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Greater ecological flexibility in furry-eared dwarf lemurs versus sympatric Sibree's dwarf lemurs: Insights from activity budgets, spatial distribution, and foraging behavior

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Abstract – Many forests in Madagascar harbor numerous and diverse species of lemur in sympatry. Whereas more distant relatives can avoid competition by occupying distinct ecological niches, more subtle niche partitioning may explain how congeners coexist in the same place at the same time. Here, we examine the behavioral ecology of sympatric furry-eared (*Cheirogaleus crossleyi*) and Sibree's (*C. sibreei*) dwarf lemurs at Tsinjoarivo- a high-altitude rainforest in central-eastern Madagascar. Specifically, we followed 24 collared individuals during the pre- and post-hibernation seasons of 2011-2014 to determine activity budgets, spatial distribution, foraging behavior and macronutrient selection. Overall, we find that furry-eared dwarf lemurs, compared to Sibree's dwarf lemurs, had smaller home ranges and traveled shorter nightly distances, spent more time foraging and less time in their resting sites. The species were somewhat spatially differentiated, with furry-eared dwarf lemurs more often found closer to forest edges and in generally more degraded habitats. Furry-eared dwarf lemurs consumed a more diverse diet, but both species foraged for fruits (and flowers) that were rich in sugars and/or fats, key nutrients particularly during the fattening season prior to hibernation. Since this study was conducted, anecdotal observations at this site strongly suggest that the furry-eared dwarf lemur is replacing Sibree's dwarf lemur, in step with ongoing habitat fragmentation and degradation. Placing our results in broader context highlights the furry-eared dwarf lemur as a more generalist species in terms of habitat occupation, geographic distribution, and ecological flexibility. In contrast, Sibree's dwarf lemur seems to be a specialist highly adapted only to Madagascar's intact and high-elevation rainforests. If this is the case, the sympatric occurrence of these two species at Tsinjoarivo may be recent, tenuous, and unsustainable in the long run. We advocate for greater research of the behavioral ecology of sympatric dwarf lemurs at this and other sites across Madagascar.

Keywords – *Cheirogaleus crossleyi*, *Cheirogaleus sibreei*, generalist, niche differentiation, specialist.

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Introduction

The lemurs of Madagascar are the most diverse primate group on Earth with more than 100 extant species belonging to 15 genera from 5 families (Mittermeier *et al.*, 2023; Everson *et al.*, 2025). In many Malagasy forests today, numerous lemur species live in sympatry, and avoid competition by occupying distinct ecological niches, creating complex and dynamic communities (Hladik *et al.*, 1980; Ganzhorn, 1989). For example, in the eastern rainforests, up to 13 lemur species, ranging in body size from 50 g to 6 kg, can coexist in the same habitat (Ganzhorn *et al.*, 1997; Wright *et al.*, 2012). Sympatric lemurs can reduce competition by eating different foods, occupying different microhabitats, or being active at different times (Ganzhorn, 1988, 1989). Classic examples of such niche partitioning across genera stem from the folivores and include the sifakas and indri selecting for different plant parts and species (trophic niche dimension) (Powzyk and Mowry, 2006) and the diurnal indri and nocturnal avahi relying on similar foods but foraging at different times of the day (temporal niche dimension) (Ganzhorn, 1988, 1989).

Lemur communities can also include different species of sympatric congeners, likely due to secondary contact (e.g., Teixeira *et al.*, 2021), with more direct potential for niche overlap. Importantly, sympatric species with overlapping niches do not necessarily come into competition if resources are abundant (Pianka, 1974), but this is rarely the case. For sympatric congeners with similar niches under competition, subtle ecological differences may allow them to coexist (Rakotondravony *et al.*, 2011). For example, sympatric bamboo lemurs (*Hapalemur* spp.) in the montane rainforest of Ranomafana have similar dietary profiles overall but avoid competition by feeding on different species of bamboo (Tan, 1999). Sympatric brown lemurs (*Eulemur* spp.) in the same rainforest vary in the proportion of foraged foods, such as unripe fruits and leaves, and in the temporal distribution of feeding bouts, which may facilitate sympatry even when seasonality limits resource availability (Overdorff, 1993).

Sympatry among congeners is particularly prevalent among the small-bodied, nocturnal, and speciose mouse (*Microcebus* spp.). and dwarf lemurs (*Cheirogaleus* spp.). To date, both biogeographic and ecological patterns have been far better studied in the former (Radespiel *et al.*, 2003, 2006; Radespiel, 2006). In mouse lemurs, sympatry generally occurs between a generalist and a specialist species (Dammhahn and Kappeler, 2008; Knoop *et al.*, 2018). For example, the widely distributed grey mouse lemur (*M. murinus*) can be found in variable sympatry with Berthe's (*M. berthae*), golden brown (*M. ravelobensis*), pygmy (*M. myoxinus*) and reddish-gray (*M. griseorufus*) mouse lemurs that all have more restricted ranges in the western or southern dry forests (Olivieri *et al.*, 2007; Dammhahn and Kappeler, 2008; Rakotondranary *et al.*, 2011a,b; Thorén *et al.*, 2011). A body of literature has examined ecological differentiation of these species (Radespiel *et al.*, 2006; Dammhahn and Kappeler, 2008; Thorén *et al.*, 2011). On the eastern side of the island, the widely distributed Goodman's mouse lemur (*M. lehilahytsara*) lives in sympatry with Jonah's (*M. jonahi*) and MacArthur's (*M. macarthurii*) mouse lemurs in montane and lower elevation rainforests (Schüßler *et al.*, 2020). One factor that may explain why sympatry is so common in mouse lemurs is that they are facultative heterotherms, i.e., they variably use daily and prolonged torpor, and hibernation depending on the species, habitat, year, and individual (Schmid, 2000; Schmid and Ganzhorn, 2009; Kobbe *et al.*, 2011; Blanco *et al.*, 2018; Schüßler *et al.*, 2025). By enabling mouse lemurs to be variably active during the dry season, heterothermy can decrease competition during the time of year when resources are most scarce.

