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RESEARCH ARTICLE

Frugivory in Four Sympatric Lemurs: Implications for the Future of Madagascar's Forests

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Although some conservationists accept that not all species can be saved, we illustrate the difficulty in deciding which species are dispensable. In this article, we examine the possibility that the integrity of a forest relies on its entire faunal assemblage. In Madagascar, one faunal group, the lemurs, accounts for the greatest biomass and species richness among frugivores. For example, 7 of the 13 sympatric lemur species in Madagascar's eastern rainforests consume primarily fruit. Because of this, we suggest that some tree species may rely heavily on particular lemur taxa for both seed dispersal and germination. In Ranomafana National Park, the diets for four of the day-active lemur frugivores have been documented during annual cycles over a 5-year period. We predicted that, although the fruit of some plant taxa would be exploited by multiple lemur species, the fruit of others would be eaten by one lemur species alone. Analyses reveal that while lemurs overlap in a number of fruit taxa exploited, 46% (16/35) of families and 56% (29/52) of genera are eaten exclusively by one lemur species. We, therefore, predict local changes in forest composition and structure if certain of these lemur species are eliminated from a forest owing to hunting, disease, or habitat disturbance. We also suggest that this result may be of global significance because carbon sequestration by the tropical forests in Madagascar may be reduced as a result of this predicted change in forest composition. *Am. J. Primatol.* 73:585–602, 2011. © 2011 Wiley-Liss, Inc.

Key words: seed dispersal; rainforest ecology; Ranomafana National Park

INTRODUCTION

There is a growing realization among some conservationists that it may be impossible to save all species. Consequently, some suggest that species should be prioritized for conservation, whereas others may have to be “let go” [Marris, 2007]. Here, we consider this possibility as it relates to frugivorous lemurs in Madagascar. In many rainforests, the primary seed dispersers are birds and bats [Bawa et al., 1990; Fleming et al., 1987; Terborgh, 1986], with an estimated 51–81% of canopy and subcanopy trees in Neotropical forests and an estimated 46–80% of trees in the Paleotropics being vertebrate-dispersed [Howe & Smallwood, 1982; Stoner et al., 2007]. However, among mammals, bats and primates comprise the majority of frugivorous species and are key to seed dispersal in most tropical forests [Bollen, 2003; Corlett, 1998; Lambert & Chapman, 2005; Lobova et al., 2003; McConkey, 2005; Peterson et al., 1995; Poulsen et al., 2002]. Primates can consume fruits with small-, medium- and large-sized seeds (Fig. 1) and excrete them intact in viable condition

[Gross-Camp & Kaplin, 2005; Overdorff & Strait, 1998; Stoner et al., 2007; Wrangham et al., 1994]. Because primates have relatively long gut retention times (1.57–38 hr) [Campbell et al., 2000, 2004; Lambert, 2002; Overdorff & Rasmussen, 1995], and often have long daily path lengths [e.g. Overdorff, 1993], chances are high that some seeds which are swallowed whole will be defecated far away from the

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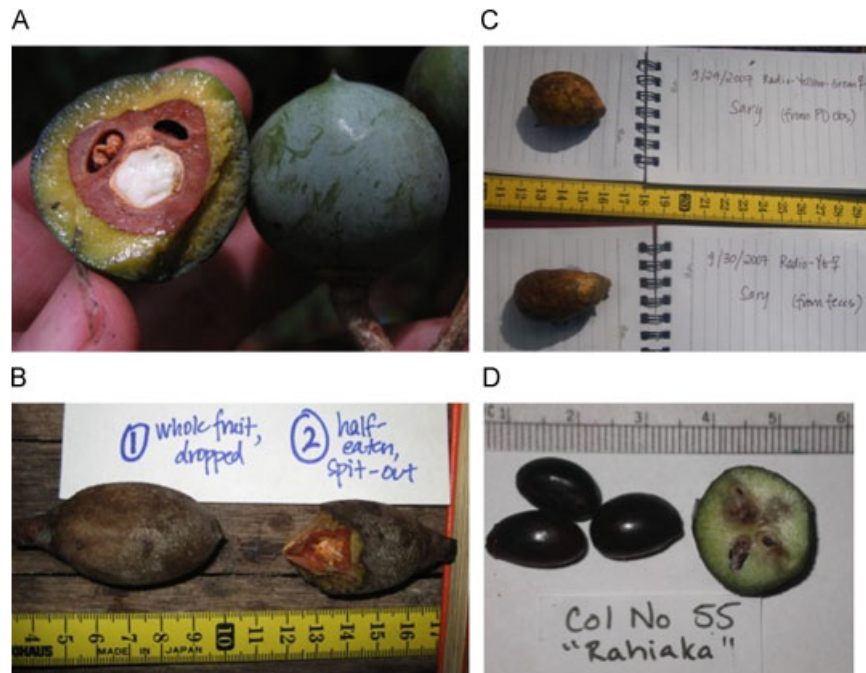


Fig. 1. Photos of fruits and seeds from Ranomafana National Park. (A) and (B) are *Canarium* spp., (C) is *Beilschmiedia* sp., and (D) is *Chrysophyllum boivinianum*. Note that the seeds in C have passed through lemur guts.

parent tree, thereby avoiding increased mortality associated with competition and microbial infection from high seed densities [Gross-Camp et al., 2009; Overdorff & Rasmussen, 1995; Stiles, 1989]. Secondary seed dispersers, such as the rodent *Nesomys* [Ryan et al., 1993] or dung beetles [Rainio & Niemala, 2006], may move or bury individual seeds, voided in clumps, to sites suitable for germination.

Madagascar, the fourth largest island in the world, has been isolated in its present position for more than 88 million years [Krause et al., 1997] and presents a special situation for seed dispersal. At approximately 1,500 km long, Madagascar supports a rich and diverse flora, including plants in rainforest, high altitude ericoid bush, brush and scrub forest, dry subtropical forest, granite outcrop forest, and spiny desert. At least 107 tree families exist on Madagascar, including 490 indigenous tree genera, 161 of which are endemic. Ninety-six percent of the 4,220 identified tree species are found nowhere else in the world [Grubb, 2003; Schatz, 2001]. In contrast, despite its reputation as a biodiversity hotspot, Madagascar lacks many of the “typical” mainland African fauna because of its biogeographical history. There are only 30 species of bat (18 endemic, 60%) found on Madagascar, 3 of which are frugivorous [MacKinnon et al., 2003; Peterson et al., 1995]. The bird fauna are equally impoverished, with only 209 breeding bird species in Madagascar (107 endemic, 51%) [Hawkins & Goodman, 2003]. Indeed, in contrast with one South American rainforest site, which boasts almost 1,000 bird species [Terborgh,

1983, 1986], Ranomafana National Park (RNP) in Madagascar contains only 116 bird species. Furthermore, of all the bird species in Madagascar, only seven are frugivorous [Langrand, 1990].

