

Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment

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Abstract. Directed dispersal is defined as enhanced dispersal of seeds into suitable microhabitats, resulting in higher recruitment than if seeds were dispersed randomly. While this constitutes one of the main explanations for the adaptive value of frugivore-mediated seed dispersal, the generality of this advantage has received little study, particularly when multiple dispersers are involved. We used probability recruitment models of a long-lived rainforest tree in Madagascar to compare recruitment success under dispersal by multiple frugivores, no dispersal, and random dispersal. Models were parameterized using a three-year recruitment experiment and observational data of dispersal events by three frugivorous lemur species that commonly disperse its seeds. Frugivore-mediated seed dispersal was nonrandom with respect to canopy cover and increased modeled per-seed sapling recruitment fourfold compared to no dispersal. Seeds dispersed by one frugivore, *Eulemur rubriventer*, had higher modeled recruitment probability than seeds dispersed randomly. However, as a group, our models suggest that seeds dispersed by lemurs would have lower recruitment than if dispersal were random. Results demonstrate the importance of evaluating the contribution of multiple frugivores to plant recruitment for understanding plant population dynamics and the ecological and evolutionary significance of seed dispersal.

Key words: *Cryptocarya crassifolia*; demography; directed dispersal; lemurs; Madagascar; primates; seed dispersal; tropical forest.

INTRODUCTION

Frugivores act as seed-dispersal agents in many ecosystems (Herrera 2002). In tropical systems, for example, up to 90% of trees have traits adapted for animal-mediated seed dispersal (zoochory; Howe and Smallwood 1982). A critical step for understanding the adaptive value of zoochory is quantifying the effect of seed deposition patterns on seed fate. A large body of work has suggested that escape of seeds from distance- and density-dependent effects of falling under a parent tree (escape hypothesis; Janzen 1970, Connell 1971, Howe and Smallwood 1982) may be a primary selective advantage of zoochory for plants (see reviews in Wright [2002], Freckleton and Lewis [2006]). However, the enhanced dispersal of seeds into microhabitats favorable for germination and recruitment (directed dispersal; Howe and Smallwood 1982, Wenny 2001) could also be critical for seeds that do escape such effects. For directed dispersal to be an adaptive strategy for zoochorous plants, the advantage of dispersal into specific microhabitats must be greater than expected under random dispersal (i.e., in which seeds reach microhabitats in proportion to their availability).

Studies exploring directed dispersal have generally focused on the behavior of a single disperser species (e.g., Green et al. 2009, Hirsch et al. 2012) or extreme situations in which seeds have very limited viability unless deposited in specific and very limited microhabitats (Carlo and Aukema 2005, Green et al. 2009, Spiegel and Nathan 2012). However, most fruiting plants are dispersed by multiple frugivores (who may differ in the locations to which they disperse seeds) and seeds are exposed to a gradient of suitable microhabitats (Brodie et al. 2009). Given the inherent difficulty in tracking seeds dispersed by multiple seed-dispersers, empirical evidence supporting the generality of the directed-dispersal hypothesis is limited. One such study by Wenny and Levey (1998) demonstrated that one of five frugivorous bird species distributed seeds of a Neotropical tree nonrandomly with respect to microhabitat characteristics resulting in higher plant recruitment. However, there is little understanding of how general such effects might be or how a suite of frugivores may together contribute quantitatively to plant demography through directed dispersal. Nonrandom dispersal could be a selective advantage for plants with multiple frugivores if plants have fruit traits to attract dispersers sharing certain foraging behaviors, habitat preferences, or probabilistic patterns of seed dispersal that favor recruitment (Wenny 2001) or if one or a few dominant dispersers drive net-advantageous dispersal patterns. Conversely, if trees attract dispersers that have nonran-

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dom dispersal patterns, there would be evolutionary pressure to adapt to these microhabitats. Such mechanisms would allow directed dispersal to arise through evolutionary adaptations of the plant despite the diffuse interactions between individual dispersers and their host plants (Wenny 2001).

