Supplemental information

Linking colony size with quantitative estimates of ecosystem services of African fruit bats

Mariëlle L. van Toor, M. Teague O'Mara, Michael Abedi-Lartey, Martin Wikelski, Jakob Fahr, Dina K.N. Dechmann

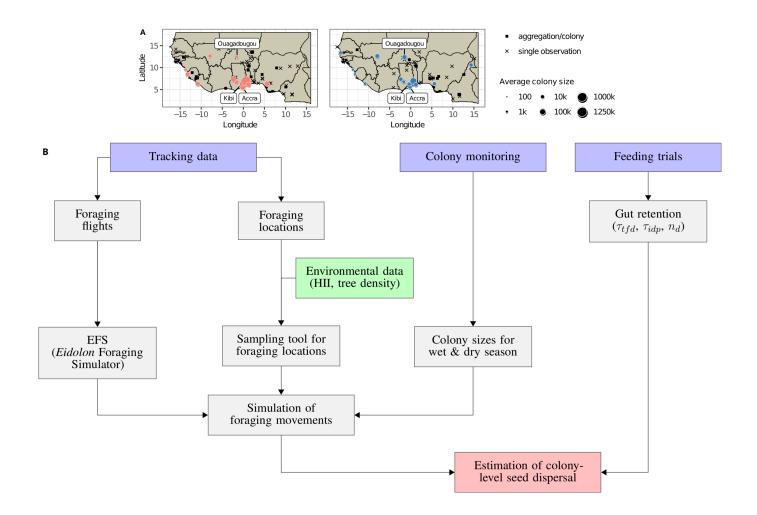
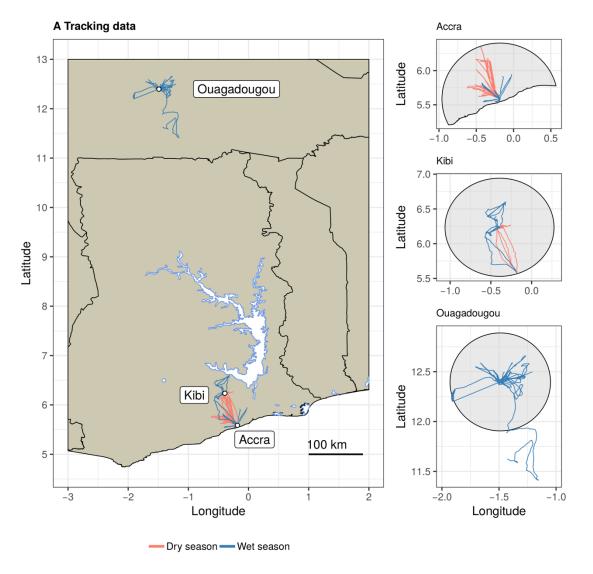


Figure S1: **A** Maps showing the colonies monitored by the *Eidolon* Monitoring Network in West Africa, along with sightings of *Eidolon helvum* from iNaturalist. Data for the dry season shown on the left, data for the wet season on the right. Dispersal distances for the monitored colonies are available in Figure 1 in the main manuscript. **B** The flowchart describes how we used the available data to derive colony-level estimates of seed dispersal.



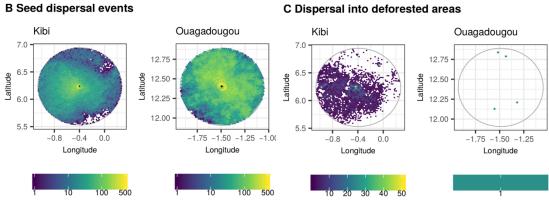


Figure S2: **A** Map of the study area showing the tracks collected for the colonies in Accra, Kibi in Ouagadougou, with close-ups of the tracking data on the right. Pinkish lines how tracks recorded during the dry season, blue lines tracks recorded during the wet season. Maps in **B** show the total number of simulated seed dispersal events thought to occur during a single night for Kibi (79,000 in total) and Ouagadougou (110,000 in total). Maps in **C** show the number of simulated dispersal events occurring in deforested areas in Kibi and Ouagadougou. All hexagons have a diameter of 2.5km, and summarize the results of events occurring in each hexagon representing an area of 5.3km². The black dot in the middle of the circles marks the location of the colony. See Figure 1 in the main document for results from the Accra colony.

Supplemental experimental procedures

Study species

The straw-coloured fruit bat (*Eidolon helvum*, Kerr 1792) is a keystone seed disperser [S1]. It is arguably the most numerous mammal of Africa [S1-S3] and occurs in colonies from thousands to millions of individuals across sub-Saharan Africa [S1-S3] (Figure S1 A). These bats commute up to 88km from a central colony each night to forage on fruit and nectar [S4]. Large fruits with medium to large seeds are typically shuttled over tens to hundreds of meters between the fruit trees and feeding perches [S5, S6]. However, seeds of small-seeded fruits of pioneer tree species such as figs (*Ficus spp.*), or economically valuable species like Iroko (*Milicia excelsa*) can be dispersed over many kilometers. *Eidolon* has the largest known capacity for long distance seed dispersal with up to 75km [S4]. *Eidolon* is also one of the few migratory African bat species, probably following the phenological waxing and waning of food resources across sub-Saharan Africa [S3, S7] causing large seasonal population fluctuations. Monitored colonies have decreased sharply in size, partially due to hunting and persecution [S8], and the overall population size is assumed to be declining which has led to a IUCN re-classification of the species as near threatened [S19, S20].