What effect does this dearth of fruit-eating bats and birds have on the ecology of the Madagascar rainforest? Many primates in Madagascar consume fruits and, therefore, are the primary seed dispersers on the island [Balko, 1998; Bollen, 2003; Britt, 2000; Ratsimbazafy, 2002; Wright & Martin, 1995; Wright et al., 2005]. Black-and-white ruffed lemurs (*Varecia variegata*), red-bellied lemurs (*Eulemur rubriventer*), and brown lemurs (*Eulemur fulvus rufus*), all medium-sized (2–4 kg) day-active primates, pass vine and tree seeds intact, which sprout faster and with less mortality than seeds not passed through a primate gut [Dew & Wright, 1998]. Although the Milne-Edwards’ sifaka (*Propithecus edwardsi*), a large rainforest lemur, is known to be primarily a seed predator [Dew & Wright, 1998; Hemingway, 1996, 1998]; older individuals with worn teeth are known to pass intact seeds, and therefore they also may contribute as seed dispersers [King et al., 2005]. It should be noted that because of strong seasonality in climate and resources, and long periodicity in the availability of fruits [Bollen & Donati, 2005], many rainforest lemurs rely on bamboo or leaves for a portion of their annual diet [Ganzhorn, 1988, 1989, 1993; Ganzhorn et al., 1999; Grassi, 2001, 2006; Tan, 1999; Wright, 1999]. Even so, fruits compose 45–95% of the annual diet of both diurnal (*Eulemur*, *Varecia*, *Propithecus*), and nocturnal (*Microcebus*, *Cheirogaleus*)

lemurs [Atsalis, 1999; Baden et al., 2008; Balko, 1998; Balko & Underwood, 2005; Britt, 2000; Erhart & Grassi, 2009; Hemingway, 1996, 1998; Lahann, 2007; Overdorff, 1991, 1993; Overdorff & Strait, 1998; Powzyk & Mowry, 2003; Tecot, 2008; Wright & Martin, 1995] (Table I). Furthermore, during fruit scarcity, many species continue to eat fruit, but spend more time on fewer, select species [e.g. Johnson, 2002; Overdorff, 1993; Tecot, 2008]. Many of these lemur species are critically endangered [Mittermeier et al., 2006; Wright et al., 2008a], and long-lived [King et al., 2010; Wright et al., 2008b] with slow reproductive potential [Erhart & Overdorff, 2008a; Godfrey et al., 2005; Pochron & Wright, 2003; Pochron et al., 2004; Richard et al., 2002; Wright, 1995, 1999]. Thus, if one or more of these lemur species is eliminated from the rainforest as a result of hunting or other factors, there may be a long-term impact on future forest composition. It is possible that, as these larger sized lemurs are removed from the ecosystem, they may be offset by a density increase in smaller lemurs [Peres & Dolman, 2000]; however, this faunal shift may mean nothing in terms of seed dispersal and plant regeneration because of their inability to pass large seeds intact [Barrera Zambrano et al., 2008; Bollen, 2003]. Although zoochorous plant taxa have not often been found to rely solely upon one frugivore for dispersal, Madagascar's depauperate guild of frugivores, particularly those capable of dispersing large seeds, indicates that presently this may be the case for at least a few plant taxa [Bollen, 2003].

In this article, we examine fruit selection by the four primary day-active lemur frugivores in the Ranomafana rainforest of Madagascar: *V. variegata*, *E. fulvus rufus*, *E. rubriventer*, and *P. edwardsi* (Fig. 2). We test the hypothesis that some plants are

candidates for dispersal by a single lemur species, and thus largely dependent upon its presence. We predict that, for some tree families and genera, there is only a single lemur species that is the primary consumer and potential disperser of its seeds. Although we recognize that these data are preliminary, we believe that this study is the first step in assessing the impact that removing even a single lemur species from the forest may have on seed dispersal and long-term forest composition.

METHODS

Study Site

RNP, established in 1991, is 43,500 ha of continuous rainforest located in southeastern Madagascar at 21°16'S latitude and 47°20'E longitude [Wright, 1992; Wright & Andriamihaja, 2002] (Fig. 3). The park is 25 km from Fianarantsoa and 60 km from the Indian Ocean. RNP consists of continuous mountainous rainforest with steep slopes, fast-flowing streams, and occasional *Pandanus* and palm swamps. Botanically, RNP is one of the most diverse rainforests in the world [Lowry et al., 1997]. This area has had a nonhunting tradition, and impact of human predation on lemurs has been minimal over at least the last 50 years [Wright, 1997]. The faunal diversity in RNP is high for Madagascar, with 116 species of birds, 6 species of carnivores, 4–5 species of bats, and 13 species of primates [Wright et al., 2005]. Elevations range from 600 to 1,470 m within the park, and annual rainfall ranges from 1,600 to 4,017 mm (RNP records). More than half of the annual rainfall occurs from December to March throughout the range of elevations [RNP records; Arrigo-Nelson, 2006; Tecot, 2008]. Temperatures range from lows in

TABLE I. Frugivorous Lemur Species in the Rainforest Site of Ranomafana With an Annual Diet of $\geq 45\%$ Fruits

Latin name	Common name	Average body mass (g)	% fruit in monthly diet	Reference
<i>Cheirogaleus major</i> ^{a,b,c}	Fat-tailed dwarf lemur	366	69	Lahann [2007]
<i>Daubentonia madagascariensis</i> ^{a,c}	Aye-aye	2,620	15–85	Sterling et al. [1994], Smith and Jungers [1997]
<i>Eulemur fulvus rufus</i>	Red-fronted brown lemur	2,180	62–98	Glander et al. [1992], Overdorff [1993]
<i>Eulemur rubriventer</i>	Red-bellied lemur	1,980	57–99	Glander et al. [1992], Overdorff [1993], Tecot [2008, 2010]
<i>Microcebus rufus</i> ^a	Brown mouse lemur	43	10–55	Atsalis [1998]
<i>Propithecus edwardsi</i>	Milne-Edwards' sifaka	5,940	3–89	Glander et al. [1992], Arrigo-Nelson [2006]
<i>Varecia variegata</i>	Black-and-white ruffed lemur	3,630	67–94	Balko [1998], Erhart and Grassi [2009], Baden et al. [2008]

^aNocturnal; not included in this study.

^bPercent monthly fruit consumption unavailable; presented as average % annual diet.

^cData derived from studies conducted in locations outside Ranomafana National Park.



