

RESEARCH ARTICLE

Patterns of Movement and Seed Dispersal by Three Lemur Species

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We combined data on gut-passage times, feeding, and movement to explore the patterns of seed dispersal by *Eulemur rubriventer*, *Eulemur rufifrons*, and *Varecia variegata editorum* lemurs in Ranomafana National Park, Madagascar. These lemur species deposited less than half of their consumed seeds >100 m away from conspecific trees (40–50%). Long-distance dispersal (>500 m) was rare and average dispersal distances were short relative to those reported of similar-sized haplorrhine primates. The three lemur species showed no significant differences in mean seed-dispersal distances. However, they differed in the shape of their frequency distributions of seed-dispersal distances as a result of differences in how they moved through their habitats. The short distances of seed dispersal we observed and the depauperate frugivorous fauna in Madagascar suggest seed-dispersal may be more limited than in other tropical forests with important implications for plant-community dynamics, biodiversity maintenance, and restoration efforts in Madagascar. *Am. J. Primatol.* © 2013 Wiley Periodicals, Inc.

Key words: gut-passage time; local dispersal; Madagascar; movement; primate; seed dispersal

INTRODUCTION

In tropical forests, primates constitute between 25% and 40% of the frugivorous biomass [Chapman, 1995; Eisenberg & Thorington, 1973] and are critical for seed dispersal of plant communities across the tropics [Chapman, 1995; Chapman & Russo, 2006; Fleming, 1979; Norconk et al., 2011]. Primates play an even larger role in Madagascar because of the island's relatively depauperate frugivorous bird and bat communities [Hawkins & Goodman, 2003; Langrand, 1990]. Since the spatial distribution of seed dispersal is determined by the movement of dispersers, the non-random way primates move while utilizing resources within their habitats [Garber, 1989, 2000; Garber & Jelinek, 2006; Janmaat et al., 2006] may have important consequences for the spatial patterning of plant diversity [Chapman & Russo, 2006; Cousens et al., 2010; Wehncke et al., 2003]. However, studies exploring both primate movement patterns and seed-deposition patterns have been limited [see Chapman & Russo, 2006; Russo et al., 2006; Wehncke et al., 2003], particularly for Madagascar's primates [but see Moses & Semple, 2011; Spehn & Ganzhorn, 2000].

The temporal and spatial patterning of frugivorous-primate movement combined with seed passage-time in the gut determine how far they disperse seeds from parent trees [Karubian & Durães, 2009; Russo et al., 2006; Westcott & Graham, 2000; Westcott et al., 2005]. Dispersal distance is important because it can strongly affect plant recruitment

patterns at different scales [Spiegel & Nathan, 2007]. At the local scale, seed dispersal allows seeds and seedlings to escape density-dependent mortality resulting from higher levels of natural enemies (pathogens, seed-predators, and herbivores), and competition in the vicinity of parent or conspecific adult trees [Connell, 1971; Howe & Smallwood, 1982; Janzen, 1970]. At larger scales, long-distance dispersal events can facilitate colonization of newly opened habitats and increase the spread rate of plant populations [Cain et al., 2000; Higgins et al., 2003; Nathan, 2006].

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Our objective in the present study was to examine movement and seed-dispersal patterns of a guild of seed-dispersing primates in the southeastern rainforests of Madagascar. Lemurs may differ from other primate species in their role as seed dispersers because of their relatively small home and day ranges [Crowley et al., 2011; Harvey & Clutton-Brock, 1981], and their low metabolic rates relative to body size [Ross, 2008] that might constrain daily movement [Sparrow & Newell, 1998]. If so, primate-driven dispersal dynamics in Madagascar's forests may differ substantially from other tropical forests.

Resolving the functional role of primate seed-dispersers in forest communities is becoming urgent given the increasing population declines of primates globally [Chapman, 1995; Stoner et al., 2007], and the reliance of up to 90% of tropical trees on seed dispersal by frugivorous vertebrates [Terborgh et al., 2002]. In Madagascar, this is especially critical given that lemurs are thought to be the dominant seed dispersers in the ecosystem [Bollen et al., 2004; Ganzhorn et al., 1999; Wright et al., 2011], and that 91% of lemurs are currently classified as at risk of extinction [IUCN, 2012], making them one of the most endangered groups of vertebrates in the world. As habitat loss, hunting and climatic changes continue to put their populations at risk [Barrett & Ratsimbazafy, 2009; Dewar & Richard, 2012; Dunham et al., 2008, 2011; Parga et al., 2012; Ratsimbazafy et al., 2013], studies of their role in ecosystem processes are becoming even more urgent.

We describe the movement patterns of three frugivorous Malagasy primates in Ranomafana National Park (RNP) and explore the resulting patterns of seed dispersal. Using data on foraging, defecations, movement and estimations of gut-passage duration, we estimated the distances that lemurs carried seeds away from parent trees. We then created frequency distributions of estimated seed-dispersal distances for each lemur species. Finally, we discuss the relevance of lemur seed-dispersal to the maintenance of tropical forests in the region, and how their role compares to non-lemur primates.

METHODS

Study Site and Species

This study was conducted in RNP located in the south-eastern rainforest of Madagascar (21° 16'S and 047° 20' E), which encompasses 41,000 ha of montane forest [Wright et al., 2012]. Mean monthly rainfall ranges from 10 to 1,200 mm [Dunham et al., 2011] and mean annual temperature ranges from 4 to 32°C [Wright et al., 2011]. The precipitation in RNP is highly variable with a peak wet season in January to March (average monthly rainfall of 508 mm), and the dry season peaks in June–October (average monthly rainfall of 143 mm) [Dunham et al., 2011]. The

elevation in Ranomafana ranges between 600 and 1,500 m [Wright & Andriamihaja, 2002].