Population monitoring

Many frugivores do not qualify as efficient seed dispersers as they never leave the canopy cover, defecate or drop seeds near the parent tree and/or predate seeds entirely [S10, S11]. Most frugivorous species move seeds over distances of 20–500m [S1, S12-S18]. In addition, individual tracks give some insight, it is necessary to expand to the population level for a more comprehensive understanding of the impact a species has on seed dispersal. Colonies of *Eidolon* have been subject to long-term counts throughout their distribution range as part of a standardized monitoring scheme by the "*Eidolon* Monitoring Network",

where colonies are counted at the roosting sites on a roughly monthly basis. Our three colonies are located in Accra and Kibi (both in Ghana), and Ouagadougou (in Burkina Faso). The Accra and Kibi colonies are located in the tropical forest zone approximately 80km apart. Colony sizes peak during the dry season, though some individuals stay all year around. Ouagadougou is located in the savanna zone and the colony is only occupied for a few months during the wet season. Count data were available from Accra since February 2008, from Kibi since August 2012, and from Ouagadougou since April 2010, providing a detailed picture of colony fluctuations throughout the year. We determined the minimum and maximum number of individuals present at the colonies for each year since the start of monitoring. To determine peak and minimum colony size across years, we calculated the median for both minimum and maximum colony counts for the colonies in Accra (dry season: 152,306, wet season: 4,017), Kibi (dry season: 41,435, wet season: 4,005), and Ouagadougou (wet season: 68,900), respectively. We ignored incomplete years, as these could bias the estimates by inflating the minimum colony size (minimum colony size not yet been observed) or underestimating the peak colony size (peak has not yet been observed).

Feeding trials and gut retention time

Results from feeding trials with *Eidolon* were available from a previous study [S5]. During the trials, 20 bats were fed with fresh and ripe fruit from four tree species: *Milicia excelsa*, *Anthocleista nobilis* and two fig species (*Ficus sur*, *F. trichopoda*). All four species have small seeds; figs are considered pioneering species, whereas *Milicia excelsa* is an economically valuable species of hardwood. Fruits were individually color-marked so that the sequence of gut passage could be accurately reconstructed.

We derived an empirical cumulative distribution to identify the probability of a defecation event as a function of time since feeding or last defecation event. We calculated the time between feeding event and first defecation, τ_{ttd} , and the time between consecutive defecation events, or inter-defecation period τ_{idp} , from the feeding trial data. We pooled the data for the feeding trials of all individuals and computed an empirical cumulative distribution function for both τ_{tfd} and τ_{idp} . The median time between ingestion of a fruit and the first defecation τ_{tfd} was 54.8 min (n=57, 95% confidence intervals: [35,75]), and the median time between defecation events τ_{idp} was 28.8 min (n=61, 95% confidence intervals: [15,40]). In addition, we counted the number of defecation events resulting from a single fruit, n_d (range: 1–4). We derived these numbers for each feeding trial, and for each of the fruits fed during the trial separately. The data and additional details are available in Data S1.

Capture and tracking of *Eidolon* in Accra, Kibi, and Ouagadougou

Bats were caught at the colonies in Ghana during both the wet season (Accra: n=8, Kibi: n=8) and the dry season (Accra: n=9, Kibi: n=4) from 2009 to 2013, and at the colony in Ouagadougou, Burkina Faso, during the wet season in 2014 (n=14). All bats were equipped with loggers that recorded the GPS-locations of individuals every 2.5–5min during flight (see Data S1), as well as bursts of 3D-accelerometry. Animal handling protocols followed the Sikes $et\ al.$ [S21] and requirements of the Ghana Wildlife Division, Forestry Commission.

Ghana:

We tracked bats on the grounds of the 37 Military Hospital, Accra (5.586° N, 0.185° E) from 2009 to 2013, and in the garden of the king's palace in Kibi (6.234° N, 0.395° E) from 2011 to 2013 to quantify bat movements. We tracked bats between periods of high (January-March) and low (August-October) colony size in both landscapes to assess the effect of seasonal variation in movement patterns on seed dispersal distances [SError! Reference source not found.]. We captured bats with canopy mist nets [SError! Reference source not found.] and a 10 m-high macro net [S4] as they returned from foraging at dawn (03:00h-06:00h), and kept them in soft cloth bags until processing. We fitted 27 adult males in Accra (body mass 272.9±24.3g) and 14 adult males at Kibi (body mass 268.4±14.1g) with GPS loggers (e-obs, Munich, Germany). The mean mass of logger plus collar was 21.0±1.8g and 24.8±1.8g, for Accra and Kibi. Logger mass was 8.6±1.0% of the bats' body mass, below the recommendation of O'Mara et al. [S22] that the weight of tags should not exceed 10% of the body mass of larger bats. The attachment method ensured that the bats would loose the tags after a few days (see below for details). Loggers were programmed according to cohort 3 (Accra, dry season), cohort 1 and 2 (Accra, wet season, n=4 for each cohort), and cohort 4 (Kibi, both dry and wet season).

