Original Article

Frugivory and Seed Dispersal Patterns of the Red-Ruffed Lemur, *Varecia rubra,* at a Forest Restoration Site in Masoala National Park, Madagascar

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Abstract

Frugivorous primates can play a critical role in the regeneration of degraded habitats by dispersing seeds of their food plants. We studied the diet and seed dispersal patterns of 3 groups of habituated red-ruffed lemurs *(Varecia rubra)* in a rain forest restoration site in Masoala National Park, Madagascar, to assess the species' seed dispersal effectiveness. Fruits accounted for 61% of the diet, with an average foraging time of 10 min per fruit patch per day. Seeds from 75% of the consumed fruit species were recovered in the collected *V. rubra* feces. We traced the potential parent plants of 20 dispersed-seed species to calculate a gut passage range (63–423 min; mean = 225, n = 35). The median seed dispersal distance from the potential parent plant was 48 m (mean = 83 m, range 0–568 m, n = 194). The home ranges of 2 of the 3 groups overlapped with the regenerating forest parcels. Although 92% of fecal samples with seeds were dispersed into the undisturbed forest, *V. rubra* fed on the fruits of the non-native pioneer shrub *Clidemia hirta,* while also dispersing native and non-native seed species into the regenerating forest parcels.

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Introduction

Seed dispersal by animals is a critical mutualistic interaction that plays an important role in the reproductive success, demography, colonization, gene flow, distribution, and evolution of plants [Howe and Smallwood, 1982; Wang and Smith, 2002]. Habitat fragmentation and degradation has threatened both plants and large-

bodied frugivores that rely on this interaction in tropical forests [Cordeiro and Howe, 2001; Farwig and Berens, 2012]. In Madagascar, human activities have resulted in the conversion of more than half of the eastern evergreen rainforest into agriculture or secondary forest [Dufils, 2003], leading to changes in animal disperser communities. It is recognized that effective conservation and restoration of tropical rainforests should consider plant-animal interaction processes, such as seed dispersal, and incorporate conservation practices to preserve such interactions [Corlett and Hau, 2000; Webb and Peart, 2001; Corlett, 2007]. A large body of literature supports the important role of frugivorous primates as seed dispersers in tropical forests [e.g. Chapman, 1995; Kaplin and Lambert, 2002; Gross-Camp and Kaplin, 2005; Chapman and Russo, 2006; Norconk et al., 2011]. However, the effectiveness of primates as seed dispersers can be influenced by several factors like body size, gut passage time, ranging patterns, diet, food availability, habitat fragmentation, and other landscape scale disturbances [Howe, 1989; Kaplin et al., 1998; Lambert and Garber, 1998; Ganas et al., 2004; Chapman and Russo, 2006; Jordano et al., 2007; Schupp et al., 2010].

One way to assess the importance of seed dispersers is to examine the quantitative and qualitative aspects of their seed dispersal effectiveness (SDE), which determines the probability of a dispersed seed producing a new adult plant [Schupp, 1993; Schupp et al., 2010]. Several variables can be used to define these attributes of SDE [Schupp et al., 2010]. For instance, the quantity of dispersed seeds can be defined by the frugivore's visitation rate at a food patch combined with the number of fruits and seeds consumed [Vazquez et al., 2005; Schupp et al., 2010]. The gut passage time (i.e. the time it takes for a seed to travel through an animal's gut) is also critical in assessing the effectiveness of dispersers as it affects the seed dispersal distance and arrival at suitable habitats for germination [Zhang and Wang, 1995; Holbrook and Smith, 2000; Chapman and Russo, 2006]. The distance of seeds from conspecific and parent plants and habitat suitability can all strongly influence the patterns of plant recruitment [Spiegel and Nathan, 2007]; these factors allow seeds and seedlings to escape density-dependent mortality effects and competition for resources [Janzen, 1970; Nathan and Muller-Landau, 2000; Hubbell et al., 2001], and they facilitate colonization of new habitats [Howe and Smallwood, 1982; Nathan, 2006].

In Madagascar forests, frugivorous lemurs are likely the primary seed dispersers of the island's diverse large-seeded or fleshy fruit-bearing plant species [Dew and Wright, 1998; Ganzhorn et al., 1999; Bollen et al., 2004; Wright et al., 2011] because of relatively low frugivorous bird and bat assemblages [Langrand, 1990; Böhning-Gaese et al., 1999; MacKinnon et al., 2003]. However, despite the large-scale forest loss in Madagascar, few studies have examined how seed-dispersing lemurs might contribute to the restoration of degraded habitats [e.g. Dausmann et al., 2008].