Dwarf lemurs, the larger cousins of mouse lemurs, are primarily frugivorous and the only obligate hibernators among primates (Dausmann and Warnecke, 2016; Blanco *et al.*, 2018). Because the hibernation season coincides with the dry season, i.e., best time of year to do field work, dwarf lemur ecology and biogeography are relatively understudied compared to that of mouse lemurs. We are only now appreciating the full extent of sympatric occurrence, with many forests throughout Madagascar's east hosting 2-3 distinct species (Blanco and Godfrey, 2014; Herrera *et al.*, 2016; Blanco *et al.*, 2025). For example, in the littoral forests of southeastern Madagascar, Greater (*C. major*) and Thomas' (*C. thomasi*) dwarf lemurs occupy similar areas and rely on similar foods but feed at different heights in the canopy (Lahann, 2007).

In the high-altitude rainforests of eastern Madagascar, the furry-eared (*C. crossleyi*) and Sibree's (*C. sibreei*) dwarf lemurs live in sympatry (Groeneveld *et al.*, 2010; Blanco *et al.*, 2013; Blanco and Godfrey, 2014). Whereas the furry-eared dwarf lemur has a broad geographic range and is found in pristine and degraded montane eastern rainforests and fragmented forests across the central highlands (Blanco *et al.*, 2018, 2025), Sibree's dwarf lemur is restricted to high-altitude rainforests generally above 1500 m (Blanco *et al.*, 2009, 2025). Based on this distribution alone, the furry-eared dwarf lemur is predicted to be more ecologically flexible (Herrera *et al.*, 2016) and sparse ecological data from the Tsinjoarivo forest support this prediction. At this site, furry-eared dwarf lemurs, compared to Sibree's dwarf lemurs, enter hibernation later and show more individual variation in hibernation duration (Blanco *et al.*, 2013, in press; Blanco and Godfrey, 2014); use both tree holes and nests as sleeping sites, whereas Sibree's dwarf lemurs only use tree holes (Blanco *et al.*, in press); and preliminary data on foraging ecology highlight that furry-eared dwarf lemurs eat a more diverse diet (Domoinaharivelo, 2014), with more robust and confirmatory data needed.

Here, we contribute to the understanding of ecological differentiation among sympatric furry-eared and Sibree's dwarf lemurs by studying behavioral ecology and spatial usage. Under the hypothesis that subtle differences in species' ecology allow sympatric congeners to co-exist (Overdorff, 1993), we expect to find that our focal species differ in e.g., areas of occupancy, home-range size, nightly travel distances, activity budgets, foraging behavior, and/or macronutrient selection that may contribute to trophic, spatial, and/or temporal differentiation. In addition, under the hypothesis that sympatry in dwarf lemurs, as in mouse lemurs, occurs between a generalist and a specialist (e.g. Henke-von der Malsburg and Fichtel, 2018), we expect to find greater ecological flexibility and variability among furry-eared dwarf lemurs, with furry-eared dwarf lemurs consuming a wider array of food items while Sibree's dwarf lemurs will prioritize a smaller number of high-quality items. Ultimately, these data will contribute to a broader understanding of how lemur assemblages are maintained, including among close relatives.

Methods

STUDY SITE AND SUBJECTS

We conducted our study in Andasivodihazo, one of the forest fragments at Tsinjoarivo, a high-altitude rainforest in central-eastern Madagascar (19°41′15″S, 47°46′25″E, 1660 m), between 2011 and 2014. Our study subjects were 24 dwarf lemurs (16 adults, 6 subadults, 2 juveniles), including 13 *C. crossleyi* (8 females, 5 males) and 11 *C. sibreei* (5 females, 6 males) (table S1 in the Supplementary material) (fig. 1).

We captured dwarf lemurs in the pre-hibernation season (January-March), which generally corresponds to the fattening period. We placed live-Tomahawk traps along known trails, baited with fermented banana, set between 4 and 10 m high in the afternoon (16:00-17:00), and checked early in the mornings (4:00-5:00). All captured dwarf lemurs were brought to the research camp for processing. At the campsite, dwarf lemurs were safely sedated (Ketamine, 5-10 mg/kg), and we collected morphometrics and reproductive observations. Each lemur was fitted with an external radiocollar (ARC 400, approx. 10 g, Advanced Telemetry Systems, Isanti, MN, USA) with a unique frequency that allowed for nocturnal tracking and resting sites' location using a data receiver (Receiver R410, Advanced Telemetry System)

Figure 1. Photos of a (left) furry-eared (*C. crossleyi*) and (right) Sibree's (*C. sibreei*) dwarf lemur from Andasivodihazo, Tsinjoarivo.

and external antenna. All captured individuals were monitored until full recovery from anesthesia, offered small pieces of banana and fresh dilute sugar-water and placed in cloth bags to facilitate resting during the day. Individuals were released later in the afternoon at their capture sites.

We aimed to recapture study lemurs for collar replacement due to limited battery life. In most cases, we replaced collars in the middle of the hibernation season (e.g., July) in connection with other projects (Blanco *et al.*, 2016). For a handful of animals, we replaced collars at the onset of the post-hibernation season (September-October) once animals had emerged and were active again. In these cases, we used live trapping as described above. At the end of the post-hibernation season (e.g., November), animals were recaptured for collar removal using live trapping as described above.

