Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes

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Frugivorous birds provide important ecosystem services by transporting seeds of fleshy fruited plants. It has been assumed that seed-dispersal kernels generated by these animals are generally leptokurtic, resulting in little dispersal among habitat fragments. However, little is known about the seed-dispersal distribution generated by large frugivorous birds in fragmented landscapes. We investigated movement and seed-dispersal patterns of trumpeter hornbills (Bycanistes bucinator) in a fragmented landscape in South Africa. Novel GPS loggers provide high-quality location data without bias against recording long-distance movements. We found a very weakly bimodal seed-dispersal distribution with potential dispersal distances up to 14.5 km. Within forest, the seed-dispersal distribution was unimodal with an expected dispersal distance of 86 m. In the fragmented agricultural landscape, the distribution was strongly bimodal with peaks at 18 and 512 m. Our results demonstrate that seed-dispersal distributions differed when birds moved in different habitat types. Seed-dispersal distances in fragmented landscapes show that transport among habitat patches is more frequent than previously assumed, allowing plants to disperse among habitat patches and to track the changing climatic conditions.

Keywords: movement ecology; fragmentation; climate change; land-use; frugivory; long-distance seed dispersal

1. INTRODUCTION

Over recent decades, tropical and subtropical forests have become smaller and more fragmented [1,2]. This results in increasing difficulties for plant and animal species to move among these fragments. The isolation of forests and forest fragments, and limited exchange of individuals, can have severe demographic and genetic consequences [3–5]. Exchange of individuals among fragmented populations is important to allow organisms to adapt to changing environmental conditions [6,7]. This problem is further accelerated by global climate change, which forces organisms to track changes in the geographical position of their preferred climatic niche [8,9]. Dispersal limitations are particularly pressing for organisms that cannot disperse by themselves, such as fruit-bearing trees [7].

Most tropical and subtropical tree species are dispersed by frugivorous animals (frequently birds) [10,11]. For these trees, dispersal among forest fragments requires the movement of birds among these fragments. To be efficient seed dispersers, birds have to move large distances and should be able to cross the ‘matrix habitat’, often farmland, which separates the forest fragments. Large fruit-eating bird species have the potential to move within fragmented landscapes and to fly between patches of forest [12–14]. Species that should be able to act as seed dispersers among forest fragments in an agricultural landscape are hornbills in Southeast Asia and Africa, and toucans in the Neotropics [15–17]. Nevertheless, to our knowledge no study has so far investigated seed dispersal of large frugivorous birds such as hornbills in a fragmented landscape containing only small and distant patches of suitable habitat.

To quantify the seed-dispersal pattern of trees, one possible approach is to track the movement patterns of the birds using radio-telemetry, to measure gut passage times (GPTs) of seeds, and to combine both distributions to calculate an average seed-dispersal distribution [18]. So far, this approach has been used very successfully for quantifying short-distance seed-dispersal patterns within habitats (i.e. within forests [16,18–21]; for a definition of short- and long-distance seed dispersal, see [22]).

In contrast, little is known about long-distance seed-dispersal patterns among forests or forest fragments [6,7,23]. For example, movement patterns of hornbills have been studied within a tropical rainforest in Cameroon [16]. Some data demonstrate that in periods of fruit scarcity in the forest, birds appear to start long-distance movements of up to 290 km [24]. A telemetry study on toucans demonstrated that these birds move readily among forest patches through farmland [15].
Nevertheless, to our knowledge no quantitative data on long-distance movement patterns and seed dispersal among forests and forest fragments exist for hornbills or toucans. Furthermore, it is not known whether seed-dispersal distributions differ if a bird is moving within continuous habitat (e.g. within a large forest) or among patches of suitable habitat (e.g. forest patches in an agricultural matrix).

An important region for studying large-scale movement patterns of birds is South Africa. The few forests occur mostly along the east coast and are heavily fragmented. These forests are a global hotspot for tree diversity [25] and are expected to suffer profoundly from global climate change [26]. The trumpeter hornbill (Bycanistes bucinator) is the largest obligate frugivorous bird in South Africa and the species is abundant along the east coast [17,27]. We predicted trumpeter hornbills to be the most promising long-distance seed-dispersal agents in eastern South Africa. To assess whether the tree diversity along the east coast can be conserved under climate change, one prerequisite is to demonstrate whether trumpeter hornbills are able to disperse seeds among forest fragments.