The species used in our study constitute a guild of three closely related (Family Lemnidae), diurnal and highly frugivorous lemur species: red-bellied lemur (*Eulemur rubriventer*, body mass: 1.6–2.1 kg), red-fronted brown lemur (*Eulemur rufifrons*, body mass: 2.2–2.3 kg), and southern black-and-white ruffed lemur (*Varecia variegata editorum*, body mass: 2.5–4.8 kg) [body masses from Baden et al., 2008; Glander et al., 1992]. These species are the largest frugivores in the rainforest of Ranomafana and are suggested to be important seed dispersers because of their ability to swallow large-sized seeds, which they pass undamaged and with increased germination success [Dew & Wright, 1998; Wright et al., 2011]. Their populations have declined in several sites within RNP [Wright et al., 2012] and are currently declining throughout their range [IUCN, 2012].

Proper permits and authorizations were obtained from Madagascar's government prior to data collection and we adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of primates. Research did not involve any direct contact or manipulation of animals.

Data Collection

Data on movement and foraging patterns were collected between June 2010 and June 2011 with a total of 1,572 observation hours on seven groups of *E. rubriventer* (average group size: $3.44 \pm \text{SD } 0.55$), eight groups of *E. rufifrons* (average group size: $7.13 \pm \text{SD } 3.67$) and nine groups of *V. v. editorum* (average group size: $2.82 \pm \text{SD } 1.21$) accessed from four research sites within the park (Fig. 1: Mangevo, Talatakely, Valohoaka, and Vatoharanana). The majority of these groups have at least one collar-tagged individual from previous studies [Wright et al., 2012] that we used to identify the focal group. For groups without tagged individuals, we were able to identify individuals based on their physical characteristics, which allowed us to track the same group [Wehncke & Dominguez, 2007].

We located a focal group, starting at about 0700 hr, and attempted to continuously track them until they were no longer active (about 1700 hr) or until we could no longer locate them. We used observations of a focal individual within each group as the basis for our group movement data. Locations were recorded every 15 min using a hand-held Global Positioning System (GPS) unit (Garmin 60 series). Our GPS coordinate points had a mean accuracy of $7.52 \pm \text{SD } 3.99$ m ($N = 830$, 64% of points were within accuracy of less than 5 m), which allowed us to track relatively exact paths. Every time the group stopped to feed, we recorded the location and identity of each feeding-tree species with the help of local botanical

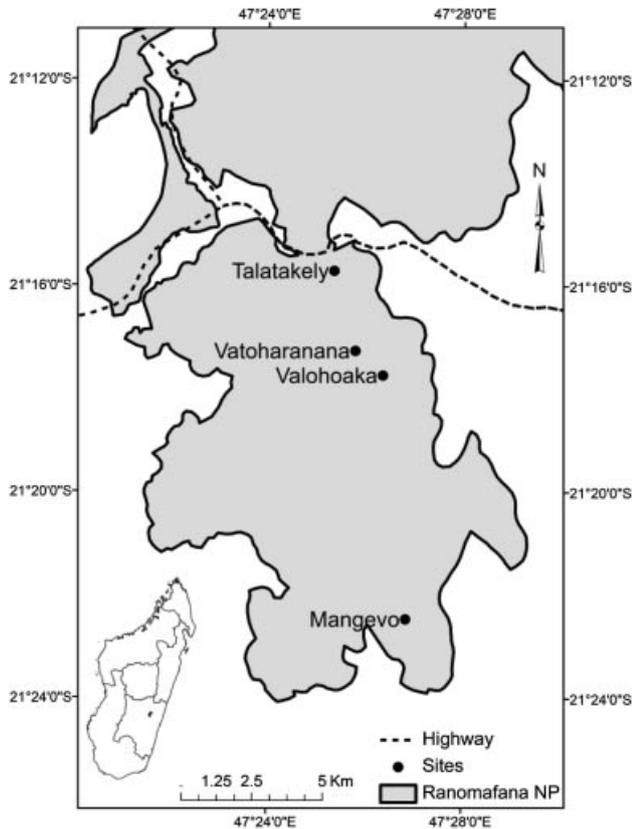


Fig. 1. Location of study sites in Ranomafana National Park, Madagascar. The inset corresponds to the map of Madagascar and does not fit to scale.

experts. Specimens from unknown plant species were collected and dried for later identification.

During lemur observations, we collected all observed fecal depositions by group members and recorded the geographic coordinate points of defecations. We then extracted, identified and counted all seeds of size >1 mm in each fecal sample [Stevenson, 2000]. Local research technicians familiar with the local flora were able to identify passed seeds to at least their vernacular names.

Parameter Estimation

All location records were transformed into a metric x and y coordinate system in ArcGIS 10.0 (Environmental Systems Research Institute Inc., Redlands CA) and MATLAB 7.12.0 (The MathWorks, Inc., Natick, MA) for parameter estimation including home-range size, daily path length, speed, turning angles, and seed-dispersal distance. We used MATLAB for initial error-checking, to manipulate the database and to calculate movement parameters. In cases where a series of location points of less than 45 min was missing because an animal was out of sight, we interpolated the missing points based on the location points before and after the missing values.

Data with missing points of more than 45 min were excluded from analyses. We also excluded path segments that suggested obvious errors in location data [Di Fiore & Suarez, 2007] based on visual examination of initial movement plots.

We used the “Minimum Bounding Geometry” function in ArcGIS to calculate the home-range sizes of each group with a convex-hull polygon method based on location points of individuals, feeding sites, and defecation sites collected over the duration of the study [Wehncke et al., 2003]. Daily paths were measured by joining successive point location records within a day that constituted more than 7 hr of observation. Location data recorded every 15 min was used to calculate step lengths (defined as distance between 15 min location points), speed (during a movement bout) and turning angles [Westcott & Graham, 2000]. Turning angles (-180° to 180°) represented the angle of direction lemurs moved relative to their previous location [Garber, 1989; Zimmerman, 1979]. A value of 0° indicates no change of direction, a positive value indicates movement to the right, negative value indicates movement to the left, and values near -180° or $+180^\circ$ indicate a reversal of movement (i.e., backtracking) [Erhart & Overdorff, 2008b; Will & Tackenberg, 2008].