NOCTURNAL TRACKINGS

We collected observational data during 50 nocturnal trackings in total, including 28 in the pre-hibernation (January-March) and 22 in the post-hibernation (September-November) seasons from 2011-2014. Although we aimed to observe all animals in both seasons, this was not always possible: due to natural population turnover, some individuals were only observed in the pre-hibernation season ($n = 11$); because some animals entered hibernation soon after collaring, some individuals were only observed in the post-hibernation season ($n = 7$). See table S1 in the Supplementary material for more information.

Trackings were generally conducted between 18:00 hours and 23:00 hours, except when this was not possible due to challenging weather conditions or site accessibility. Each night, we followed a single lemur using 2-min scan sampling and a simplified ethogram. This protocol was adjusted for data collection on small-sized, nocturnal lemurs while minimizing disturbance of natural behaviors. Every 2 minutes, we turned on the flashlight to locate the individual and record behavior; we turned off the flashlight between scans. Our ethogram included resting, moving, grooming, and feeding behaviors. We also noted if the individual was inside a resting site. If the individual was feeding, we recorded the plant name and food part (e.g., fruit, flower) and estimated the height of the lemur in the canopy to the nearest meter. We recorded out of sight (OOS) when the individual was not in the resting site and could not be directly observed.

We recorded GPS coordinates every time the focal lemur moved at least 5 m in any horizontal direction. When the individual was not directly observed but the signal in the receiver was 1 bar (equivalent to about 5-10 m distance) we recorded a GPS coordinate to mark the approximate location of the individual. We used these coordinates in our calculations of nightly distances. We also opportunistically collected GPS points of resting and hibernation sites by tracking collared animals during the day. In general, we aimed to record resting sites daily during the pre-hibernation and post-hibernation seasons, and hibernation sites weekly during the hibernation season. We used GPS data both from nocturnal trackings and resting/hibernation site-monitoring in our estimations of home range sizes. Descriptions of resting sites are included elsewhere (Blanco *et al.*, in press).

ANALYSES OF ACTIVITY BUDGETS AND FORAGING PATTERNS

Our behavioral dataset for analyses included data from 24 dwarf lemurs (1-4 trackings per individual). For each tracking, we calculated activity patterns by dividing the number of scans per behavior (e.g., inside resting site, resting, moving, foraging) over the total number of scans "in view" (i.e., we discarded the OOS scans). For lemurs that were observed on multiple nights, we calculated mean percentages per individual, such that each animal was only included once in the dataset. We computed Wilcoxon (two independent samples) nonparametric tests to determine if any behaviors differed between species and between sexes within species.

We then isolated the foraging data and determined which plant species and parts were most consumed during the pre-hibernation and post-hibernation seasons for *C. crossleyi* and *C. sibreei*. Because individual animals were represented differently in our dataset, both within and between seasons, and foraged on different items, we scaled this analysis to the species. We divided the total number of feeding scans per food item across all conspecifics by the total number of feeding scans among conspecifics to determine the relative proportion of each item. We additionally examined foraging behavior by feeding bout, i.e., by combining continuous feeding scans by an individual on the same item into a single feeding event. We present information on the longest individual feeding bouts.

We calculated the lemurs' heights in the canopy during foraging, by averaging values per individual across nocturnal trackings, such that each lemur was only represented once. We then computed a Wilcoxon test to determine if foraging height differed between species.

ANALYSES OF NIGHTLY DISTANCES AND HOME RANGES

We compiled GPS data for 55 nocturnal trackings (27 pre-hibernation, 28 post-hibernation) from 23 of the dwarf lemurs (1-4 trackings per individual) and used these data to estimate travel distances. Discrepancies between behavioral data (50 trackings) and nightly distances (55 trackings) are due to gaps in our dataset (see table S1 in the Supplementary material for details on which individuals contributed to which analysis). For each individual and per nocturnal tracking, we calculated the nightly distance traveled using the Points to Line tool in ArcGIS Pro v.3.4.3 (ESRI, Redlands, Calif., USA), where GPS coordinates were arranged temporally from start to end. Each distance included between 4-19 GPS coordinates per individual per night. To account for differences in the tracking duration, we divided total distance by number of tracking minutes (meters by minute) and multiplied this by 300 to estimate distance covered during the standard 5-h period. We used mean values per individual per season in the analysis. We then computed Wilcoxon tests to determine if nightly travel distances differed between species, and between sexes within species, within each season.

Next, we calculated home range sizes for the 22 individuals (12 *C. crossleyi* and 10 *C. sibreei*) for whom we had at least 10 GPS coordinates. To calculate individual home range sizes, we compiled GPS coordinates from nocturnal trackings and resting/hibernation sites collected during the day. Home ranges were estimated using the Kernel Density tool in ArcGIS Pro, using the 95% density value as the threshold. In sum, we estimated kernel density, extracted values to points to identify 95% density value and created a layer with all points equal or greater than the threshold. We then used the raster to polygon tool to calculate the general home range area in hectares. We computed Wilcoxon tests to determine if home ranges differed between species and between sexes within species.

