



Original article

The effect of feeding time on dispersal of *Virola* seeds by toucans determined from GPS tracking and accelerometers

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ABSTRACT

Seed dispersal is critical to understanding forest dynamics but is hard to study because tracking seeds is difficult. Even for the best-studied dispersal system of the Neotropics, *Virola nobilis*, the dispersal kernel remains unknown. We combined high-resolution GPS/3D-acceleration bird tracking, seed-retention experiments, and field observations to quantify dispersal of *V. nobilis* by their principal dispersers, *Ramphastos* toucans. We inferred feeding events from movement data, and then estimated spatio-temporally explicit seed-dispersal kernels. Wild toucans moved an average of 1.8 km d⁻¹ with two distinct activity peaks. Seed retention time in captive toucans averaged 25.5 min (range 4–98 min). Estimated seed dispersal distance averaged 144 ± 147 m, with a 56% likelihood of dispersal >100 m, two times further than the behaviour-naïve estimate from the same data. Dispersal was furthest for seeds ingested in the morning, and increased with seed retention time, but only up to 60 min after feeding. Our study supports the long-standing hypothesis that toucans are excellent dispersers of *Virola* seeds. To maximize seed dispersal distances trees should ripen fruit in the morning when birds move the most, and produce fruits with gut-processing times around 60 min. Our study demonstrates how new tracking technology can yield nuanced seed dispersal kernels for animals that cannot be directly observed.

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1. Introduction

Seed dispersal is one of the key processes determining plant reproductive success, the spatial structure of plant populations and the species composition of plant communities (Nathan and Muller-Landau, 2000; Jansen et al., 2008). Documenting seed dispersal distances and seed deposition patterns therefore is an important goal in plant community ecology. Measuring seed dispersal directly, however, is complicated by the fact that individual seeds are notoriously hard or even impossible to track (Wang and Smith, 2002). The difficulty of tracking seeds has seriously limited our understanding of seed dispersal and its role in ecosystems (Nathan and Muller-Landau, 2000). This problem is particularly pervasive for endo-zoochorous plant species, which may comprise >90% of all tree species in tropical forests (Howe and Smallwood, 1982).

To some degree, the problem of tracking animal-dispersed seeds can be overcome by mechanistic models that predict seed-dispersal kernels from animal movement rates and seed retention time (Murray, 1988; Wehncke et al., 2003; Westcott et al., 2005). These models combine the probability of seed passage over time with an analysis of the distance an animal typically moves in that time period to estimate the “dispersal kernel”, the probability distribution of seed dispersal distance (Cousens et al., 2008). This simple approach, however, has been criticized for not incorporating spatial patterns of animal movement and feeding behaviour, failing to account for clumping of seed deposition, and thus overestimating seed dispersal effectiveness (Muller-Landau et al., 2005; Russo et al., 2006).

New spatially explicit mechanistic models that incorporate behaviour offer a more accurate alternative. For example, Russo et al. (2006) used observations on spider monkey movement and behaviour to show high spatial variance in dispersed seed density caused by the daily aggregation of seeds around monkey sleeping sites, which contrasted with the scattering of seeds during foraging

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bouts. Similarly, Westcott et al. (2005) found that including daily patterns of cassowary movement created much different seed shadows depending on the time of day a fruit was eaten, with seeds eaten in the morning being dispersed three times further than seeds eaten in the afternoon.

Accounting for animal behaviour in estimating seed dispersal kernels gives more accurate dispersal estimates, but collecting the necessary detailed animal movement and behaviour data in the field requires exceptional effort, and is often not possible. This type of studies has therefore been largely limited to habituated animals (e.g. Westcott et al., 2005; Russo et al., 2006; Mcconkey and Chivers, 2007). However, most frugivores are not possible to study in this way, either because they are too shy to be habituated, or they cannot be followed as they quickly move from site to site.

Here we use new tracking technologies to describe the behaviour and movement of *Ramphastos* toucans and combine these data with seed – transition times to estimate the dispersal kernel of the *Virola nobilis* (Myristicaceae) for which the toucans are the principal dispersers in Central Panama. Howe and co-workers have extensively studied the dispersal ecology of this tree species (Howe, 1981, Howe and Vande-Kerckhove, 1981; Howe, 1993), making this one of the best-documented dispersal system in the tropics (Howe and Westley, 1997). However, the actual seed distributions produced by the toucans have always remained unknown, despite exceptional effort, because it was physically impossible to follow the seeds and/or the birds, which are shy and move fast through the upper canopy of dense tropical forest. In general, *Virola* fruits are an important food source for *Ramphastos* toucans, making up 11–38% of their diet (Galetti et al., 2000), and toucans in turn are the most important disperser for many *Virola* species (Howe, 1981).

Toucans are thought to be high-quality dispersers to these tree species because they are able to fly for long distances, and may cross a variety of landscape types (Graham, 2001), potentially moving seeds between their ingestion and regurgitation or defecation.