In this study, we report on some components of the quality and quantity of SDE by *Varecia rubra* (red-ruffed lemur) to help assess a forest restoration program in Masoala National Park (MNP). We determined the quantity of seed dispersal via the diet, the proportion of frugivory, and the amount and diversity of seeds passed by *V. rubra*. To explore the quality of SDE, we calculated the gut passage time, estimated a seed dispersal kernel based on the distances seeds were dispersed from a potential parent plant, and examined the frequency that *V. rubra* dispersed seeds in the regenerating forest parcels.
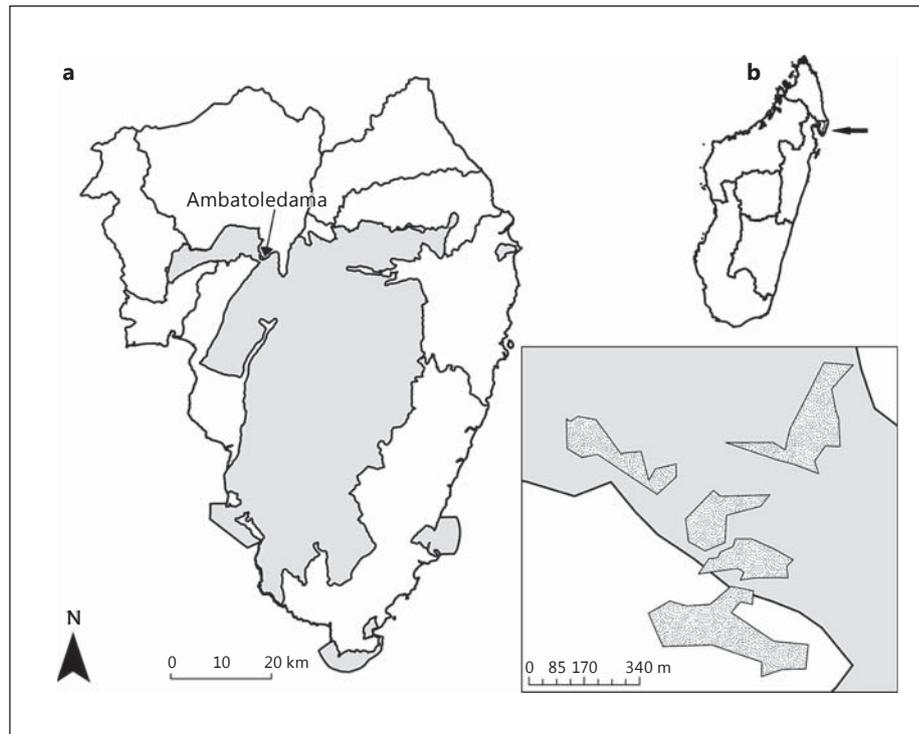
Fig. 1. a Map of the Masoala Peninsula showing the extent of MNP (gray) and the location of Ambatoledama. **b** Location of the Masoala Peninsula in Madagascar. **Inset** Ambatoledama field site within the National Park boundaries (gray) and non-forest regenerating parcels (stippled).

Methods

Study Site

This study was conducted in Ambatoledama in MNP located in northeastern Madagascar between 50°0′E, 15°16′S, and 50°1′E, 15°17′S (fig. 1). The vegetation is tropical evergreen forest and the altitude at the site ranges from 300 to 700 m. The climate of the Masoala peninsula is humid, with annual mean precipitation varying from 2.2 to 6.0 m [Kremen, 2003], and a mean monthly temperature range of 19–31.6°C [Vasey, 1997].

The mature forest cover at the Ambatoledama site is narrow, i.e. about 2.5 km in width, surrounded by a matrix of agriculture and secondary forest of various ages. Prior to the creation of the park, there were subsistence farming parcels surrounded by primary forest at Ambatoledama. A forest restoration project was established at Ambatoledama in 1997 where park staff planted saplings of lemur food trees in multiple former farming parcels [Holloway, 2000]. One main goal of the restoration project in 1997 was to entice frugivorous lemurs into the regenerating parcels, so they would disperse seeds from interior forest trees [Holloway, 2003]. In 2006 and 2007, when we carried out this study, the regenerating parcels consisted of a discontinuous canopy of pioneer tree species such as *Harungana madagascariensis* (family Clusiaceae) and *Dombeya andapensis* (family Malvaceae), and an understory approximately 2 m in height of native and non-native shrubs such as *Afromomum angustifolium* (family Zingiberaceae) and *Clidemia hirta* (family Melastomataceae) [Dokolahy, 2004]. Other vegetation in the parcels at the time of this study in-