We estimated seed-dispersal distance of each dispersal event by measuring the straight-line distance between the location of the seed(s) in a fecal deposition and a likely parent tree. Multiple conspecific seeds in the same fecal deposit were counted as one dispersal event. We determined probable parent trees by selecting trees of the same species as the dispersed seed(s), for which feeding events occurred before dispersal but within the estimated range of gut passage times for the disperser (description below). If there was more than one candidate parent-tree, we took an average of potential dispersal distances as our estimate. While this introduced some uncertainty to our estimates, it allowed us a large enough sample size to test hypotheses on the social-group level and avoid pseudo-replication, common in many primate studies.

The ranges of gut-passage times used in selecting potential parent trees for dispersal events were based on minimum and maximum values of both our observations and from published direct measurements from captive lemurs. Specifically, in captive lemurs, the gut-passage times from feeding experiments using solute or plastic markers were 155–270 min for *E. rubriventer*, 60–155 min for *E. rufifrons* (*E. fulvus* in original paper) [Overdorff & Rasmussen, 1995], and 30–210 min for *V. v. editorum* (*V. variegata* in original paper) [Cabre-Vert & Feistner, 1995]. We estimated gut-passage times from our observational records based on fruits from plant species eaten only once the day of observation for which a seed dispersal event was later observed and prior to defecation, which occurred at least 5 hr after the start of observations [Moses & Semple, 2011; Stevenson,

2000; Wehncke et al., 2003]. Following these criteria, the gut-passage times for wild *E. rubriventer* ranged between 96 and 433 min (mean = 214.16 min, $N = 12$), for *E. rufifrons* 72–371 min (mean = 190.08 min, $N = 12$), and for *V. v. editorum* 42–468 min (mean = 194.81 min, $N = 32$). To our best knowledge, these are the first accounts of gut-passage times for wild *E. rubriventer* and *E. rufifrons*. The mean gut-passage time for *V. v. editorum* is less than the findings of Moses and Semple [2011] in wild *V. variegata* ($260 \pm \text{SD } 160$ min) in Manombo rainforest, located southeast of RNP.

Data Analyses

We used SPSS 20.0 (IBM, Inc., Armonk, NY) to perform all statistical analyses. We used Pearson χ^2 tests to examine how lemur species differed in the frequency distributions of their turning angles (bins of 30°) and dispersal distances (bins of 25 m). We performed a Multivariate General Linear Model (GLM), evaluated with Pillai's trace test, to evaluate how lemur species differed simultaneously in home range size and movement variables, including daily path length and speed. Replicates of dependent variables were based on means of individual social-group estimates. Data were normally distributed, thus meeting the assumptions for a multivariate GLM.

To explore how lemur movement was associated with seed-dispersal distance, we used a generalized linear model with lemur species as a fixed factor. Group-level estimates of home range and movement variables, including daily path length and speed, were reduced to independent, uncorrelated variables through a principal component analysis (PCA). We retained one principal component with an eigenvalue > 1 [Peres-Neto et al., 2005], which explained 57.23% of the total variation. We examined the influence (loadings) of our movement variables on the remaining PCA score and then tested if it could explain significant variation in mean seed-dispersal distances among social-groups with lemur species as a fixed factor in a full factorial analysis.

We also used a nested generalized linear model to explore the relationship between gut passage time and associated seed-dispersal distances, with lemur species as a fixed factor. Variables in this analysis were derived from seed-dispersal events used to calculate gut-passage time of the three species (see Methods section). We did not include dispersal events

for which dispersal distance was estimated based on a range of measured gut passage times. Distances were nested within day of observation which was nested within group.

RESULTS

Movement and Foraging Patterns

The estimated mean group home-ranges of these lemur species are presented in Table I. Since the home ranges were estimated based on our limited study period, they may underrepresent year-long range sizes because ranges may shift over seasons in relation to resource availability [Erhart & Overdorff, 2008a]. Indeed, cumulative estimates of daily home-range sizes did not reach an asymptote by the end of the sampling period. The observed daily path of the three lemur species consisted of movement bouts (traveling between periods of foraging and resting) of variable length (e.g., Fig. 2) and speed (Table I).

The three studied lemur species differed significantly in how they moved through their habitat (multivariate-GLM: Pillai's Trace, $F_{6,40} = 3.090$, $P = 0.003$). However, tests of between-subjects effects revealed no significant differences in the lemurs' speed ($F_{2,21} = 2.222$, $P = 0.133$) or home range-size ($F_{2,21} = 1.964$, $P = 0.165$), and marginally non-significant differences in mean daily path-lengths ($F_{2,21} = 3.122$, $P = 0.065$). *V. variegata editorum* appear to have the longest average daily path length, which was more than double that of *E. rubriventer*, which was the shortest of the three lemurs (Table I). The three species showed a non-uniform distribution of observed turning angles (Fig. 3). They often returned to the same feeding trees and resting areas, and tended to repeatedly use the same pathways between resting and feeding trees. The frequency distribution of their turning angles differed significantly among species (Pearson Chi-square: $\chi^2 = 46.063$, $df = 22$, $P = 0.002$). The two *Eulemur* spp. were observed to backtrack more often than *V. v. editorum*, which had a higher tendency for more direct and linear routes between points (Fig. 3). This was especially more apparent for *E. rufifrons*.

Seed-Dispersal Patterns

Eulemur rubriventer was observed to disperse 23 out of 44 fruit species (plus 3 species not observed in their diet), while *E. rufifrons* was observed to disperse

TABLE I. Mean \pm Standard Deviation of Home-Range Size, Daily Path Lengths, Speed, and Absolute Turning Angles of the Three Frugivorous Lemur Species in Ranomafana National Park, Madagascar

Lemur species	Home range (ha)	Daily path length (m)	Speed (m/s)
<i>E. rubriventer</i>	13.70 ± 04.56 ($N = 7$)	519.33 ± 367.16 ($N = 17$)	0.075 ± 0.069 ($N = 114$)
<i>E. rufifrons</i>	22.06 ± 12.19 ($N = 8$)	796.91 ± 475.01 ($N = 33$)	0.093 ± 0.092 ($N = 233$)
<i>V. v. editorum</i>	29.10 ± 21.89 ($N = 9$)	$1,079.95 \pm 692.65$ ($N = 75$)	0.079 ± 0.078 ($N = 504$)