We used a combination of high-resolution GPS locations and accelerometer activity sensors to describe the daily pattern of toucan behaviour, directly measure movement, and relate these to patterns of seed passage obtained from trials with captive individuals. We used these data to estimate dispersal kernels for seeds that were eaten at different times of the day, as in Westcott et al. (2005). Our expectation was that toucans follow a bimodal activity pattern – typical for diurnal birds (Aschoff, 1966) – with high activity in the morning followed by a lull in mid-day, a secondary peak in the afternoon, and a complete cessation of movement during the night as they remain motionless at a roost. Therefore, we predicted that seeds eaten in the morning should be dispersed the farthest because this is the animal's most active period. Meanwhile, midday and afternoon meals should have more limited dispersal distances as birds move relatively little during midday, and because birds may not regurgitate seeds consumed in the afternoon until they have returned to their night roost, where they would accumulate in a clumped pattern.

2. Materials and methods

2.1. Site and species

Animal-tracking fieldwork was carried out in Soberanía National Park (9°7.54N, 79°41.41 W), a site that encompasses 22,000 ha of lowland moist forest along the Panama Canal in Central Panama. We captured birds along a dirt road leaving the town of Gamboa by a tourist resort. The local forest is a mixture of secondary forest (20–80 yr old, mostly around the dirt road) and old-growth forest. Annual rainfall averages 2226 mm with 4.1 dry

months (<100 mm rainfall) (Park et al., 2010). Additional observations of toucan feeding behaviour at *Virola* trees were carried out in forests on nearby Barro Colorado Island, 9°9.37 N, 79°50.88 (Leigh, 1999).

V. nobilis A.C. Smith (formerly known from Panama as *Virola surinamensis*) and *Virola sebifera* Aubl. are wild nutmegs (Myristicaceae) common in Central Panama. Both species are dioecious canopy trees that produce classic bird fruits: green fibrous capsules that dehisce when ripe to display a large seed covered in a 1 mm thick bright-red aril with extremely high fat and protein content (Howe, 1981, 1993). The arillate seeds weigh 2–6 g in *V. nobilis* (Howe, 1993) and 1 g in *V. sebifera* (Howe, 1981). Both species' fruits typically dehisce during the early and midmorning, and in small amounts, supposedly to enhance feeding by birds (Howe, 1993); Howe (1993) called these *Virola* species “early-morning specialists”. Primary dispersal of *V. nobilis* seeds is by a variety of birds and mammals, but particularly by toucans (Howe, 1993; Forget and Sabatier, 1997). Scatter-hoarding rodents such as the agouti (*Dasyprocta punctata*) may provide secondary dispersal (Forget and Milleron, 1991). *Virola* strongly depend on seed dispersal for recruitment as weevil infestation causes near-complete mortality of offspring around parent trees (Howe, 1993).

The Keel-billed toucan (*Ramphastos sulfuratus*) and the Chestnut-mandibled toucan (*Ramphastos swainsonii*) are the major dispersers of *Virola* (Howe and Vande-Kerckhove, 1981). Both species are common throughout their ranges in Central America and north western South America and locally have been estimated to live at densities of 16 and 12 individuals per 100 ha, respectively (Robinson et al., 2000). Both species are large birds (ca. 400 & 650 g, respectively) that “gulp” *Virola* seeds by swallowing the arillate seeds entirely, making no attempt to separate pulp from seeds before swallowing (Levey, 1987). Large seeds are processed in the crop to separate them from the aril, and then regurgitated.

2.2. Seed passage time

Feeding experiments with captive animals are the traditional way of obtaining data on times frugivores retain seeds in their gut. Retention time of *Virola* seeds has previously been evaluated by feeding captive toucans with seeds inserted into papaya chunks (Holbrook et al., 2007). We followed this approach by feeding 67 fresh *V. sebifera* seeds stuck into berries to four captive *Ramphastos sulfuratus* in Summit Botanical Garden, Panama. Additionally, we conducted experiments in which we fed semi-fresh *V. nobilis* with the aril attached, i.e. real fruits to 5 captive toucans (*R. sulfuratus*) at the Rotterdam zoo, The Netherlands. The fruits were freshly collected on BCI from the ground below various fruiting tree. The *Virola* fruits were then transported to the Netherlands on dry ice by courier with export permits from the Panama Autoridad Nacional del Ambiente. We fed a total of 100 fruits to the 5 birds (14–28 per bird) and then observed the birds to record each regurgitation time. We used hierarchical models to test for differences in survival (Therneau and Lumley, 2009) in R 2.8.1 (R Development Core Team., 2008) and fitted six accelerated failure time models with different error distributions to the lumped regurgitation times and compared their AICs.

2.3. Animal movement and behaviour

Toucans in Panama are too shy and fast-moving to actively follow, but we did observe animals at feeding trees to characterize their feeding behaviour. We collected these observations by hiding near six fruiting *V. sebifera* trees and watching all feeding birds. We watched quietly from the ground from 6:30–10:30, with 3–6 replications per tree, for a total of 117 h of observation. Whenever

a bird arrived in a tree we watched it continuously to record the number of seeds swallowed and the length of visit.

To track birds, we first captured them with mist nets mounted in the forest canopy. We fitted six toucans (four *R. sulfuratus* (400 g) and two *Ramphastos swainsonii* (640 g) with 17 g backpacks containing a GPS (E-Obs, <http://www.e-obs.de>), 3-axis accelerometer, remote data readout, and VHF radio transmitter, and released them directly (cf. Holland et al., 2009). All animal handling protocols were approved by the IUCAC of Princeton University. The back pack represented less than 4.3% of the bird's body weight, and was designed to fall off the bird within 10 d. The GPS units were set to attempt a fix every 15 min from 4:30–19:30. The accelerometer was set to measure animal activity for 50 s every 3 min, day and night. The radio-transmitter allowed us to find and approach birds to within 200 m, at which point we could download the data from the data logger. Tags ran out of batteries or fell off birds after 5–9 days.

