ORIGINAL ARTICLE

WILEY **bio**TROPICA · ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests

Veronarindra Ramananjato[1] 🆔 | Zafimahery Rakotomalala[1] | Daniel S. Park[2] |
Camille M. M. DeSisto[2] | Nancia N. Raoelinjanakolona[1] | Nicola K. Guthrie[3] |
Zo E. S. Fenosoa[1] | Steig E. Jonhson[3] | Onja H. Razafindratsima[4] 🆔

[1]Mention Zoologie et Biodiversité Animale, Faculté des Sciences, University of Antananarivo, Antananarivo, Madagascar

[2]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

[3]Department of Anthropology and Archaeology, University of Calgary, Calgary, AB, Canada

[4]Department of Natural Resource Management, South Dakota State University, Brookings, SD, USA

Correspondence
Veronarindra Ramananjato, Mention Zoologie et Biodiversité Animale, University of Antananarivo, BP 906, Faculté des Sciences, 101 Antananarivo, Antananarivo, Madagascar.
Email: vero.narindra@gmail.com

Abstract

Fruit-eating animals play important roles as seed dispersal agents in terrestrial systems. Yet, the extent to which seed dispersal by nocturnal omnivores may facilitate germination and the recruitment of plant communities has rarely been investigated. Characterizing their roles in seed dispersal is necessary to provide a more complete picture of how seed dispersal processes affect ecosystem functioning. We investigated the roles and impacts of two species of nocturnal omnivorous lemur species, *Microcebus jollyae* and *M. rufus*, on seed dispersal in Madagascar's rain forests, through analysis of fecal samples and germination experiments. Data show that these lemur species, which are among the world's smallest primates, dispersed 22 plant species from various forest strata and that the defecated seeds germinated faster and at higher rates than control seeds for the eight plant species we tested. Even though mouse lemurs dispersed both native and non-native plant species, non-native plant species represented a relatively small proportion (17%). These results demonstrate that overlooked nocturnal omnivores can act as important seed dispersers, which may have critical implications for forest regeneration and the maintenance of plant diversity in fragmented/degraded forests. Finally, we provide critical insights into the previously unobserved behavior and diet of endangered nocturnal lemurs for their effective conservation.

Abstract in Malagasy is available with online material.

KEYWORDS
conservation, Madagascar, *Microcebus*, mouse lemur, primates, regeneration, seed dispersal, tropical forest

1 | INTRODUCTION

Animal-mediated seed dispersal provides key advantages to ecosystem functioning and resilience by influencing plant fitness, diversity maintenance, gene flow among populations, and plants' ability to escape local environmental changes (Beckman et al., 2019; Howe & Smallwood, 1982). While previous studies have greatly contributed to knowledge on the mechanisms and impacts of animal-mediated seed dispersal, the majority have focused on predominantly frugivorous species. However, other trophic groups, such as carnivores and omnivores, can also disperse seeds (Herrera, 1989; Hulme &

Benkman, 2002; Yang, Zhang, Deng, & Yi, 2019). Studies investigating the impacts of omnivores as seed dispersers are scarce, especially for small-bodied and nocturnal species. Understanding their role in seed dispersal may provide new knowledge and insights to advance the field of seed dispersal ecology and plant community assembly.

Omnivores could help shape forest structure through seed dispersal because their diets often include many plant species from different strata (Motta-Junior & Martins, 2002; Platt et al., 2013; Radespiel, Reinmann, Rahelinirina, & Zimmerman, 2006). Additionally, they often exhibit ecological characteristics and behavior different from those of frugivores (Herrera, 1989; Motta-Junior & Martins, 2002). For instance, they can travel considerable distances when foraging, which could facilitate long-distance seed dispersal (Beckman et al., 2019). Also, by consuming and defecating different species of plant neighbors during successive feeding events, they could transport diverse plant assemblages to other locations and influence their spatial distribution (Génin & Rambeloarivony, 2018; Hämäläinen et al., 2017). Furthermore, they may have dietary overlap with sympatric frugivores (Valenta & Lehman, 2016), which could be advantageous for some plant species that suffer from seed predation by certain frugivores (Dew & Wright, 1998).

Here, we examine the roles of nocturnal omnivores in seed dispersal in Madagascar's rain forests, focusing on mouse lemurs (*Microcebus* spp.). We tested the hypothesis that they disperse diverse plant species from different forest strata. We also tested whether mouse lemurs provide advantages to the plants they consumed, through mechanical and/or chemical digestion, by enhancing seed germination and seedling growth.

2 | METHODS

We conducted this research in two southeastern Madagascar's rain forests (Figure S1): Ranomafana National Park (RNP) and Kianjavato Classified Forest (KCF). We trapped mouse lemurs in six sites within the continuous forest of RNP, six forest fragments in its surroundings, and three forest fragments and six reforestation parcels in KCF (Table S1). RNP is dominated by evergreen montane rain forest (400–1,500 m a.s.l.), mainly comprised of native plant species (Razafindratsima & Dunham, 2016). KCF fragments consist of moderately degraded lowland forests at higher elevations (>50 m a.s.l.) and degraded secondary forests in lower elevations (<70 m a.s.l.; Louis et al. 2013). Both sites are characterized by a tropical humid climate with an annual average temperature of 12–30°C and precipitation of 1,500–2,400 mm (Dunham, Erhart, & Wright, 2011; Manjaribe, Frasier, Rakouth, & Louis, 2013).