Burkina Faso:

In Ouagadougou the colony was situated in the Parc Urbain Bangr-Weoogo (12.398° N, 1.489° W). We caught bats in the local wet season in August-September 2014 and June-July 2013. We followed the same procedure as in Accra and Kibi, and captured bats in canopy nets at dusk and dawn, weighed them, and measured their forearm. Only adult males with body mass >270g in good condition were equipped with GPS loggers (e-obs, Munich, Germany, mass 24g). Logger mass made up 9.5±0.5% (n=5) in 2013 and 9.3±0.6% (n=8) of bats' mass in 2014. Loggers were programmed according to cohorts 3 (n=2) and 4 (n=12). Bats were released under the colony immediately after processing.

Logger settings:

We tracked bat movements during 18:00h-06:00h local time with logger settings as described by Fahr *et al.* [S4]. The GPS loggers are capable of recording several types of data (GPS locations, 3-axial acceleration data, flight speed and height). Loggers were programmed according to regimes consecutively called Cohorts 1-4. Acceleration data were collected all day at intervals of 15s per minute at a byte count of 1188 (56.23Hz). Acceleration axes for all loggers were X=left-right, Y=backward-forward, and Z=up-down. Cohort 1 and Cohort 2 (2009) were programmed for delayed start at 06:00h on the morning following release. Cohort 1 collected GPS-fixes at a regular interval of 600s during GPS on-times. Cohort 2 collected GPS-fixes at the same rate until the animal was moving at a speed of 5ms⁻¹, after which they switched to a GPS-interval of 300s. Cohort 3 (2011) and Cohort 4 (2012-2013) started data collection immediately at release of the animal; GPS-on times were 18:10h-06:00h and 17:59h-06:01h. GPS-fixes for Cohort 3 and Cohort 4 were acceleration-informed. They collected fixes every 1800s until the bat started flying, then switched to fixes every 300s (Cohort 3) and 150s (Cohort 4). All loggers stopped data collection when the battery voltage fell below 2.7V to ensure sufficient power for data download.

Logger attachment:

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 [S4]. 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 [S22]. 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.

Data availability

Some of the tracking data from Accra and Kibi were previously published [S4, S5] and all data are accessible on the Movebank Data Repository under DOI 10.5441/001/1.44183438. Data from the feeding trials are available in Data S1. Colony count data were made available to us by the "Eidolon Monitoring Network", and can be requested from the network via contact with J. Fahr (see also the AfriBats project on iNaturalist).

Simulating seed dispersal at the colony level

Eidolon Foraging Simulator

Foraging distances of *Eidolon* change dramatically between the wet season when they feed on fruit and the dry season when they switch to nectar and pollen (straight-line distance from the colony up to 88km one way [S4]). We simulated their foraging movements with a movement model (empirical Random Trajectory Generator, eRTG [S23, S24]) that generates conditional random trajectories with a fixed start and end location while remaining well within the distributions of step lengths and turning angles observed in actual *Eidolon* foraging movements. The eRTG is conditional, i.e. it simulates the movement between two locations with a fixed number of steps based on a dynamic drift derived from a step-wise joint probability surface. The process is attracted to the destination location and the strength of attraction is modulated by the time left to reach the target. Thus, the eRTG is similar to a biased correlated random walk and can be best described as a mean-reverting Ornstein-Uhlenbeck process [S25]. The eRTG uses empirical tracking data as a template, and takes empirical distributions of several characteristics of animal movement at a fixed sampling interval as input. This enables the model to simulate random conditional trajectories resembling the template tracking data at the same temporal scale.

We extended this basic conditional movement model by including a stochastic switch between flying movements (commuting) and remaining in a single location (foraging and resting). A single simulated trajectory can include several foraging locations. As a consequence, the *Eidolon* foraging simulator (EFS) required several additional parameters in the form of empirical distributions. These are the duration of time spent at a foraging location ($\tau_{foraging}$), the Euclidean distance between subsequent foraging locations ($d_{locations}$), and the number of foraging locations visited during the entire night ($n_{foraging}$). We derived all the required information from the tracking data (see above), and provide details on how this was achieved in the Supplemental method details (see below). The model was based on data from all individuals and seasons.