We tested the accuracy of E-Obs GPS tags by placing 18 tags under forest canopy and recording 2071 fixes over one day. The average linear error was 21.9 m (range 0.1–250.5 m), SD = 23.5 m, 50% CI = 14.5 m, and a 95% CI = 62.5 m. The accuracy of the GPS mounted on free-ranging toucans will have been greater than this because satellite reception will be better in the mid-story and canopy of the forest where these birds typically live. We analysed toucan movement trajectories using the adehabitat package for R (Calenge, 2006), and used the *mindistkeep* function to filter out movements smaller than 50 m, considering them a mix of GPS error and within-tree movements. This function works by replacing a location <50 m away with the previous coordinates, thus would not remove a directed series of small movements that sum up to >50 m. We used the standard deviation of the accelerometer value from one 50-s burst of data as a measure of activity. For this activity index, we used only the acceleration measured along the dorso-ventral axis of the bird, as this is an unequivocal indicator of flight (Shepard et al., 2008; Holland et al., 2009).

We analysed toucan movement data in two ways. In both analyses, the key measure was the net displacement over time from a fixed point as an indication of how far a seed would be moved away from its mother tree. First, following traditional protocol, we weighed all times of the day equally (Murray, 1988; Wehncke et al., 2003). Second, to reflect the animals' temporal patterns of feeding and moving, we implied feeding events based on their movement patterns and used these as starting points for analysis of seed movement (cf Westcott et al., 2005). Based on the results from our observations at feeding trees, we characterize toucans as active foragers, rapidly moving from tree to tree and consuming fruits within one tree in less time than the interval between our GPS fixes (15 min). These foraging bouts are followed by rest periods where animals do not move as frequently. Therefore we choose any location preceded by a movement of 50 m or more as an indication of a likely feeding location. This is also the approximate 95% confidence limit for the accuracy of our tracking tags, and thus minimizes the effect of GPS error on our analysis.

To infer the movement of seeds from the movement of animals, we analysed the displacement distances of toucans for 150 min. We created starting points for these inferred seed movements either by drawing evenly across the day for one analysis, or by using the likely feeding locations as described above. Feeding events were classified into three time periods: 5:00–9:15 (morning), 9:30–14:45 (midday), and 15:00–19:15 (afternoon). These time boundaries were chosen as to have an equal amount of implied feeding events in each period. We fitted exponential-rise-to-max functions through the parameter estimates across post-feeding intervals, and estimated the distribution parameters for other interval lengths from these functions.

2.4. Estimating seed dispersal kernels

To create an estimate of the linear distance that seeds were moved by toucans, we simulated regurgitation times by randomly drawing 1000 times t from the fitted lognormal distribution of regurgitation time. Then, for each time t , we took the corresponding parameters μ and σ from the fitted distributions of animal movement to characterize the lognormal distribution of net post-feeding displacement distances, and randomly drew a net flight distance d from that distribution, representing a distance at which a seed was deposited. Thus, we obtained 1000 simulated seed dispersal events that each were a combination of one regurgitation time t and one net flight distance d . To create a two dimensional map of the probability of seed dispersal from a parent tree we centred all inferred feeding events at the same point (0,0) and summed the probability of seed regurgitation based on the actual movements of toucans away from their presumed feeding points as recorded by the GPS, and the probability of seed regurgitation over time.

3. Results

3.1. Feeding trials

Regurgitation times were significantly longer for *V. nobilis* seeds ingested with aril (mean time 25.5 min, range 4–98, $n = 100$ seeds) than for *V. sebifera* seeds embedded in an artificial fruit (15.0 min, $n = 66$; Figure S1; Cox regression, with birds as random factor: Wald = 54.1, df = 4.59 df, $p < 0.001$). As aril and species effects were confounded, we cannot tell which effect caused the difference observed. However, it is likely that the adhesion of the aril increases processing time. If so, then trials with seeds in artificial fruits probably yield underestimations of regurgitation time. Therefore, we used the regurgitation times of the arillate seeds for modelling the dispersal kernel. The probability distribution of regurgitation time was best-fitted by a lognormal with $\mu = 2.96$ (meanlog) and $\sigma = 0.72$ (sdlog) (Fig. 1a).

3.2. Animal movement and behaviour

Our observations at fruiting *V. sebifera* trees showed that toucan visits represented 83% of all 114 frugivore birds visits. Visitation rate was not significantly different between the two species (*R. swainsonii* 3.1 ± 2.2 , *R. sulfuratus* 2.5 ± 1.7 visits/tree/morning; Mann–Whitney U test: $Z = -0.7$, $P = 0.5$). However, *R. swainsonii* removed significantly more fruits per visit (3.9 ± 6.3 vs. 1.1 ± 3 , Mann–Whitney U test: $Z = -4.7$, $P < 0.05$). Visits of both birds were brief, with those of *R. swainsonii* being longer than *R. sulfuratus* (9 ± 4.9 min vs. 3.6 ± 2.1 min, T -Test: $t = 5.0$, $P = 0.002$). Spider monkeys (*Ateles geoffroyi*) passed through the trees on two occasions but did not feed on fruits.