Fig. 2. Photos of four day-active, frugivorous lemur species in Ranomafana National Park. (A) *Eulemur fulvus rufus*, (B) *Propithecus edwardsi*, (C) *Varecia variegata*, and (D) *Eulemur rubriventer*. Photos courtesy of A. Baden, S. Tecot, and J. Jernvall.

June–September (4–12°C) to highs in December–February (30–32°C). Five trail systems, each approximately 5 km², have been developed within the southern parcel of RNP for lemur observations.

Madagascar rainforest phenology plots show that many canopy species produce flowers and fruit on prolonged, irregular, asynchronous, or alternate year cycles [Bollen & Donati, 2005; Dunham et al., 2008; Hemingway, 1995; Overdorff, 1993; Powzyk, 1997; Tecot, 2008; Wright, 1999; Wright et al., 2005]. In fact, fruiting cycles are not necessarily the same across the five trail systems within the continuous rainforest of RNP, even when controlling for species [Arrigo-Nelson, 2006; Baden, unpublished data; Tecot, 2008]. To control for confounding variables of different feeding data collected in different years or different sites within the park, we have chosen to limit our analysis to one site, Vatoharanana (VATO).

VATO ranges from 1,100 to 1,200 m elevation with the canopy estimated at 20–25 m high [Hemingway, 1995; Overdorff, 1991; Tecot, 2008]. Although the forest of VATO underwent selective logging from 1987 to 1988, it has experienced little human disturbance overall [Balko, 1998; White et al., 1995]. Here, we present feeding data collected on four day-active lemur species. Data on *V. variegata*, *E. fulvus rufus*, and *P. edwardsi* (Fig. 2) were collected from January 2001 to July 2003 (EME) and data on *E. rubriventer* (Fig. 2) were collected from January 2004 to March 2005 (SRT). Although the possibility remains that fruit availability during the two studies differed, one assumption of this study is that the duration of the first study is sufficient to encompass a large portion of the interannual variation in fruiting in this forest. If our assumption is wrong, we expect the least amount of overlap in

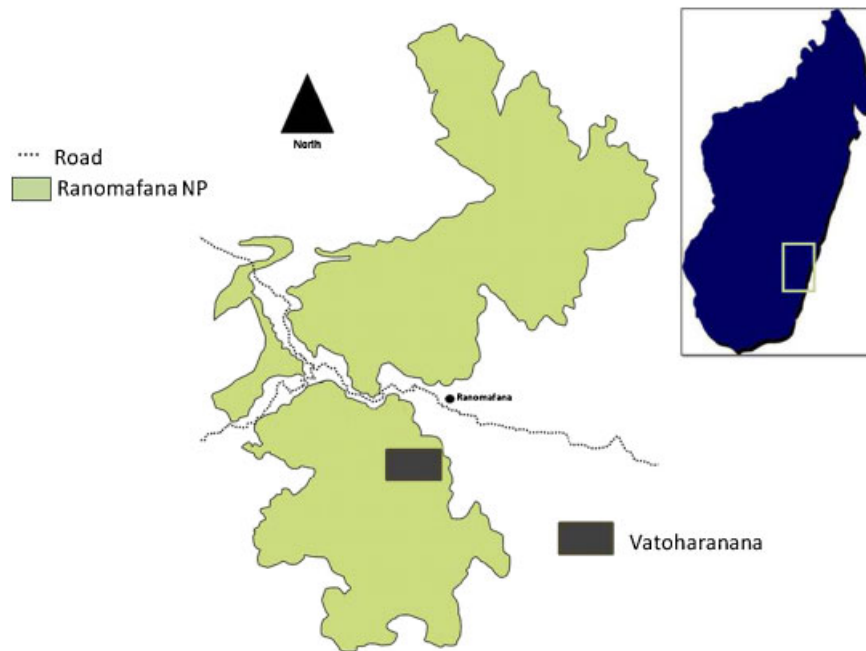


Fig. 3. The inset map illustrates the location of Ranomafana National Park in southeastern Madagascar. The enlarged map details the park boundary, the research site Vatoharanana, and the town of Ranomafana.

fruit-bearing plants consumed to exist between *E. rubriventer* and each of the other lemur species.

Our research complied with the laws of Madagascar pertaining to biological field research, was authorized by the Madagascar National Parks, CAFF/CORE, and the Madagascar Ministry of the Environment, and was approved by the IACUC animal care committee at Stony Brook University and Texas State University-San Marcos. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Lemur Observations

All feeding data were collected using focal animal sampling and continuous recording [Altmann, 1974]. In addition to the duration of feeding behavior, food type (fruit, leaf, seed, flower), ripeness stage (ripe, unripe), and plant taxonomy were recorded. Throughout the study and in previous studies at this site, the home ranges of each of the study species overlapped at least partially and at times extensively [Erhart, unpublished data; Erhart & Overdorff, 1999, 2008b; Overdorff, 1991; Tecot, unpublished data]. Groups, therefore, had access to many of the same, if not identical fruit resources. We noted all polyspecific associations during feeding bouts and found that all our study species occasionally fed simultaneously from the same trees, with the exception of *V. variegata* and *P. edwardsi* [Erhart, unpublished data; Tecot, unpublished data].

During data collection, we studied two groups each of *V. variegata*, *P. edwardsi*, *E. fulvus rufus*

[cf. *Eulemur rufifrons*, Groves, 2006; Pastorini et al., 2003], and *E. rubriventer*. All focal animals were followed for 2 hr intervals and total sample times were balanced between group members, with the exception of *E. rubriventer*, who were followed continuously from dawn to dusk. In the 2001–2003 study, focal groups and species were rotated on a weekly basis so that total sample times were balanced between groups and species; this also ensured that every group and species was studied throughout the year. In the 2004–2005 data set, *E. rubriventer* focal groups and individuals were rotated on a daily basis. Within each study, all observers were trained by a single individual and interobserver reliability greater than 90% was achieved; four of the five observers worked on both studies. It should be noted that we recorded data only on lemurs and did not examine fruit eating by other taxa, such as bats, rodents, and birds.

Plant Observations

Local research technicians trained by the Missouri Botanical Garden staff identified plants by their vernacular names. Research technicians were tested annually to be sure plant identification was consistent. The authors then assigned (when possible) each vernacular name to species, genus, and family. Because 21% of the fruits eaten by lemurs in this study are from plants whose species names are unknown [Erhart, unpublished data; Tecot, unpublished data], we analyzed all plant data at the genus and family levels. Furthermore, botanists note that it

is difficult to decide how many species to recognize for plant genera in Madagascar [Grubb, 2003].