We focused on a long-lived rainforest tree, *Cryptocarya crassifolia*, in southeastern Madagascar and three frugivorous lemur species that commonly disperse its seeds to assess the advantages of directed dispersal by multiple frugivores to plant recruitment. We tested three main hypotheses: (1) seed dispersal by frugivores would be distributed nonrandomly across microhabitats with varying canopy covers, (2) recruitment would be higher for seeds nonrandomly dispersed than seeds fallen under the parent tree (no dispersal) or randomly dispersed, and (3) the three species of frugivores would differ in their contribution to plant recruitment. To do this, we carried out direct observations of dispersal events by the three frugivores and parameterized probability recruitment models using dispersal observations and results of a 3-yr recruitment experiment across different microhabitats.

METHODS

Study site and system

This study was conducted in the evergreen rainforest of Ranomafana National Park (RNP), Madagascar (47°18'–47°37' E, 21°02'–21°25' S). Established as a protected area in 1991, RNP comprises 41 600 ha (Wright and Andriamihaja 2002). With an average annual rainfall of 2830 mm, the precipitation in RNP is seasonal with a peak wet season in January–March (average monthly rainfall of 508 mm) and a dry season in June–October (average monthly rainfall, 143 mm; Dunham et al. 2011). Elevation in RNP ranges between 600 and 1500 m (Wright and Andriamihaja 2002). Our work was conducted in four study sites (Mangevo, Talatakely, Valohoaka, and Vatoharanana) within the southern block of forest in the park (see map, Appendix A), which is home to 330 known tree and large shrub species.

Our study tree species, *Cryptocarya crassifolia* Baker (syn. *Ravensara crassifolia* Danguy; family, Lauraceae), locally known as Tavolomanitra (see Plate 1), is a long-lived canopy tree endemic to the southeastern rainforests in Madagascar. It is a successional-climax species that produces large, brown-colored fleshy fruits (length, 20 mm; diameter, 19 mm) with one large, ovoid seed (length, 18 mm; diameter, 17 mm) and sets fruit annually from March to October (O. H. Razafindratsima and A. E. Dunham, unpublished data). In RNP, *Cryptocarya* seeds are commonly dispersed through defecation by three frugivorous lemur species (Razafindratsima et al. 2014), which are also the largest-bodied frugivores in the system (2.0–3.4 kg; Razafindratsima et al. 2013): *Eulemur rubriventer* (red-bellied lemur), *Eulemur rufifrons* (red-fronted brown lemur), and *Varecia variegata editorum* (southern black-and-white ruffed lemur, see

Plate 1). These species' reported densities in RNP are 5.46 individuals/km² for *E. rubriventer*, 6.70 individuals/km² for *E. rufifrons*, and 2.23 individuals/km² for *V. v. editorum* (Wright et al. 2012). They are arboreal and disperse seeds while travelling, resting, or feeding in the canopy; however, they differ in their patterns of foraging and movement through their habitats (Razafindratsima et al. 2014). Surveys of *V. v. editorum* suggest they prefer areas with closed canopy covers (Herrera et al. 2011).

Sampling microhabitats of seed deposition

We determined patterns of seed dispersal by each lemur species into different microhabitats through direct observations of defecation events. Our sample included observations of eight prehabituated groups of each species (average group size: *E. rubriventer*, 3.05 ± 0.71; *E. rufifrons*, 6.16 ± 3.48; *V. v. editorum*, 2.94 ± 1.23) which were distributed across four sites (Mangevo, Talatakely, Valohoaka, and Vatoharanana) from June 2010 to June 2011. There was extensive overlap among groups and between species at each site. Groups and species were alternated daily (when locating another group was possible) to ensure comparable data were collected across all groups under study. During lemur group follows, a team of two to four observers collected as many fecal samples as they could from all group individuals (total: 1340 samples; Appendix B). All seeds within each fecal sample were identified to species. Conspecific seeds in the same fecal deposition were considered as one dispersal event. For each fecal deposition, we also identified the nearest adult neighboring tree and measured canopy cover above the fecal deposition using a spherical densiometer (Model C, Forestry Densiometers, Bartlesville, Oklahoma, USA). We categorized canopy cover as gap (<55% canopy cover), medium-shaded (55–75%), and shaded (>75%). The gap category was representative of observed recent tree-fall gaps in the park. The shaded category (>75%) was chosen such that it was the minimum interval that was represented by at least 10% of the forest within each of the study sites.