The GPS-tracking of the six animals yielded 40 animal-days of movement trajectory, including 2012 locations. All tracking data are available online at <http://www.movebank.org> and archived with doi:10.5441/001/0000003. The 95% Kernel home range ranged between individuals from 19.9 to 88.8 ha (mean 44.5 ± 28.1). Minimum total distances moved per day across all 40 animal-days ranged from 324 to 4891 m (mean 1870 ± 982). Toucans were more likely to have moved larger distances at larger time intervals (Fig. 1b). Of the two parameters that characterize these lognormal distributions (Figure S2), μ increased with interval length (implying that birds on average got farther away as time elapsed), while σ was relatively constant for $t > 30$ min (so the variation in distance was not strongly time-dependent after 30 min). For both parameters,

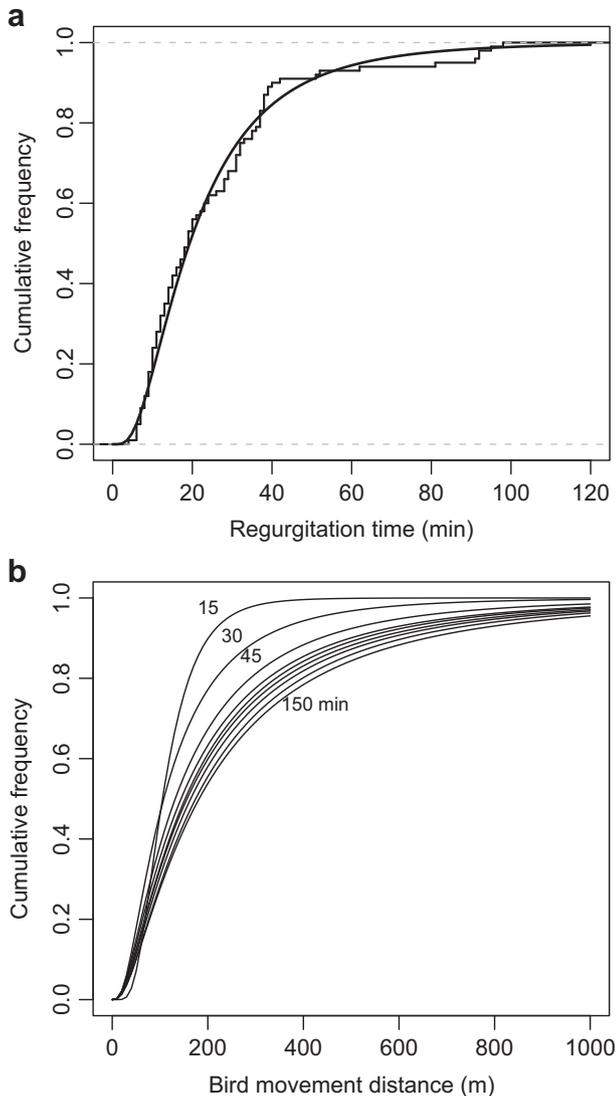


Fig. 1. Frequency distributions for seed retention (a) and animal movement (b) of *Ramphastos* toucans eating *Virola* seeds. In (a) the thin black line is the observed data while the bold line is the fitted lognormal distribution that we used to generate random regurgitation times in the stochastic model. The curves in (b) show displacement distance of GPS-tagged toucans at different time intervals after implied feeding events; each line is a lognormal distribution fitted to the observed data for sequential 15 min time intervals. We used these distributions in our stochastic model of seed dispersal.

the increase over time was well-fitted by exponential rise-to-max functions (Figure S2).

The accelerometer data showed that the toucans had a typical avian daily activity pattern with a peak of activity and movement in the morning followed by a lull at midday, a secondary peak in the afternoon, and complete inactivity all night (Fig. 2). Although we did not collect GPS locations at night, comparisons of the last three fixes in the evening (19:00–19:30) with the first three fixes the following morning (4:30–5:00) confirmed that the animals did not move at night; this last evening location and first morning location were always within the expected error of the GPS (18.8 ± 11.5 m, max 45.7 m). Accelerometer measurements collected at 3 min intervals all night confirmed that no activity occurred during this period (Fig. 2). The toucans repeatedly visited a limited number of roost sites, we documented 18 roost locations used on 29 nights by 6 different birds.

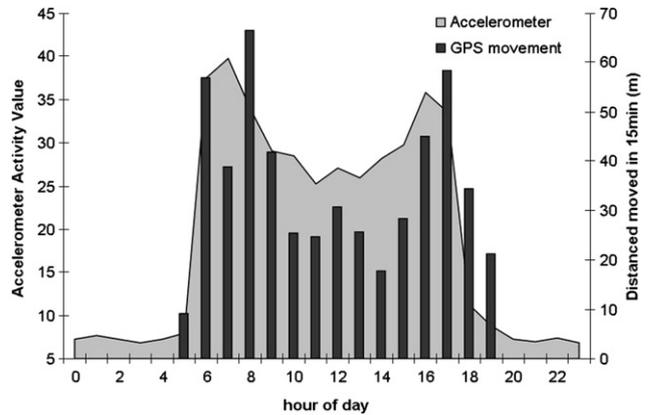


Fig. 2. Daily patterns of toucan activity and movement. Accelerometer activity values are the standard deviation of acceleration measured on the dorso–ventral axis of the bird collected every 3 min, day and night. Distance values are the average distance moved between successive GPS fixes, excluding those movements <50 m which could be due to GPS error or local movements within the crown of a tree. GPS data were not collected at night, but accelerometers confirm that there was no flight during this time.