Table 1. Composition of the *V. rubra* groups observed during our study seasons, total hours and days of observation, and proportion of fruit in the diet of the focal females based on all-occurrence feeding observations

	Adults, n	Infants, n	Others, n	Total observation time, h	Total observation time, days	Proportion of fruit in the diet (focal female)
November, 2006, to January, 2007						
Piste	1♀, 1♂	3		160	17	0.86
JJ	1♀, 1♂	4		86.7	10	0.83
JP	1♀, 1♂	2	1 juvenile ♀ born before 2006	86.2	10	0.87
August to November, 2007						
Piste	1♀, 1♂	0	2 juveniles	617.5	60	0.47
JJ	1♀ died in 2007		Not observed	–	–	–
JP	2♀, 1♂	0	2 juveniles	482.3	50	0.53
						Mean = 0.61

cluded a few naturally recruited remnant trees, which were left standing prior to agricultural development. The sizes of the regenerating parcels range from about 2 to 5 ha (fig. 1).

Study Animal

The red-ruffed lemur, *V. rubra,* is endemic to the Masoala Peninsula and is classified by the International Union for the Conservation of Nature as 'Critically Endangered' [Schwitzer et al., 2013]. *V. rubra* is described as living in multimale/multifemale groups with a fission-fusion social organization including subgroups, affiliates, and core groups [Vasey, 2006]. During our study period, *V. rubra* appeared to range within core groups of 2–6 individuals. In this paper, we refer to the core groups as 'groups' and distinguish the group from the 'focal females' where necessary. We focused on *V. rubra* because it is the largest extant diurnal frugivorous primate in MNP [Vasey, 2004] and the genus *Varecia* has been characterized as sensitive to disturbed forests [White et al., 1995; Balko and Underwood, 2005; Ratsimbazafy, 2006].

Data Collection

Fieldwork was conducted from November 2006 to January 2007 and from August to November 2007 for a total of 85,960 min of observations over 99 days (daily mean = 585 min, SD ±120). Prior to data collection, 3 groups (table 1) were habituated to human presence from August to November 2006 by local guides who followed the groups 5 days per week. We affixed Telonics brand MOD-205 radio collars (Telonics Inc., Mesa, Ariz., USA) to 4 adult females and 1 adult male in November 2006. Following a standard protocol for primate capture [Glander et al., 1991], lemurs were immobilized and captured using a CO_2-powered dart gun with a dose of 25 mg/kg of Telazol® (0.3 ml per 2.5–3 kg animal). The methodology was approved by the University of Minnesota's Institutional Animal Care and Use Committee (protocol No. 0603A83626).

When following a group, we monitored behavior through binoculars via either all-day (6.00–18.00 h) or half-day observations (6.00–12.00 h) from November 2006 through January 2007 and from August through November 2007 (table 1). We collected all-occurrence feeding behavior [Altmann, 1974] for focal females, which included recording every feeding bout lasting longer than 1 min; the feeding bout data from the focal females served as a representative sample for the group. We focused on the adult females because, in the genus *Varecia*, females are dominant to males in social and feeding contexts [Kaufman, 1991; Morland, 1991]; therefore, we assumed they fed on preferred foods. A feeding bout was recorded as the start and end time of feeding in the same food patch. We refer to the feeding sites as 'food patches' since *V.*
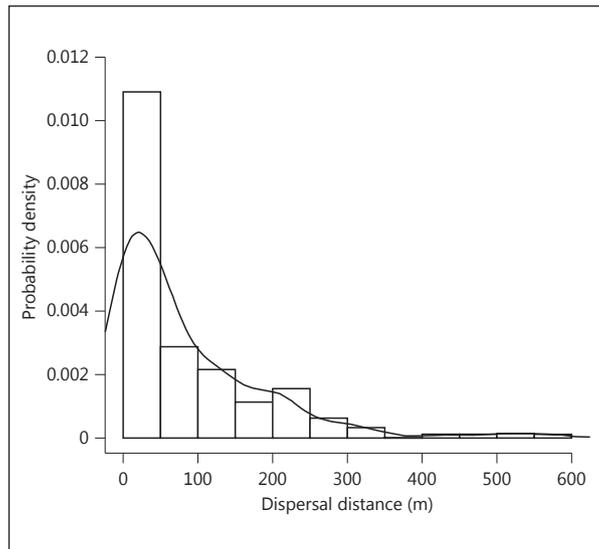
Fig. 2. Dispersal kernel of seeds dispersed by *V. rubra* at Ambatoledama, MNP.