For both *Eulemur fuvulus rufus* and *E. rubriventer*, more than 75% of their monthly diet comprised five plant species (whether for fruit, flowers, or leaves) [Overdorff, 1991]; moreover, there were never more than five genera or families from which these lemurs ate fruit for more than 5% of their monthly feeding time. For this reason, we chose to analyze only the top five plant genera and families exploited monthly as food resources in this study. The top five plant genera exploited each month were determined by calculating the proportion of time spent feeding upon each genus. From this list, we selected only those genera exploited specifically for fruit. Genera not exploited for fruit were excluded (and thus the number of top genera was less than five in some months). The percentage of time each of the remaining genera were exploited for only fruit was then calculated for each lemur species. Top five genera were used in the analysis, except in cases when foods eaten were not fruit and except if <5% of the diet. We then calculated the top five families, using the same methods as described previously. To better understand the use of fruit resources by each of the four study species, we analyzed the number of shared plant taxa (n) relative to the cumulative number of plant taxa selected by each lemur pair (N) at the genus and family levels (Tables II and III).

Statistics

In this study, anywhere from one to four lemur species were observed to exploit fruit from a particular genus or family (i.e. we exclude fruit genera or families that were never exploited by any of the four lemur species included in this study). Although we recognize that relative resource availability within a species' home range will inevitably influence its exploitation, for the purposes of statistical analyses we assume that each lemur species has an equal probability of consuming each plant taxon. Moreover, given that our study species fall within a relatively small range of body sizes (2–6 kg), and the fact that even the smallest species, *E. rubriventer*, is capable of dispersing large (>23 mm long) seeds [Overdorff & Strait, 1998], we believe that each lemur taxon is equally likely to be physically capable of exploiting the same food resources. From the observed numbers of fruit genera and families exploited by each of the four lemur species, we calculated the probability that fruit from any particular genus or family would be eaten by one, two, three, or four lemur species if chance alone were operating. We adjusted calculated probabilities to account for cases where fruit from a genus or family was eaten by none of the lemur species. We used these probabilities to derive null expectations. To

determine whether fruit taxa were exploited at random, we then compared our observations with the null expectation (explained further, below). We used χ^2 tests, using SPSS 17.0 (SPSS, Inc., Chicago, IL) to test the significance of differences between the observed and expected numbers of fruit taxa that are eaten by one, two, three, or four lemur species, with the significance level set at $\alpha = 0.05$.

RESULTS

Fifty-two fruit-bearing plant genera comprise the top five genera with fruits consumed by our four lemur species each month (Table II). Thirty-five fruit-bearing plant families comprise the monthly top five families for the same four lemur species (Table III). Each lemur species exploits fruit from multiple genera and families, such that there is considerable overlap in the fruit taxa consumed by each of the four lemur species (genus: 11–30%, family: 14–33%; see below). Table IV summarizes the proportion of fruit genera and families that are eaten by each of the four lemur species.

Using the data summarized in Table IV, we calculated the number of plant genera and families that would be eaten by one, two, three, or four lemur species owing to chance alone (the null expectation). We used the observed number of plant genera and families exploited by each lemur species to determine the probabilities that each species does or does not exploit fruit from a particular taxon (Table V). We then used those probabilities to calculate the likelihood that fruit from a genus or family might be exploited by one, two, three, or four lemur species. For example, there are four possible ways in which fruit from any particular genus could be exploited by a single lemur species: (1) it could be exploited exclusively by *E. rubriventer*; (2) exclusively by *E. f. rufus*; (3) exclusively by *P. edwardsi*; and (4) exclusively by *V. v. variegata* (Table VI). We calculated the probability for each possibility by combining the probability that a particular lemur will feed on fruit from a particular genus with the probabilities that the remaining three lemurs will *not* feed from that genus. The total probability of a plant genus being exploited by only a single lemur is the sum of the probabilities of each scenario. Because chance, but not our analytical protocol, could result in a plant genus being exploited by zero lemur species, we corrected probabilities to account for that disallowed scenario. Table VI presents the calculation of null expectations for fruit genera and Table VII presents the calculations of null expectations for fruit families. Expected and observed values are shown in Figure 4. Using chi-square tests, we found that the numbers of genera and families with fruit consumed by lemur species differed significantly from null expectations (genera, $P < 0.003$; families, $P < 0.02$) (Table VIII). At both the plant

TABLE II. Top Five Genera With Fruit Comprising $\geq 5\%$ of Monthly Diets for Each Lemur Species

Genus	<i>E. rubriventer</i>	<i>E. f. rufus</i>	<i>P. edwardsi</i>	<i>V. v. variegata</i>	Total number of consumers
Albizia	X	—	—	—	1
Beilschmiedia or Potameia	X	—	—	—	1
Cabucala or Voacanga	X	—	—	—	1
Cinnamosma	X	—	—	—	1
Genus indet. 1 “sena”	X	—	—	—	1
Pauridiantha	X	—	—	—	1
Psychotria	X	—	—	—	1
Anthocleista	—	X	—	—	1
Dombeya	—	X	—	—	1
Garcinia	—	X	—	—	1
Genus indet. 2 “tsimatahodakato”	—	X	—	—	1
Grewia	—	X	—	—	1
Mussaenda	—	X	—	—	1
Psidium	—	X	—	—	1
Smilax	—	X	—	—	1
Symphonia	—	X	—	—	1
Clerodendrum	—	—	X	—	1
Genus indet. 3 “andriambolamena”	—	—	X	—	1
Glennia	—	—	X	—	1
Polyscias	—	—	X	—	1
Schefflera	—	—	X	—	1
Treculia	—	—	X	—	1
Allophylus	—	—	—	X	1
Canarium	—	—	—	X	1
Carissa	—	—	—	X	1
Dilobeia	—	—	—	X	1
Medinilla	—	—	—	X	1
Ravenea	—	—	—	X	1
Sideroxylon	—	—	—	X	1
Bakerella	—	—	X	X	2
Erythroxylum	—	X	—	X	2
Harungana	—	X	—	X	2
Mammea	X	—	—	X	2
Micronychia	X	X	—	—	2
Noronhia	X	X	—	—	2
Protorhus	—	X	—	X	2
Ravensara	—	X	—	X	2
Scolopia	X	X	—	—	2
Streblus	—	X	—	X	2
Vitex	X	X	—	—	2
Ambavia	X	X	—	X	3
Canthium	X	X	—	X	3
Chrysophyllum	X	X	—	X	3
Cissus	—	X	X	X	3
Cryptocarya	X	X	—	X	3
Mendoncia	X	X	—	X	3
Ocotea	—	X	X	X	3
Plagioscyphus	—	X	X	X	3
Dichapetalum	X	X	X	X	4
Ficus	X	X	X	X	4
Oncostemum	X	X	X	X	4
Syzygium	X	X	X	X	4
Total # of genera used	21	30	14	26	

For each lemur species, the X denotes that the plant genus was found in the top five foods exploited monthly.

genus and family levels, the deviations from expectations were primarily owing to unexpectedly high numbers of fruit taxa being eaten by only a single

lemur species (genus $N = 29$; family $N = 19$) and concomitantly low numbers of fruit taxa being eaten by two lemur species (genus $N = 11$; family $N = 8$).