We used a novel telemetry device—GPS loggers (e-obs GmbH, Munich, Germany [28])—to track movement patterns of trumpeter hornbills in large remnants of continuous forest and in the agricultural landscape containing little suitable habitat. We conducted feeding trials of captive hornbills to assess GPTs, and combined movement patterns and GPTs to derive seed-dispersal distributions. To assess how habitat influenced movement patterns and seed-dispersal distributions, we quantified seed-dispersal distributions at times when birds moved within continuous forests and at times when they foraged in the agricultural landscape with few, small and distant patches of suitable habitat.

2. MATERIAL AND METHODS

(a) Study site and species

Forests occur in South Africa mostly along the east coast. The study area lies within one of the recognized global hotspots of biodiversity: the Maputaland-Pondoland-Albany hotspot, which contains nearly 600 tree species (the highest tree diversity of any of the world’s temperate forests) [25]. Climate change is expected to have severe consequences for South Africa, and in particular for the forests along the east coast, which are expected to shift their altitudinal and latitudinal position [26]. At the same time, these forests are expected to suffer profoundly from global climate change [26]. The trumpeter hornbill is the largest obligate frugivorous bird in South Africa [17]. Even during the breeding season, 89 per cent of its food items are fruits [17]. The trumpeter hornbill is a medium-sized hornbill, with an average body weight of 550 g for females and 720 g for males. Trumpeter hornbills have a large gape width, which allows them to swallow and also to transport large seeds. In Oribi Gorge, trumpeter hornbills are among the most abundant frugivores [27].

(b) Trapping and tracking of trumpeter hornbills

Trumpeter hornbills were caught using canopy mist nets in fruiting fig (Ficus spp.) or mahogany trees (Trichilia spp.), or using free-standing nets placed in flying routes to and from these trees. The birds were weighed, measured and ringed. Only males were fitted with GPS loggers, because females enclose themselves in cavities during breeding and we were worried loggers could interfere with their breeding behaviour. A logger weight of 27 g is below the generally accepted threshold of <3–5% body weight [32] (males weighed on average 743 g; range 600–835 g). GPS loggers were attached like a backpack. We used Teflon strings with predetermined breakage points as backpack straps, allowing loggers to drop-off eventually.

The GPS loggers measure the position of the bird with GPS quality at predetermined times. In our case, they were programmed to measure the position in time intervals of 15 min during daytime, the activity period of the hornbills. At night, the loggers were switched to standby mode as the GPS data was stored in the logger and can be downloaded to a handheld base station through a radio link. Using yagi antennas, handheld as well as fixed on the roof of a car, we improved the range for a successful download to distances up to 2 km. The battery of the loggers lasted on average 18 days for data sampling (maximum 26 days). A data download is possible also after the GPS logger stopped recording locations, because the battery saves energy for a last download process. Once we released the birds, we searched for them, systematically starting from the trapping point and continuously extending the area. Successful data downloads led us to new habitat patches used by the birds for foraging or for spending the night.

We tested the precision of the location data by placing loggers in the open and under tree canopies, and measuring the distance between the true location and the location recorded by the logger.

(c) Feeding trials

To determine GPTs, we made feeding trials on two captive trumpeter hornbills (one male, one female), housed at the Max-Planck Institute for Ornithology, Radolfzell, following established methods (e.g. [20,33]). The birds were kept in three inter-connected cages of about 3 × 4 m area (3 m height) and were tame, tolerating the presence of observers close to and in the cage without signs of distress. We fed each individual five differently sized types of fruit/seed:
cocktail tomatoes (median seed size 0.0002 g), grapes (0.020 g), tangerines (0.20 g), lychees with small seeds (0.28 g) and lychees with large seeds (2.04 g). Birds ingested these fruits readily; lychees are also consumed in the wild (B. Peckham 2009, personal communication). We conducted two feeding trials per bird and fruit type. Fruits were fed in the morning; non-consumed fruits were removed after 18 min during the experiment and the night before the birds were offered seedless food. All seeds were defaecated except the large lychee seeds, of which 90 per cent were regurgitated. We recorded the time and place of each defecation on the floor of the cage. Faeces were collected after defecation, passed through a sieve and inspected for seeds. Defaecations were collected until all ingested seeds were recorded or until no seed was detected for a 2.5 h time period after the last seed was recorded in the faeces. We determined the GPT of each seed for each experiment. We defined the starting point of the gut passage as the mid-point between start of fruit presentation at the beginning of the experiment and the removal of non-consumed fruits. We then determined for each experiment and each seed the time interval between this mid-point and the time the seed was defaecated. In case the seeds were regurgitated, we calculated the time between swallowing and regurgitation of the seeds. We calculated for each experiment the median and maximum GPT of the seeds. As we conducted two feeding trials per fruit type and bird (n = 20 experiments), we were able to test whether median and maximum GPT per trial differed between the five fruit/seed size types, between defaecated and regurgitated seeds, and between the two individuals.