We studied two nocturnal omnivorous lemur species: rufous mouse lemur (*Microcebus rufus*) and Jolly's mouse lemur (*M. jollyae*, Family: Cheirogaleidae), which are among the smallest primates in the world with body mass of up to 61 g and total body length of up to 25 cm (Mittermeier et al., 2010; Razafindratsima, Yacoby,

TABLE 1 Summary table of the linear mixed-effects models of germination and growth parameters

	Microcebus rufus		*Microcebus jollyae*		
	Petri dish	Forest ground	Petri dish	Semi-shaded plot	Shaded plot
Experiment	**N = 150 (88)**	**N = 75 (7)**	**N = 528 (70)**	**N = 660 (233)**	**N = 377 (47)**
Germination rate	$\beta = 1.09$	$\beta = 23.29$	$\beta = 2.37$	$\beta = 0.95$	$B = -0.89$
	$z = 2.60$	$z = 0.001$	$z = 4.26$	$z = 3.57$	$z = -2.73$
	$p < .01$	$p = .99$	$p < .001$	$p < .001$	$p < .01$
	$R^2M = 0.05$	$R^2M = 0.93$	$R^2M = 0.18$	$R^2M = 0.04$	$R^2M = 0.02$
	$R^2C = 0.27$	$R^2C = 0.95$	$R^2C = 0.33$	$R^2C = 0.28$	$R^2C = 0.18$
Mean germination time	$\beta = -11.28$	$\beta < 0.001$	$\beta = 24.79$	$\beta = 15.16$	$\beta = -18.78$
	$z = -0.68$	$z = 1.00$	$z = 2.59$	$z = 1.12$	$z = -1.16$
	$p = .52$	$p = .47$	$p < .05$	$p = .34$	$p = .29$
	$R^2M = 0.06$	$R^2M = 0.24$	$R^2M = 0.49$	$R^2M = 0.15$	$R^2M = 0.16$
	$R^2C = 0.06$	$R^2C = 0.25$	$R^2C = 0.49$	$R^2C = 0.16$	$R^2C = 0.16$
Mean seedling length	$\beta = 15.54$	$\beta < 0.001$	$\beta < 0.001$	$\beta = 1.08$	$\beta < 0.001$
	$z = 2.45$	$z = 1.00$	$z < 0.001$	$z = 0.37$	$z = 1.48$
	$p < .1$	$p = .48$	$p < .1$	$p = .73$	$p = .22$
	$R^2M = 0.21$	$R^2M = 0.25$	$R^2M = 0.46$	$R^2M = 0.008$	$R^2M = 0.24$
	$R^2C = 0.76$	$R^2C = 0.25$	$R^2C = 0.46$	$R^2C = 0.53$	$R^2C = 0.24$

Note: β, estimates of the models; N, sample size (values in brackets are observations from which analyses were based); P, probabilities of deviation; R^2C, conditional R^2 (proportion of variance explained by both the fixed and random factors); R^2M, marginal R^2 (proportion of variance explained by the fixed factors alone), z, fitted models.

& Park, 2018a,b). *Microcebus rufus* is restricted to RNP and few surrounding forests, and *M jollyae* has 95 percent of its population in KCF (Louis et al., 2006). Both species are omnivorous; however, fruits make up a high proportion of *M. rufus'* diet during the peak of the fruiting season (up to 84%; Atsalis, 1999). Mouse lemurs are tolerant of habitat degradation (Knoop, Chikhi, & Salmona, 2018), making them an important biological model to assess the impacts of seed dispersal on ecosystem function in the context of environmental change.

We collected seeds from fecal materials of captured individuals, from July 2017 to December 2018. We set up 3–4 transects of 300–400 m in each site, along which we deployed a trap (H.B. Sherman Traps, Inc.) every 25 m (140 traps in total; Supporting Information 1). In total, we captured 256 individuals: 193 *M. rufus* and 63 *M. jollyae*; we collected any feces from these captured individuals (for a total of 193 and 50, respectively) in the trap before releasing the individual;

otherwise, we kept the individual in a breathable cloth sack until it defecated (Table S2).

We extracted, identified, and measured all seeds from each feces without removing any fecal matter (in total, 2,570 seeds from *M. rufus* and 3,882 seeds from *M. jollyae* with 1–600 seeds per feces). Trained local research technicians identified the defecated seeds to their vernacular name, which we later matched with the corresponding scientific names using existing data bases of plants in the region (Manjaribe et al., 2013; Rafidimanana, Holmes, Johnson, Louis, & Rakouth, 2017; Razafindratsima, Jones, & Dunham, 2014; Razafindratisma, unpbl.). We preserved the seeds in small paper envelopes stored in a bag containing silica gel until germination experiments.