We tested for nonrandom patterns of seed deposition by comparing observed deposition microhabitats with availability in each study site. To quantify availability, we established nine straight-line transects in each of the four study sites that overlapped with the ranges of the lemurs. Transects were 500 m long × 4 m wide (Brodie et al. 2009), ran perpendicular to a main trail system at each site, and were spaced at least 100 m apart. Total area sampled per site was 18 000 m². To estimate the relative availability of adult *Cryptocarya* trees, we surveyed tree composition in each transect by identifying and counting all adult trees (defined as minimum size of reproduction, estimated from known stems by trained local botanists). We estimated the availability of each canopy-cover category by measuring canopy cover at points every 10 m along each transect using a densiometer (for microhabitat availability, see Appendix C).

Seed-fate experiment

We conducted an experiment with *Cryptocarya* seeds to assess seed germination, removal/predation, and seedling survivorship across different canopy covers and under conspecific trees. This experiment was conducted in Talatakel, because its accessibility allowed for monitoring every two weeks. Seeds used in the experiment were extracted from fresh ripe fruits collected on the ground or from fruiting trees of *Cryptocarya* trees rather than from lemur defecations because of logistical challenges in collecting enough seeds in lemur scat. However, our germination rates for *Cryptocarya* seeds were similar to rates found for seeds passed through the gut of the three lemur species in a previous study (Dew and Wright 1998). Seeds were thoroughly mixed and then planted under conspecific trees or in one of three microhabitat treatments: (1) under canopy comprised of gap habitat (<55%), (2) medium-shaded habitat (55–75%), and (3) shaded habitat (>75%). Each treatment was replicated 10 times. All heterospecific sites were located >15 m away from a *Cryptocarya* tree. The locations of experimental plots were selected in close proximity to small trails for ease of access and were at least 100 m apart.

To separate the effects of seed removal/predation from germination, each plot was composed of paired subplots containing a rodent enclosure and an open treatment in each of our replicated microhabitats described above. Enclosure subplots consisted of wire cages (mesh size: 1 cm²) measuring 30 × 30 × 15 cm pinned to the ground with wooden stakes in each corner (Brodie et al. 2009). Open subplots were located ~25 cm from enclosure subplots and marked with wire flags. Five seeds were placed on the surface of each paired subplot (4 microhabitat types × 10 locations × 2 enclosure treatments × 5 seeds = 400 seeds total). For the open subplots, seeds were each tethered to a buried garden staple with 150-cm thread glued to each seed with scent-free, nontoxic cyanoacrylate adhesive to enable tracking of seed fate (Forget and Cuijpers 2008). Since seed removal and predation were difficult to disentangle in many cases, we combined them into a single category (seed removal/predation).

Plots were monitored every 2 weeks for 3 months (June–September 2010) for seed removal/predation, germination, and survivorship. To quantify seed removal/predation, we counted the number of seeds missing or with obvious signs of predation. No signs of rodents entering the cages were evident during the experiment. Unfortunately, after an initial 3 months of monitoring, new park regulations required that we remove cages from our enclosure subplots. All plots were then monitored to assess 1-yr and 3-yr survivorship.

Data analyses

We used a general linear model in SPSS 20.0 (IBM, Armonk, New York, USA) to examine how the three disperser species differ in the estimates of the quantity of

Cryptocarya seeds dispersed per adult tree in their habitat per fruiting season (see Appendix D). Sampling level was per group with species treated as a fixed effect. When site was included as a random factor, it was not a significant predictor ($F_{3,2.33} = 0.45$, $P = 0.74$), so was excluded from the analysis. Data met assumptions of a parametric test. Patterns of seed deposition bias into specific microhabitat categories (based on availability; see Appendix D) were compared between disperser species and relative to a null expectation with a chi-square test. We also used a paired t test to determine if social groups of dispersers deposit *Cryptocarya* seeds under conspecific trees more frequently than expected based on tree abundances in the groups' habitats. Replicates were based on means of individual lemur group estimates.