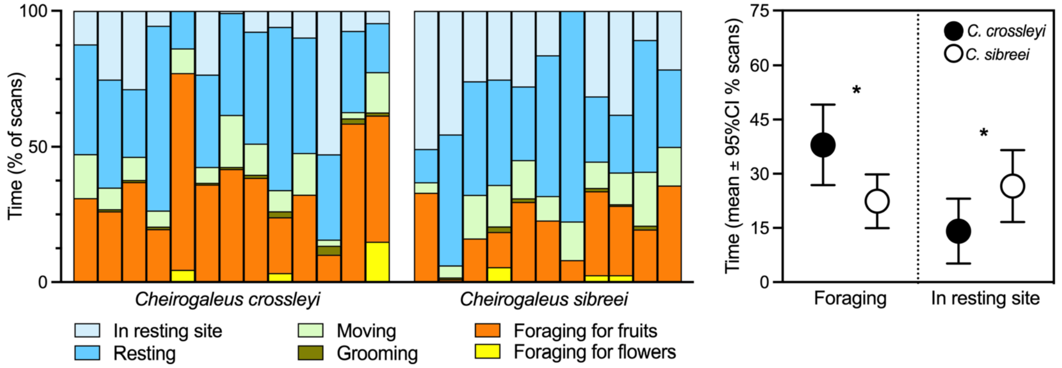

Figure 2. Behavior of study dwarf lemurs, depicted as stacked bar charts of activity patterns by individual lemur (left) and the proportion of time spent foraging and in resting sites averaged across conspecifics, for furry-eared dwarf lemurs (*C. crossleyi*) (black) and Sibree's dwarf lemurs (*C. sibreei*) (right) $*p < 0.05$.

PLANT SAMPLING AND ANALYSIS

We collected a subset of fruits and flowers from the plants consumed by study dwarf lemurs for nutritional analysis, when possible, from the same trees where they were observed. Fresh samples were dried in the field using a portable Coleman oven. We maintained internal temperature around 50°C until materials were fully dried. Samples were exported to Hamburg University, Germany, for further analysis. We obtained sugar and fat content, following protocols in Donati *et al.* (2011). We calculated mean values for multiple samples of same plant material.

In summary, we obtained soluble sugar content as equivalent of galactose after acid hydrolyzation of 50% methanol extract. Fat content was determined by extraction for 4 h with petrol-ether in a Soxhlet apparatus, as fat is dissolved in petrol-ether. After the ether is evaporated, the amount of fat could be weighed.

Results

ACTIVITY PATTERNS

Furry-eared dwarf lemurs were in view approx. 58% (1094 scans) of the tracking time (min 34%, max 87%, SD = 14.8), whereas Sibree's dwarf lemurs were in view approx. 44% (686 scans) of the time (min 11%, max 67%, SD = 17.0). When in view, furry-eared dwarf lemurs spent, on average, 38% (400 scans) of the time feeding (SD = 18.4), 37% (429 scans) resting (SD = 15.0), 9.8% (97 scans) moving (SD = 5.3) and 1% (14 scans) self-grooming (SD = 1.0), whereas Sibree's dwarf lemurs spent 38% (264 scans) resting (SD = 18.3), 22% (154 scans) feeding (SD = 11.1), 12% (75 scans) moving (SD = 4.9) and 0.7% (5 scans) self-grooming (SD = 0.7). Furry-eared dwarf lemurs spent significantly more time feeding than did Sibree's dwarf lemurs (Wilcoxon's $z = -2.32$, $p = 0.02$), whereas Sibree's dwarf lemurs spent significantly more time inside resting sites than did furry-eared dwarf lemurs (27% vs. 14%; Wilcoxon's $z = 2$, $p = 0.046$) (fig. 2). We found no significant differences between sexes.

FORAGING BEHAVIOR, MACRONUTRIENTS, AND FEEDING EVENTS

Both species fed primarily on fruits and, to a lesser degree, flowers (furry-eared: 95.4 and 4.6%, respectively; Sibree's: 95.7 and 4.3%, respectively). We identified 25 plant species consumed by dwarf lemurs, 21 of which were consumed by furry-eared dwarf lemurs, 15 of which were consumed by Sibree's dwarf lemurs, and 11 of which were shared between species (tables 1 and 2). Of these plants, only three (fruit and/or flower) were consumed by both species during both the pre- and post-hibernation seasons: *Bakerella clavata* (Tongoalahy), *Tambourissa purpurea* (Ambora), *Mendoncia flagellaris* (Vahivoraka).

Table 1. List of plant species consumed by sympatric dwarf lemur species during pre-hibernation at Tsinjoarivo.

Common name	Scientific name	Plant part	*C. crossleyi*		*C. sibreei*		Nutrition (%DM)	
			Rank	%	Rank	%	Sugar	Fat
Takaloparihy	*Embelia concinna*	Fruits	1	47.5%			*15.9%*	*10.3%*
Vahivovo	*Gynoctodes umbrellata*	Fruits	2	25.8%	4	6.6%	*20.2%*	5.4%
Tongoalahy	*Bakerella clavata*	Fruits	3	9.0%	1	34.6%	9.4%	*20.6%*
Nonoka	*Ficus reflexa*	Fruits	4	6.5%	2	26.0%	7.9%	2.0%
Tsaramaso Hazo	*Petchia erythrocarpa*	Fruits			3	17.3%	*12.1%*	*15.7%*
Fantsikahitra	*Canthium* sp.	Fruits	5	4.7%				
Taimbolavo	*Erythroxylum* sp.	Fruits			5	4.2%	7.9	*10.7*
Vahitafoaka	*Gouania* cf. *mauritiana*	Fruits	6	2.4%				
Anamamibe	*Phytolacca dodecandra*	Fruits	7	1.7%			*10.0%*	8.9%
Vahivoraka	*Mendoncia flagellaris*	Fruits	8	1.3%	6-8	2.1%	6.5%	1.9%
Manalo II	*Schefflera monophylla*	Fruits	9-10	0.4%	6-8	2.1%	*17.0%*	6.5%
Vahivoraka	*Mendoncia flagellaris*	Flowers			6-8	2.1%	*15.5%*	1.7%
Ambora	*Tambourissa purpurea*	Fruits	9-10	0.4%	9-10	1.7%	*23.9%*	1.7%
Vahy Mivoraka	n/a	Fruits			9-10	1.7%		
Total				99.6%		98.3%		

Plants with fat and/or sugar content above 10% of dry matter are highlighted in italics.