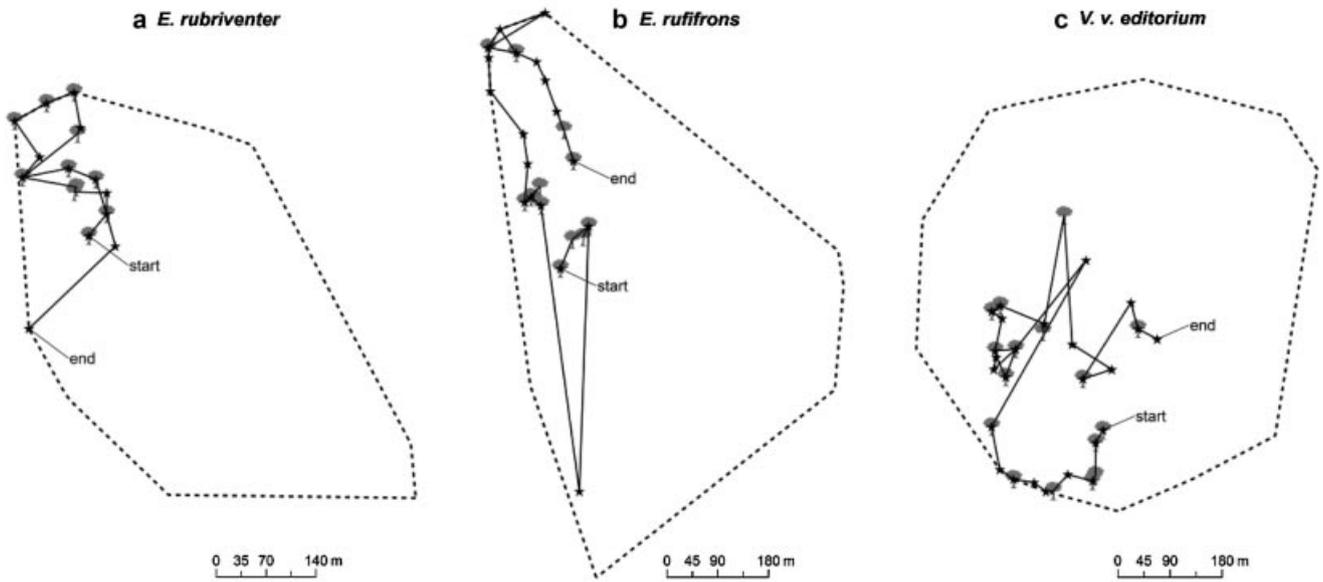


Fig. 2. Representative examples of a daily path for one selected group of each lemur species within the group's home range (dashed line): (a) *E. rubriventer*, (b) *E. rufifrons*, and (c) *V. v. editorum*. The star symbol indicates location every 15 min, and the grey tree-symbols represent feeding trees. The daily path from start in the morning until the end of observations in late afternoon is indicated by the thick black line.

the seeds of 23 out of 64 fruit species that they consumed during our study period (plus 2 species not observed being consumed), and for *V. v. editorum* 20 out of 53 fruit species (Appendix I). During our study, 21 of the 42 fruiting plant species dispersed by the lemurs were only dispersed by one of the three lemur species (i.e. not dispersed by multiple lemur species). However, our sample size was limited and more sampling over a longer time period is needed to get a better understanding of both dietary and seed-dispersal overlap. All lemur species deposited a large proportion of seeds away from conspecific trees, and at distances of more than 100 m (42.4% for *E.*

rubriventer, 43.8% for *E. rufifrons*, and 50% for *V. v. editorum*). *Eulemur rubriventer* was estimated to disperse seeds away from parent trees by a mean distance of 119.81 m (max: 358.7 m), 95.59 m (max: 417.1 m) for *E. rufifrons*, and 116.86 m (max: 630.3 m) for *V. v. editorum*. The frequency of seed deposition at different distance categories from potential parent trees differed significantly among the lemur species (Fig. 4, Pearson: $\chi^2 = 518.82$, $df = 40$, $P < 0.0001$). All three lemur species showed a peak frequency of seed distribution within 25 m of the parent tree. Seed deposition frequency then declined slowly with distance for *V. v. editorum*; however, the patterns

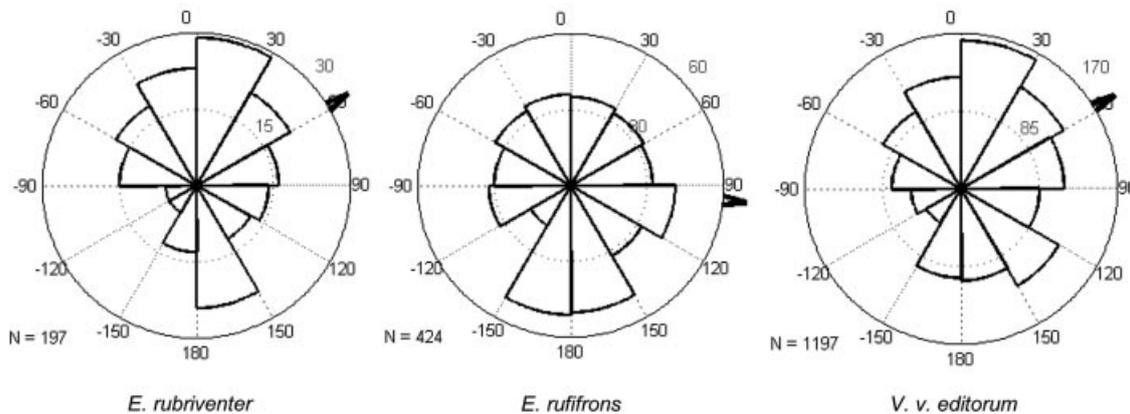


Fig. 3. Circular distribution of the turning angles between consecutive steps. *E. rufifrons* (middle panel) tends to do more backtracking (moving in a direction counter to the prior point) than *E. rubriventer* (left panel) and *V. v. editorum* (right panel), which progress in relatively straight lines. The grey numbers are scales of the number of counts in the various angle classes. Arrows represent vector means.