We performed a full-factorial generalized linear model (GLM) with negative binomial distribution and log-link function in SPSS 20.0 to assess the effects of canopy cover and nearest adult-tree conspecificity on *Cryptocarya* recruitment success and vital rates. The methods used for the estimations of the seed-dispersal parameters and vital rates are detailed in Appendix D.

We assessed the relative contribution of each disperser to the 3-yr recruitment of their host plant relative to random dispersal and no dispersal with a probability recruitment model performed in MATLAB R2011a (MathWorks, Natick, Massachusetts, USA) parameterized by our observational and experimental data (Appendix D).

RESULTS

Patterns of seed deposition into different microhabitats

Frugivore species differed significantly in the quantity of seeds dispersed per adult tree in the habitat ($F_{2,18} = 3.77$, $P = 0.04$; Fig. 1A). *Eulemur rubriventer* dispersed about three times more *Cryptocarya* seeds per tree than *E. rufifrons* (Least significant difference [LSD] post hoc test, $P = 0.03$) or *V. v. editorum* ($P = 0.02$). There was no significant difference between the quantity of seeds dispersed per tree by *E. rufifrons* and *V. v. editorum* ($P = 0.10$). All three lemur species in our study dispersed seeds into microhabitats nonrandomly with respect to availability of canopy cover categories. This was true when we only considered dispersal events under heterospecific trees (Fig. 1B; *E. rubriventer*, $\chi^2 = 166.9$, $df = 23$, $P < 0.0001$; *E. rufifrons*, $\chi^2 = 288.9$, $df = 23$, $P < 0.0001$; *V. v. editorum*, $\chi^2 = 456.6$, $df = 23$, $P < 0.0001$) or when conspecific trees were included in the analysis (Appendix E). All three lemur species dispersed seeds into medium-shaded areas and away from shaded areas significantly more than expected by chance (Fig. 1B). The two *Eulemur* spp. also had a tendency to differentially disperse seeds into gaps, while there was no bias for *V. v. editorum* (Fig. 1B). *E. rufifrons* dispersed *Cryptocarya* seeds under the crowns of conspecific adult trees more than expected by chance ($t_5 = 3.07$, $P = 0.03$; Fig. 1C), but there was no significant difference for *E.*