rubra feed in trees, lianas, and shrubs. For each feeding bout, we recorded the vernacular name of the consumed plant species, the plant part (fruits, leaves, and flowers or nectar), and the GPS coordinates of the food patch (Garmin GPSMAP® 60CS). We scanned all of the individuals in the groups every 10 min to record their behavioral activities and GPS coordinates; in this paper, we use scan data associated with feeding behavior and locations only. Fecal samples were stored in plastic bags and later washed and sifted through a 1-mm-thick mesh sieve to extract and identify seeds [Stevenson, 2000]. Seed species less than 1 mm in length in fecal samples numbered in the hundreds and were noted as 'occurrences'. Food items and passed seeds were identified, when possible, to the family level by a parataxonomist on site or at the Tsimbazaza Botanical Park in Antananarivo, Madagascar. We recognize that our data collection methods may have introduced bias given the potential differences between age-sex classes and sampling intervals during behavioral observation [Altmann, 1974; Stevenson et al., 2005].

We mapped the regenerating parcels by walking around the perimeters and recording the geographic coordinates using GPS units (fig. 2). The coordinates were transformed into polygon shapefiles in ArcMap 10.1 (Environmental Systems Research Institute) and adjusted for accuracy when overlaid with a 10-meter resolution orthorectified digital aerial photograph mosaic created from flyovers of MNP in November and December 2007 (courtesy of the Wildlife Conservation Society Conservation Flight Association).

Data Analyses

We estimated the percentage of frugivory in *V. rubra* by calculating the mean of the proportion of minutes focal females spent consuming fruit divided by the minutes they spent consuming all foods per day. We estimated the visitation rate at food patches by calculating the mean feeding bout in minutes per fruit patch. To measure the variation in the daily proportions of fruits, leaves, and flowers (or nectar), the proportions were arcsine square root transformed and analyzed in a one-way analysis of variance (ANOVA) using JMP 9.0 (SAS Institute Inc., Cary, N.C., USA). We estimated a gut passage range by tracing the origin of passed seeds back to a potential parent plant based on the time of seed ingestion to deposition. If the passed seed was from the focal female, the beginning of the feeding bout was used as the time of ingestion; otherwise, for seeds passed by other group members, we used the observation time for a foraging event from the 10-min scan

sample as the time of ingestion. We did not have the capability to trace seeds back to parent plants genetically. Therefore, to reduce the uncertainty in assigning a potential parent to each seed, we used the following criteria similar to Stevenson [2000] to calculate the gut passage time: passed seeds were collected from known individual *V. rubra* who were continuously observed during the sampling day; the passed seeds originated from a fruit species consumed during either one feeding bout or successive feeding bouts at the same single food patch in the sampling day, and seed deposition occurred at least 5 h from the start of the observation day. However, we also included seed deposition as early as at 1.20 h under the following circumstances in the calculation of the gut passage time: when the groups were found in the previous night's sleeping site, when the groups were followed to a food patch, and when passed seeds of that species were found before 5 h from the start of the observation day. We justify inclusion of these data because captive *V. rubra* gut passage times range from 0.30 to 2.30 h, with a median time of 1.40 h [CabreVert and Feistner, 1995]. Passed seeds that did not meet the criteria were excluded from the estimate of gut passage times.

We calculated an empirical dispersal kernel and descriptive statistics for *V. rubra*-dispersed seeds using R 3.0.1 [R CoreTeam, 2013]. A dispersal kernel is a probability density that describes the scatter of dispersed and undispersed seeds from a parent plant [Clark et al., 1999]. In this study, we created a combined dispersal kernel for multiple species of dispersed seeds only; we did not consider undispersed seeds. The dispersal kernel was based on a sample of recovered seeds; we only included the seeds that fell within the calculated gut passage time range. We calculated the euclidian distance in meters between the GPS locations of the parent plants and the defecated seeds. We used the following criteria for a best estimate of seed dispersal distances from potential parent plants [Stevenson et al., 2000; Wehncke et al., 2003; Moses and Semple, 2011; Razafindratsima et al., 2014]: seeds were defecated within the calculated gut passage time range; fruit species were consumed at only one food patch in the sampling period, and, when there were multiple feeding bouts at the same food patch in a day, the earliest bout time was used as the time of ingestion as a single data point per passed seed in a fecal sample.