(d) Data analysis

We included in all analyses only days for which at least 30 valid coordinates were available (76.9% of relocations of a day in summer season and 63.9% of a day in winter season). This reduced sample size by on average 1.4 days per bird (from a mean number of 18.2 to a mean number of 16.8 days per bird). To test whether birds had to adapt to the GPS loggers, we tested whether the birds flew shorter distances on the first days on which they carried loggers. We calculated for each bird the cumulative flight distance per day. We tested whether the flight distance on the first (second, third, etc.) day differed significantly from the mean flight distance averaged over all later days. We found that from the fourth day on, daily flight distances did not differ significantly from those of the later days (Wilcoxon one-sided signed-rank test: \( p > 0.1 \)). We conducted all the following analyses excluding the first 3 days the birds carried GPS loggers. This reduced the sample size again from a mean number of 16.8 to a mean number of 12.5 days per bird. For this analysis and all following analyses, we used the open-source software R [34].

We first calculated displacement distributions of birds. We randomly selected starting points in the movement track of each bird and measured the distance to the location each bird had 15, 30, 45, 60, 75, 90, 105, 120, 135 or 150 min later, following established methods (e.g. [20,33]). The time intervals (15, 30, 45 min, etc.) were drawn from a uniform distribution. The maximum time interval of 150 min represented the maximum GPT (see §3). Thus, we randomly selected a starting point in the movement track of each bird, then randomly selected a movement time interval from the uniform distribution (15, 30, 45 min, etc.) and finally calculated the Euclidean distance between the chosen starting point and endpoint. We randomly drew 1000 displacement distances per individual bird. We chose starting points such that the earliest starting point was about 1 h before sunrise and the latest endpoint about 1 h after sunset. Displacement distances were thus calculated uniformly over the activity period of the hornbills. We determined the displacement distributions for each of the birds separately and then calculated for each time interval (15, 30, 45 min, etc.) the mean and standard error across the birds.

We then combined the individual displacement distributions of each bird with the mean GPT distribution. The test of median and maximum GPT per feeding trial showed that there were no significant differences in median and maximum GPT between the five fruit/seed size types, between defaecated and regurgitated seeds, nor between the two individuals (see §3). We therefore determined a mean GPT distribution across the 20 feeding trials. We calculated the mean proportion of seeds that were defaecated or regurgitated on average 15, 30, 45, 60, 75, 90, 105, 120, 135 or 150 min (each ± 7.5 min) later across the 20 feeding trials. These proportions were 12.1, 19.9, 20.8, 13.7, 12.7, 12.9, 2.9, 2.8, 0.4 and 1.6 per cent of the seeds, respectively (figure 1). We then repeated the procedure described above, but now the time intervals (15, 30, 45 min, etc.) were drawn not from a uniform distribution but from the distribution of GTPs (i.e. after randomly selecting a starting point, 12.1 per cent of the distances were calculated for a time interval of 15 min, 19.9 per cent for an interval of 30 min, etc.) This procedure weights the displacement distribution with the GPT distribution.