TABLE III. Top Five Families With Fruit Comprising $\geq 5\%$ of Monthly Diets for Each Lemur Species

Family	<i>E. rubriventer</i>	<i>E. f. rufus</i>	<i>P. edwardsi</i>	<i>V. v. variegata</i>	Total number of consumers
Cannellaceae	X	—	—	—	1
Family indet 1 “sena”	X	—	—	—	1
Leguminosae	X	—	—	—	1
Family indet 2 “tsimatahodakato”	—	X	—	—	1
Loganaceae	—	X	—	—	1
Marantaceae	—	X	—	—	1
Smilacaceae	—	X	—	—	1
Tiliaceae	—	X	—	—	1
Andriambolamena	—	—	X	—	1
Araliaceae	—	—	X	—	1
Verbanaceae	—	—	X	—	1
Acanthaceae	—	—	—	X	1
Arecaceae	—	—	—	X	1
Burseraceae	—	—	—	X	1
Melastomaceae	—	—	—	X	1
Proteaceae	—	—	—	X	1
Apocynaceae	X	—	—	X	2
Erythroxylaceae	—	X	—	X	2
Flacourtiaceae	X	X	—	—	2
Lamiaceae	X	X	—	—	2
Loranthaceae	—	—	X	X	2
Mendonciaceae	X	X	—	—	2
Oleaceae	X	X	—	—	2
Anacardiaceae	X	X	—	X	3
Annonaceae	X	X	—	X	3
Clusiaceae	X	X	—	X	3
Dichapetalaceae	—	X	X	X	3
Rubiaceae	X	X	—	X	3
Sapindaceae	—	X	X	X	3
Sapotaceae	X	X	—	X	3
Vitaceae	—	X	X	X	3
Lauraceae	X	X	X	X	4
Moraceae	X	X	X	X	4
Myrsinaceae	X	X	X	X	4
Myrtaceae	X	X	X	X	4
Total # of families used	17	22	11	20	

For each lemur species, X denotes that the plant family was found in the top five foods exploited monthly.

TABLE IV. Number of Fruit-Bearing Plant Genera and Families Eaten by Only One of the Study Species; Number Shared With Other Study Species and Proportion Out of the Total Number of Fruit-Bearing Plant Genera and Families Eaten by Each Study Species

	Fruit genera (52 total)			Fruit families (35 total)		
	Solitary/shared	Total	Proportion of total fruit genera	Solitary/shared	Total	Proportion of total fruit families
<i>E. rubriventer</i>	7/14	21	0.40	3/14	17	0.49
<i>E. f. rufus</i>	9/21	30	0.58	5/17	22	0.63
<i>P. edwardsi</i>	6/8	14	0.27	4/7	11	0.31
<i>V. v. variegata</i>	7/19	26	0.50	5/15	20	0.57

We found that the three primarily frugivorous species *V. variegata*, *E. f. rufus*, and *E. rubriventer* overlapped in a greater proportion of fruit genera

and families compared with the seed predator species *P. edwardsi* (Tables IX and X). The proportion of shared fruit genera was qualitatively highest for

TABLE V. Probability That a Lemur Species Does or Does Not Exploit Any Particular Fruit Genus or Family

Lemur	Probability of exploiting a particular fruit genus of the 52 total fruit genera	Probability of NOT exploiting a particular fruit genus of the 52 total fruit genera	Probability of exploiting a particular fruit family of the 35 total fruit families ^a	Probability of NOT exploiting a particular fruit family of the 35 total fruit families
<i>E. rubriventer</i>	21/52 = 0.404	10.404 = 0.596	17/35 = 0.486	10.486 = 0.514
<i>E. f. rufus</i>	30/52 = 0.577	10.577 = 0.423	22/35 = 0.629	10.629 = 0.371
<i>P. edwardsi</i>	14/52 = 0.269	10.269 = 0.731	11/35 = 0.314	10.314 = 0.686
<i>V. v. variegata</i>	26/52 = 0.5	10.5 = 0.5	20/35 = 0.571	10.571 = 0.429

^aData from Table IV.

E. f. rufus and *V. variegata*, whereas the proportion of shared fruit families was qualitatively highest for *E. f. rufus* and *E. rubriventer*.

DISCUSSION

In tropical forests, there is some indication of a primate/plant codependency, with some trees relying on primates to disperse their seeds at a distance from the parent tree [Chapman & Onderdonk, 1998; Dominy & Duncan, 2005; Lambert, 2002; Lambert & Chapman, 2005; Lambert & Garber, 1998; Link & Di Fiore, 2006; Stevenson, 2005]. Although coevolutionary arguments in plant–frugivore interactions are highly controversial [Bollen et al., 2005; Chapman & Chapman, 2002; Herrera, 1985], the exclusive or nearly exclusive feeding by lemurs on certain fruit taxa, in theory, may have enough ecological importance to modify entire plant communities. In an earlier research, *E. rubriventer*, *E. fulvus rufus*, and *V. variegata* have been shown to be excellent seed dispersers [Dew & Wright, 1998] and the fourth species (*P. edwardsi*) is a seed predator [Dew & Wright, 1998; Overdorff & Strait, 1998], with older individuals occasionally passing seeds intact [King et al., 2005; Wright et al., 2005]. We found that while lemurs have some dietary overlap in fruit taxa consumed at our research site, many fruits are eaten exclusively by a single lemur species; therefore, their seeds are potentially dependent on only one lemur species for their dispersal. This is the case for 56% (29/52) of the plant genera and 46% (16/35) of the plant families recorded in this study. These results are consistent with those from a similar study in which Bollen [2003] investigated dietary overlap and seed dispersal by lemurs, flying foxes, birds, and rodents in a littoral forest in St. Luce, Madagascar. She found that *E. fulvus collaris* was the sole disperser of large seeds; in fact, five large-seeded fruits were highly dependent upon *E. f. collaris* for dispersal and recruitment [Bollen, 2003]. Taken in concert, such findings of species-specific frugivory suggest the possibility that plant genera, and also entire families, may be more vulnerable to extinction owing to the removal of even a single lemur taxon.

