecific is not necessarily

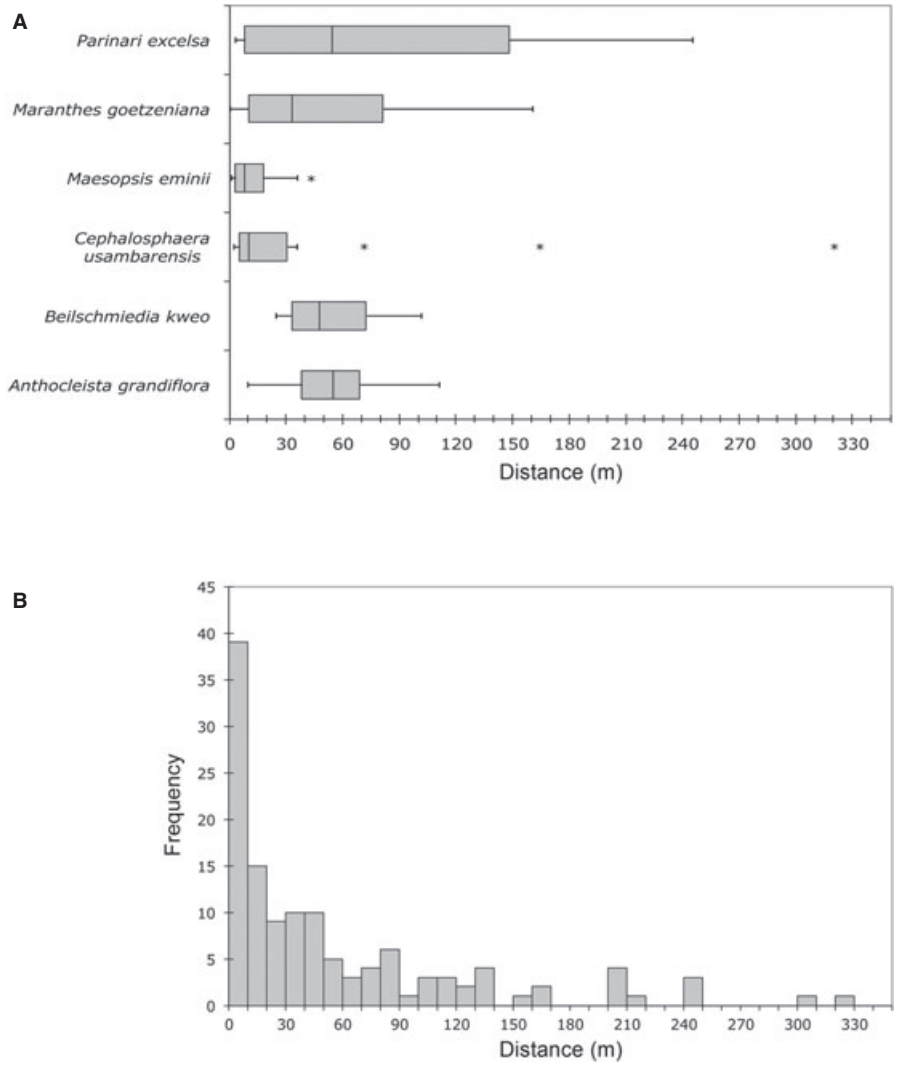


FIGURE 2. Minimum dispersal distances beyond nearest conspecific tree canopy for bat-dispersed species in the East Usambara Mts. (A) Box plots display the minimum dispersal distances for six tree species with $N \geq 7$. (B) Histogram of minimum dispersal distances for all species together ($N = 127$).

the original source (Hardesty *et al.* 2006); (2) in several instances, the nearest conspecific was not located, so no distance was recorded (distances searched ranged from 50 to 325 m from feeding roosts); and (3) all distances are from spat out fruit or seeds, but defecation of ingested, small-seeded species likely occurs over larger distances (such as those modeled by Tsoar *et al.* 2010). For these reasons, we suspect that the actual dispersal distances are often further than recorded here (Fig. 2). African fruit bats are certainly capable of dispersing large-seeded species hundreds of meters. In the fragmented landscape surrounding the Amani Nature Reserve, movement of bats between small patches of forest, isolated trees, or low-density stands in farmland likely facilitates the transport and deposition of seeds to distant sites.