We set defecated (*N* = 18 species) and control seeds (*i.e.*, seeds manually extracted from fresh fruits, *N* = 8 species) to germinate in either petri dishes with constant humidity (Huenneke & Vitousek, 1990) or directly on the forest floor to examine seed performance in the forest (Razafindratsima & Dunham, 2015). As shade intensity varies among forest fragments and reforestation parcels in KCF, we also set experimental microhabitats with two different canopy covers: semi-shaded and shaded areas (Supporting Information 2).

For each experiment, we assessed three parameters: germination rate, germination time, and mean seedling length after three-month monitoring (Table S3). We fitted linear mixed-effects models in R 3.6.1 (R Core Team 2018) with the packages "lme4" (Bates, Mächler, Bolker, & Walker, 2015) and "lmerTest" (Kuznetsova, Brockhoff, & Christensen, 2017) to investigate how each parameter differed between defecated and control seeds. As we were not able to collect all the control seeds from all 18 species during fieldwork, we only used eight species for the statistical analysis. We ran one model per experiment set (*i.e.*, petri dish, forest ground, and semi-shaded and shaded areas) and per mouse lemur species with 1,295 defecated seeds, 495 control seeds, and 445 seedlings in total. We set treatment (defecated versus. control) as a fixed effect, and plant species as random effects because of their species-specific needs and responses to the environment to trigger germination. Additionally, we performed a survival analysis to examine the timing of germination across different predictors using the package "survival" (McNair, Sunkara, & Forbish, 2012). We fitted a Cox model with frailty to assess the significance of variation between treatments per experiment sets and mouse lemur species, with plant species as frailty effect.
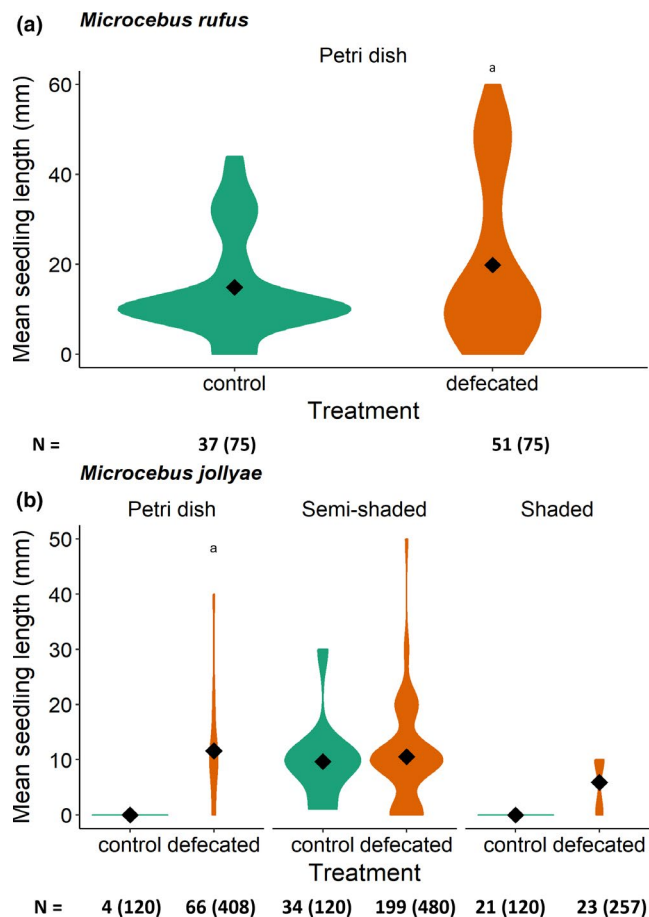

FIGURE 1 Mean seedling length after three-month monitoring of planted seeds from *Microcebus rufus* (a) and *Microcebus jollyae* (b). Asterisks (*) indicate significant variation of the parameter among treatments (*** < 0.001; ** < 0.01; and * 0.05, ᵃ < 0.1). The violin represents the variation of germination time and seedling length after three months, and the black diamonds represent arithmetic means. The values *N* in the table under each panel represent the total number of germinated seeds with the total number of seeds planted in parentheses

3 | RESULTS

3.1 | Diversity and size of defecated seeds

The two mouse lemurs defecated seeds from 22 different plant species, spanning 13 families (Table S4). We identified three non-native plant species (from 23 fecal samples), one of which was the highly invasive strawberry guava, *Psidium cattleianum* Sabine. Seeds defecated from *M. rufus* had length that ranges from 1 to 15.60 mm and width from 1 to 12.30 mm (*N* = 2,570), while those defecated from

M. jollyae had length that ranges from 0.32 to 8.48 mm and width from 0.21 to 5.00 mm (*N* = 3,882).

3.2 | Germination and growth parameters

Eighty-three percent of the 18 defecated species from the two mouse lemurs germinated and produced viable seedlings (Table S5). With the eight species tested, defecated seeds from both mouse lemur species had significantly higher germination rate than control seeds in all experiments, except the seeds from *M. rufus* set on forest ground (Table 1). However, we found no significant difference in germination time between defecated and control seeds, except seeds from *M. jollyae* in petri dishes (Figure S2b). No control seeds and only seven seeds defecated from *M. rufus* germinated on the forest ground (Figure 1a). Additionally, after three months, seedlings from defecated seeds from both mouse lemur species were taller than control seeds in all experiments (Figure 1a,b), but this difference was only marginally significant in all petri dish experiments (β = 15.54, t = 2.45, p = .09 for *M. rufus*, and β < 0.001, t = 2.45, p = .08 for *M. jollyae*; Table 1).