To evaluate whether bird displacement and seed-dispersal distributions differed between habitat types, we calculated both distributions over time periods when birds moved within large continuous forests and over time periods when they foraged in the agricultural landscape. To evaluate habitat cover, we used the latest KwaZulu-Natal Land-Cover database (GeoTerraiImage; www.geoterraiimage.com; preliminary 2005, modified 2008). We defined ‘continuous forests’ as the large continuous forest of Oribi Gorge Nature Reserve (1930 ha), the densely wooded parts of the Mazikhulu River valley 7 km to the north of Oribi Gorge and the forest within Mbumbasi Nature Reserve (trees and bush cover >70%; 880 ha). These three forests are the largest natural forests within about 30 km of Oribi Gorge. The agricultural

Figure 1. Distribution of average gut passage times (GPTs) of two trumpeter hornbills. Mean percentage of seeds (± s.e.) defaecated in each 15 min interval. n = 20 feeding trials.
landscape was defined as the following habitat types: all types of farming (e.g. sugarcane, exotic plantations), old cultivated fields, bush land, grassland, wetlands, roads and expanses of water. Within the agricultural landscape, patches of natural forest are small (<156 ha) and there are tree rows, isolated trees and farm gardens frequented by the hornbills. The rest of the habitat types (e.g. suburban areas, rural communities) were subsumed under an ‘other habitat types’ category.

We identified in the movement track of each bird time periods with a minimum duration of 150 min (representing the maximum GPT; see §3) in which all locations were in the same habitat type, either ‘continuous forest’ or ‘agricultural area’. We then selected starting points randomly in the ‘continuous forest’ and in the ‘agricultural area’ sub-datasets (all birds) and calculated seed-dispersal distributions for the two habitat types separately, using the same procedure as described above. We drew 100 displacement distances randomly per individual bird and habitat type.

To describe the dispersal distributions in the two habitat types mathematically, we fitted five different probability density functions (normal, logistic, Cauchy, Student t and Weibull) to the dispersal distance distributions, separately for the two habitat types [35,36]. We estimated parameters of each distribution based on maximum likelihood using R package BBLME2010 [34,37]. To identify the best-fitting model for the bimodal distribution in the agricultural landscape, we first partitioned the data into two unimodal distributions, based on visual inspection (see also [38,39]). We first fitted distributions to the first and the second peak separately and then tested all possible linear combinations of the five functions using the parameters estimated from the separate fits as starting points. We applied the Akaike information criterion (AIC) to assess model fit.

3. RESULTS

We caught 10 male and 8 female trumpeter hornbills in two field seasons. Of the males, six were caught in July 2008 and four in April 2009; both were non-breeding seasons. We were able to relocate all 10 tracked birds. We obtained data for a mean number of 18.2 days per bird (range 6–26 days; the bird with only 6 days of recording lost his backpack). After eliminating days with less than 64 per cent valid location data and after dropping the first 3 days’ data, an average of 12.5 days per bird (range 2–22 days were available). The analyses are based on a mean number of 675.6 locations per bird (minimum 193, maximum 955). Median measurement error of the loggers placement distribution averaged across the 10 birds is 8.0 m (25% quartile: 4.5 m; 75% quartile: 14.0 m; n = 142 locations, 71 in the open, 71 under tree canopies). The distribution of measurement errors shows a peak at about 5.6 m (see electronic supplementary material, figure S1).

Mean median GPT in the 20 feeding trials was 57 min, mean maximum GPT was 77 min and the absolute maximum GPT was 155 min (figure 1). Median and maximum GPT per fruit/seed size type and trial did not differ between the five fruit/seed size types or the two individuals (two-factor ANOVAs, median GPT: fruit/seed type: $F_{1,14} = 2.2, p = 0.12$; individual: $F_{1,14} = 1.5, p = 0.24$; maximum GPT: fruit/seed type: $F_{1,14} = 2.0; p = 0.15$; individual: $F_{1,14} = 3.4, p = 0.086$). Median and maximum GPT did not differ between regurgitated and defaecated seeds (two-factor ANOVAs, median GPT: digestion mode: $F_{1,16} = 2.6, p = 0.12$; individual: $F_{1,16} = 0.3, p = 0.61$; maximum GPT: digestion mode: $F_{1,16} = 0.9; p = 0.35$; individual: $F_{1,16} = 0.9, p = 0.35$). This shows that GPTs were rather independent of fruit seed size, digestion mode and individual, and may be representative for natural fruits more generally.