How representative is the bat-dispersed flora of the EUM for other places in Africa? We suspect that other moist forests may have similar proportions of bat-dispersed species because: (1) fruit bats are found throughout African forests: and (2) several plant species and genera in this study are widely distributed. Frugivory and seed dispersal by bats for 16 species and 20 genera was corroborated by literature records from all over the continent (Tables S2 and S3). The wide distribution of fruit bats and some of their favored plants suggests that the EUM are not anomalous, but rather that Africa has many more bat-dispersed species than have been published to date. Of African studies, the most extensive sampling has been on islands such as Pemba (Entwistle & Corp 1997), Madagascar (Bollen 2007, Picot *et al.* 2007, Racey *et al.* 2009), and Mauritius (Nyhagen *et al.* 2005), except for one unpublished dissertation from Ivory Coast (Thomas 1982). Studies in Zambia (Richter & Cumming 2006) and Benin (Djossa *et al.* 2008) that used remains below feeding roosts to record bat diets (combined with direct observation or fecal samples, respectively) found only six species each under feeding roosts. We suggest that these low numbers may not be representative of African

forests because Richter and Cumming (2006) limited their observations to the season of *Eidolon helvum* migration and to *E. helvum* diets, and Djossa *et al.* (2008) carried out their study in an area that was more savanna than forest, with correspondingly lower tree diversity than evergreen African forests. With a more intensified approach to studying bat feeding roosts elsewhere in Africa, we predict similar proportion of bat-dispersed trees in other Afrotropical forests.

We suspect that there is considerable overlap in the dietary preferences of fruit bats and other animals, as 45 percent and 49 percent of bat-dispersed species in the EUM have been observed to also be consumed by primates or large birds (Table S2). Given the diffuse relationship between plants and their animal dispersers, fruit bats might act as effective dispersers in fragmented or heavily degraded habitats after primates and other larger vertebrates disappear (but see Vanthomme *et al.* 2010). Predicting which seed dispersers continue to function in altered landscapes requires an analysis of fruits consumed and seeds dispersed not only by bats (*e.g.,* Geiselman *et al.* 2002 for the Neotropics) but also by all major vertebrate dispersers in Africa, as well as the differential contributions of animal species to patterns of seed dispersal (Jordano *et al.* 2007, Nathan *et al.* 2008). African fruit bats clearly disperse seeds, but studies quantifying subsequent seed fates are needed to measure their effectiveness and relative importance as dispersers for different plant species.

Although bats are seldom hunted in East Africa (with the exception of Pemba Island), hunting large fruit bats such as *Eidolon helvum* is much more widespread in central and west Africa (Mickleburgh *et al.* 2009). Degradation and habitat loss are, however, growing issues for Afrotropical forests, and no studies to date have evaluated how African fruit bats are impacted by these activities. In any event, loss of fruit bats, as found in Pacific islands, limits recruitment of late successional, large-seeded species in native forests (McConkey & Drake 2006), and affects bat-dispersed species of high economic and agroforestry value, such as the Shea nut *Vitelleria paradoxa* of western Africa (Djossa *et al.* 2008). It is necessary to understand the role that bats play in seed dispersal to predict the impact of habitat loss or bushmeat hunting on the plant communities in Africa.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Plant species found below bat feeding roosts, grouped by seed size and alphabetized by family.*

TABLE S2. *Additional information about plant species from Table S1.*

TABLE S3. *Published observations of bat dispersal of different plant species in the same genera as species in Table S1.*

FIGURE S1. Photographs of fruits, seeds, and seedlings below bat feeding roosts.

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