3.3 | Survival analysis

Overall, germination probabilities of defecated seeds were higher in all experiments (Figure 2 and Figure 3), which shows that gut passage affected seed germination and hastened the timing of germination, and supports the linear mixed-effects models. Germination probabilities were highest and significant in defecated seeds from *M. rufus* set in petri dishes (Figure 2 and Table 2).

4 | DISCUSSION

Although seed dispersal by frugivores has been shown to shape plant community diversity in many ecosystems (Terborgh et al. 2002; Razafindratsima & Dunham, 2016; Baños-Villalba et al., 2017), studies examining the roles and impacts of omnivorous and nocturnal animals, in particular, as seed dispersal agents have been lacking. Here, we demonstrate that omnivorous and nocturnal mouse lemurs contribute to the dispersal of diverse fruiting plant species in Madagascar's tropical forests and can have beneficial impacts, by increasing seed germination and seedling growth. These findings highlight the importance of considering the relative contributions of
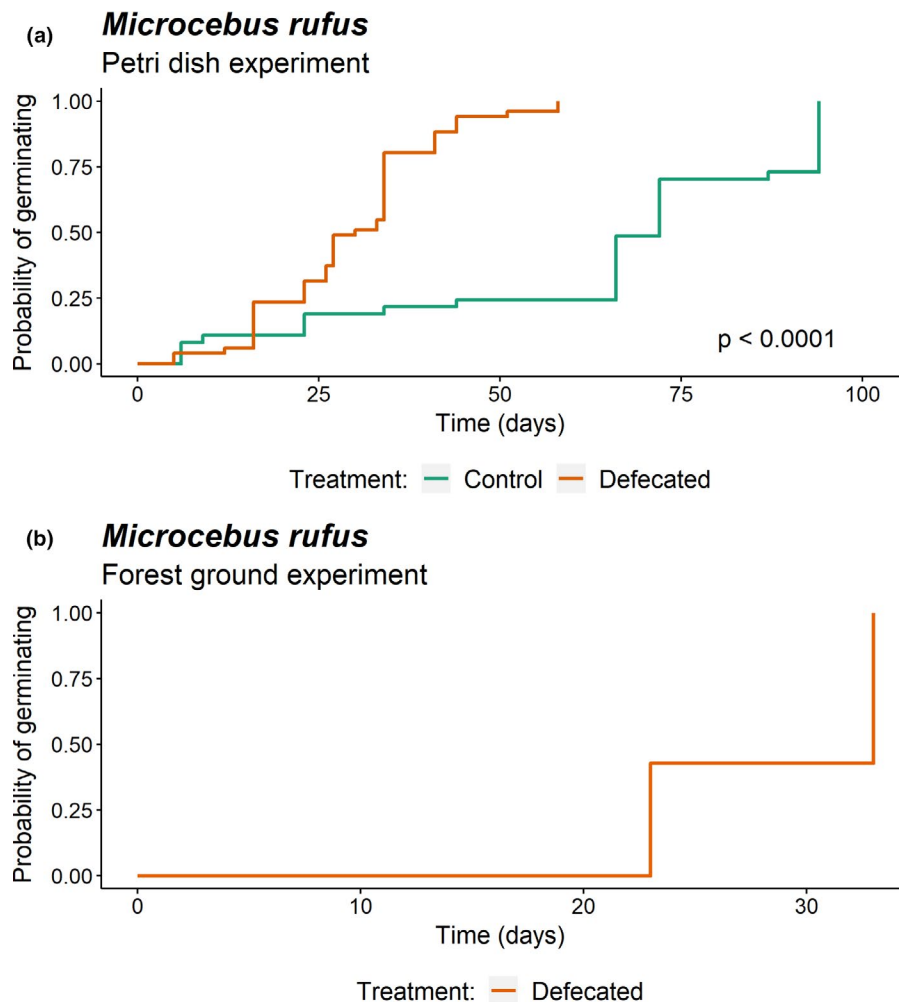