But what is the advantage to lemurs specializing on certain fruits? Body size may be a simple explanation, as larger lemurs have been found to ingest fruits with larger seeds [Campbell et al., 1999, 2000; Lahann, 2007; Wright et al., 2005]. As expected by the comparatively small body size of lemurs, 33% of the seeds passed by these species are in the small range [<5 mm in length, after Janson, 1983] [Dew & Wright, 1998]. However, lemur/plant codependency may be based on more than body size. For example, 56% of the seeds passed by these lemurs are in the large range [>10 mm in length, after Janson, 1983] [Baden, unpublished data; Dew & Wright, 1998]. Seed size is also not consistently related to body size within the four lemur species: *E. rubriventer* (adult body mass 2.0 kg), *E. f. rufus* (adult body mass 2.1 kg) [Overdorff, 1991], and *V. variegata* (adult body mass 3.6 kg) [Baden et al., 2008] pass seeds in small and large seed size categories [Dew & Wright, 1998], whereas *P. edwardsi* (adult body mass 5–8 kg) pass only small seeds [Dew & Wright, 1998]. Furthermore, even the two closely related *Eulemur* species that are of comparable body size eat certain fruits exclusive of the other, possibly as a means of niche separation [Overdorff, 1993], which may have a greater influence on the species-specific fruit–frugivore relationships that we report here. There is also some indication that trees may select certain seed dispersers over others by using chemical deterrents. After millions of years of evolution, some lemurs have evolved digestive specializations to enable them to detoxify foods, such as cyanide in bamboo [Tan, 1999; Yamashita et al., 2009] and alkaloids or tannins in leaves [Ganzhorn et al., 1985]. Most fruits are found to have fewer toxins, making them attractive to seed-dispersing vertebrates [Janson, 1983]. However, it has been suggested that trees may reduce inefficient foraging on fruits through chemical defense [Howe, 1983]. This may be the case in Madagascar and should be studied in the future.

Two previous studies investigating seed dispersal in these four lemur species [Dew & Wright, 1998; Overdorff & Strait, 1998] found that, after passing through the guts of *E. fulvus rufus*, *E. rubriventer*, and *V. variegata*, some seeds of select plant taxa germinated [Overdorff & Strait, 1998] and that

TABLE VI. Computation of Null Expectation of Fruit Genera Eaten by One, Two, Three, or Four Lemur Species if Chance Alone is Operating, Using the Probabilities From Table V

Fruit genus eaten by	<i>E.r.</i>	<i>E.f.</i>	<i>P.e.</i>	<i>V.v.</i>	Probability <i>E.r.</i>	Probability <i>E.f.</i>	Probability <i>P.e.</i>	Probability <i>V.v.</i>	Total probability	Corrected probability ^a	Null expectation
Zero lemur species ^a	-	-	-	-	0.596	0.423	0.731	0.5	0.0921	No fruit genus is eaten by zero lemurs	
One lemur species	Probability a fruit genus is eaten by zero lemur species								0.0921		
	X	-	-	-	0.404	0.423	0.731	0.5	0.0625		
	-	X	-	-	0.596	0.577	0.731	0.5	0.1257		
	-	-	X	-	0.596	0.423	0.269	0.5	0.0339		
	-	-	-	X	0.596	0.423	0.731	0.5	0.0921		
Two lemur species	Probability a fruit genus is eaten by one lemur species								0.3142	0.3461	18/52
	X	X	-	-	0.404	0.577	0.731	0.5	0.0852		
	X	-	X	-	0.404	0.423	0.269	0.5	0.0230		
	X	-	-	X	0.404	0.423	0.731	0.5	0.0625		
	-	X	X	-	0.596	0.577	0.269	0.5	0.0463		
	-	-	X	X	0.596	0.423	0.269	0.5	0.0339		
	-	X	-	X	0.596	0.577	0.731	0.5	0.1257		
Three lemur species	Probability a fruit genus is eaten by two lemur species								0.3765	0.4147	21/52
	X	X	X	-	0.404	0.577	0.269	0.5	0.0314		
	X	-	X	X	0.404	0.423	0.269	0.5	0.0230		
	X	X	-	X	0.404	0.577	0.731	0.5	0.0852		
	-	X	X	X	0.596	0.577	0.268	0.5	0.0463		
Four lemur species	Probability a fruit genus is eaten by three lemur species								0.1858	0.2047	11/52
	X	X	X	X	0.404	0.577	0.269	0.5	0.0314		
	Probability a fruit genus is eaten by four lemur species								0.0345	2/52	

^aBy definition, the condition in which a fruit genus is exploited by zero lemur species is not allowed. Probabilities are corrected by dividing computed expected probabilities by 0.9079 (= 1-0.0921).

TABLE VII. Computation of Null Expectation of Fruit Families Eaten by One, Two, Three, or Four Lemur Species if Chance Alone is Operating, Using the Probabilities From Table V

Fruit family eaten by	<i>E.r.</i>	<i>E.f.</i>	<i>P.e.</i>	<i>V.v.</i>	Probability <i>E.r.</i>	Probability <i>E.f.</i>	Probability <i>P.e.</i>	Probability <i>V.v.</i>	Total probability	Corrected probability ^a	Null expectation
Zero lemur species ^a	—	—	—	—	0.514	0.371	0.686	0.429	0.0561	No fruit family is eaten by zero lemurs	
One lemur species	X	—	—	—	0.486	0.371	0.686	0.429	0.0561		
	—	X	—	—	0.514	0.629	0.686	0.429	0.0531		
	—	—	X	—	0.514	0.371	0.314	0.429	0.0951		
	—	—	—	X	0.514	0.371	0.686	0.571	0.0270		
Two lemur species	X	X	—	—	0.486	0.629	0.686	0.429	0.2539	0.2690	9.4/35
	X	—	X	—	0.486	0.371	0.314	0.429	0.0900		
	X	—	—	X	0.486	0.629	0.686	0.571	0.0242		
	—	X	X	—	0.514	0.629	0.314	0.429	0.0706		
	—	—	X	X	0.514	0.371	0.314	0.571	0.0436		
	—	X	—	X	0.514	0.629	0.686	0.571	0.0342		
Three lemur species	X	X	X	—	0.486	0.629	0.686	0.429	0.1227	0.4124	14.4/35
	X	—	X	—	0.486	0.629	0.314	0.429	0.3893		
	X	—	—	X	0.486	0.371	0.314	0.571	0.0412		
	X	X	—	X	0.486	0.629	0.686	0.571	0.0323		
	—	X	X	X	0.514	0.629	0.314	0.571	0.1197		
Four lemur species	X	X	X	X	0.486	0.629	0.686	0.571	0.0580	0.2662	9.3/35
	X	X	X	—	0.486	0.629	0.314	0.571	0.2512		
	X	X	—	X	0.486	0.629	0.686	0.571	0.0548	0.0581	2.0/35

^aBy definition, the condition in which a fruit family is exploited by zero lemur species is not allowed. Probabilities are corrected by dividing computed expected probabilities by 0.9439 (= 1–0.0561).