Simulating foraging movements with the EFS

We simulated foraging movements at each of the three colonies for a single night during both the wet and the dry season with the EFS. The number of simulated trajectories corresponded to the median number of bats present at the colonies during the highest and lowest population count. Prior to initiating the simulation of individual foraging movements, we determined the initial location, corresponding to a bat's first food tree during that night, according to two environmental parameters (tree density [S26] and human influence index [S27]). As we do not know how individuals of single colonies disperse in the landscape to forage, we applied two different schemes for a weighted random sampling of foraging locations. The first

sampling scheme assumed that covering large distances to the feeding grounds comes at no cost to the individual bat (environmental sampling, or "ES scheme"). The second sampling scheme assumed that traveling large distances does come at a cost to foraging bats (distance-scaled environmental sampling, or "DES scheme"). For both sampling schemes, the initial foraging locations of simulated bats were sampled from a circle surrounding colonies, with the radius corresponding to the maximum observed foraging distance for the respective colony and season. We rounded these distances up to the nearest kilometer, resulting in circles with radii of 88km (dry season) and 44km (wet season) in Accra, 76km for both seasons in Kibi, and 51km in Ouagadougou. All sampled foraging locations were weighted by environmental information: initial as well as later foraging locations were positively weighted by tree density and negatively weighted by human influence index, meaning that locations were more likely to be sampled from areas with high tree cover and low human impact. The sampling was additionally weighted by inverse distance from the colony for the DES scheme. We have provided more detail for the sampling of initial foraging locations in section and the corresponding R-code in Data S1.

We simulated the foraging movements for the Accra and Kibi colonies during dry season and of all three colonies during the wet season with the EFS; and repeated the process for both the ES and DES sampling scheme.

Simulating seed dispersal

For the simulation of defecation along the foraging simulations, we made the assumption that bats ingested fruit right before leaving the foraging sites. We established a time counter for each foraging location the bats used and set it to zero the moment the bat left the respective location, i.e. there was a separate counter for each foraging location. After each subsequent relocation (every 5min), the time counter was updated with the time since leaving the foraging location, and we performed a binomial experiment with two possible outcomes: no defecation, or defecation at that location. The probability of a defecation event was determined by the time since leaving the foraging location and the empirical cumulative distribution function for time to first defecation τ_{ttd} . If a defecation event occurred, the time counter was reset to zero. The binomial experiment was repeated for each subsequent location of the trajectory until the individual reached the colony, but after the first defecation event τ_{ttd} was exchanged for τ_{tdp} , representing the interval between defecation events (see Data S1 for corresponding R-code).

Seed dispersal distances

After finishing all simulation processes, we removed defecation locations above water bodies. We used the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG [S28]) to identify

the spatial dimensions of water-bodies in the study area using the GSHHG Level 1 (seashore) and Level 2 (lakes) at the highest available resolution (mean point separation of 178 m [S28]). Subsequently, we calculated the distance between foraging location and the corresponding dispersal events for each trajectory using geodesic distances as an indicator of dispersal distance. We then used non-parametric bootstrapping (1000 replicates) to determine the median dispersal distance for each colony, season, and sampling scheme, and computed the corresponding 95% confidence intervals for the median.

Seed dispersal into deforested areas

Median estimates of monetary value provided by forest ecosystems range between \$1127 and \$2355 per hectare per year [S29], making long-distance seed dispersal and its effects for the regeneration of cleared areas a crucial ecosystem service. Identifying which species contribute substantially to seed dispersal and forest regeneration, and understanding how these services are affected by changes in population size, is thus pivotal to the understanding and conservation of forest ecosystems [S30]. To assess areas of recent forest loss in the vicinity of the colonies, we used publicly available high-resolution global maps of forest loss [S31]. These maps are derived from LandSat imagery and provide information whether, and during which year a 30x30m pixel was deforested (data are available for 2001-2016). We converted deforested pixels within the corresponding circles around each colony to polygons coded by the year when deforestation occurred.

We then counted the number of seeds dropped in each of the deforested pixels using a point-in-polygon or spatial overlay algorithm. This algorithm tested for each seed dispersal event whether the corresponding defecation location was located within any of the deforested pixels. This also allowed us to determine the number of deforested pixels into which seeds were dispersed during a single night. We then estimated the median percentage of pixels and corresponding 95% confidence intervals that might become reforested by an entire colony within a single night using non-parametric bootstrapping (1000 replicates) using the different years as replicates. Similarly, we estimated the median number of seeds dropped in deforested pixels and 95% confidence intervals by non-parametric bootstrapping (1000 replicates) over the different years. Again, we computed these numbers for each of the colonies, seasons, and sampling schemes.

We also estimated the monetary effect of the ecosystem services provided by the colonies in Ghana. Damnyag *et al.* [S32] estimated that deforestation in Ghana results in a loss in annual gross revenue of \$133,650,000 for an average deforestation of 128,733ha. This gross revenue was estimated for six forest areas in Ghana, and included estimates for the value of edible fruit, stumpage fees, loss in soil fertility, and avoided carbon emission [S32]. Using the estimates from the study, we calculated the lost revenue per hectare of forest to estimate the additional revenue resulting from reforestation as \$1038.195 per hectare.

We then computed the deforested area affected by *Eidolon* seed dispersal as indicated above, and calculated the additional revenue if these areas were to be reforested. Finally, we calculated the additional revenue provided by the regeneration of forest patches cleared during 2001–2016 affected by *Eidolon* seed dispersal per individual bat in the corresponding colony and season. Please note that these estimates do not directly represent the contribution of *Eidolon* colonies to ecosystem services, but rather the monetary value of ecosystem services of deforested areas - if deforestation were reversed - and which were affected by *Eidolon* seed dispersal in our simulations.