FIGURE 2 Probability of germination of defecated and control seeds from *Microcebus rufus* in Ranomafana National Park in petri dishes (a) and on the forest ground (b), based on survival analysis. *p*: probabilities of deviation
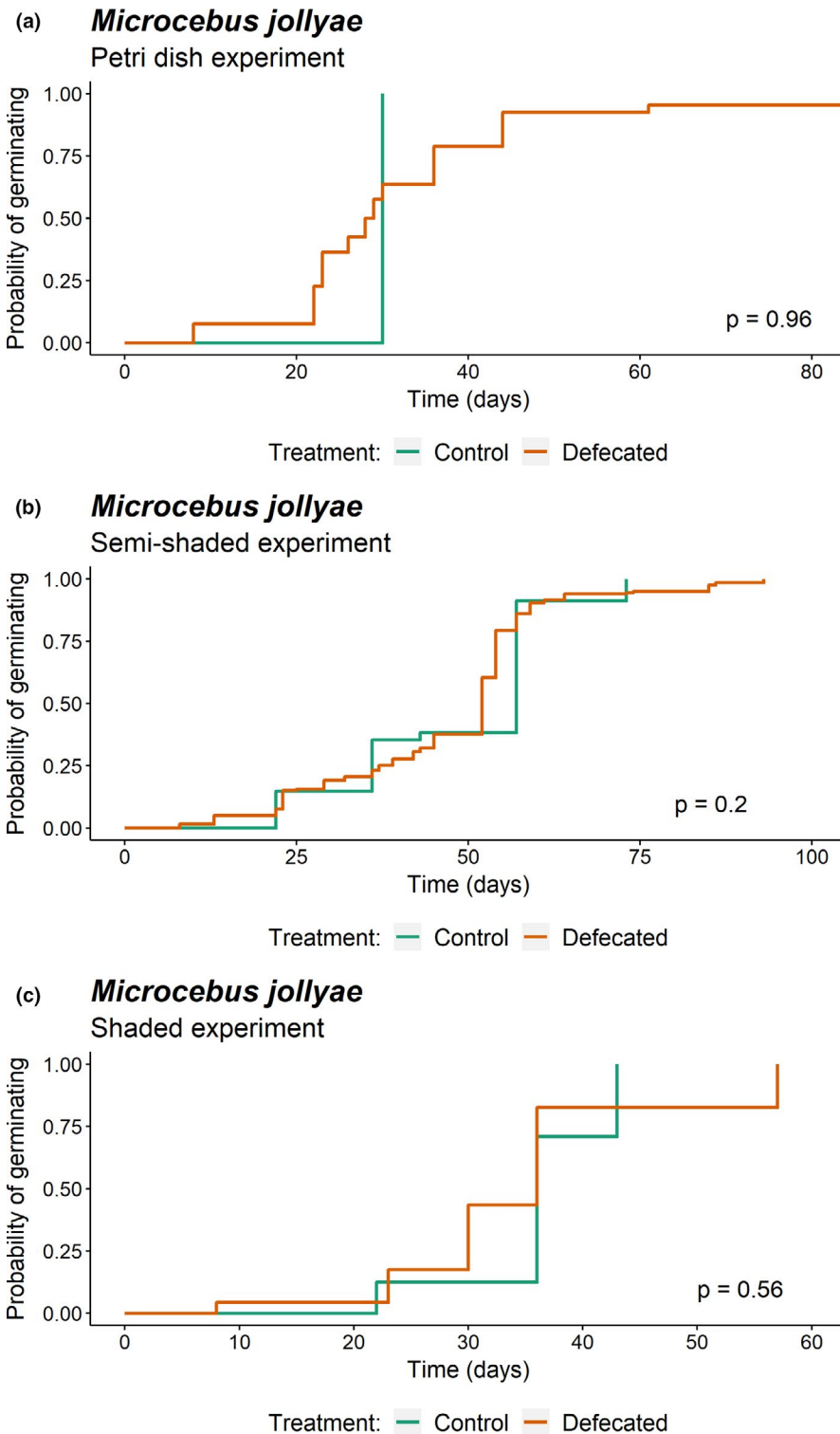
(a) *Microcebus jollyae*
Petri dish experiment

(b) *Microcebus jollyae*
Semi-shaded experiment

(c) *Microcebus jollyae*
Shaded experiment

FIGURE 3 Probability of germination of the defecated and control seeds from *Microcebus jollyae* in Kianjavato Classified Forest in petri dishes (a), semi-shaded experimental plots (b), and shaded experimental plots (c), based on survival analysis. *p*: probabilities of deviation

a suite of fruit/seed consumers to better understand the adaptive advantages of animal-mediated seed dispersal.

Microcebus rufus and *M. jollaye* could act as important primary seed dispersers of certain plant species in Madagascar's southeastern rain forests. They dispersed small- and medium-sized seeds (<10 mm) of native and non-native plant species. Although they were dispersing a smaller diversity of plants than the large-bodied diurnal frugivores (*Eulemur rubriventer*, *E. rufifrons*, and *Varecia variegata editorum*) in RNP

(Dew & Wright, 1998; Razafindratsima et al., 2014), they dispersed more than another mouse lemur, *M. griseorufus*, in Berenty Special Reserve (10 plant species; Génin & Rambeloarivony, 2018). Additionally, *M. rufus* disperse up to three understory plant species, which are also dispersed by *Philepitta castanea*, a small-sized bird in RNP (Rakotomanana, Hino, Kanzaki, & Morioka, 2003; Razafindratsita & Zach, 2009). Importantly, the two mouse lemurs disperse some plant species that might not be dispersed by other animals in these areas (Table S6).