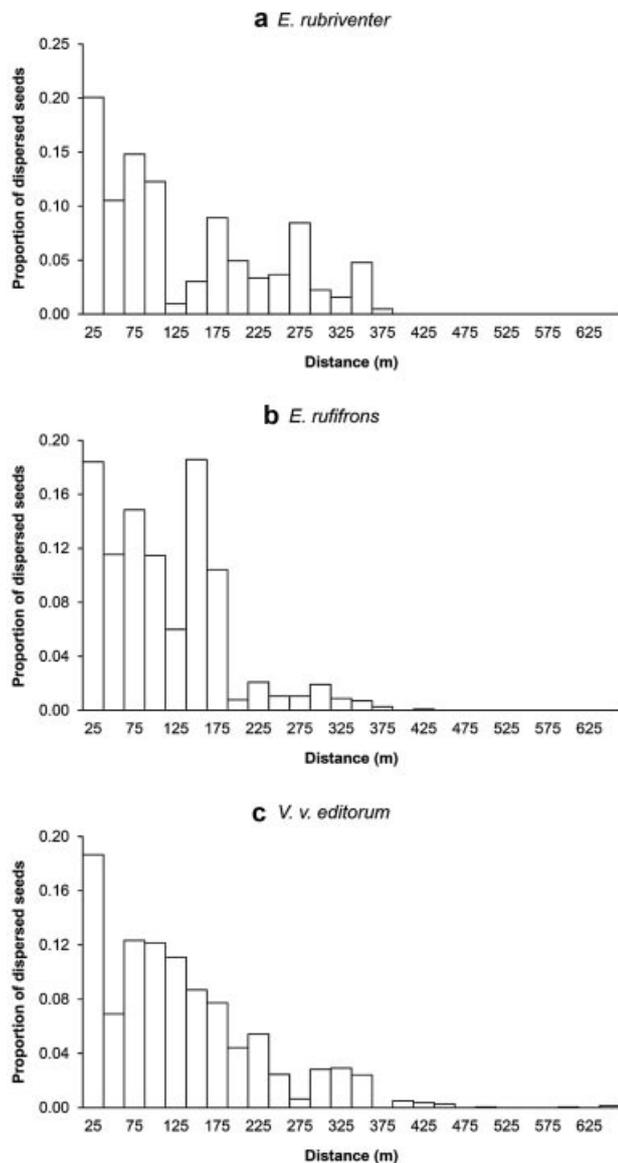


Fig. 4. Frequency distribution of estimated distances that seeds are dispersed from most likely parent trees by (a) *E. rubriventer*, (b) *E. rufifrons*, and (c) *V. v. editorum* of all the plant species they disperse in RNP. Seed count excludes plant species with seeds <1 mm in length such as *Ficus* spp. and *Psidium* spp. which were found in large quantities in fecal samples.

for *Eulemur* spp. appear bimodal with a second smaller peak occurring at about 150–175 m from the seed origin for *E. rubriventer*, and a second peak at 125–150 m for *E. rufifrons* (Fig. 4).

In our PCA of movement variables, all three movement variables had similar loadings of same sign (mean speed: 0.778; mean daily path length: 0.763; and mean home range-size: 0.728). When the principal component score (PC-1) was used in a full-factorial, generalized linear model with lemur species as a fixed factor, it explained significant variation in mean seed-dispersal distance, while species identity

and interaction terms were not significant (Table II). At the seed-level, gut-passage time was associated with seed-dispersal distance, independent of species identity (Wald $\chi^2 = 320.717$, $df = 22$, $P < 0.0001$).

DISCUSSION

This study demonstrates that frugivorous lemurs disperse less than half (42–50%) of all consumed seeds more than 100 m from their parent trees. Long-distance dispersal (>500 m) was rare and only observed for *V. v. editorum*. The three species differed in the way that they moved through their habitats resulting in interspecific differences in the frequency distributions of seed dispersal distances from likely parent trees. However, mean seed-dispersal distance was not significantly different across species. Although the principal component score of movement variables was found to be an important predictor of dispersal distance, the variation found between groups was greater than between lemur species.

Results also showed that lemurs repeatedly used certain paths and feeding trees, which is likely to confer aggregated patterns of seed dispersion and constrain seed dispersal distance (especially if the disperser tends to reverse their direction and return to the same feeding trees). *Eulemur rufifrons*, in particular, uses a lot of backtracking behavior (as seen in Fig. 2), which may increase their probability of depositing seeds in a clustered pattern. Backtracking behavior in *E. rufifrons* is suggested to be due to the large size of their groups, and their dependence on large fruiting trees as food resources, to which they frequently return over the course of a day and on successive days [Erhart & Overdorff, 2008b]. As the three largest frugivores in the system, the dispersal patterns conferred by these primates may help shape the recruitment patterns of many plant species in the forest and affect the colonization and expansion of plant populations [Cain et al., 2000; Higgins et al., 2003; Muller-Landau & Hardesty, 2005; Nathan, 2006].

Seed Dispersal Patterns

The distance that a seed is dispersed from parent trees is critical for seed survival and recruitment

TABLE II. Generalized Linear Model Full-Factorial Test Examining Differences in Dispersal Distances Versus the Principal Component Score and Species Identity

Factors	Wald χ^2	df	P
Species	3.525	2	0.172
PC-1	4.502	1	0.034
Species \times PC-1	0.884	2	0.643

probabilities because of density-dependent mortality associated with proximity to conspecific adult trees [Connell, 1971; Janzen, 1970; Johnson et al., 2012; Liu et al., 2012]. This conspecific density-dependent effect may disappear at a distance of 15 m away [Hubbell et al., 2001]; thus dispersal distances of more than 100 m are often considered long-distance dispersal [Cain et al., 2000]. The three lemur species in this study disperse a majority of seeds well beyond 15 m from potential parent trees, and often at a distance of more than 100 m. However, dispersal beyond 500 m was rare in our study and only observed by *V.v. editorum*. Because tails of dispersal distributions consist of rare events and are inherently difficult to quantify, they are not well resolved in our study. However, we expect that occasional long-distance dispersal of seeds may be facilitated by these lemurs when sub-adult or adult lemurs transfer groups or immigrate to new areas and thus move long distances rapidly. Theoretical studies have suggested that even very rare long distance dispersal events can enhance species range expansion and survival of species in dynamic landscapes [see Nathan, 2006 for review]. Events that are rare on the timescale of 1 year may still be quite important over the demographic timescale relevant for a long lived rainforest tree, some of which may live hundreds of years. These three lemur species were observed to emigrate from their natal groups at least once in their lifetime [Baden, 2011; Overdorff & Tecot, 2007; Overdorff et al., 1999]; therefore they may contribute to long dispersal of their food trees that are fruiting during their emigration period. Primates with more fluid social structures, such as group fission-fusion strategy observed in *E. rufifrons* [Erhart & Overdorff, 2008a; Overdorff et al., 1999], can also cover large ranges leading to a higher probability of seed dispersal across different microsites and a scattered seed dispersal pattern [Chapman & Russo, 2006].