Table 2. List of plant species consumed by sympatric dwarf lemur species during post-hibernation at Tsinjoarivo.

Common name	Scientific name	Plant part	*C. crossleyi*		*C. sibreei*		Nutrition (%DM)	
			Rank	%	Rank	%	Sugar	Fat
Nonoka	*Ficus reflexa*	Fruits	1	13.7%			7.9%	2.0%
Tavolo	*Cryptocaria* sp.	Fruits	2	12.6%				
Kalafambakaka	*Oncostemum acuminatum*	Fruits	3	11.3%	6-7	5%	*17.5%*	3.5%
Vahivoraka	*Mendoncia flagellaris*	Fruits	4	10.7%	6-7	5%	6.5%	1.9%
Sakaihazo	*Allophylus pinnatus*	Fruits	5	10.2%				
Rafy	*Maesa lanceolata*	Fruits	6	8.6%			*10.1%*	*17.3%*
Manalo I	*Bakerella* sp.	Fruits	7	7.5%	1	47.5%	*10.1%*	3.6%
Ambora	*Tambourissa purpurea*	Fruits	8	5.9%	4	10%	*23.9%*	1.7%
Kininina	*Eucalyptus* sp.	Flowers	9	5.4%			*16.4%*	7.4%
Seva	*Solanum mauritianum*	Fruits	10	4.3%			*20.6%*	9.5%
Kimba ditinina	*Symphonia microphylla*	Fruits	11	2.9%	2-3	12.5%		
Sohitrasisika	*Gaertnera* aff *bieleri*??	Fruits	12	2.7%				
Tongoalahy	*Bakerella clavata*	Flowers	13	2.4%	2-3	12.5%		
Tongoalahy	*Bakerella clavata*	Fruits	14	1.3%			9.4%	*20.6%*
Hazomainty	*Diospyros* sp.	Fruits			5	7.5%		
Total				99.5%		100%		

Plants with fat and/or sugar content above 10% are highlighted in italics.

During the pre-hibernation season, both dwarf lemur species were observed consuming the fruits of *Schefflera monophyla* (Manalo II), *Embelia concinna* (Takaloparihy) and *Gynoctodes umbrellata* (Vahivovo) (table 1). During the post-hibernation season, both dwarf lemur species were observed consuming the fruits of *Oncostemum acuminatum* (Kalafambakaka), *Bakerella* sp. (Manalo I) and *Symphonia microphylla* (Kimba ditinina) (table 2).

Table 3. Plant species with longest feeding events (FED) during pre-hibernation. Fr = fruits.

Common name	Scientific name	FED (min)	Species	ID	Date
Takaloparihy (Fr)	*Embelia concinna*	86	*C. crossleyi*	"Ly"	23 March 2012
		58	*C. crossleyi*	"Nes"	18 March 2013
		56	*C. crossleyi*	"Ne"	15 March 2013
		40	*C. crossleyi*	"Ne"	9 March 2013
		28	*C. crossleyi*	"Ne"	15 March 2013
		24	*C. crossleyi*	"Nes"	18 March 2013
		20	*C. crossleyi*	"Ne"	9 March 2013
		20	*C. crossleyi*	"Nes"	13 March 2013
		20	*C. crossleyi*	"Nes"	18 March 2013
Vahivovo (Fr)	*Gynoctodes umbrellata*	66	*C. crossleyi*	"Na"	20 March 2013
		60	*C. crossleyi*	"BLu"	21 March 2013
Nonoka (Fr)	*Ficus reflexa*	36	*C. sibreei*	"Ra"	13 February 2013
Tongoalahy (Fr)	*Bakerella clavata*	32	*C. sibreei*	"Am"	25 February 2013
		26	*C. sibreei*	"Pa"	23 February 2013
		24	*C. crossleyi*	"Mar"	8 March 2013
		24	*C. sibreei*	"Sy"	11 February 2013
Fantsikahitra (Fr)	*Canthium* sp.	20	*C. crossleyi*	"Ag"	22 March 2012

Two of the plant species consumed by both dwarf lemur species in both seasons rank high in nutritional value: *Bakerella clavata* had the greatest value for fat content and *Tambourissa purpurea* the greatest value for sugar content (tables 1 and 2). Of the remaining four fruits with fat content values above 10% dry matter, two were almost exclusively used by furry-eared dwarf lemurs (*Embelia concinna* and *Maesa lanceolata*) and two by Sibree's dwarf lemurs (*Petchia erythrocarpa* and *Erythroxylum* sp.). Three plant species showed sugar content values above 20% dry matter. Of these, *Gynoctodes umbrellata* and *Tambourissa purpurea* were consumed by both species, and *Solanum mauritianum* was only consumed by furry-eared dwarf lemurs.

We counted a total of 270 feeding events (177 by furry-eared dwarf lemurs; 93 by Sibree's dwarf lemurs), although 66.7 % corresponded to short periods comprising 1-4 consecutive scans (2 to 8 estimated minutes per event). When considering the longest feeding events, the chosen plant foods differed between seasons (tables 3 and 4).