We estimated the expected frequency with which each *V. rubra* group dispersed seeds into the regenerating parcels based on the proportion of seeds dispersed and the area of overlap between the group's home range and the regenerating parcels. The home range of each group was estimated with a gaussian kernel density estimation (KDE) of habitat use in Geospatial Modelling Environment (GME; Spatial Ecology, LLC) [Beyer, 2012], with a 95% contour of intensity of utilization, using all GPS location points of feeding patches, fecal samples, and 10-min scan samples. To create the kernels, we selected cell sizes of 10 m and a plugin bandwidth. The 95% contours of KDE were used to estimate the area of overlap between home ranges for each group and the regenerating parcels. We performed a one-tailed χ^2 test to determine if the observed frequencies of seed dispersal occurrences in undisturbed forest versus the regenerating parcels were equal to the expected number of dispersal occurrences.

Results

Diet

We observed *V. rubra* consume the leaves, fruits, or flowers of at least 97 plant species from 28 different families (see online suppl. appendix; for all online suppl. material, see www.karger.com/doi/10.1159/000363408). The mean daily proportion of frugivory ranged from 0.47 to 0.86 by focal female and study season, but the daily mean over both study seasons and all focal females was 0.61 (SD ±0.32, n = 147; table 1). There was a significant difference in the mean daily proportion of time spent feeding on fruits, leaves, and flowers ($F_{2, 440}$ = 101.3, p < 0.0001). A post hoc Tukey HSD test showed that the proportion of fruit in the diet on a daily basis was greater than that of leaves and flowers (q = 2.35, α = 0.05). In both study seasons, focal females

spent an average of 10 min feeding per fruit patch per day (range 1–135 min, n = 300 food patches).

Seed Processing and Dispersal

The groups of *V. rubra* consumed the ripe fruits of 56 species, swallowing whole fruits or whole seeds along with pulp, and they passed seeds of 41 different species (75%). We collected 862 fecal samples, 90% of which contained at least one seed. Passed seeds were relatively large in length and width as described by Razafindratsima and Martinez [2012]. The seeds of 2 native tree species (*Calophyllum milvum* and *Garcinia verrucosa,* family Clusiaceae), 1 non-native shrub (*C. hirta,* family Melastomataceae), and multiple native *Ficus* spp. (family Moraceae) accounted for 70% of all passed seed occurrences in the fecal samples (see online suppl. appendix). On average, the focal female *V. rubra* passed 7 seeds (>1 mm in length) per feeding bout per food patch (range 1–124 passed seeds, n = 71 observations) and had 7 feeding bouts per day (range 1–21, n = 147 observations).

We traced the potential parent plant for 20 of the dispersed-seed species from 35 fecal samples to calculate a mean gut passage time of 225 min (range 63–423 min). The median seed-dispersal distance from the potential parent was 48 m (mean = 83 m, range 0–568 m, n = 194). For 72% of the observations, seeds were dispersed at least 10 m away from the potential parent food patch. The probability distribution of seed dispersal distances (dispersal kernel) was unimodal with positive skewness to the right ($\gamma_1 \geq 2.0$) and leptokurtic ($\gamma_2 = 8.1$) with an acute peak around the mean (fig. 2).

Seed Dispersal in Regenerating Parcels

Eight percent (n = 703, number of samples with reliable information on the group and GPS coordinates) of the collected seed-containing fecal samples landed in the parcels, representing 8 species from 6 families. Four of the dispersed-seed species were the same as those saplings planted by park staff for the restoration project at Ambatoledama (table 2). *C. hirta,* a non-native pioneer shrub in Madagascar, occurred in 53% of the fecal samples collected in the parcels. All of the observations of seeds dispersed into the parcels occurred in the 2007 study period. The Piste group had the greatest percentage of fecal samples with seeds in the parcels (13%), whereas we recovered only 2 fecal samples with seeds from the JP group (1%) and 0 samples from the JJ group (table 3). There was spatial overlap between the 95% kernel home ranges of the 3 groups and the regenerating parcels (fig. 3); however, the degree of overlap constituted relatively small percentages of the total home ranges for the 3 groups, i.e. 10, 2, and 0.1% (table 3). Based on the expected and observed seed dispersal events relative to the spatial overlap of the home ranges and the 2 land classes (forest and regenerating parcels), the observed and expected frequencies of seed dispersal events by land class differed significantly for the Piste group ($\chi^2 = 4.2$, p = 0.03), but not for the JP and JJ groups ($\chi^2 = 1.7$, p = 0.19, and $\chi^2 = 0.02$, p = 0.88, respectively).