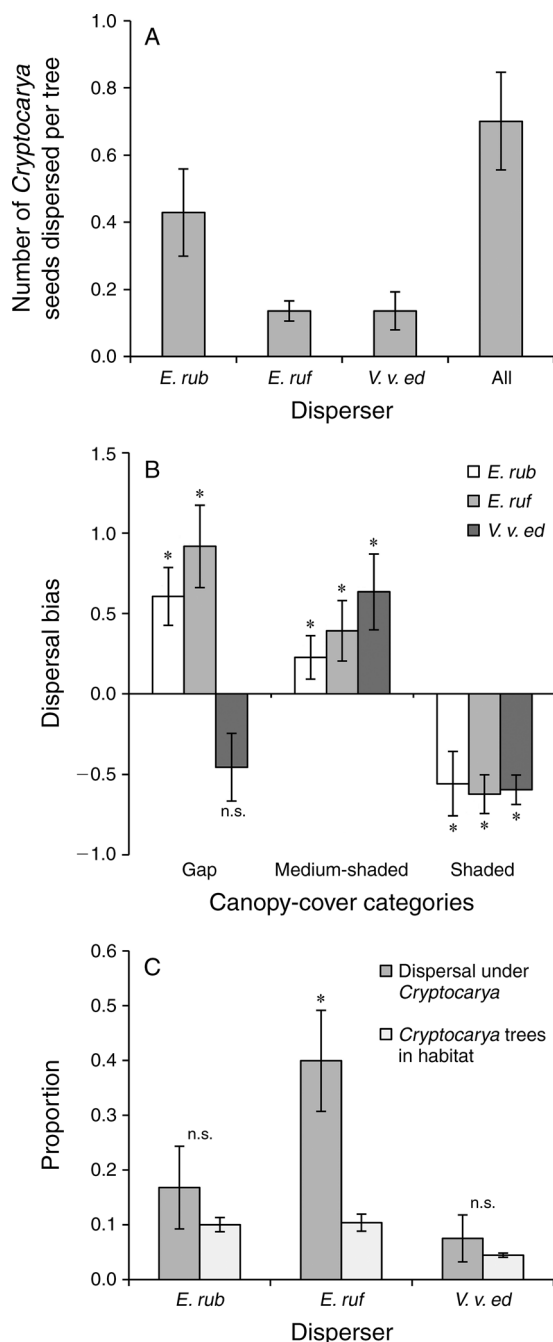


FIG. 1. (A) Quantity of *Cryptocarya* seeds dispersed by each frugivore species (*E. rub*, *Eulemer rubriventer*; *E. ruf*, *E. rufifrons*; *V. v. ed*, *Varecia variegata editorum*) per tree during the plant species' fruiting season and for all dispersers combined (All). (B) Dispersal events by the three frugivore species under heterospecific trees with different microhabitat categories (gap, <55% cover; medium-shaded, 55–75%; shaded, >75%) relative to availability in their habitats. 1, proportional dispersal; >1, more seeds deposited in the microhabitat category than expected based on availability; <1, fewer seeds dispersed in the microhabitat than expected. (C) Proportions of dispersal of *Cryptocarya* seeds under conspecific trees relative to tree availability in the habitats of each disperser. Values are means; error bars represent standard error across groups and composite standard error for the All category.

* $P < 0.05$; n.s., not significant.

rubriventer ($t_6 = 0.88$, $P = 0.41$) or *V. v. editorum* ($t_3 = 0.91$, $P = 0.43$).

Seed fate across microhabitats

The 3-yr sapling recruitment differed significantly with canopy cover category (Wald $\chi^2 = 8.62$, $df = 2$, $P = 0.01$). Recruitment rates were >3 times higher in gaps than in medium- and heavily shaded sites (0.28 vs. 0.09; Fig. 2). Recruitment was also significantly lower near conspecific adult neighbors when controlling for canopy cover (Wald $\chi^2 = 3.99$, $df = 1$, $P = 0.046$). Interaction terms (canopy-cover category and conspecificity) were not quite significant (Wald $\chi^2 = 2.53$, $df = 1$, $P = 0.11$). Both canopy cover and conspecificity had significant effects on 1–3 y transition probabilities (Wald $\chi^2 = 9.52$, $df = 2$, $P = 0.01$; Wald $\chi^2 = 9.81$, $df = 1$, $P = 0.002$, respectively) with a significant interaction between variables (Wald $\chi^2 = 6.50$, $df = 1$, $P = 0.01$). However, there was no significant effect on germination rates (canopy cover, Wald $\chi^2 = 0.40$, $df = 2$, $P = 0.82$; conspecificity: Wald $\chi^2 = 0.01$, $df = 1$, $P = 0.91$), 3 month to 1 y transition probabilities (canopy cover, Wald $\chi^2 = 4.63$, $df = 2$, $P = 0.10$; conspecificity, Wald $\chi^2 = 0.60$, $df = 1$, $P = 0.44$), or removal/predation rates (canopy cover, Wald $\chi^2 = 0.57$, $df = 2$, $P = 0.75$; conspecificity, Wald $\chi^2 = 0.30$, $df = 1$, $P = 0.58$).