Code availability

We have provided complementary R-code and data in Data S1 to explain the key steps performed in this study. Please not that we used custom computer code written for R to run the empirical Random Trajectory Generator (eRTG [S23]). The package and accompanying paper are currently under development.

Supplemental detailed results

The EFS uses the movement geometry of empirical trajectories (step lengths, turning angles, their covariance and their auto-correlation) to realistically capture the foraging trajectories of tracked individuals. Consequently, the foraging movements simulated with the EFS are representative of actual foraging movements of the individuals that informed it. We simulated the foraging movements of 541,326 individuals from three colonies during two seasons, using two different schemes for sampling initial foraging locations. Out of these simulations, 20,126 (about 9.6%) failed due to errors that can occur randomly (e.g. if the single foraging site for the night was located very close to the colony), or due to the eRTG aborting the simulation (the simulation failed to reach a foraging location or the colony within the available amount of time). Consequently, the results for dispersal distances and dispersal into deforested areas represent estimates for about 89% (Accra, wet season) to 99% (Ouagadougou, wet season) of the individuals present at the colonies.

Our simulations suggest that an individual *Eidolon* commutes for substantial distances in a single night (median: 67.1km, 25%-quantile: 45.3km, 75%-quantile: 90.1km; measured from the initial foraging location and not including shuttling flights between fruit trees and feeding roosts). Bats defecate seeds about 2-3 times (range: 0-14) during commuting flights. Numbers of individual defecation events within a single night ranged from about 5,448 (Accra during the population minimum) to 338,342 (Accra during the population maximum) for the entire colonies. While the density of dropped seeds increased towards the site of the colony, substantial numbers of seeds were defecated further away. The numbers of seeds dispersed outside a 5km radius around a colony ranged between 5'316 (Accra during the wet season,

92.1% of all dispersal events) and 336,362 (Accra during the dry season, 94.2% of all dispersal events). Overall, the percentage of seeds dropped outside this 5km radius was greater than 91% for all colonies, seasons, and sampling schemes.

We found that the results from the seed dispersal simulations did not differ between the sampling schemes, with similar estimates for dispersal distances and dispersal into deforested areas for both the ES and DES scheme. Below, the results for the ES are listed in the text, and results for the DES in parentheses.

Seed dispersal distances

The combined simulation of foraging movements of *Eidolon* and defecation events allowed us to derive estimates of seed dispersal distances. Seed dispersal distances varied greatly, ranging from a minimum of five meters to a maximum of 95.7km (see Figure 1 A in the main document). Here, we report the median distances, and the 95% confidence intervals (95% CIs) on the median, which we determined by 1000-fold non-parametric bootstrapping

Accra colony

The highest median dispersal distance was observed for the colony in Accra during the dry season (Figure 1 A in the main document), where dispersal distances averaged to 21.4km with 95% CIs of 21.26km-21.51km (DES scheme: 21.52km [21-39-21.66]km). During the wet season, when only about 4,000 individuals are present at the colony, the average dispersal distances were considerably smaller with a median of 12.55km with 95% CIs of 12.15-12.95km (DES scheme: 12.68km [12.34-13.05]km).

Kibi colony

Our simulations suggested a median dispersal distance of 17.70km with 95% Cls of 17.55-17.86km (DES scheme: 17.89km [17.72-18.05]km) for the Kibi colony during the dry season. This did not differ much from the wet season, for which we found median dispersal distances of 17.72km with 95% Cls of 17.17-18.31km (DES scheme: 17.34km [16.87-17.84]km).

Ouagadougou colony

The colony in Ouagadougou is only present during the wet season. Our predictions suggested a median dispersal distance of 13.71km with 95% CIs of 13.62-13.79km (DES scheme: 13.83km [13.76-13.92]km).

Colony-level dispersal into deforested areas

Accra colony

In the years from 2001 to 2016, between 9,323 and 203,023ha were deforested each year in the area surrounding the Accra colony (circle with radius of 88km). The simulation of seed dispersal suggested that during the dry season, about 853 of a total of 338,342 defecation events (bootstrapped median of years 2001-2016, 95% CIs: 612-1075 events, see Figure 1 D in the main document) occurred above deforested pixels (DES scheme: 845.44 [600-1627.84]). These seeds were deposited in areas corresponding to about 1.7% of the average area deforested per year (bootstrapped median of years 2001-2016, 95% CIs: [1.60-1.74]%; DES scheme: 1.7% [1.55-1.73]%). During the wet season (population minimum), individuals from the Accra colony dropped about 20 (95% CI: 11-43 seeds) out of a total of 5,448 seeds per night in deforested pixels (DES scheme: 10 seeds [5.17] seeds), which were dropped above about 0.1% (95% CIs: 0.096-0.112%) of the deforested pixels (DES scheme: 0.08% [0.06-0.1]%).