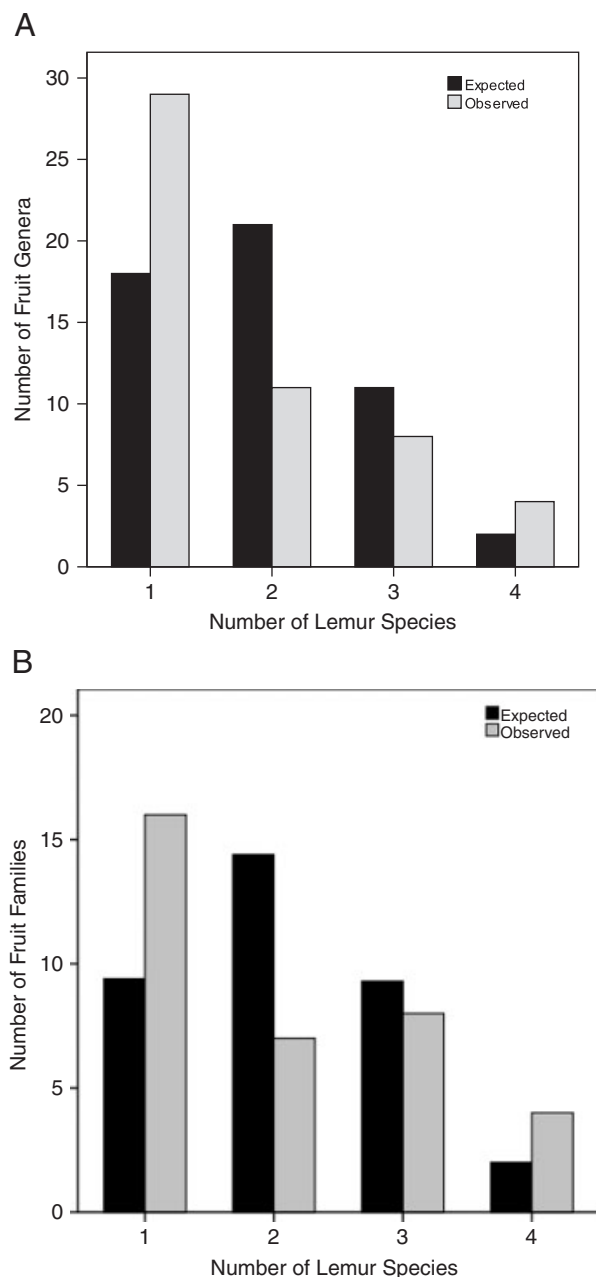


Fig. 4. Expected and observed numbers of fruit-bearing genera (A) and families (B) that are eaten by one, two, three, or four lemur species.

TABLE VIII. Expected and Observed Numbers of Fruit-Bearing Genera and Families That Were Eaten by One, Two, Three, or Four Lemur Species. Chi-Square Tests Confirm That the Observed Distribution of Fruit-Bearing Plants Among the Four Lemur Species is Nonrandom

Lemur species	Fruit genera (N = 52)					Fruit families (N = 35)				
	Expected	Observed	χ^2	df	P	Expected	Observed	χ^2	df	P
1	18	29	14.302	3	<0.003	9.4	16	10.649	3	<0.02
2	21	11				14.4	7			
3	11	8				9.3	8			
4	2	4				2.0	4			

germination was improved (faster and higher numbers; range sprouting success 60–80%) [Dew & Wright, 1998]. According to this study, fruit from the Acanthaceae family was eaten by only *V. variegata*, and seeds were passed intact in the feces (no data on Acanthaceae germination success, or on the fruit of other plant taxa consumed by a single lemur species, have been reported). Results from a second study indicate that feeding and traveling behavior may act to disperse some seeds more efficiently than others. For example, *E. rubriventer* often feed, rest, and then defecate in the same tree, thus depositing seeds within the shadow of the parent tree [Overdorff & Strait, 1998]; therefore, reducing the chances of germination success. However, *E. rubriventer* also travel immediately after consuming some fruits [Overdorff & Strait, 1998] and the likelihood of germination success can thus vary. Although these studies indicate that these lemurs can be excellent seed

TABLE IX. Number of Shared Fruit-Bearing Plant Genera (n) Relative to the Total Number of Plant Genera Selected by Each Lemur Pair (N)

Lemur pair	Proportion
<i>E. rubriventer</i> × <i>P. edwardsi</i>	0.11
<i>E. f. rufus</i> × <i>P. edwardsi</i>	0.16
<i>V. variegata</i> × <i>P. edwardsi</i>	0.20
<i>V. variegata</i> × <i>E. rubriventer</i>	0.21
<i>E. f. rufus</i> × <i>E. rubriventer</i>	0.25
<i>E. f. rufus</i> × <i>V. variegata</i>	0.30

TABLE X. Number of Shared Fruit-Bearing Plant Families (n) Relative to the Total Number of Plant Families Selected by Each Lemur Pair (N)

Lemur pair	Proportion
<i>E. rubriventer</i> × <i>P. edwardsi</i>	0.14
<i>E. f. rufus</i> × <i>P. edwardsi</i>	0.21
<i>V. variegata</i> × <i>P. edwardsi</i>	0.26
<i>V. variegata</i> × <i>E. rubriventer</i>	0.27
<i>E. f. rufus</i> × <i>V. variegata</i>	0.31
<i>E. f. rufus</i> × <i>E. rubriventer</i>	0.33

dispersers, they also indicate that germination success can vary a great deal for different plant taxa. One of our goals in this study was to determine which plant taxa might be of primary importance for future studies of seed dispersal in this forest. Because the two studies discussed took place over the course of 2 [Overdorff & Strait, 1998] and 3 [Dew & Wright, 1998] months and are limited to taxa fruiting during those time periods, they do not lend insight to whether the seed taxa identified in our study are dispersed away from the parent tree nor whether germination success is improved by passing through the guts of these lemurs. Future studies focusing on dispersal distance and germination success in these plant-lemur pairs will help us more fully understand the importance of these relationships.