Sapling recruitment

Results of our probability recruitment model suggest that *Cryptocarya* seeds dispersed by lemurs will have on average a four times higher 3-yr recruitment rate than seeds falling directly under the canopy of the parent tree. For each lemur species, this difference was supported by nonoverlapping 95% confidence intervals (CI; Fig. 3). The model suggested that directed dispersal of *Crypto-*

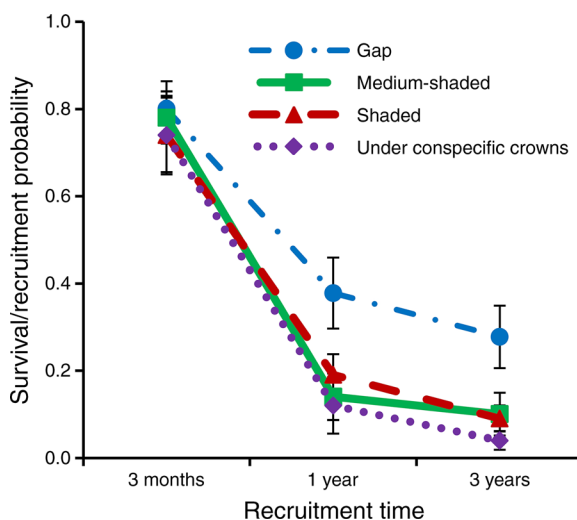


FIG. 2. Survival and recruitment of *Cryptocarya* in microhabitats with different canopy covers (gap, <55% cover; medium-shaded, 55–75%; shaded, >75%) and under conspecific crowns. Error bars represent standard errors.

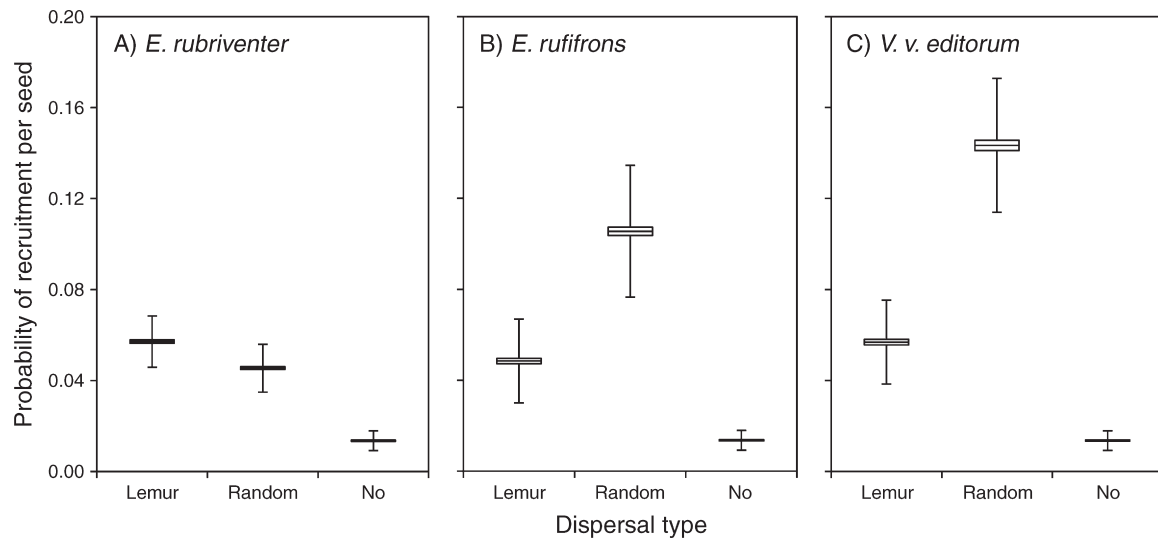


FIG. 3. Probability recruitment model results. The estimated per capita seed recruitment probabilities are presented for seeds dispersed by each frugivore species (A, *E. rubriventer*; B, *E. rufifrons*; C, *V. v. editorum*) vs. seeds fallen under parent tree (no dispersal) and randomly dispersed seeds (relative to microhabitat availability). Middle lines, boxes, and error bars show mean, 95% bootstrap confidence intervals, and SD respectively.

carya seeds was performed by *E. rubriventer* but not *E. rufifrons* or *V. v. editorum*. Seeds dispersed by *E. rubriventer* were estimated to have 1.3 times higher recruitment success than randomly dispersed seeds. However, random dispersal was estimated to be more advantageous for recruitment than lemur dispersal by *E. rufifrons* and *V. v. editorum* (random dispersal was 2.2 and 2.5 times higher respectively; nonoverlapping 95% CI).