The observed frequency distribution of estimated seed-dispersal distances by *V. v. editorum* showed a peak close to the parent tree, followed by a rapid decline and a long tail. However, the distributions of seed-dispersal distances by the two *Eulemur* species appear bimodal. Most notably, *E. rufifrons* made equally likely seed depositions near the parent and at around 150 m from the parent tree, resulting in a high probability that seeds would be transported to that distinct distance class. The first peak may be explained by the common lemur behavior of feeding, resting and then defecating in the same tree [Overdorff & Strait, 1998]. The second peak might be explained by the mean distance moved after foraging bouts when they do travel immediately after foraging, and/or may be related to the spatial distribution of favored feeding trees in their habitat, however more research is necessary. Backtracking may also be a factor leading to these patterns.

Seed Dispersal Distance Relative to Other Primates

The lemur species in our study are clearly effective at depositing a large portion of ingested seeds beyond the risk of density-dependent mortality. However, the dispersal distances estimated from our study and from other studies of lemurs [Moses & Semple, 2011; Spehn & Ganzhorn, 2000] are notably shorter than those of primate frugivores in other tropical regions (Fig. 5, Appendix II). Small body size of lemurs may account for some of these differences. Indeed, the mean seed dispersal distance of arboreal frugivorous primate species is strongly associated with body mass (Fig. 5; $R^2 = 0.422$, $F_{1,12} = 8.765$, $P = 0.012$). However, both *Cebus capucinus* [Wehncke et al., 2003] and *Cebus apella* [Zhang & Wang, 1995] disperse seeds at least twice as far, on average, as the similar-sized *V. v. editorum*. We thus suspect that the relatively small home-range sizes and day-range lengths of lemurs relative to other primates [Crowley et al., 2011; Harvey & Clutton-Brock, 1981] may contribute to the relatively short distances they disperse seeds. This also means that short dispersal distances by lemurs may be common in other forested regions of Madagascar as well, and warrants further study.

It is also important to note that Madagascar's lemur communities have changed with the large-scale extinction of large-bodied lemurs that disappeared after the Holocene [Godfrey et al., 2012; Razafindratsima et al., 2013], and today's forests may be missing an important part of their frugivore community. While it is uncertain which extinct lemurs, if any, were once present at our study site, some extinct species are suspected to have been important for long-range seed dispersal in Madagascar [Crowley et al., 2011].

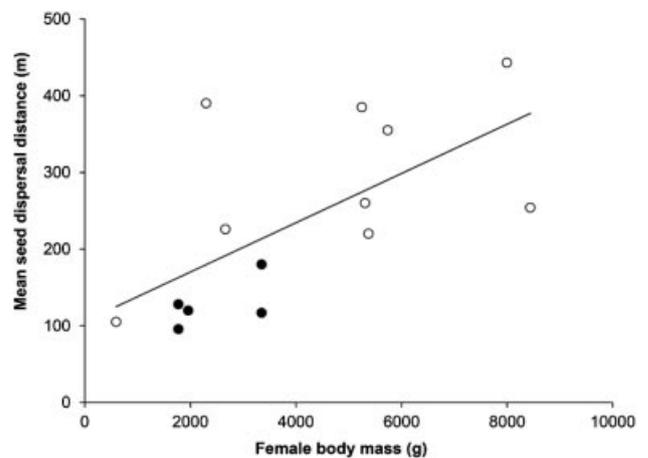


Fig. 5. Significant relationship between female body mass and seed dispersal distance across arboreal lemur (black circles) and non-lemur (open circles) primates. Lemurs have among the shortest seed dispersal distances measured in primates (data and citations in Appendix II).

CONCLUSIONS AND FUTURE DIRECTIONS

Together, the extinction of Madagascar's largest primate-frugivores, the naturally depauperate bird and bat communities [Hawkins & Goodman, 2003; Langrand, 1990], and the relatively short range of seed dispersal by extant lemur frugivores may be indicative of restricted seed dispersal of Madagascar's trees relative to other tropical forests. A cross-site comparison of congeneric *Commiphora* trees in Madagascar and South Africa (dispersed primarily by birds), showed much shorter dispersal distances in Madagascar relative to South Africa [Bleher & Böhning-Gaese, 2001]. Similar cross-site comparisons of dispersal differences on a community scale are required to determine if Madagascar forests do indeed differ in dispersal regimes through limited local dispersal relative to other regions.

The implications of local dispersal may be large. Short dispersal distances may result in more local clustering of adult-tree distributions [Bleher & Böhning-Gaese, 2001], thus increasing the heterogeneity of the forest. Limited dispersal has also been emphasized in the coexistence literature as a potentially important mechanism for reducing competitive exclusion and maintaining tree biodiversity within diverse tropical forests [Hubbell & Foster, 1986; Snyder & Chesson, 2003; Tilman, 1994]. Local seed-dispersal has even been suggested to enhance plant speciation [Baak, 2005]. Thus, if narrow distribution patterns of dispersed seeds are common and have existed throughout Madagascar's history, they may have been a contributing factor to the incredible diversity of plants on the island.