Simply put, our overarching goal was to determine whether dietary separation exists among the diurnal frugivorous lemurs at this site. The patterns we present indicate that, regardless of the distribution of plants in the forest, more than half of the plant taxa consumed are done so by only a single lemur species. Our results complement other studies of lemur seed dispersal in eastern rainforests of Madagascar and across the various forests types of Madagascar [Birkinshaw, 2001; Bollen, 2003; Dausmann et al., 2008; Dew & Wright, 1998; Lahann, 2007; Overdorff & Strait, 1998; Simmen et al., 2003; Spehn & Ganzhorn, 2000]. It may be that lemurs play a particularly important role in seed dispersal, as birds and bats on Madagascar have low population densities and are primarily insectivorous [Langrand, 1990; MacKinnon et al., 2003]. Whether these results are representative of a broader pattern found across Madagascar remains to be addressed. An interesting question arising from this study concerns the mechanisms promoting such a separation (e.g. the distribution of plants in the environment, the extinction of large frugivorous species, competitive exclusion), particularly if similar patterns are found in other sites. Moreover, in forests where moderate-sized lemur frugivores are absent, are dependent plant taxa also absent? Analyses in this study are based on the simple assumption that each lemur species is equally likely to encounter and exploit all food resources. In reality, this is probably not the case and we anticipate that future research will consider the relative abundance of each fruit genus and family within each lemur species' home range.

Mammals, including primates, are increasingly hunted within tropical forests [Corlett, 2007; Fa et al., 2005; Peres & Lake, 2003; Peres & Palacios, 2007; Robinson & Bennet, 2004]. Humans hunt lemurs in many forests in Madagascar and the larger sized diurnal lemurs are preferred prey items [Golden, 2009; Lehman & Wright, 2000; Lehman et al., 2005]. In fact, of the hunters surveyed, three of the four frugivores in this study (*V. variegata*, *Eulemur*

fulvus, and *E. rubriventer*) were chosen as top prey items [Golden, 2009]. Moreover, in many forests, the frugivorous day-active lemurs have been hunted to extinction [Irwin et al., 2005; Lehman et al., 2005]. Is it possible that if certain lemurs are eliminated from a community, others will experience competitive release, thereby replacing the eliminated species in seed dispersal? Peres and Dolman [2000] found that as the larger sized primates [>4 kg] were severely reduced or eliminated from Amazonian forests, the population density of nonhunted medium-sized species [1.5–4.0 kg] increased. The top three frugivorous lemur species examined in this study are medium in body size [2.0–3.6 kg], with only small nocturnal species (43–366 g) to replace them. In a study of sympatric nocturnal lemur frugivory, Lahann [2007] showed that *Cheirogaleus* and *Microcebus* consume fruits with a small seed size (3.8–10.1 mm) and avoid fruits with a large seed size (25–30 mm). They pass many seeds whole, but fruit selection may limit the range of seeds that are dispersed. It follows that these nocturnal cheirogaleids cannot switch to eating the fruits currently eaten by larger sized diurnal lemurs, because the larger sized seeds exploited by diurnal lemurs are simply too large for nocturnal lemurs to ingest [Dew & Wright, 1998]. This constraint reinforces the fact that nocturnal lemurs, with their small body sizes, cannot replace the larger lemur species as seed dispersers for these plant taxa [see also Barrera Zambrano et al., 2008]. Following this line of reasoning, one might predict changes in local forest composition over time where seed dispersers have been eliminated from the community. However, simply put, trees may live longer than lemurs. Therefore, even if a lemur species were to go locally extinct, trees for which that species serves as a disperser will persist for a time after a local extinction. This implies that a longitudinal study of declining lemur populations and documented local extinctions should include data on forest composition, to determine whether these possible ecological consequences can indeed be inferred. In addition, we recommend that more studies, such as this, be conducted at several sites within Madagascar to determine if this emerging trend is seen in other locations. Finally, we would like to follow-up on this study and the two previous studies of seed germination at this site [Dew & Wright, 1998; Overdorff & Strait, 1998], with a more thorough investigation of the effects of lemur gut passage on seed germination success by focusing on the tree species identified herein. Overdorff and Strait [1998] showed that the passage of seeds through the guts of *Eulemur* resulted in germination, and Dew and Wright [1998] showed that germination success improved for several plant taxa, but long-term study is needed to determine the impact of such processing on germination and recruitment of the taxa identified

in this study. Moreover, investigating the chemical composition of the fruits in this study might provide additional insights into plant–lemur coevolution. The nearly exclusive feeding by lemurs on certain fruit taxa may imply that these species are important to maintain plant communities and their absence may have the ability to modify them. Therefore, these data in conjunction with the further studies suggested here may be able to shed additional light on these debates.

There are distinct environmental repercussions to our finding that different species of lemurs seem to specialize on the fruits of certain trees that are of global importance. In general, tropical forests store 340 billion tons of carbon, equivalent to more than 40 years' worth of human fossil fuel emissions [Canadell et al., 2007]. Tropical deforestation and degradation are responsible for an estimated 20% of global carbon emissions to the atmosphere [Myers, 2007]. In these same forests, overhunting is pushing many animals to extinction [Milner-Gulland & Bennett, 2003; Peres, 2000; Walsh et al., 2003]. Losses from overhunting are particularly severe among large-bodied animals, including lemurs, because these species tend to be preferentially hunted and have slower population growth rates [Dunham et al., 2008; Golden, 2009; Lehman & Wright, 2000; Lehman et al., 2005; Peres, 2000; Peres & Palacios, 2007; Wright et al., 2008b]. By removing the animal dispersers of carbon-rich tree seeds, hunting may be changing future forest composition [Chapman & Onderdonk, 1998; Peres & Palacios, 2007; Peres & Van Roosmalen, 2002; Wang et al., 2007; Wright et al., 2007]. Overhunting can, in turn, reduce the globally important carbon sink provided by tropical forests. Although overhunting consequences have not yet been addressed in Madagascar rainforests, many of the most carbon-dense tree species in mainland Africa and Asia rely on large vertebrates to transport their seeds and ensure successful reproduction [McConkey, 2005; Pochron et al., 2004; Walsh et al., 2003; Wang et al., 2007]. Terborgh et al. [2008] have found that there is a substantial shift in Peruvian rainforest species composition as large-seeded trees are replaced by smaller seeded species. Brodie and Gibbs [2009] suggest that overhunting can drive degradations of carbon storage, as large-seeded trees with high wood density are deprived of their seed-dispersing animals [Bunker et al., 2005]. Therefore, our finding that each lemur species tends to exploit certain tree taxa that are not exploited by other lemurs could be an important link to understanding the effects of hunting lemurs on future forest composition, as well as anthropogenic disturbance of the carbon cycle.

The next step in determining the importance of lemurs for forest composition is to use these results to study the success of dispersal of the plant genera and families whose fruit was consumed by only one

lemur species. We have presented some evidence that there might be a change in forest composition and carbon sequestration over the long term, if certain lemur species went locally extinct and no longer dispersed seeds in that forest. Our hope is that these results will inspire the necessary actions to protect these species and their rainforest homes.

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