The distance moved after implied feeding events varied over the day, with toucans moving further after feeding in the morning (316 m after 2 h) and afternoon (230 m) than in midday (208 m, Fig. 3). This agrees with the relatively low activity during that period. The lognormal distributions fit to post-feeding movements for these three time periods separately all had μ increasing with interval length – birds on average get farther away as time elapses – but much more so for the morning than for midday and especially the afternoon (Figure S2). Again, the variation of these relationships (σ) was relatively constant for $t > 30$ min for morning and afternoon feeding, but not for midday feeding, where the variation in distance was not strongly time-dependent.

3.3. Temporal and spatially explicit seed dispersal kernels

Time of feeding had a strong influence on the dispersal kernel that the simulations produced. When not considering time of day

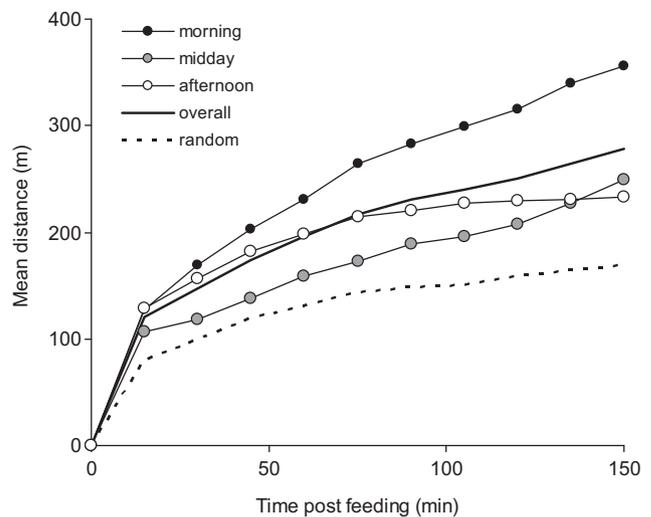


Fig. 3. Mean movement distance of GPS-tagged *Ramphastos* toucans after implied feeding during different times of the day and for all feeding events combined (continuous line). Toucans moved much further after feeding in the morning than after feeding around noon. Movement distance of toucans after random times, regardless of feeding activity, is shown for comparison (dashed line). The mean seed retention time for toucans was 25.2 min, with a maximum of 98 min.

for feeding, the frequency distribution of distance based on 1000 simulated dispersal events had $\mu = 4.14$ and $\sigma = 0.90$. The corresponding mean dispersal distance was 69 m and the probability of seeds being dispersed >100 m was 0.47 (Table 1). When considering the daily pattern of toucan feeding and movement across morning, midday, and afternoon, the estimated dispersal kernel of toucans shows more movement, with a $\mu = 4.72$ and $\sigma = 0.68$ (Fig. 1c). The resulting probability of being dispersed >100 m was higher, as was the mean dispersal distance (Table 1). Most of the longer-distance dispersal resulted from morning feeding.

By mapping out the estimating feeding locations of toucans we could also visualize the patterns of their movement after feeding in two dimensions. Combining this with regurgitation probabilities yielded a two dimensional probability estimate for the dispersal of seeds away from a feeding tree (Fig. 5). This estimate is inaccurate in not representing the likely variation in passage rates between the different species of seeds eaten by toucans, but does show the symmetry of dispersal across all directions, as well as the spatial distribution of rare dispersal events > 200 m.

4. Discussion

4.1. Better to be breakfast, lunch or dinner?

Seed dispersal kernels play a key role in contemporary seed dispersal research (Cousens et al., 2008) but have remained hard to measure, especially for plants dispersed by animals in which dispersing seeds are hard or impossible to follow (Wang and Smith, 2002). For this reason, the seed dispersal kernel of the best-studied dispersal system in the tropics – Central American *Virola* seeds and *Ramphastos* toucans – has remained unknown, despite extensive research effort (Howe and Vande-Kerckhove, 1981; Howe, 1981, 1993; but see recent work on related South American species by Holbrook and Loiselle, 2007). In this paper, we estimated this missing dispersal kernel by combining GPS based bird movement data with seed retention times obtained from traditional feeding experiments. We also extended traditional kernel estimation by relating the detailed movement tracks with data on toucan feeding behaviour, making the estimates temporally and spatially explicit. This extension not only improved our kernel estimate over traditional estimates that disregard space and time, but also allowed new predictions about the coevolution of plants and their bird dispersers. Additional improvements of this type of model in the future could include investigating the effects of foraging strategies employed by different species, sexes, or individuals.