The movement tracks differed widely among individuals. Some birds stayed in Oribi Gorge Nature Reserve or in the surrounding area; others moved between Oribi Gorge Nature Reserve and the coast (figure 2). The displacement distribution averaged across the 10 birds is shown in figure 3a. It was very slightly bimodal with a very slight first peak at about 25 m, and a higher second peak at about 630 m. Weighting the displacement distribution (figure 3a) with GPT (figure 1) yielded the potential seed-dispersal distribution, averaged over the 10 hornbills (figure 3b). It was also very weakly bimodal with a slight first peak at about 25 m and a second slightly higher peak at about 630 m. The seed-dispersal distances of the individuals showed a similar pattern; 9 of the 10 birds had a bimodal seed-dispersal distribution (electronic supplementary material, figure S2). Maximum potential seed-dispersal distance was 14.5 km. Overall, the largest spatial extent over which a bird moved within the study period was 37 km.

Seed-dispersal distributions differed considerably among habitat types. The seed-dispersal distribution in the forest was based on seven birds and the one in the agricultural area on nine birds, as not all birds spent 2.5 h continuously in each of the two habitat types. Birds spent on average 30 per cent of their time in the three larger forests (range 0–99%, n = 10 birds), 50 per cent in agricultural areas (range 1–85%) and the remaining 20 per cent in other habitat types (range 0–80%). The seed-dispersal distribution in continuous forest was unimodal with a best fit by the Weibull function with an expected mean seed-dispersal distance of 86 m and a maximum seed-dispersal distance of 3016 m (figure 4a and table 1). The seed-dispersal distribution in the agricultural area was strongly bimodal (figure 4b). This distribution was fitted best by two different functions that had similar AIC values (ΔAIC < 2). The first function was a linear combination of the Weibull function for the first peak and a normal function for the second peak; the second function was a linear combination of two normal functions for both peaks (table 1). The first, larger peak was placed at about 18 m and the second, smaller peak at about 512 m dispersal distance; maximum seed-dispersal distance was 8914 m (figure 3e).

4. DISCUSSION

Our data showed that movement patterns of trumpeter hornbills in fragmented landscapes with a patchy occurrence of forests resulted in very slightly bimodal seed-dispersal distribution with a maximum seed-dispersal distance of 14.5 km. Seed-dispersal distributions differed among habitat types, with a unimodal seed-dispersal distribution within continuous forests and a strongly bimodal distribution in agricultural areas.

The distribution of measurement errors of the loggers demonstrates that the first peak in the movement and seed-dispersal distributions of the birds was not caused...
by measurement error. The peak in the measurement error distribution at 5.6 m (electronic supplementary material, figure S1) is located at a considerably smaller distance than the first peak of the dispersal distribution at about 25 m (figure 3a,b).

In general, it has been assumed that the seed-dispersal kernels generated by mobile animals in continuous landscapes are more or less leptokurtic with a peak close to the seed source, followed by a rapid decline and a long tail. Such a pattern in a fragmented landscape would result in little dispersal among fragmented habitat patches, and would make long-distance dispersal events and transport of seeds among fragmented habitat patches exceedingly rare. The novel GPS data loggers we used allowed us to quantify the movement behaviour of the birds precisely without bias with regard to movement distances. That is, at times in which birds moved large distances, the number and quality of the location data were as high as at times with short movement distances. Rare long-distance flights of the birds between gorges or to coastal areas could be located with the same high probability as short-distance flights. The data generated by the GPS loggers showed that the movement patterns of trumpeter hornbills were more complex than previously anticipated. Different movement behaviour of the birds in the two habitat types resulted in distinctly different dispersal distributions for continuous forests and the fragmented agriculture landscape (figure 4a,b). Seed-dispersal distances averaged over the 10 individuals (figure 3b) were similar to those of the agricultural habitat (figure 4b), probably because birds spent on average 50 per cent of their time in agricultural areas and only 30 per cent in continuous forests (and 20% in other habitat types).