There were a total of 702 food patches visited by all 3 groups. In 2006, five patches were located in the parcels; in 2007, 41 food patches were in the parcels. *V. rubra* fed on 11 unique plant species from 8 different families in 4 of the 5 parcels. Of the time the groups spent feeding in the parcels, 69% was spent consuming the ripe fruits of *C. hirta.* Further, only the Piste group during the 2007 season foraged on *C. hirta* within a single parcel for a maximum bout of 115 min (mean = 29, SD = 31, n = 38 bouts).

Table 2. Seed species dispersed into the regenerating parcels; proportions of occurrences in all fecal samples collected in the parcels (n = 55)

Family	Genus and species	Vernacular name	Proportion instances	Seed size[a]	Habit and status of the species in the regenerating parcel
Melastomataceae	*Clidemia hirta*	Trotrobaritra	0.37	Small	Non-native pioneer shrub; not planted by staff in parcels
Moraceae	*Ficus* spp.	Multiple, including: amotana, nonosay, and hodipaso	0.36	Small	Liana or tree; not planted by staff in parcels
Clusiaceae	*Calophyllum milvum*	Vintanona	0.14	Large	Tree; planted by staff in parcels
Rubiaceae	Unidentified	Valotra	0.12	Small	Liana; not planted by staff in parcels
Lauraceae	*Cryptocarya* sp.	Tavolo madinidravina	0.08	Large	Tree; planted by staff in parcels
Myrtaceae	*Eugenia* sp.	Ompa	0.02	Medium	Tree; the same genus was planted by staff in parcels

[a] Small: <1 mm, medium: 5–10 mm, and large: >10 mm in length.

Table 3. Percentage of fecal samples with seeds (dispersal events) that were dispersed within the regenerating parcels and forest, and home range overlap with the parcels and forest

	Seed dispersal events			Home range overlap				
group	parcels, %	forest, %	total feces with seeds	KDE 95% contour, ha	overlap with parcels, ha	overlap with the forest, ha	χ^2	p
Piste	13	87	420	9.30	0.885 (10%)	8.41 (90%)	4.7	0.03
JP	1	99	258	16.77	0.314 (2%)	16.46 (98%)	1.7	0.19
JJ	0	100	25	5.42	0.005 (0.1%)	5.42 (99.9%)	0.02	0.88

The χ^2 test statistic applied to the proportions of fecal samples with seeds that were deposited in the forest and regenerating parcels relative to the acreage of each group's home range and the area of overlap with the regenerating parcels.

Discussion

Frugivory

Previous research based on year-round observations has shown that *Varecia* species spend 74–90% of their time feeding on fruit [Morland, 1991; Vasey, 1997; Balko, 1998; Vasey, 2004]. During our study periods at Ambatoledama, the percentage of time *V. rubra* focal females spent feeding on fruit averaged 61%, but this varied by group and season from 47 to 87%. The observed differences may be due to the
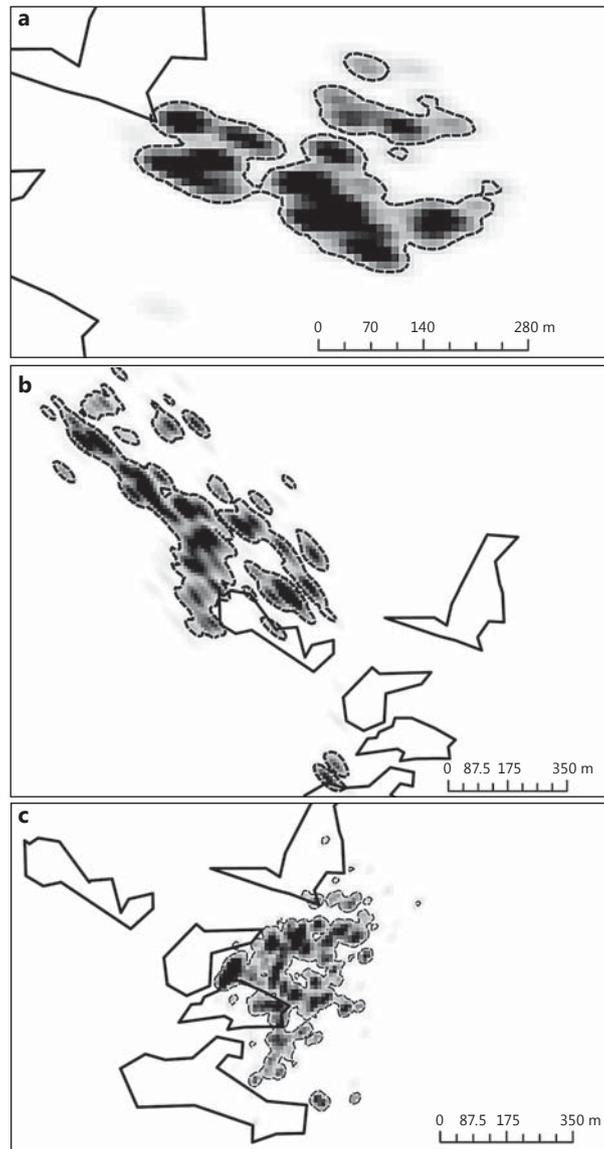
Fig. 3. Home ranges for each group represented by 95% contours of KDE (shaded and within hatched lines) and locations of the regenerating parcels (within solid lines) for each group: JJ (**a**), JP (**b**), and Piste (**c**).