Kibi colony

In the years from 2001 to 2016, between 15,747 and 352,295ha were deforested each year in the area surrounding the Kibi colony (circle with radius of 76km). During the dry season, the Kibi colony dispersed about 259 (95% CIs: 15-374 seeds, see Figure S2 C) of a total of 79,212 seeds into deforested pixels (DES scheme: 263 seeds, [155-409] seeds). The affected area corresponded to 0.37% (95% CIs: 0.33-0.39%) of the total deforested area (DES scheme: 0.37% [0.32-0.39]%). During the wet season, individuals dropped about 27 seeds (95% CI: 12-41 seeds) out of a total of 7,780 seeds per night in deforested pixels (DES scheme: 24 [13-33] seeds), affecting about 0.04% (95% CIs: 0.04-0.04%) of the cleared pixels (DES scheme: 0.04% [0.03-0.4]%).

It should be mentioned that the foraging areas of the Accra and Kibi colonies overlapped by about 9,300 km², which probably leads to cumulating effects. In addition, the West African forest zone is home to many more colonies and smaller aggregations of these fruit bats (see Figure S1 A), likely leading to a much greater impact of this species than estimated here.

We also estimated the monetary effects of forest regeneration services provided by the colonies in Accra and Kibi using the estimates of a lost gross revenue of \$133,650,000 per year due to deforestation in Ghana published by Damnyag *et al.* [S32]. We found that the deforested areas affected by *Eidolon* seed dispersal during the dry season would, if deforestation in these areas were completely reversed, bring an additional annual revenue of \$280,831.7 for the Kibi colony (affected deforested area: 270.5ha), and \$858,068.2 (affected deforested area: 826.5ha) for the Accra colony, assuming all individuals forage on small-seeded fruit. For the wet season, additional annual revenue would amount to \$25,435.8 (affected

deforested area: 24.5ha) in Kibi and \$11,939.2 (affected deforested area: 11.5ha) in Accra, respectively. These results suggests that during a single night, every individual of the *Eidolon* colonies in Ghana feeding on small-seeded fruit contributes seeds to an area, that if completely reforested, could provide an additional annual revenue of \$6 (median estimate for the Accra and Kibi colonies during both dry and wet season). Even though the dispersal of seeds into deforested areas is only the first step to reforestation, *Eidolon* colonies might contribute substantially to the agricultural gross revenue on the African continent, as conservative figures put the global population size of the species at about 10 million individuals.

Ouagadougou colony

The sparsely forested savanna habitat around the colony located in Ouagadougou (circle with a radius of 51km) suffered from annual deforestation of about 24-3,015ha in the years from 2001 to 2016. We did not observe substantial dispersal events into deforested areas despite the overall number of 110,731 dispersal events (see Figure S2 C).

Building the *Eidolon* foraging simulator

We derived all the empirical estimates required to inform the EFS from the available tracking data. The tracks of individual *Eidolon* were previously assigned a "percent flying" during a 15-s period of 3D-accelerometry logged during the sampling of GPS-locations using the approach described by Abedi-Lartey *et al.* [S5]. We used this information to filter the entire tracking data for GPS-locations marked as 100% flying behavior. We identified the parts of the data where at least four such consecutive fixes (i.e., no missing locations and a sampling interval of five min±30s) were available. From these short parts of data, we calculated the flight speed of the individual as geodesic distance divided by the time between subsequent locations, the turning angle, as well as the change of both flight speed and turning angle at a lag of one step. We then calculated the distance covered within 300s, or 5min from the flight speed estimate assuming a constant speed, which we used as our estimate for step length.

To derive the required empirical estimates for the extensions made for the EFS, we segmented the foraging trips made by the tracked *Eidolon* individuals. We used an expectation-maximization binary clustering approach with a temporal smoothing on the scale of one hour (EmbC [S33]) to behaviorally annotate the tracking data. The EmbC returns up to four behavioral classes, which are usually interpreted as resting, intensive search, travelling/relocation, and extensive search behaviors. We subsequently reclassified these into "foraging" (grouping behavioral classes characterized by low speed) and "commuting" (grouping behaviors characterized by high speed). We then split the data according to changes between these two behaviors excluding locations within 1000m of the colony site to not confuse foraging and resting at foraging locations with roosting behavior at the colony. For each individual and

night, we then identified unique foraging locations, which often consisted of a food tree and a feeding roost, and determined the time the individual spent there t_i . We also determined the distances between subsequently used foraging locations d_i , and the number of foraging locations the individual used during the night n_i .

Sampling schemes for selecting initial foraging locations

We simulated foraging movements of bats during a single night, with the number of simulations corresponding to the median number of bats present at the colonies during the highest and lowest population count (see section C). The number of simulations varied between 0 (during the dry season in Ouagadougou) and 152,306 individual trajectories (during the dry season in Accra).