The seed-dispersal distribution within large continuous forests was unimodal, with a best fit by the Weibull function and an expected dispersal distance of 86 m. For seed dispersal by birds in continuous forests, previous studies found, in general, leptokurtic distributions [20,21,40]. Some of these dispersal kernels were distinctly leptokurtic with only a small proportion of seeds dispersed over long distances. Nevertheless, some studies also showed a small second peak at longer dispersal distances [16,18,19,39]. Dispersal distributions for Asian hornbills also showed that these birds have a high potential for transporting seeds across the landscape and for occasional long-distance dispersal [41]. Comparisons of these seed-dispersal distributions with those of the trumpeter hornbills presented here are difficult because of differences in the scaling of the dispersal distances. The fact that dispersal distributions in continuous forest were unimodal can also explain why bird (i) was the
only individual that did not have a bimodal seed-dispersal distribution (electronic supplementary material, figure S1, bird (i)). This bird was the only bird that spent almost all its time (99%) within the continuous forest of Oribi Gorge.

In contrast, movement and seed-dispersal distributions in agricultural areas were bimodal, with a first peak at about 18 m and a second peak at about 512 m. Here, the first peak was best fitted by a Weibull or a normal function and the second peak by a normal function. Goméz [42] found a bimodal seed-dispersal pattern for jays within and between oak forests, but with much smaller dispersal distances than trumpeter hornbills. Other seed-dispersal kernels measured in heterogeneous landscapes have been leptokurtic in most cases [33,38].

In agricultural areas, trumpeter hornbills often moved only short distances within and between the crowns of neighbouring trees while foraging within a forest fragment or a farm garden, probably resulting in the first peak in their displacement distribution. However, the birds made equally likely long-distance flights with a preferred distance of about 512 m, resulting in a surprisingly high probability that seeds were transported to such distinct long-distance classes. It is possible that the first peak at about 18 m is caused by the mean size of forest fragments or farm gardens in the study area, and the second peak at about 512 m by the mean distance between suitable habitat patches. To answer this question requires a larger sample size of birds, and more detailed analyses of the habitat choice, size and spatial distribution of suitable habitat patches, and of the movement tracks of the birds and is beyond the scope of the present study.

Here, we would like to emphasize that seed-dispersal distributions differed considerably between continuous forests and agricultural areas. Seed-dispersal distributions in agricultural areas were more complex than in forests. Furthermore, modal and maximum seed-dispersal distances were much larger in agricultural areas (maximum 8914 m) than in forests (maximum 3016 m). This shows that landscape structure strongly influences the movement behaviour, and thus the movement and seed-dispersal pattern, of trumpeter hornbills. Previous radio-tracking studies of frugivorous birds within continuous habitats might have, in general, underestimated the ability of large birds to cope with large distances between forests in fragmented, agricultural areas. Trumpeter hornbills regularly moved between forest fragments and between the large continuous forests in the study region. These birds therefore have the potential to disperse seeds over large distances and among patches of suitable habitat. This also allows seeds to move between patches and to reach new sites. The high-mobility, frequent, long-distance flights and the high abundance of these birds suggest that trumpeter hornbills play an essential role for long-distance seed dispersal among the fragmented forests of eastern South Africa.
Table 1. Best-fitting probability density functions to seed-dispersal distributions within continuous forest and the agricultural landscape (figure 4a,b). Fit of the Weibull function to the seed-dispersal distribution within continuous forest (all other functions differed by ΔAIC > 9 from the best model). The two best-fitting linear combinations of two probability density functions to the bimodal seed-dispersal distribution within the agricultural landscape (all other linear combinations differed by ΔAIC > 3 from the best model); a = linear combination parameter.

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<th>r²</th>
<th>AIC</th>
<th>ΔAIC</th>
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<table>
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<th>agricultural landscape function</th>
<th>parameters (± s.e.)</th>
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<th>second peak</th>
<th>a</th>
<th>r²</th>
<th>AIC</th>
<th>ΔAIC</th>
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<tr>
<td>Weibull/normal</td>
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<td>0.493</td>
<td>0.877</td>
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<td>normal/normal</td>
<td>mean = 1.275 (± 0.025) s.d. = 0.375 (± 0.018) mean = 2.716 (± 0.023) s.d. = 0.438 (± 0.022)</td>
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To conclude, our results show that seed transport among habitat patches might be more frequent than previously assumed. The long seed-dispersal distances quantified here emphasize the ability of large frugivorous birds to disperse seeds among habitat patches in fragmented landscapes and their crucial role in allowing plants to adapt to global climate change.

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REFERENCES
20 Westcott, D. A., Bentrupperhäuser, J., Bradford, M. G. & McKeown, A. 2005 Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on