Furry-eared dwarf lemurs foraged at greater heights in the canopy than did Sibree's dwarf lemurs (mean = 9.3 m, SD = 3.4 and mean = 8.4 m, SD = 3.1 respectively; Wilcoxon's $z = -2.1$, $p = 0.0359$).

NIGHTLY DISTANCES AND HOME RANGES

Sibree's dwarf lemurs traveled significantly longer paths than did furry-eared dwarf lemurs, during both the pre- and post-hibernation seasons. Within either species, we found no significant differences between the sexes. During pre-hibernation, Sibree's dwarf lemurs moved on average 511 m (SD = 131) compared to just 330 m (SD = 136) by *C. crossleyi* (Wilcoxon's $z = 2.1$, $p = 0.039$) during the first half of the night (5 h). During post-hibernation, Sibree's dwarf lemurs traveled on average 635 m (SD = 203) compared to just 410 m (SD = 87) by furry-eared dwarf lemurs (Wilcoxon's $z = 2.2$, $p = 0.026$) (fig. 3).

Sibree's dwarf lemurs primarily occupied the western area of the study area while furry-eared dwarf lemurs occupied the eastern and southern areas of the forest fragment, with some overlap between species in the middle (fig. 4). Sibree's dwarf lemurs also had much larger home ranges than did furry-eared dwarf lemurs (mean = 3.7 ha, SD = 2.5 vs. mean = 1.9 ha, SD = 1.9 respectively) though these differences were not statistically significant (Wilcoxon's $z = 1.9$, $p = 0.06$). However, once we removed

Table 4. Plant species with longest feeding events (FED) during post-hibernation.

Common name	Scientific name	FED (min)	Species	ID	Date
Ambora (Fr)	*Tambourissa purpurea*	34	*C. crossleyi*	"Br"	26 November 2011
Tavolo (Fr)	*Cryptocaria* sp.	32	*C. crossleyi*	"Je"	19 September 2014
Rafy (Fr)	*Maesa lanceolata*	30	*C. crossleyi*	"Lu"	23 September 2013
Vahivoraka (Fr)	*Mendoncia flagellaris*	30	*C. crossleyi*	"Ly"	16 November 2011
Kininina (Fl)	*Eucalyptus* sp.	28	*C. crossleyi*	"Nes"	21 September 2013
Manalo I (Fr)	*Bakerella* sp.	26	*C. sibreei*	"Ran"	18 September 2013
		24	*C. crossleyi*	"BLu"	20 September 2013
Sakaihazo (Fr)	*Allophylus pinnatus*	24	*C. crossleyi*	"Fi"	28 October 2011
		24	*C. crossleyi*	"Fi"	23 November 2011

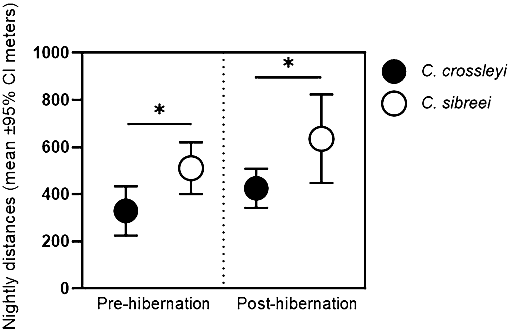

Figure 3. Nightly travel distances by furry-eared (*C. crossleyi*) and Sibree's (*C. sibreei*) dwarf lemurs relative to season.

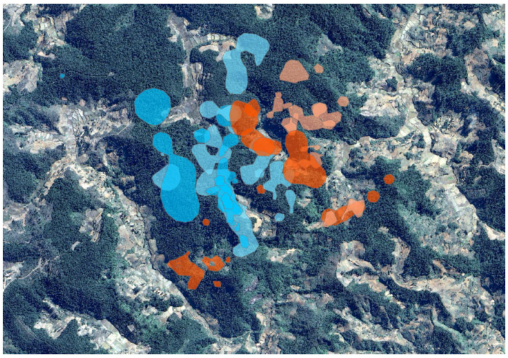

Figure 4. Home ranges for Sibree's dwarf lemurs (light blue) and furry-eared dwarf lemurs (orange). Darker colors refer to males in both species.

data from two outlier males (one per species with values of 7 ha and 9 ha), the difference between species became significant (mean = 3.1 ha, SD = 1.7 vs. mean = 1.5 ha, SD = 1.1; Wilcoxon's $z = 2.1$, $p = 0.04$). Within species and excluding the outliers, female Sibree's dwarf lemurs had home ranges that were significantly larger than their male counterparts (females = 5, males = 4, Wilcoxon's $z = -1.97$, $p = 0.0491$). We found no such differences between the sexes in furry-eared dwarf lemurs (females = 7, males = 4, Wilcoxon's $z = 0.66$, $p = 0.51$). Given these small samples sizes, these results should be taken with caution.

The large home ranges of the two outlier males merit further explanation. We reason that the large home range of the male Sibree's dwarf lemur was due to his dispersal from his natal group. This male was monitored over two consecutive years (2011 and 2012). In year one, he was a subadult and was seen sharing a resting site with another subadult male, presumably a littermate. He then hibernated in an underground location far from this area, perhaps close to his natal site, but returned to the foraging area after emergence. In year two, he was an adult and was seen foraging with an infant, suggesting he had found a mate and together they established a territory. The male furry-eared dwarf lemur was studied only during the post-hibernation season, which coincides with the reproduction season. His use of numerous sleeping sites over a large area perhaps points to his roaming in search of a new potential mate and/or estrous females.