TABLE 2 Summary table of the Cox model with frailty

| Experiment | Microcebus rufus | | Microcebus jollyae | | |
	Petri dish	Forest ground plot	Petri dish	Semi-shaded plot	Shaded plot
Sample size	N = 150 (88)	N = 75 (7)	N = 528 (70)	N = 660 (233)	N = 377 (47)
Statistics	X^2 = 20.62 df = 1 p < .0001	X^2 = NA[a] df = NA[a] P = NA[a]	X^2 = 66.08 df = 1 p = .96	X^2 = 1.60 df = 1 p = .20	X^2 = 0.30 df = 1 p = .56

Note: df, degree of freedom; *N*, sample size (values in brackets are observations from which analysis were based); *P*, probabilities of deviation; X^2, chi-square value.

[a]Failure of the control seeds to germinate precluded statistical analysis.

Seed dispersal by the two mouse lemurs substantially enhanced seed germination and seedling growth, corroborating other findings on the positive effects of animal gut passage on seeds (Traveset & Verdú, 2002), which has also been used as a component of the measure of effectiveness of animal-mediated seed dispersal (Schupp, 1993; Schupp, Jordano, & Gómez, 2010). Although germination rates are often species-specific, if we consider the sprouting success after gut passage for other dispersers, the overall quality of seed dispersal service by the two mouse lemurs (83%) is on par with that of the highly frugivorous *E. rubriventer* and *V.v. editorum* (both 80%; Dew & Wright, 1998). However, it is slightly higher than that of *E. rufifrons* (60%; Dew & Wright, 1998) and *P. castanea* (7%–8%; Rakotomanana et al., 2003). Such comparisons suggest that mouse lemurs could be at least as effective as highly frugivorous lemurs at facilitating germination. Many factors, such as fruit/seed maturity, germination drivers of each plant species, and climatic and/or edaphic conditions, may also influence germination time in addition to the potential scarification that gut passage may provide (Finch-Savage & Leubner-Metzger, 2006). However, as control seeds were collected from one or two individuals per species, the low number of control seeds and their source in tested plant species in our study could have introduced potential bias, which could be avoided with a larger sample size that includes different stages of fruit maturity. Nevertheless, we have documented an overlooked trend in seed dispersal ecology, dispersal by small-bodied and nocturnal omnivores, which needs further investigation.

Previous studies have shown that, by using non-native plants as a food source, some native animals might contribute to the spread of invasive species in tropical ecosystems (Gérard, Ganzhorn, Kull, & Carrière, 2015; Gosper, Stansbury, & Vivian Smith, 2005; Huenneke & Vitousek, 1990). However, despite a diet mixing native and non-native plants, *M. rufus* is unlikely to be a significant vector for biological invasions. Even though we sampled during the fruiting season of the invasive *P. cattleianum* in RNP when it may attract many frugivores, *M. rufus* maintained a diverse diet, dispersing mostly native species (Table S4). On the other hand, soap bush (*Clidemia hirta* D.Don), a pioneer herbaceous exotic species, was overrepresented among the seeds dispersed by *M. jollyae* in KCF, probably because of its abundance in the understory of the region. By foraging on *C. hirta*, *M. jollyae* could facilitate the regeneration process within these parcels because it fruits year-round (Wester & Wood, 1977), which may attract mouse lemurs and other frugivores, allowing forest plant species to be dispersed and colonize these areas. Non-native shrubs have indeed been found to be critical for the initiation of forest regeneration in other systems in Madagascar (Martinez & Razafindratsima 2014). Nevertheless, *M. jollyae* could potentially disperse *C. hirta* into the old growth forest fragments; therefore, close monitoring of this species in these reforestation parcels is recommended for invasion management.

The short germination time (Figure S2) and high germination rate (Figure S3) in the semi-shaded plots indicate that mouse lemurs could play a significant role in habitat restoration and early-forest succession. The ability of animal seed dispersers to take seeds into disturbed forests could be critical in influencing the capacity of the forest to recover from disturbances (Carlo & Morales, 2016), given that seed dispersal limitation is a critical structuring factor in both early- and late-forest successions (Makoto & Wilson, 2019). This is acutely important in KCF as it is undergoing active reforestation processes. Mouse lemurs extensively use the newly reforested areas (Guthrie, unpbl.), which provide semi-opened areas where they could deposit seeds, and promote forest regeneration, extension, and connectivity. Furthermore, as mouse lemurs dispersed seeds from various strata, their dispersal service could favor the development of early-forest succession and preservation of fragmented/degraded habitats.

In summary, this study provides new insights into the potential roles of nocturnal omnivorous species in dispersing and structuring plant communities, which are the major factors for forest regeneration. Our findings also highlight the potential applications of animal-mediated seed dispersal in forest fragment connectivity, maintenance of plant diversity, and community structure. Further studies conducted throughout the annual cycle could help to better assess the effectiveness of seed dispersal by nocturnal omnivores. Future studies could also focus on examining the potential of non-traditional seed dispersers in filling the functional gap of losing large-bodied frugivores – a major concern in Madagascar (Schwitzer et al., 2014) and worldwide (Aslan, Zavaleta, Tershy, & Croll, 2013).