Prior to initiating the simulation of individual foraging movements, it was necessary to determine the initial location, corresponding to a bat's first food tree during that night. As we do not know how individuals of single colonies disperse in the landscape to forage, we used the ES and the DES schemes. Foraging locations were sampled from a circle around each colony using the maximum observed distances from the colony during both population maximum and minimum. We rounded these distances up to the nearest kilometer, resulting in circle radii of 88km (maximum) and 44km (minimum) in Accra, 76km for both population maximum and minimum in Kibi, and 51km in Ouagadougou. In Accra the computed circle was intersected with the coastline of Africa to exclude non-terrestrial habitat from sampling. Both the ES and DES sampling scheme sampled foraging locations randomly, but according to environmental correlates, with locations that were more similar to actual foraging locations of Eidolon (as determined from the tracking data) having a higher probability of being sampled. To describe foraging locations environmentally, we used two available remote sensing products with a resolution of 1km2, namely tree density (MODIS Vegetation Continuous Fields version 5.1 [S26]) and human influence index (HII, [S27]). We annotated the actual foraging locations identified from the tracking data with these products, and derived 2D-kernel density estimates for the values for tree density and HII for each of the colonies separately. We then mapped the density estimates back onto a raster with 1km² resolution representing the potential foraging area (circle with a radius respective to colony and season around each colony).

Simulating the foraging movements of *Eidolon* with the EFS

For each simulated trajectory, we initially sampled the number of foraging locations the individual would visit during its trip, and the time it would spend at each of these sites according to the empirical distributions obtained from the tracking data. Subsequently, we sampled the initial foraging location for the

individual. To do so, we applied a random spatial sampling on the sampling raster to choose one of the raster cells available in the circle around the colony. The sampling was weighted by the probability of cells being chosen according to the corresponding sampling scheme. Finally, we performed a random spatial sample within the chosen cell of 1km^2 size to determine the starting location. In case the bat would use more than one foraging site, we sampled distance ($d_{\text{locations}}$) and commuting time (τ_{foraging}) to the subsequent foraging location according to the 2D-kernel density of the empirical estimates. We then drew a circle with the radius of $d_{\text{locations}}$ around the current foraging location, cropped the environmental sampling layer to the boundaries of the circle, and sampled a location according to the procedure of the ES scheme. We determined the required number of steps n_{step} between foraging locations using

$$n_{step} = d_{locations} / (v_{avg} * 300s) (1[BC1])$$

where v_{avg} corresponds to the average speed of the bat, which multiplied with 300 seconds results in an average step length for a five minute interval. If the number of required steps was one, we assumed a beeline movement without initiating the movement model. If the number of required steps was smaller than five (the minimum number of steps required by the empirical Random Trajectory Generator; hereafter eRTG) yet larger than one, we divided the step length distribution of the EFS by five and initiated the eRTG between locations (with a step duration of 1min rather than 5min and assuming that movement parameters on these scales are part of the same distributions).

After a bat visited its last foraging locations, we initiated the eRTG between the location of last foraging and the colony. The number of available steps for the simulation was determined by dividing the distance between foraging location and colony by the average step length, and rounding up the resulting value. The simulation terminates as soon as the bat reaches the colony.

Supplemental References

- [S1] Racey, P. 8,000,000 fruit bats: Africa's best-kept wildlife secret. Bats 22, 1–5 (2004).
- [S2] Sørensen, U. G. & Halberg, K. Mammoth roost of nonbreeding straw-coloured fruit bat *Eidolon helvum* (Kerr, 1792) in Zambia. *Afr. J. Ecol.* **39**, 213–215 (2001). 10.1046/j.1365-2028.2000.00281.x.
- [S3] Richter, H. V. & Cummings, G. S. Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *J. Zool.* **268**, 35–44 (2006). 10.1111/j.1469-7998.2005.00020.x.
- [S4] Fahr, J. *et al.* 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**, e0138985 (2015). 10.1371/journal.pone.0138985.
- [S5] Abedi-Lartey, M., Dechmann, D. K. N., Wikelski, M., Scharf, A. K. S. & Fahr, J. Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Glob. Ecol. Conserv.* **7**, 12–24 (2016). 10.1016/j.gecco.2016.03.005.