Our stochastic models of seed dispersal demonstrate that toucans are indeed excellent seed dispersers, as Howe and co-workers predicted (Howe, 1981). We estimated that toucans disperse seeds an average of 144 m from the mother tree, with a 56% probability of dispersing seeds >100 m away. In addition, there was a long tail to this relationship (Fig. 4) such that some

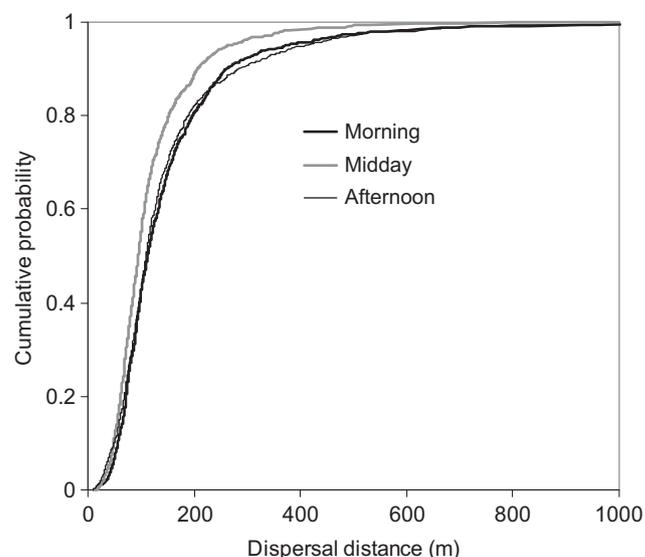


Fig. 4. Estimated dispersal kernels, or probability distributions, of seed movement distance for *Virola* seeds consumed by *Ramphastos* toucans at different times of the day. The kernels were obtained by simulation using stochastic models of movement of GPS-tagged toucans after presumed feeding events and regurgitation rate for *Virola* seeds.

seeds will eventually be dispersed at scattered sites much greater than 200 m away (Fig. 5). These results are generally similar to those found for toucans moving *Virola flexuosa* seeds in South America, where seeds had a 72% probability of moving >100 m, with a long tail to the relationship (Holbrook et al. 2007). This long tail was also found for movement of *Virola calophylla* by spider monkeys (*Ateles paniscus*), which had an average dispersal distance of 151 m (Russo et al., 2006). By following individual monkeys, Russo et al. (2006) were also able to model the spatial heterogeneity of seed dispersal, and found it strongly affected by the deposition of seeds around monkey resting sites. Thus, toucans are similar to other large birds in serving as excellent seed dispersers by most seeds >100 m away, and the potential to move some >1 km (Westcott et al., 2005; Sun et al., 1997; Lenz et al., 2010).

Our high-resolution GPS data allowed us to infer feeding and roost sites, despite the fact that it was impossible to physically follow and observe toucans after seed ingestion, and thereby estimate the spatio-temporal variation in seed dispersal. We found that the behavioural rhythm of toucans affected seed movement, with seeds ingested in morning (breakfast) and afternoon (dinner) being more likely to achieve significant dispersal than seeds ingested mid-day (lunch). This phenomenon agrees with the fact that both *Virola* species are “early-morning specialists” (sensu Howe, 1993): their fruits typically dehisce during the early and midmorning and are quickly removed by birds. Compared with spider monkeys (Russo et al., 2006), however, the risk of *Virola* seeds accumulating under toucan roosting trees was low regardless of feeding time because of the relatively short seed retention time of toucans.

The observed daily activity pattern of toucans is typical for most tropical bird species (Aschoff, 1966), and we suggest that there is a broadly important selective pressure for trees targeting bird dispersers to ripen their fruits in the morning. If general bird activity is related to the distance they move, as we found in toucans, then seeds consumed earlier in the day would be more likely to be moved greater distances, and thus more likely to escape seed predators and diseases concentrated near the mother tree (Janzen, 1970; Connell, 1971; Mangan et al., 2010). This is likely the case for birds with large territories, and was found for the southern cassowary (*Casuaris casuaris*), which dispersed seeds much further

Table 1

Estimated (modeled) dispersal distances of *Virola nobilis* seeds ingested by feeding toucans in Central Panama.

Feeding time	Fitted lognormal μ, σ	Dispersal distance (m) mean \pm stdev	Probability dispersal >100 m
Morning	4.78, 0.65	152 \pm 154	0.58
Midday	4.57, 0.59	95 \pm 83	0.55
Afternoon	4.73, 0.72	149 \pm 152	0.57
Total (weighted by time of day)	4.72, 0.68	144 \pm 147	0.56
Total (ignoring time of day)	4.14, 0.90	69 \pm 130	0.47

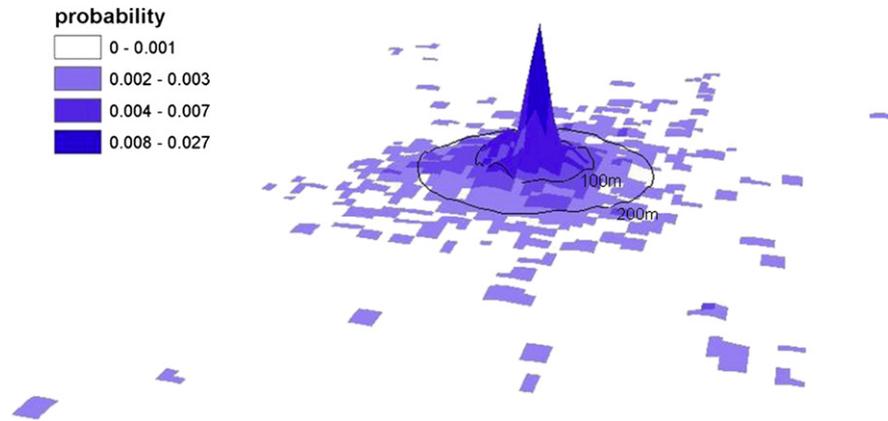


Fig. 5. Spatially explicit map of the probability of seed dispersal away from inferred feeding trees by toucans. This is built by relating the probability of seed regurgitation over time with actual 2d movements of toucans away from the location of feeding trees inferred based on GPS data. Seeds have a 56% probability of being dispersed >100 m, and an 18% chance of moving >200 m.

after feeding in the morning than in the afternoon (Westcott et al., 2005). However, smaller birds moving around in smaller territories may have less of a relationship between time and displacement distance, as found in mammals (Carbone et al., 2005). Additional tracking data are needed to test this prediction.