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

VR and OHR conceived the ideas. VR, NKG, OHR, DSP, ZR, and SEJ designed the protocols for data collection. VR, CMMD, NNR, NKG, and ZESF collected and curated data. VR analyzed the data and led the writing of the manuscript with inputs from all co-authors. All authors contributed critically to the review and editing of the drafts and gave final approval for publication.

ETHICAL APPROVAL

Ethical and legal approval was obtained prior to the start of the study. Animal trapping and handling were performed in accordance with the ethics of the permit from the University of Calgary's Animal Ethics n° AC19-0026 and the Ministère de l'Environnement et du Développement Durable of Madagascar.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k0p2ngf50 (Ramananjato et al. 2020).

ORCID

Veronarindra Ramananjato (iD) https://orcid.org/0000-0003-2398-3671

Onja H. Razafindratsima (iD) https://orcid.org/0000-0003-1655-6647

REFERENCES

Aslan, C. E., Zavaleta, E. S., Tershy, B., & Croll, D. (2013). Mutualism disruption threatens global plant biodiversity. *PLoS ONE*, *8*, e66993.

Atsalis, S. (1999). Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *20*(2), 193–199.

Baños-Villalba, A., Blanco, G., Díaz-Luque, J., Dénes, F. V., Hiraldo, F., & Tella, J. L. (2017). Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Scientific Reports*, *7*, 7373.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-effects Models using lme4. *Journal of Statistical Software*, *67*(1), 1-48.

Beckman, N. G. et al. (2019). Advancing an interdisciplinary framework to study seed dispersal ecology. *AoB Plants*, plz048.

Carlo, T. A., & Morales, J. M. (2016). Generalist birds promote tropical forest regeneration and increase diversity via rare-biased seed dispersal. *Ecology*, *97*(7), 1819–1831.

Dew, L. J., & Wright, P. C. (1998). Frugivory and seed dispersal by four species of Primates in Madagascar's eastern rainforest. *Biotropica*, *30*, 425–437.

Dunham, A. E., Erhart, E. M., & Wright, P. C. (2011). Global climate cycles and cyclones: Consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, *17*, 219–227.

Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Physiol.*, *171*, 501–523.

Génin, F., & Rambeloarivony, H. (2018). Mouse lemurs (Primates: Cheirogaleidae) cultivate green fruit gardens. *Biological Journal of the Linnean Society*, *124*(4), 607–620.

Gérard, A., Ganzhorn, J. U., Kull, C. A., & Carrière, S. M. (2015). Possible roles of introduced plants for native vertebrates conservation: The case of Madagascar. *Restoration Ecology*, *23*(6), 768–775.

Gosper, C. R., Stansbury, C. D., & Vivian Smith, G. (2005). Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. *Diversity and Distributions*, *11*(6), 549–558.

Hämäläinen, A., Broadley, K., Droghini, A., Haines, J. A., Lamb, C. T., Boutin, S., & Gilbert, S. (2017). The ecological significance of secondary seed dispersal by carnivores. *Ecosphere*, *8*(2), e01685.

Herrera, C. M. (1989). Frugivory and seed dispersal by carnivorous animals, and associated fruit characteristics, in Mediterranean habitats. *Oikos*, *55*, 250–262.

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228.

Huenneke, L. F., & Vitousek, P. M. (1990). Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: Implications for management of native Hawaiian forests. *Biological Conservation*, *53*, 199–211.

Hulme, P. E., & Benkman, C. W. (2002).Granivory. In C. M. Herrera & O. Pellmyr (Eds.), *Plant-animal interactions: an evolutionary approach* (pp. 132–154). Oxford, UK: Blackwell.

Knoop, S., Chikhi, L., & Salmona, J. (2018). Mouse lemurs' use of degraded habitat: A review of the literature. *Lemur News*, *21*, 20–31.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Test in linear mixed effects models. *Journal of Statistical Software*, 1–26.

Louis, E. E., Coles, M. S., Andriantompohavana, R., Sommer, J. A., Engberg, S. E., Zaonarivelo, J. R., ... Brenneman, R. A. (2006). Revision of the mouse lemurs (*Microcebus*) of Eastern Madagascar. *International Journal of Primatology*, *27*(2), 347–389.

Louis, E. E., Ranaivoarison, J. F., McGuire, S., & Johnson, S. (2013). Kianjavato. In C. Schwitzer, R. A. Mittermeier, N. Davies, S. Johnson, J. H. Ratsimbazafy, J. Razafindramanana, E. E. Louis & S. Rajaobelina (Eds.), *Lemurs of Madagascar: a strategy for their conservation 2013–2016* (pp. 95–97). Bristol, UK: IUCN.

Makoto, K., & Wilson, S. D. (2019). When and where does dispersal limitation matter in primary succession? *Journal of Ecology*, *107*, 559–565.

