Current Biology
Magazine

CellPress

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

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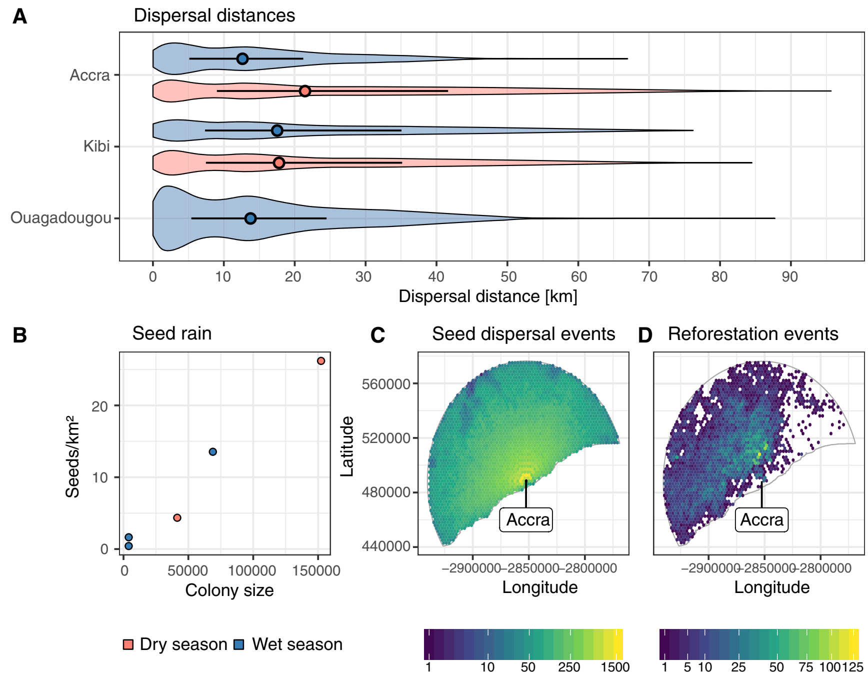

Figure 1. Results of the seed dispersal simulations.
(A) Seed dispersal distances for each of the focal colonies. Violin plots show the entire distribution of simulated seed dispersal events. Points indicate the median dispersal distance, and the line represents the range between the 25% and 75% quantiles. (B) Spatial density of dispersed seeds within the area from which foraging locations for simulated bats were sampled as a function of colony size. Maps in (C) and (D) show the range of foraging movements for the Accra colony during the dry season (note that Accra is a coastal town). All hexagons have a diameter of 2.5 km, and summarize the results of events occurring in each hexagon representing an area of 5.3 km². (C) Total number (N = 338,000) of simulated seed dispersal events predicted to occur during a single night. (D) Number of simulated dispersal events occurring over deforested areas. See Figure S2 for the results for the Kibi and Ouagadougou colonies.

Animal-mediated seed dispersal is a pivotal component of functioning forest ecosystems all over the globe. Animals that disperse seeds away from their parental plants increase the seeds' chances of survival by releasing them from competition and specialised predators and so contribute to maintain the biodiversity of forests. Furthermore, seeds dispersed into deforested areas provide the opportunity for reforestation. Forest regeneration especially depends on animals that cover large distances easily and cross forest gaps, in particular large-bodied frugivores or mobile species such as birds and bats [1]. Yet, frugivores have started to disappear from forests everywhere, with potentially dramatic consequences for forest composition, regeneration and overall forest biomass [2,3]. Identifying which species contribute substantially to the dispersal of viable seeds, and how these services are affected by fluctuations in population size, is thus pivotal to the understanding and conservation of forest ecosystems [4]. Here, using simulations based on tracking data, gut retention times and population counts we show that the seed dispersal services of the straw-coloured fruit bat are unique, not only in terms of dispersal distance, but also in the number of dispersed seeds per night as well as the potential for forest regeneration.

The straw-coloured fruit bat (*Eidolon helvum*) is a prime candidate for a keystone seed disperser. This large fruit bat is one of the most numerous frugivores in Africa, occurring in colonies of thousands to millions of individuals from which bats fly out each night to forage on fruit and nectar. Previous efforts have established that *Eidolon* can displace medium and large seeds over several hundred meters and has the largest known capacity for the dispersal of small-seeded plant species, with dispersal distances of up to 75 km [5]. The vast dispersal distances provided by *Eidolon* have led to suspicions that the species might have assisted the spread of non-native plant species. Yet we think that these effects are outweighed by the ecosystem services *Eidolon* provides [6]. The species is an important seed disperser of small-seeded pioneering plants, such as figs, and for economically valuable species such as Iroko (*Milicia excelsa*). Similar to other species of frugivorous bats [1,7], it is thought that handling by *Eidolon* does not harm, or even enhances, the germination of seeds. *Eidolon* is also one of the few migratory African bat species, probably following the waxing and waning of food resources. An Africa-wide monitoring network has revealed large seasonal fluctuations in colony size [8] with strong effects on local ecosystem services that are amplified by increasing pressure through hunting and persecution.