Compared with our toucan data, the long seed retention times of cassowaries (171–1800 min) made night-time deposition around a roost a particular risk for seeds eaten in the afternoon (Westcott et al., 2005). Seeds dispersed to roosting sites are not moved as far, on average, and may suffer high mortality due to predators attracted to the accumulated seeds. This suggests an interesting trade-off in the section of gut passage times for particular seeds. Plants are generally thought to evolve mechanisms to prolong gut passage times (Tewksbury et al., 2008). However, if gut passage is too slow, and seeds are eaten in the afternoon, this would increase the risk of being deposited under a sleeping roost. In the case of toucans, dispersal distance increases with gut retention time up to about 60 min, while risk of being deposited under a roost becomes important after about 75 min of gut retention (Fig. 3).

4.2. Sensor-derived behaviour improves seed dispersal kernels

The importance of animal behaviour for seed dispersal has been recognized, but not often quantified, because of the difficulty of observing these behaviours in wild animals (Westcott et al., 2005; Russo et al., 2006; McConkey and Chivers, 2007). We show that animal behaviour relative to seed dispersal can be measured remotely through sensors, which is a growing field as technology continues to improve (Cooke et al., 2004; Wikelski et al., 2007, 2010; Rutz and Hays, 2009). As this technology continues to miniaturize, it will offer new scientific opportunities to terrestrial biologists, as it has already done for marine ecologists (Weimerskirch et al., 2005; Ponganis, 2007). We used observations of toucans at feeding trees to interpreted fine-scale movement data and differentiate potential feeding sites from rest sites. The mean dispersal distance of our behaviourally informed kernel was twice as far as a naïve estimate from the same data, showing the significance of accounting for behaviour. Our relatively simple protocol also allowed us to add both a spatial and temporal component to our results, offering new hypotheses about the coevolution of trees and their dispersers.

For species in which feeding behaviour is less well-defined there are a variety of new methods to classify movement patterns into different behavioural classes (Patterson et al., 2008) and statistically note the change point between behaviours (Gurarie

et al., 2009). The number of different behaviours that might be delimited by movement patterns is somewhat limited, but tri-axial accelerometers offer more specific sensor-based measure of behaviour (Shepard et al., 2008; Sakamoto et al., 2009). Although we used accelerometer data simply as a measure of activity in toucans, they have the potential to be used to classify specific behaviours, and could be combined with GPS to produce a geo-referenced time series of behaviours that would be immediately relevant to their dispersal of seeds, and other ecosystem functions (Holland et al., 2009). The most important animal behaviours for estimating dispersal kernels are the ingestion and defecation (or regurgitation) of seeds, which would probably not be detected by accelerometers, but might be recorded through the development of new implanted physiological sensors (Weimerskirch et al., 2005; Signer et al., 2010).

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Appendix. Supplementary material

Supplementary material associated with this paper can be found, in the online version, at doi:10.1016/j.actao.2011.06.007.

References

- Aschoff, J., 1966. Circadian activity pattern with two peaks. *Ecology* 47, 657–662.
- Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.
- Carbone, C., Cowlshaw, G., Isaac, N.J.B., Rowcliffe, J.M., 2005. How far do animals go? Determinants of day range in mammals. *Am. Nat.* 165, 290–297.
- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. In: Den Boer, P.J.,