DISCUSSION

Understanding the effects of nonrandom frugivore-mediated seed dispersal on plant recruitment is critical for understanding plant population dynamics and the ecological and evolutionary consequences of seed dispersal. Nonrandom, directed movement of seeds towards suitable microhabitats (directed dispersal) is frequently discussed as an adaptive advantage of seed dispersal by frugivores (Farwig and Berens 2012, Beckman and Rogers 2013). Unfortunately, the difficulty in tracking seeds dispersed by multiple frugivores has meant we have limited understanding of such advantage to plant recruitment. Demographic analyses incorporating variation of microhabitats into which seeds are dispersed are important for assessing the population-level consequences of nonrandom seed dispersal (Brodie et al. 2009, Loayza and Knight 2010). Our model allowed us to address the relative contribution of different dispersers to the partial recruitment of their host plant and to predict the value of nonrandom dispersal for seed recruitment success.

Results from our probability recruitment models suggest that nonrandom dispersal is not currently an overall advantage of having traits associated with

zoochory by lemur frugivores for *Cryptocarya crassifolia*, a long-lived tree species in a Madagascar rainforest. While all frugivores in our study dispersed seeds nonrandomly with respect to microhabitat, their patterns of dispersal differed from each other. One of the plant's three frugivores (*Eulemur rubriventer*) may provide directed dispersal for the plant, with modeled sapling recruitment of dispersed seeds 1.3 times higher than for seeds dispersed randomly; however, recruitment of seeds dispersed by the other two frugivorous lemurs (*Eulemur rufifrons* and *Varecia variegata editorum*) were 2–2.5 times lower than for seeds dispersed randomly. The overall contribution to sapling recruitment, by the three dispersers as a group, was modeled to be lower than if those seeds were dispersed randomly in the habitat. This was true even though the most effective disperser (*E. rubriventer*) was estimated to disperse more seeds per adult tree than the other two frugivore species combined. However, all three frugivorous lemurs did provide *Cryptocarya* trees an advantage by moving seeds away from the crowns of parent trees, resulting in a fourfold higher recruitment probability.

Frugivores differed in the microhabitats where they tended to deposit seeds, resulting in differences in recruitment outcomes relative to random dispersal models. Both *Eulemur* spp. biased dispersal into gaps but *V. v. editorum* did not. *Eulemur rufifrons* biased dispersal under conspecifics where recruitment was low. These differences are likely due to the way the three species use their habitat. For example, *V. v. editorum* is not frequently observed in habitat with open canopies (Herrera et al. 2011), whereas *E. rufifrons* frequently backtracks to the same fruiting