seasonal and asynchronous fruit availability in the Madagascar rainforest [Morland, 1991; Overdorff, 1993; Powzyk, 1997; Balko, 1998; Wright, 1999; Ratsimbazafy, 2006]. In 2006, our study period occurred during the mid- to late 'hot and dry' season characterized by peak fruit and flower production, whereas in 2007 our observations were during the end of the 'cold and rainy' season and the start of the 'hot and dry' season when fruit production typically is not yet at its peak [Vasey, 2005]. The variation in the diet of *V. rubra* suggests that the time frame of a field study can affect conclusions about the magnitude of the effectiveness of seed dispersers when

considering frugivory as a main variable. However, the potential for *V. rubra* to disperse numerous seed species in MNP is high, as they were observed feeding on at least 50 fruit species. At Andranobe in MNP, *V. rubra* consumed at least 132 different plant species over 1 year [Vasey, 2000a, 2004]. In addition, the focal females in our study spent an average of 10 min feeding per fruit patch per day, which suggests there can be numerous opportunities for *V. rubra* to disperse seeds from multiple food sources.

V. rubra dispersed a large number and percentage of intact seeds (41 species, 75% of the consumed fruit species) during our study seasons. We reported elsewhere that most of the seeds dispersed by *V. rubra* were large in size (85% of passed seeds had a length >10 mm), viable, germinated more frequently than nonpassed seeds extracted from ripe fruits, and showed an increased seedling growth [Razafindratsima and Razafimahatratra, 2010; Razafindratsima and Martinez, 2012]. Large-seeded fruit species are relatively immobile and rely on large-bodied animal dispersers to move the seeds beyond the crowns of the parent plants [Wheelwright, 1985; Kitamura et al., 2002; Peres and van Roosmalen, 2002], although secondary seed dispersers, like scatter-hoarding rodents, can also effectively disperse large-seeded plant species [Jansen et al., 2012]. In MNP, *V. rubra* is the largest extant primate (body mass: 3.3–3.6 kg) [Vasey, 2004] and it is likely the only primary seed-dispersing species able to consume and disperse the larger-sized seeds. However, there is some overlap with the sympatric species *Eulemur albifrons,* which is a smaller frugivore (body mass: 2–2.6 kg) [Mittermeier et al., 2006] that also disperses the large seeds of *G. verrucosa* and *C. milvum* [pers. obs.].

Gut Passage Time

The gut passage time plays an important role in determining seed distribution patterns [Westcott et al., 2005] and can affect seed survival and seedling recruitment. For example, the germination success of a large-seeded tree species dispersed by the red-tailed guenon *Cercopithicus ascanius* in Uganda was less correlated with the distance from the parent tree but more correlated with seed cleaning before spitting, which reduced fungal infestation of the seeds [Lambert, 2001]. Likewise, in a Malagasy southeastern forest, the passage of *Grewia* seeds through the digestive tract of brown lemurs, i.e. *E. fulvus rufus,* reduced seed predators [Spehn and Ganzhorn, 2000]. *V. rubra* had a relatively fast gut passage time ranging from 63 to 423 min (mean = 225 min), comparable to what was observed in its close relative *V. variegata* in the rainforests of Ranomafana (mean = 194.8 min) [Razafindratsima et al., 2014] and Manombo (mean = 260 min) [Moses and Semple, 2011]. A fast gut passage time appears to be typical in frugivorous lemurs since the structure of their digestive tract is simple and short [Campbell et al., 2004; Sato, 2012]. The gut passage time could affect whether seeds are deposited in clumped or scattered patterns, which may affect seed survival and seedling recruitment [Schupp and Milleron, 2002; Muller-Landau and Hardesty, 2005] such that it might decrease the effects of competition at seedling stages [Wright, 2002; Paine et al., 2008; Stevenson, 2008]. For example, a study of *Cebus capucinus* in Panama found that a relatively fast gut passage time of 100 min resulted in fewer seeds per fecal sample and a scattered seed dispersal pattern [Wehncke et al., 2003]. The likelihood of density-dependent seed mortality may be reduced under these conditions [Howe and Smallwood, 1982; Howe, 1989].