If limited local dispersal is wide-spread in Madagascar, it may have important implications for restoration as it may slow recovery of the already highly fragmented and disturbed forests in Madagascar. Such information may be critical for informing approaches for current and future forest restoration activity in Madagascar. This does not imply that lemurs do not play a critical role in seed dispersal in Madagascar's forests. In contrast, the loss of the local dispersal that does exist could be devastating to plant communities. Given the low diversity and potential for redundancy of frugivores in this system, impacts of lemur extinction may be tremendous for Madagascar's forests. With 91% of lemurs currently facing high risks of extinction [IUCN, 2012], Madagascar's plant communities may face changes as major dispersers are lost from the system.

We are not aware of any other taxa in RNP that may act as alternative seed dispersers for the majority of plant species dispersed by these lemurs. Among the frugivores in RNP, the large-sized lemur species, *Propithecus edwardsi* (mean body mass: 5.6 kg) [King et al., 2011] is primarily a seed predator, masticating the majority of seeds it consumes [Dew & Wright, 1998]. However, it is known to pass intact

seeds when advancing age results in overly worn teeth [King et al., 2005]. Birds and nocturnal frugivorous-primates such as *Microcebus rufus* and *Cheirogaleus crossleyi* may also contribute to the seed dispersal of plant species in Ranomafana like their congeners in the littoral rainforest of south-east of Madagascar [Lahann, 2007], but they may not disperse many of the large-seeded species in the forest. However, studies on seed dispersal services by these frugivores in RNP are lacking [but see Rakotomanana et al., 2003].

Given the limited seed-dispersal distance by lemurs observed in our study, we recommend that conservation action should incorporate ways of encouraging the movement and dispersal of seed-dispersing lemurs via corridors and regenerating habitats across anthropogenic barriers (such as roads) to promote regeneration of native habitats [Razafindratsima & Martinez, 2012]. Although we lack data on seed-dispersal services by other frugivores in RNP forests, we recommend consideration of the whole frugivore community in conservation actions because the richness and abundance within a frugivore assemblage can have positive effects on the effectiveness of seed dispersal [Garcia & Martinez, 2012].

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APPENDIX I. Fruit Species Consumed and Dispersed by *E. rufifrons*, *E. rubriventer* and *V. v. editorum* in Ranomafana National Park from June 2010 to June 2011: Presence and Relative Proportion of Intact Seed Species in Defecations Relative to Total Defecated Seeds During Study Period.

Family	Species names	Local names	<i>E. rubriventer</i>	<i>E. rufifrons</i>	<i>V. v. editorum</i>
Anacardiaceae	<i>Abrahamia thouvenotii</i>	Sandramy fotsy		x	
	<i>Abrahamia turkii</i>	Sandramy	1.018	0.106	11.360
Anisophylleaceae	<i>Anisophyllea fallax</i>	Hazoharaka			x
Annonaceae	<i>Ambavia capuronii</i>	Ramiavontoloho			x
	<i>Xylopia buxifolia</i>	Ramiavona	x		
Aphloiaceae	<i>Aphloia theaformis</i>	Fandramanana	x	x	
Apocynaceae	<i>Carissa edulis</i>	Fantsy		x	x
	<i>Craspidospermum verticillatum</i>	Vandrika	0.157	x	
	<i>Plectaneia sp</i>	Vahikondro	x		x
Arecaceae	<i>Dyopsis decipiens</i>	Sihara			7.410
	<i>Dyopsis nodifera</i>	Sirahazo	x		
	<i>Ravenea robustior</i>	Lafa			1.188
Asteraceae	<i>Mikania sp</i>	Vahivahia	x	x	x
Burseraceae	<i>Canarium madagascariensis</i>	Ramy			1.328
Burseraceae	<i>Canarium madagascariensis</i>	Ramy boribory		x	0.140
Canellaceae	<i>Cinnamosma madagascariensis</i>	Fanamangidy		x	
Celastraceae	<i>Brexiella sp</i>	Voamasoandro		0.053*	
Clusiaceae	<i>Garcinia goudotiana</i>	Kimbaletaka	x		x
	<i>Garcinia sp</i>	Voamalambotaho	x		
	<i>Mammea bongo</i>	Natojabo			x
	<i>Mammea vatoensis</i>	Natovoraka		x	1.783
	<i>Psorospermum androsaemifolium</i>	Fanerandahy		x	
Connaraceae	<i>Agelaea pentagyna</i>	Vahihetrotra	x	x	
Cucurbitaceae	<i>Raphidocystis sp</i>	Vahimbarongy		x	
Cunoniaceae	<i>Weinmannia bojeriana</i>	Maka	2.741	1.856	
	<i>Weinmannia rutenbergii</i>	Lalona		x	
Dichapetalaceae	<i>Dichapetalum chlorinum</i>	Vahindavenona			x
	<i>Dichapetalum sp</i>	Vahimavo	1.175		x
Ebenaceae	<i>Diospyros gracilipes var. lecomtei</i>	Hazomainty		2.174	
Fabaceae	<i>Abrus precatorius</i>	Vahimboamena		x	
Gentianaceae	<i>Anthocleista amplexicaulis</i>	Dendemy	x	x	
Lamiaceae	<i>Clerodendrum petunioides</i>	Voalatakakohoala		x	
	<i>Premna corymbosa</i>	Odimamo			x
Lauraceae	<i>Cryptocarya crassifolia</i>	Tavolomalady	2.741	3.924	1.538
	<i>Cryptocarya crassifolia</i>	Tavolomanitra	17.933	8.643	3.530
	<i>Cryptocarya parareolata</i>	Tavolomaintso			0.140
Lauraceae	<i>Cryptocarya sp</i>	Tavolomalady fotsy	0.078*	0.530*	0.629
	<i>Cryptocarya thouvenotii</i>	Tavolopina	10.180	13.786	2.377
	<i>Ocotea nervosa</i>	Varongy	0.078	x	x
	<i>Ocotea racemosa</i>	Varongy fotsy			x
	<i>Potameia rubra</i>	Sary			0.035
Loranthaceae	<i>Bakerella sp</i>	Tongoalahy		x	
Malvaceae	<i>Grewia sp</i>	Hafipotsy		4.507	
Melastomataceae	<i>Medinilla sp</i>	Kalamasimbarika		x	
Monimiaceae	<i>Ephippiandra madagascariensis</i>	Tambonetra			x
	<i>Tambourissa perrieri</i>	Ambora lahy	1.488*	x	
Moraceae	<i>Ficus botryoides</i>	Voararano	x	x	x
	<i>Ficus lutea</i>	Amontana	x	x	x
	<i>Ficus politoria</i>	Famakilela	x	x	
	<i>Ficus reflexa</i>	Nonoka	n	n	n
	<i>Ficus rubra</i>	Nonoka vaventy			x
	<i>Ficus tiliifolia</i>	Voara	n	n	
	<i>Streblus dimepate</i>	Mahanoro	7.204	2.863	
Myrtaceae	<i>Eugenia louvelii</i>	Voabe	3.759	x	x
	<i>Psidium cattleianum</i>	Goavy tsinahy	n	n	
	<i>Psidium guajava</i>	Goavy vaventy	n	n	
	<i>Syzygium emirnense</i>	Robary		x	x