In this simulation study, we investigated the theoretical potential of *Eidolon* colonies for long-distance dispersal of small seeds and seed rain into deforested areas. We quantitatively estimated seed dispersal by three colonies of *Eidolon* in West Africa using a movement model integrating *Eidolon* foraging ecology with colony monitoring data, high-resolution tracking data (n = 43), and gut retention of small seeds estimated from feeding trials (n = 20). We simulated foraging movements of all bats present at the colonies during the dry and wet season, and quantified seed dispersal and dispersal distances. These predictions were made under the theoretical assumption that all individuals feed exclusively on small-seeded fruit. We also quantified seed dispersal into deforested areas as an estimate of the colonies' contribution to forest regeneration, and approximated the potential value of these ecosystem services (for details on data collection and analyses, see Supplemental information; for documented R-code and data, see Data S1).

We found that the average bat covered a distance of 67.1 km from its foraging tree to the colony, and visited one to three different trees each night. It dispersed seeds over distances of up to 95 km, with averages ranging between 12.6 and 21.4 km, depending on colony and season (Figure 1A). For the entire colony in Accra (Ghana), which consists of about 152,000 individuals during the dry season, we estimated up to 338,000 dispersal events during a single night, producing an average seed rain of 26.2 dispersal events per km^2 (Figure 1A). During the wet season, when the colony is occupied by only 4,000 individuals, the number of dispersal events per night dropped to a mere 5,500. Results for the colonies in Kibi (Ghana) and Ouagadougou (Burkina Faso) scaled similarly with colony size.

We used seed rain over clear-cut areas to estimate the potential contribution of *Eidolon* to forest ecosystem services. Especially in Ghana, deforestation affects 128,733 ha on average per year, and reduces the country's gross revenue by US$133,650,000 every year [9]. During the dry season, at peak colony size in Accra and Kibi, bats dispersed seeds into 826.5 and 270.5 ha of the areas deforested in the period between 2001 and 2016 (Figures 1C,D). Complete reforestation of these areas could contribute an additional annual gross revenue of $858,068 (Accra) and US$280,832 (Kibi) through e.g. stumpage fees. During the wet season, when most bats migrate away, this potential contribution dropped to 11.5 ha (Accra; additional annual gross revenue of $11,939) and 24.5 ha (Kibi; $25,436). In this naturally sparsely forested savanna habitat surrounding the colony in Ouagadougou, the number of dispersal events into clear-cut areas were negligible. The estimates for additional gross revenue were made for fully matured forest for which seed rain as provided by *Eidolon* is merely a first step.

Especially in forested landscapes, *Eidolon* form enormous colonies consisting of hundreds of thousands of individuals. Conservative figures put the global population size of the species at about 10 million individuals, suggesting that such super-colonies might assist forest regeneration through substantial seed dispersal, and thereby help to maintain valuable forest ecosystem services. Yet, populations of *Eidolon* and many other frugivores are in decline, and forests are becoming increasingly fragmented throughout the tropics [6]. This development severely endangers not only the functioning and maintenance of forest ecosystems [3], but together with increasing deforestation also the livelihood of people. Quantitative studies that estimate the effect of these species on the landscape level and link them to population size remain scarce. Our study indicates that the loss of *Eidolon* might endanger the functioning of forest ecosystem by limiting recruitment and gene flow. Below a certain threshold level, the beneficial effects of seed dispersal services provided by *Eidolon* might decrease disproportionately, and even collapse entirely [10]. The protection of large fruit bat colonies should thus be a winning strategy.

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures, supplemental experimental procedures, and supplemental references, and can be found at https://doi.org/10.1016/j.cub.2019.02.033.

ACKNOWLEDGEMENTS

We thank the Executive Director and staff, and especially Richard Suu-Ire of the Forestry Commission in Ghana for help with logistics and research permission. Work on the grounds of the 37 Military Hospital was under permission of Colonel Samuel Bel-Nono. We thank Kofi and Husein Bagulo (Accra), Isaac Agyare (Kibi), and Ambroise Ouedraogo (Ouagadougou) for help in the field. David Kayman, Kate Baker, Andres Fernandez Loras and David Turkson contributed to the colony estimates. Anne Scharf annotated and organized the data. Daisy Dent and two anonymous reviewers provided feedback on a previous version of this manuscript. The study was funded by the Max Planck Institute for Ornithology (Radolfzell), and a grant from the International Max Planck Research School for Organismal Biology to M.A.

AUTHOR CONTRIBUTIONS

M.T., M.O., J.F. and D.D. conceived the experiment; M.A., J.F., M.W., and D.D. collected the data; M.T. performed the analyses; M.T., M.O., and D.D. wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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