Manjaribe, C., Frasier, C. L., Rakouth, B., & Louis, E. E. (2013). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology*, *2013*, 1–12.

Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a

forest restoration site in Masoala National Park, Madagascar. *Folia Primatology (basel)*, 85(4), 224–243.

McNair, J., Sunkara, A., & Forbish, D. (2012). How to analyse seed germination data using statistical time-to-event analysis: Non-parametric and semi-parametric methods. *Seed Research Science*, 22(2), 77–95.

Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., & Rylands, A. (2010). *Lemurs of Madagascar*, 3rd ed. Arlington, TX: Conservation International-Tropical Field Guide Series.

Motta-Junior, J. C., & Martins, K. (2002). The frugivorous diet of the Maned wolf, Chrysocyon brachyurus, in Brazil: ecology and conservation. In D. J. Levey, R. Silva & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 291–303). Oxford, New York, NY: CABI.

Platt, S. G., Elsey, R. M., Liu, H., Rainwater, T. R., Nifong, J. C., Rosenblatt, A. E., … Mazzotti, F. J. (2013). Frugivory and seed dispersal by crocodilians: An overlooked form of saurochory? *Journal of Zoology*, 291, 97–99.

Radespiel, U., Reinmann, W., Rahelinirina, M., & Zimmerman, E. (2006). Feeding ecology of sympatric mouse lemur species in northwestern Madagascar. *International Journal of Primatology*, 27(1), 311.

Rafidimanana, D. A., Holmes, S. M., Johnson, S., Louis, E. E., & Rakouth, B. (2017). Relationship between vegetation characteristics and the presence of lemurs: *Varecia variegata*, *Eulemur rubriventer* and *Eulemur rufifrons* in Kianjavato forest fragments. *Lemur News*, 20, 15–19.

Rakotomanana, H. F., Hino, T., Kanzaki, M., & Morioka, H. (2003). The role of the velvet Asity *Philepitta castanea* in regeneration of understory shrubs in Madagascan rainforest. *Ornithological Science*, 2, 49–58.

Ramananjato, V., Rakotomalala, Z., Park, D. S., DeSisto, C. M. M., Raoelinjanakolona, N. N., Guthrie, N. K. … Razafindratsima, O. H. (2020). Data from: The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. Dryad Digital Repository https://doi.org/10.5061/dryad.k0p2ngf50

Razafindratsima OH., Dunham Amy E.. (2015). Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology*, 96(1), 24–30.

Razafindratsima, O. H., & Dunham, A. E. (2016). Frugivores bias seed-adult tree associations through nonrandom seed dispersal: A phylogenetic approach. *Ecology*, 97(8), 2094–2102.

Razafindratsima, O. H., Jones, T. A., & Dunham, A. E. (2014). Patterns of movement and seed dispersal by three lemur species. *American Journal of Primatology*, 76, 84–96.

Razafindratsima, O. H., Yacoby, Y., & Park, D. S. (2018a). MADA: Madagascar animal trait data archive. *Ecology*, 99(4), 990.

Razafindratsima, O. H., Yacoby, Y., & Park, D. S. (2018b). *MADA: Madagascar animal trait data archive*. Retrieved from https://doi.org/10.5061/dryad.44tt0

Razafindratsita, V., & Zach, S. (2009). Frugivory and facilitation of seed germination by the velvet Asity, *Philepitta castanea* (Müller, 1776), in the rainforest understory of Ranomafana National Park. *Malagasy Nature*, 2, 154–159.

Schupp, E. W. (1993).Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107, 15–29.

R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, 188, 333–353.

Schwitzer, C., Mittermeier, R. A., Johnson, S., Donati, G., Irwin, M. T., Peacock, H., … Wright, P. C. (2014). Averting lemur extinction amid Madagascar's political crisis. *Science*, 343, 842–843.

Terborgh, J., Pitman, N., Silman, H., Schichter, H., & Nunez, P. (2002). Maintenance of tree diversity in tropical forests. In D.J. Levey, W.R. Silva & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 1-17). Oxford, UK: CABI Publishing.

Traveset, A., & Verdú, M. (2002). A meta-analysis of the effect of gut treatment on seed germination. In D.J. Levey, W.R. Silva & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 339–350). Oxford, New York: CABI Publishing.

Valenta, K., & Lehman, S. M. (2016). Seed dispersal by mouse lemurs: do Microcebus represent a unique frugivorous guild? In S. M. Lehman, U. Radespiel & E. Zimmermann (Eds.), *The Dwarf and mouse lemurs of Madagascar: biology, behavior, and conservation biogeography of the Cheirogaleidae* (pp. 353–365). Cambridge, UK: Cambridge University Press.

Wester, L. L., & Wood, H. B. (1977). Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environmental Conservation*, 4, 35–41.

Yang, Y., Zhang, Y., Deng, Y., & Yi, X. (2019). Endozoochory by granivorous rodents in seed dispersal of green fruits. *Canadian Journal of Zoology*, 97, 42–49.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.