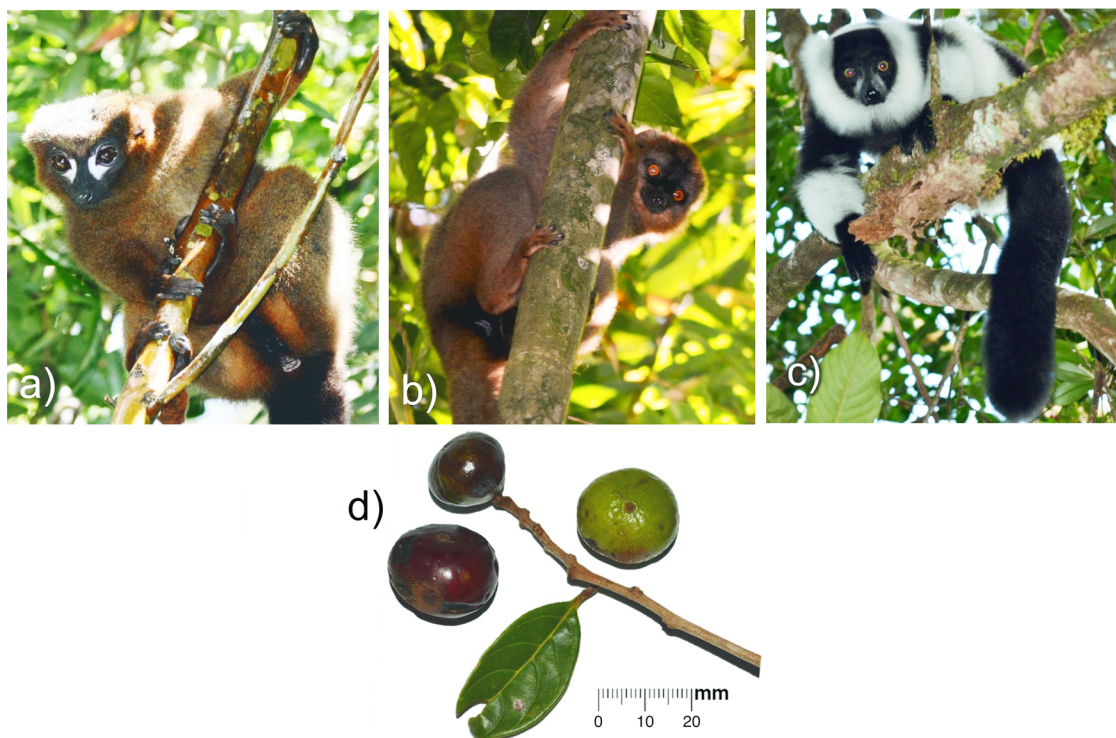


PLATE 1. The three seed dispersers in our study were (a) *Eulemur rubriventer*, (b) *Eulemur rufifrons*, and (c) *Varecia variegata editorum*. These species are the main seed dispersers of (d) *Cryptocarya crassifolia* in Ranomafana National Park, Madagascar. Photo credits: Coke Smith and Onja Razafindratsima. Photo credits: (a) Coke Smith, (c) Mamy-Fy Rakotondrainibe, (b and d) O. H. Razafindratsima.

trees during the day (Razafindratsima et al. 2014), which may lead to increased seed deposition under conspecifics.

One hypothesis for the adaptive value of animal-mediated seed dispersal is the benefit of directed dispersal to recruitment (Wenny 2001). Animal-mediated dispersal is often nonrandom, and if seeds are directed by animals towards areas that enhance recruitment, a clear advantage is obtained. In our study, lemurs, as a group, do not contribute to a directed dispersal advantage to the plant in the sense that recruitment was lower than if the total number of lemur-dispersed seeds were instead distributed randomly in the environment. However, the fact that lemurs moved some of the seeds away from conspecifics did act to greatly increase modeled seedling recruitment relative to the no-dispersal scenario. Our results stress the importance of evaluating the contribution of multiple dispersers of a shared host-plant species to recruitment to determine if nonrandom dispersal could be providing an overall advantage to plant demography.

There have been few studies that have evaluated the impact of nonrandom seed dispersal by multiple frugivores on host-plant recruitment. These few studies are supportive of our findings that frugivores often differ in their patterns of dispersal and contribution to plant recruitment (Wenny et al. 1998, Brodie et al. 2009).

Wenny and Levey (1998) demonstrated that only one of five species of birds directed seeds nonrandomly into gaps where recruitment success was high. Brodie et al. (2009) found that three frugivore species sharing a host-plant species differentially dispersed seeds into different microhabitats resulting in variable impacts on plant recruitment; however, it is unclear if the dispersal patterns qualified as directed dispersal.

While lemur-mediated dispersal is less effective than random dispersal, it still results in 4 times higher recruitment than no dispersal for their host-plant species. The functional loss of seed dispersers has become a growing problem worldwide as a result of anthropogenic factors, such as hunting and habitat fragmentation (Farwig and Berens 2012, Vidal et al. 2013). Our model contributes to other recent work (Cordeiro and Howe 2003, Brodie et al. 2009, Levi and Peres 2013) in suggesting that the absence of animal dispersers can have negative consequences for plant demography. If plant–animal dispersal webs tend to be modular, such that plants tend to specialize on animal dispersers by disperser type (e.g., Donatti et al. 2011), then there may be important consequences of disperser loss for plant populations in Madagascar, where almost all frugivorous lemurs are currently facing high risks of extinction (Schwitzer et al. 2014).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-0684.1.sm>