- Gradwell, G.R. (Eds.), Dynamics of Populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp. 298–312.
- Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* 19, 334–343.
- Cousens, R., Dytham, C., Law, R., 2008. Dispersal in Plants: A Population Perspective. Oxford Scholarship Online Monographs, Oxford, UK.
- Forget, P.M., Milleron, T., 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87, 596–599.
- Forget, P.M., Sabatier, D., 1997. Dynamics of the seedling shadow of a frugivore-dispersed tree species in French Guiana. *J. Trop. Ecol.* 13, 767–773.
- Galetti, M., Laps, R., Pizo, M.A., 2000. Frugivory by toucans (*Ramphastidae*) at two altitudes in the Atlantic forest of Brazil. *Biotropica* 32, 842–850.
- Graham, C.H., 2001. Factors influencing movement patterns of Keel-billed toucans in a fragmented tropical landscape in Southern Mexico. *Cons. Biol.* 15, 1789–1798.
- Gurarie, E., Andrews, R.D., Laidre, K.L., 2009. A novel method for identifying behavioural changes in animal movement data. *Ecol. Lett.* 12, 395–408.
- Holbrook, K.M., Loiselle, B.A., 2007. Using toucan-generated dispersal models to estimate seed dispersal in Amazonian Ecuador. In: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), *Seed Dispersal: Theory and Its Application in a Changing World*. CAB International, Wallingford, UK, pp. 300–321.
- Holbrook, K., Loiselle, B., Dennis, A., Schupp, E., Green, R., Westcott, D., 2007. Using toucan-generated dispersal models to estimate seed dispersal in Amazonian Ecuador. In: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), *Seed Dispersal: Theory and Its Application in a Changing World*. CABI, Wallingford, pp. 300–321.
- Holland, R.A., Wikelski, M., Kummeth, F., Bosque, C., 2009. The secret life of oilbirds: new insights into the movement ecology of a unique avian frugivore. *PLoS ONE* 4, e8264.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201–228.
- Howe, H.G., Vande-Kerckhove, G.A., 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62, 1093–1106.
- Howe, H.F., Westley, L.C., 1997. Ecology of pollination and seed dispersal. In: Crawley, M.J. (Ed.), *Plant Ecology*, second ed. Blackwell Science, London, UK, pp. 262–283.
- Howe, H.F., 1981. Dispersal of a Neotropical nutmeg *Virola sebifera* by birds. *Auk* 98, 88–98.
- Howe, H.F., 1993. Aspects of variation in a neotropical seed dispersal system. In: Fleming, T.H., Estrada, A. (Eds.), *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Springer, Dordrecht, The Netherlands, pp. 149–162.
- Jansen, P.A., Bongers, F., Van der Meer, P.J., 2008. Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography* 31, 43–52.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528.
- Leigh Jr., E.G., 1999. *Tropical Forest Ecology: A View from Barro Colorado Island*. Oxford University Press, Oxford.
- Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B.H., Wikelski, M., Bohning-Gaese, K., 2010. Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proc. Roy. Soc. B. Bio. Sci.* doi:10.1098/rspb.2010.2383.
- Levey, D.J., 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129, 471–485.
- Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I., Bever, J.D., 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466, 752–755.
- Mcconkey, K.R., Chivers, D.J., 2007. Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *J. Trop. Ecol.* 23, 269–275.
- Muller-Landau, H.C., Hardesty, B.D., Burslem, D., Pinard, M., Hartley, S., 2005. Seed dispersal of woody plants in tropical forests: concepts, examples and future directions. In: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*. Cambridge University Press, Cambridge, pp. 267–309.
- Murray, K.G., 1988. Avian seed dispersal of three Neotropical gap-dependent plants. *Ecol. Mon.* 58, 271–298.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285.
- Park, A., van Breugel, M., Ashton, M.S., Wishnie, M., Mariscal, E., Deago, J., Ibarra, D., Cedeno, N., Hall, J.S., 2010. Local and regional environmental variation influences the growth of tropical trees in selection trials in the Republic of Panama. *For. Ecol. Manag.* 260, 12–21.
- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State-space models of individual animal movement. *Trends Ecol. Evol.* 23, 87–94.
- Pongani, P.J., 2007. Bio-logging of physiological parameters in higher marine vertebrates. *Proc. 2005 Int. Symp. Bio-logging Sci.* 54, 183–192.
- R Development Core Team, 2008. R.8.1: A Language And Environment For Statistical Computing. URL: R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.
- Robinson, W.D., Brawn, J.D., Robinson, S.K., 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecol. Mon.* 70, 209–235.
- Russo, S.E., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* 87, 3160–3174.
- Rutz, C.G., Hays, C., 2009. New frontiers in biollogging science. *Bio. Lett.* 5, 289–292.
- Sakamoto, K.Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., Wanless, S., 2009. Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* 4, e5379.
- Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Hasley, L.G., Gleiss, A., Morgan, D.T., Myers, A.E., Newman, C., Macdonald, D.W., 2008. Identification of animal movement patterns using tri-axial accelerometry. *Endang. Species Res.* 10, 47–60.
- Signer, C., Ruf, T., Schober, F., Fluch, G., Paumann, T., Arnold, W., 2010. A versatile telemetry system for continuous measurement of heart rate, body temperature and locomotor activity in free-ranging ruminants. *Meth. Ecol. Evol.* 1, 75–85.
- Sun, C., Ives, A.R., Kraeuter, H.J., Moermond, T.C., 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* 112, 94–103.
- Tewksbury, J.J., Levey, D.J., Huizinga, M., Haak, D.C., Traveset, A., 2008. Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chillies. *Ecology* 89, 107–117.
- Therneau, T., Lumley, T., 2009. *Survival: Survival analysis, Including Penalised Likelihood*. R package Version 2.34–41. R Package Version 2.35–4.
- Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends Ecol. Evol.* 17, 379–385.
- Wehncke, E.V., Hubbell, S.P., Foster, R.B., Dalling, J.W., 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of Neotropical tree species. *J. Ecol.* 91, 677–685.
- Weimerskirch, H., Gault, A., Chereil, Y., 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86, 2611–2622.
- Westcott, D., Bentrupperbaumer, J., Bradford, M., McKeown, A., 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia* 146, 57–67.
- Wikelski, M., Kays, R., Kasdin, J., Thorup, K., Smith, J.A., Cochran, W.W., Swenson Jr., G.W., 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. *Exp. Biol.* 210, 181–186.
- Wikelski, M., Moxley, J., Eaton-Mordas, A., Lopez-Urbe, M.M., Holland, R., Moskowitz, D., Roubik, D.W., Kays, R., 2010. Large-range movements of Neotropical orchid bees observed via radio telemetry. *PLoS ONE* 5, e10738. doi:10.1371/journal.pone.0010738.