Discussion

By comparing the behavioral ecology of two species of dwarf lemur at the Tsinjoarivo forest, we find some evidence of subtle niche partitioning that may enable sympatric congeners to co-exist. Specifically, we find that furry-eared dwarf lemurs, compared to Sibree's dwarf lemurs, had smaller home ranges and traveled less each night, foraged higher in the canopy for a more diverse diet, and spent more time foraging and less time in their resting sites. The species were also somewhat spatially differentiated, with furry-eared dwarf lemurs found more often in southern and eastern areas, closer to forest edges and in generally more degraded habitats. Taken together, these results highlight ecological differentiation between species across both trophic and spatial scales, in addition to their temporal differentiation based on the timing of hibernation (Blanco and Godfrey, 2014; Blanco *et al.*, 2018, in press).

At a trophic level, the dwarf lemurs shared some dietary overlap, with both species foraging for the fruits of *Bakerella clavata*, *Tambourissa purpurea*, and *Mendoncia flagellaris* prior to and after hibernation. Prior to hibernation, the two species shared reliance on three of their respective top four most consumed plant items, namely the fruits of *B. clavata*, *Gynoctodes umbrellata* and *Ficus reflexa*. For furry-eared dwarf lemurs, *Embelia concinna* fruits were among the top four most consumed items, while *Petchia erythrocarpa* fruits were among the top four items for Sibree's dwarf lemurs. Given the preliminary nature of our data, we do not consider this list of dietary items comprehensive, particularly in the post-hibernation season. For instance, we did not directly observe insect feeding, but insect matter has been reported from dwarf lemur feces at this site (Domoinaharivelo, 2014). We likely also overestimated the foraging of *B. clavata*, by combining two species of mistletoe: *B. clavata* (large leaves) and *B. viguieri* (small leaves). Moreover, Domoinaharivelo (2014) reported that *F. reflexa* played an important role for Sibree's dwarf lemurs after hibernation, which our data did not capture, likely due to our small sample sizes.

Nevertheless, the most-consumed fruits in our database seem to be good sources of sugar and/or fat, which are particularly important nutrients at the time of year when dwarf lemurs fatten to prepare for hibernation (Blanco *et al.*, 2018). Whether these dwarf lemurs in the east, like their *C. medius* counterparts in the west, fatten primarily by endogenously converting dietary sugars (Fietz and Ganzhorn, 1999) or, like mouse lemurs (*Microcebus rufus*) in the east, fatten directly from dietary fats (Atsalis, 1999), remains to be tested. Such dietary differences could underlie compositional differences in fat depots (Blanco *et al.*, 2022), with implications for hibernation. Notably *C. medius*, fattening on fruit sugars and hibernating in the relatively warm temperatures of western Madagascar, mainly rely on monounsaturated fats to fuel hibernation (Fietz *et al.*, 2003). In so doing, they can avoid the greater oxidative stress required to burn polyunsaturated fatty acids that are crucial to cell membrane fluidity when hibernating at temperatures near freezing (Fietz *et al.*, 2003). In the central highlands, ambient temperatures are far colder during the hibernation season. Although underground hibernacula can buffer cold temperatures to some degree, it is possible that furry-eared and Sibree's dwarf lemurs must rely on polyunsaturated fatty acids to support cellular health while hibernating in this frigid environment. If so, those polyunsaturated fats would need to be deposited directly from dietary fats and not synthesized from dietary carbohydrates.

Despite the similarities in the top plant items consumed by both dwarf lemur species, we note that furry-eared, but not Sibree's, dwarf lemurs opportunistically fed on certain plants that raise questions about their tolerance to plant secondary compounds. These items included the fruits of *Phytolacca dodecandra* and *Solanum mauritianum*, and the flowers of *Eucalyptus* sp. Whereas *P. dodecandra* is toxic to some animals due to phytochemicals like triterpenoids and saponins (Desta *et al.*, 2021), *S. mauritianum* is an invasive species from South America that contains solasodine, an alkaloid that can be fatal to humans, cattle and other mammals (Olckers, 2009). Another generalist lemur, *Eulemur fulvus*, can also tolerate these fruits (Eppley *et al.*, 2022), and perhaps selects them for the relatively high sugar content (this study). *Eucalyptus* (originally from Australia) was introduced to Madagascar and is commonly found in degraded or secondary forests. All plant parts contain secondary compounds like eucalyptol that can be toxic to mammals; whether concentrations in flowers are high enough to be poisonous for lemurs is unknown. The flowers, also high in sugar (this study), are reported to be opportunistic food source for *Lemur catta* (Simmen *et al.*, 2006) and *E. rubriventer* (Overdorff, 1988). While these three plant species may play a minor role in the diets of furry-eared dwarf lemurs, it is intriguing that this species consumes them at all without obvious ill effects. Perhaps these plants are tolerated when consumed in small amounts or perhaps these dwarf lemurs (or their gut microbes) can metabolize the plant secondary compounds and thereby neutralize toxicity (Dearing and Cork, 1999; Dearing and Weinstein, 2022; Windley *et al.*, 2022). This dietary flexibility may give furry-eared dwarf lemurs a competitive edge during lean seasons or in degraded forests.