- [S6] Seltzer, C. E., Ndangalasi, H. J. & Cordeiro, N. J. Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. *Biotropica* **45**, 450–456 (2013). 10.1111/btp.12029.
- [S7] Ossa, G., Kramer-Schadt, S., Peel, A. J., Scharf, A. K. & Voigt, C. C. The movement ecology of the straw-colored fruit bat, *Eidolon helvum*, in sub-Saharan Africa assessed by stable isotope ratios. *PLoS ONE* **7**, e45729 (2012). 10.1371/journal.pone.0045729.
- [S8] Kamins, A. O. *et al.* Uncovering the fruit bat bushmeat commodity chain and the true extent of fruit bat hunting in Ghana, West Africa. *Biol. Conserv.* **144**, 3000–3008 (2011). 10.1016/j.biocon.2011.09.003.
- [S9] Convention on the Conservation of Migratory Species of Wild Animals: *Eidolon helvum*. http://www.cms.int/en/species/eidolon-helvum (2012). Accessed: 2018-04-12.
- [S10] Janzen, D. H. Seed predation by animals. *Annu. Rev. Ecol. Syst.* **2**, 465–492 (1971). 10.1146/annurev.es.02.110171.002341.
- [S11] Bodmer, R. E. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* **23**, 255–261 (1991). 10.2307/2388202.
- [S12] Westcott, D. A., Bentrupperbäumer, J., Bradford, M. G. & McKeown, A. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia* **146**, 57–67 (2005). 10.1007/s00442.005.0278.y.
- [S13] Blake, S., Deem, S. L., Mossimbo, E., Maisels, F. & Walsh, P. Forest elephants: Tree planters of the Congo. *Biotropica* **41**, 459–468 (2009). 10.1111/j.1744-7429.2009.00512.x.
- [S14] Anderson, J. T., Nuttle, T., Saldaña Rojas, J. S., Pendergast, T. H. & Flecker, A. S. Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proc. R. Soc. Lond. B* rspb20110155 (2011). 10.1098/rspb.2011.0155.
- [S15] Kays, R., Jansen, P. A., Knecht, E. M. H., Vohwinkel, R. & Wikelski, M. The effect of feeding time on dispersal of *Virola* seeds by toucans determined from GPS tracking and accelerometers. *Acta Oecol.* **37**, 625–631 (2011). 10.1016/j.actao.2011.06.007.
- [S16] Lenz, J. *et al.* Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proc. R. Soc. Lond. B* **278**, 2257–2264 (2011). 10.1098/rspb.2010.2383.
- [S17] Hirsch, B. T., Kays, R., Pereira, V. E. & Jansen, P. A. Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecol. Lett.* **15**, 1423–1429 (2012). 10.1111/ele.12000.
- [S18] Stevenson, P. R., Link, A., Onshuus, A., Quiroz, A. J. & Velasco, M. Estimation of seed shadows generated by Andean woolly monkeys (*Lagothrix lagothricha lugens*). *Int. J. Primatol.* **35**, 1021–1036 (2014). 10.1007/s10764.014.9795.z.
- [S19] Mickleburgh, S., Hutson, A. M., Bergmans, W., Fahr, J. & Racey, P. *Eidolon helvum. The IUCN Red List of Threatened Species* e.T7084A12824968 (2008). 10.2305/IUCN.UK.2008.RLTS.T7084A12824968.en
- [S20] Hayman, D. T. S. *et al.* Demography of straw-colored fruit bats in Ghana. *J. Mammal.* **93**, 1393–1404 (2012). 10.1644/11-MAMM-A-270.1.

- [S21] Sikes, R. S. & Gannon, W. L. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**, 235–253 (2011). 10.1644/10-MAMM-F-355.1.
- [S22] O'Mara, M. T., Wikelski, M. & Dechmann, D. K. N. 50 years of bat tracking: device attachment and future directions. *Methods Ecol. Evol.* **5**, 311–319 (2014). 10.1111/2041-210X.12172.
- [S23] Technitis, G., Weibel, R., Kranstauber, B. & Safi, K. An Algorithm for Empirically Informed Random Trajectory Generation between Two Endpoints. online (GIScience 2016: Ninth International Conference on Geographic Information Science, 2016). https://doi.org/10.5167/uzh-130652.
- [S24] Technitis, G., Weibel, R., Kranstauber, B. & Safi, K. On old tracks to new insight: Random trajectories on recorded paths. *Move. Ecol.* (in preparation).
- [S25] Smouse, P. E. *et al.* Stochastic modelling of animal movement. *Phil. Trans. R. Soc. Lond. B* **365**, 2201–2211 (2010). 10.1098/rstb.2010.0078.
- [S26] DiMiceli, C. *et al.* Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010, Collection 5 percent tree cover. *University of Maryland, College Park, MD, USA* (2011).
- [S27] Wildlife Conservation Society-WCS & Center For International Earth Science Information Network-CIESIN-Columbia University. Last of the wild project, version 2, 2005 (lwp-2): Global human influence index (hii) dataset (geographic) (2005).
- [S28] Wessel, P. & Smith, W. H. F. A global, self-consistent, hierarchical, high-resolution shoreline database. *J. Geophys. Res.* **101**, 8741–9743 (1996). 10.1029/96JB00104.
- [S29] de Groot, R. *et al.* Global estimates of the value of ecosystems and their services in monetary units. *Ecosyst. Serv.* **1**, 50–61 (2012). 10.1016/j.ecoser.2012.07.005.
- [S30] Stoner, K. E., Riba-Hernández, P., Vulinec, K. & Lambert, J. E. The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. *Biotropica* **39**, 316–327 (2007). 10.1111/j.1744-7429.2007.00292.x.
- [S31] Hansen, M. C. *et al.* High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013). 10.1126/science.1244693.
- [S32] Damnyag, L., Tyynelä, T., Appiah, M., Saastamoinen, O. & Pappinen, A. Economic cost of deforestation in semi-deciduous forests a case of two forest districts in Ghana. *Ecol. Econ.* **70**, 2503–2510 (2011). 10.1016/j.ecolecon.2011.08.012.
- [S33] Garriga, J., Palmer, J. R. B., Oltra, A. & Bartumeus, F. Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLoS ONE* 11, e0151984 (2016). 10.1371/journal.pone.0151984.