Seed Dispersal Distances

The distance of seed dispersal away from parent plants and adult conspecifics is critical for seed survival and seedling recruitment because of density-dependent mortality effects associated with the proximity to parent and conspecific adult trees [Janzen, 1970; Schupp, 1988; Nathan and Muller-Landau, 2000; Howe and Miriti, 2004]. In a recruitment study in a Peruvian rainforest, most recruited saplings arose from dispersed seeds and not from undispersed seeds that fell under the crowns of the parent plants [Terborgh et al., 2011]. In this study, *V. rubra* deposited a majority of seeds ≥10 m from the parent tree and long-distance dispersal was rare. Short-distance seed dispersal may be common in frugivorous lemurs as a result of their small body size and relatively small home range size [Razafindratsima et al., 2014].

Forest Restoration

Forest regeneration is, in part, limited by available seed dispersers [Nepstad et al., 1991; Holl et al., 2000]. Large-bodied frugivores are critical in the restoration of their habitat since they can disperse native plant species into degraded areas [Kaplin and Lambert, 2002]. We observed *V. rubra* traveling through the regenerating parcels while foraging on fruits and dispersing seeds. They were mainly feeding on the small, ripe fruits of *C. hirta,* a non-native fast-growing pioneer species. *C. hirta* grows close to the ground, with a maximum height of 2 m in the parcels, and lemurs forage on the ripe fruits while traveling on the ground under an open canopy. Although other studies have observed *V. variegata* feeding on *C. hirta* after decreased food availability due to cyclone damage [Ratsimbazafy, 2006], this was an unusual observation in MNP since previous studies have found that *V. rubra* spend 94% of the time feeding in the tree crowns of relatively large trees [Vasey, 2000b]. Our observations suggest that *V. rubra* is not behaviorally restricted to foraging in tall and large trees within the mature forest. Although we observed *V. rubra* ranging in the regenerating parcels, in the case of 2 groups, there was no statistical difference between the expected and observed frequencies of seed dispersal events into the parcels.

There are positive and negative aspects of *V. rubra* dispersing *C. hirta* seeds. In the short-term, foraging on *C. hirta* is beneficial for the restoration project since it provides fruits year-round [Wester and Wood, 1977] and draws lemurs into the parcels, allowing dispersal of a diversity of forest seed species. Successful restoration programs in the tropics use remnant or man-made perches [Janzen, 1988; Holl et al., 2000; Shiels and Walker, 2003] or planted food trees [Toh et al., 1999; Berens et al., 2008] to lure avian and mammalian dispersal agents into non-forest landscapes, but studies have also shown that early successional shrubs are important for the initiation of forest regeneration [Nepstad et al., 1991; Vieira et al., 1994; Zahawi and Augspurger, 1999; Duncan and Chapman, 2002]. In the long term, the structure of the forest at MNP might be affected by *V. rubra* dispersing *C. hirta* seeds into the mature forest, since this species can thrive under an open or a closed canopy [Wester and Wood, 1977]. Some of the endemic plant species dispersed into the regenerating parcels, i.e. *Calophyllum* sp. and *Cryptocarya* spp., were large seeded, which typically provides them with a competitive advantage over smaller seeds in low light [Swaine and Whitmore, 1988; Whitmore, 1989]. Such species might fare well under the cover of *C. hirta* [Balderrama and Chazdon, 2005; Dupuy and Chazdon, 2008]. Deposition of native seed species by lemurs into the regenerating parcels provides recruitment opportunities that would otherwise not occur if a seed disperser like *V. rubra* was absent.

Seed dispersal by *V. rubra* will affect the structure and composition of the regenerating forest but, because we know very little about the growth rates or requirements of the native plant species, it is beyond the scope of this paper to predict what the restored forest will look like.

Prioritization of species for conservation needs to reflect ecological function, like SDE [McConkey et al., 2012]. Although this was a relatively short-term study, it provides evidence that *V. rubra* plays a critical role in the dispersal of plant species in the mature forest and regenerating parcels. The largest extant lemur species in MNP is worth protecting, especially for the ecological service it provides as an effective seed disperser. In MNP, managers can actively lure *V. rubra* by cultivating food sources along forest edges and in regenerating parcels. This has to be coupled with active protection and communication with the local community for acceptance and to reduce the subsistence hunting of lemurs [Golden, 2009].

Acknowledgments

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