Species' differences in foraging ecology and hibernation expression may help explain some of our other findings, including that Sibree's dwarf lemurs spend more time in their resting sites but travel farther across larger home ranges, especially the females, presumably to target specific high-quality foods. Sibree's dwarf lemurs enter hibernation significantly earlier and hibernate longer than do furry-eared dwarf lemurs (Blanco and Godfrey, 2014; Blanco *et al.*, in press), meaning that they have a shorter window to amass fat reserves. To fatten fast, perhaps Sibree's dwarf lemurs prioritize particular foods, even if they must travel farther to find them, and offset energy expenditure by spending more time in their resting sites. Alternately, this species might be particularly efficient at transferring energy from food to fat. Because Sibree's dwarf lemurs are smaller than are furry-eared dwarf lemurs (approx. 250 vs. approx. 350 g), they require less food and smaller fat reserves overall. Their smaller size, and the energy required to sustain it, might be critical to supporting a longer hibernation season in cold and high-altitude habitats. Tsinjoarivo forest is perhaps the coldest place inhabited by furry-eared dwarf lemurs, but this habitat, and those at even greater elevations, are the only forests where Sibree's dwarf lemurs are found today.

Although we suggest that subtle ecological differences between sympatric dwarf lemurs at Tsinjoarivo enable their co-existence at any particular timepoint, one clear question is whether this sympatry is stable and sustainable through time. Our data from 2011-2014, show that the dwarf lemur species were generally found in different areas of the forest; however, we posit that the spatial overlap in the center of the study area is likely a relatively recent and concerning phenomenon. In our original prospection and sampling at this site in 2006 and 2007, we exclusively captured Sibree's dwarf lemurs in the forest fragment of Andasivodihazo and exclusively captured furry-eared dwarf lemurs in the lower elevation and continuous forest of Vatateza (approx. 12 km to the east, 1200 m) (Blanco *et al.*, 2009). By late 2008 and 2009, we began to capture furry-eared dwarf lemurs at Andasivodihazo for the first time, when we expanded our trapping area to include more open environments (Groeneveld *et al.*, 2010). In 2014, we failed to capture any Sibree's dwarf lemurs at Andasivohidazo, likely due to forest degradation and land clearing on the forest edge, but we captured abundant furry-eared dwarf lemurs in areas formerly used by Sibree's dwarf lemurs. Most recently, in 2019, we only captured two Sibree's dwarf lemurs after considerable effort targeting all the original sampling areas (MBB, unpublished data). These anecdotal observations strongly suggest that the furry-eared dwarf lemur is replacing Sibree's dwarf lemur at this site, in step with ongoing habitat fragmentation and degradation.

One explanation is that these dynamics between the species follow the "Jack of all trades is the master of none" hypothesis, which posits that generalists "bear some cost in each environment they can use such that a specialist in a given environment will always outcompete a generalist sharing that environment" (Remold, 2012). In other words, in pristine high-altitude forests, the specialist Sibree's dwarf lemur outcompetes the generalist furry-eared dwarf lemur. However, the "environmental filtering" associated with the adaptation by Sibree's dwarf lemur to a singular, harsh and cold environment perhaps comes at the cost of their competitive edge under different or changing conditions (Hoiss *et al.*, 2012). At Tsinjoarivo, continuing forest fragmentation is linked to the greater presence of furry-eared dwarf lemurs, perhaps driven by them either directly outcompeting Sibree's dwarf lemurs or by their occupation of habitats no longer suitable for their specialized congeners. Future research at additional sites that have a similar contact zone between these species, notably Marojejy and Ranomafana National Parks (Herrera *et al.*, 2016; Blanco *et al.*, 2025), can help confirm if sympatry between these dwarf lemurs is stable under reduced anthropogenic pressure.

Given the ongoing transformation in Madagascar's forest environments, known sympatric assemblages will be expected to change island wide, as evidenced by changes to the relative abundance and the presence/absence of species per site. Catalyzed by anthropogenic change linked to habitat loss, with downstream and significant consequences to ecosystem function, habitat homogenization, e.g., land clearing and deforestation, reduces landscape complexity and favors disturbance-tolerant species (Gámez-Virués *et al.*, 2015; Nordberg and Schwarzkopf, 2019). Understanding the ecological flexibility and resilience of each lemur species is not only essential to predicting which may survive under specific environmental scenarios, but also has implications for the temporal dynamics of complex species assemblages, including density-specific interspecies interactions (Schäffler *et al.*, 2021). Notably, dwarf lemurs at Tsinjoarivo may also face competition from generalist Goodman's mouse lemurs, but relaxed pressure from the loss of generalist common brown lemurs that have been locally extirpated, dynamics that we did not consider here. Ultimately, we advocate for greater biogeographical and ecological research at sites that harbor multiple species of dwarf lemurs in sympatry and long-term monitoring to determine the historical context by which these assemblages were established and how likely their persistence is into the future.

Supplementary materials

Data is available on https://doi.org/10.1163/14219980-bja10076 under Supplementary Materials.

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Author contributions

MBB designed the study, collected and analyzed data, wrote the manuscript; LKG analyzed data and wrote the manuscript; HNTR, NHR and BT collected data; ADY discussed and funded the study; KHD edited the manuscript and funded the study. All authors gave final approval for publication.

Conflict of interest

The authors declare no conflict of interest.

Ethics statement

This research was approved by Duke University's Institutional Animal Care and Use Committee in the USA (A040-12-02), the University of Hamburg, Germany, and the Ministère de l'Environnement et des Forêts (now Ministry of Environment and Sustainable Development) in Madagascar (permit Nos 015/11/MEF/SG/DGF/DCB.SAP/SCB; 202/11/MEF/SG/DGF/DCB.SAP/SCB; 306/12/MEF/SG/DGF/DCB.SAP/SCB;

028/13/MEF/SG/DGF/DCB.SAP/SCB; 081/13/MEF/SG/DGF/DCB.SAP/SCB; and 229/14/MEEF/ SG/DGF/DCB.SAP/SCB).

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