(Continued)

APPENDIX I. Continued

Family	Species names	Local names	<i>E. rubriventer</i>	<i>E. rufifrons</i>	<i>V. v. editorum</i>
	<i>Syzygium_emirnense</i>	Rotrafotsy	0.235	x	3.251
Myrtaceae	<i>Syzygium_parkeri</i>	Rotramena	2.036*	0.106	4.124
Oleaceae	<i>Noronhia_incurvifolius</i>	Tsilaitra fotsy		x	
	<i>Noronhia_introversa</i>	Tsilaitra	x	x	
Pandanaceae	<i>Pandanus_sp</i>	Tsirika	3.915	x	
Passifloraceae	<i>Deidamia_sp</i>	Kilelakomby		1.273	
Primulaceae	<i>Oncostemum_botryoides</i>	Kalafana			x
	<i>Oncostemum_botryoides</i>	Kalafana lg	x	x	0.070
	<i>Oncostemum_leprosum</i>	kalafana sm			x
	<i>Oncostemum_nervosum</i>	Kalafambakaka	0.157	0.053	x
Rubiaceae	<i>Antirhea_borbonica</i>	Fatsikahitra	x	x	x
Rubiaceae	<i>Danais_sp</i>	Tamborimantsina	x		x
	<i>Gaertnera_brevipedicellata</i>	Ranjopody		x	
	<i>Gaertnera_phyllostachya</i>	Bararata			x
	<i>Gyrostipula_foveolata</i>	valotra			x
	<i>Gyrostipula_foveolata</i>	Valotra tenany			x
	<i>Mussaenda_arcuata</i>	Anambahy	x	x	
	<i>Mussaenda_erectiloba</i>	Fatora	7.048	3.287	x
	<i>Psychotria_mandrarensis</i>	Fanorafa		x	x
	<i>Psychotria_reducta</i>	Fohaninasy	18.246	11.612	
	<i>Saldinia_sp</i>	Tongely	x	x	
Rutaceae	<i>Toddalia_asiatica</i>	Anakatsimba	x	x	
	<i>Vepris_sp</i>	Apody lg			x
Rutaceae	<i>Zanthoxylum_sp</i>	Voangy		x	
	<i>Zanthoxylum_tsihanimposa</i>	Tsitongamposa		x	x
Salicaceae	<i>Scolopia_madagascariensis</i>	Faritraty	11.511	32.185	
Sapindaceae	<i>Allophylus_cobbe</i>	Dikana	3.994	2.015	x
	<i>Deinbollia_neglecta</i>	Lanary madinika	x	0.424	x
	<i>Zanha_sp</i>	Zahana		0.318	0.489
Sapotaceae	<i>Chrysophyllum_boivinianum</i>	Rahiaka	4.229	10.127	59.560
	<i>Sideroxylon_betsimisarakum</i>	Nato			0.105
Smilacaceae	<i>Smilax_anceps</i>	Rohindambo	x	0.159	
Torriceleaceae	<i>Melanophylla_crenata</i>	Vavaporetaka		x	
Unidentified		Lonjo		x	
Unidentified		Vahimberana		x	
Unidentified		Vahitamboro			x
Unidentified		Voatakaboka	0.078	x	0.944

n: dispersed-seeds of <1 mm in length (count not recorded).

*: fruit species found in defecation but not observed being consumed.

x: consumed plant species but not dispersed.

APPENDIX II. Published Accounts of Mean Observed Seed Dispersal Distances of Several Lemur and Non-Lemur Primates.

Primate species	Female body mass (g)	Mean dispersal distance (m)	Reference for dispersal data
Non-lemur species			
<i>Alouatta palliata</i>	4855	–	Estrada and Coates-Estrada [1984]
<i>Alouatta seniculus</i>	5310	260	Julliot [1996]
<i>Ateles belzebuth</i>	7996	443	Link and Di Fiore [2006]
<i>Ateles paniscus</i>	8440	202.5	Zhang and Wang [1995]
<i>Cebus apella</i>	2300	390	Zhang and Wang [1995]
<i>Cebus capucinus</i>	2666	225.8	Rowell and Mitchell [1991], Valenta and Fedigan [2010], Wehncke et al. [2003]
<i>Hylobates muelleri</i>	5250	385	McConkey and Chivers [2007]
<i>Hylobates muelleri x agilis</i>	5375	220	McConkey [2000]
<i>Lagothrix lagotricha</i>	5740	300	Stevenson [2000]
<i>Leontopithecus rosalia</i>	595	105	Lapenta and Procópio-de-Oliveira [2008]
<i>Macaca leonina</i>	6480	–	Albert et al. [2013]
<i>Saguinus fuscicollis</i>	377	–	Garber [1986]
<i>Saguinus mystax</i>	586	–	Garber [1986]
Lemur species			
<i>Eulemur fulvus rufus</i>	1775	128	Spehn and Ganzhorn [2000]
<i>Eulemur rubriventer</i>	1960	119.81	This study
<i>Eulemur rufifrons</i>	1775	95.95	This study
<i>Varecia variegata</i>	3350	180	Moses and Semple [2011]
<i>Varecia variegata editorum</i>	3350	116.86	This study

Data on body mass were recorded from “All The World’s Primates” database (<<http://www.alltheworldsprimates.org/>>).