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Stable Isotopes Complement Focal Individual Observations and Confirm Dietary Variability in Reddish–Gray Mouse Lemurs (*Microcebus griseorufus*) from Southwestern Madagascar

Brooke E. Crowley,[1,2]* Emilienne Rasoazanabary,[3] and Laurie R. Godfrey[4]

[1]*Department of Geology, University of Cincinnati, Cincinnati, OH 45221*
[2]*Department of Anthropology, University of Cincinnati, Cincinnati, OH 45221*
[3]*Department of Anthropology, Stony Brook University, Stony Brook, NY 11794*
[4]*Department of Anthropology, University of Massachusetts, Amherst, MA 01003*

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ABSTRACT We examine the ecology of reddish-gray mouse lemurs from three habitats at Beza Mahafaly Special Reserve using focal follows and stable carbon and nitrogen isotope data. Focal observations indicate dietary differences among habitats as well as sexes and seasons. Both sexes consume more arthropods during the rainy season but overall, females consume more sugar-rich exudates and fruit than males, and individuals from riparian forest consume fewer arthropods and more fruit than those in xeric or dry forest. We ask whether these observations are isotopically detectable. Isotope data support differences between seasons and sexes. Nitrogen isotope values are higher during the rainy season when lemurs consume more arthropods, and higher in males than females, particularly during the dry season. However, differences among populations inferred from focal observations are not fully supported. Lemurs from riparian forest have lower isotope values than those in xeric scrub, but isotope data suggest that lemurs from the dry forest eat the least animal matter and that focal observations overestimated dry forest arthropod consumption. Overall, our results suggest that observational and isotopic data are complementary. Isotope data can be obtained from a larger number of individuals and can quantify ingestion of animal matter, but they apparently cannot quantify the relative consumption of different sugar-rich foods. Combined focal and isotope data provide valuable insight into the dietary constraints of reddish-grey mouse lemurs, with implications for their vulnerability to future habitat change. Am J Phys Anthropol 155:77–90, 2014.

Mouse lemurs (*Microcebus* spp.) are a diverse genus of small-bodied lemurs. They live in the majority of native habitats, as well as disturbed forests and plantations, across Madagascar (Mittermeier et al., 2010). Here we explore the foraging ecology, as revealed through both focal individual sampling and stable isotope analysis, of *Microcebus griseorufus*, the reddish-gray mouse lemur, at Beza Mahafaly Special Reserve (BMSR). *Microcebus griseorufus* exists at the dry extreme of ecological niches occupied by mouse lemurs in Madagascar (Rasoloarison et al., 2000; Yoder et al., 2002; Kobbe and Dausmann, 2009). This species is found throughout southern and southwestern Madagascar in some of the island's most hostile and seasonal environments (Mittermeier et al., 2010). However, there are signs that it is negatively impacted by anthropogenic activities as well as prolonged drought (Heckman et al., 2006; Génin, 2008; Rasoazanabary, 2011; Godfrey and Rasoazanabary, 2012). With continued climate change and habitat alteration, *M. griseorufus* may face conditions beyond its coping capacity. Therefore, it is of critical importance to understand this species' ecological flexibility and constraints.

Populations of *M. griseorufus* may rely on very different foods, even when living in close proximity. Plant exudates (i.e., gum), arthropods, and fruits comprise the dietary staples of *M. griseorufus* (Génin, 2008; Rasoazanabary, 2011). However, diets vary seasonally and there may be dietary differences between the sexes (Génin, 2008; Rakotondranary et al., 2011; Rasoazanabary, 2011). Given the plasticity in their omnivorous feeding patterns, reddish-gray mouse lemurs are ideal subjects for a study of the relationship between habitat and feeding ecology. Continued human-induced environmental change may eliminate exactly those resources that are

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*Correspondence to: Brooke E. Crowley, Department of Geology, 500 Geology and Physics Building, University of Cincinnati, Cincinnati, OH 45221, USA. E-mail: brooke.crowley@uc.edu

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most critical to this species' survival and reproduction. Establishing how much the diets of reddish-gray mouse lemurs vary among habitats, sexes, and seasons may provide important insights into their potential resilience (Kobbe and Dausmann, 2009; Rasoazanabary, 2011; Varner and Dearing, 2013).

Observational data from focal individuals provide valuable information about the feeding ecology of mouse lemurs (e.g., Génin, 2008). However, because of the challenges involved in following and observing radio-collared nocturnal small-bodied primates in the canopy, uncertainties remain as to the extent to which focal feeding observations reflect ingested and assimilated foods or represent average dietary intake for a population. Stable isotope values from fur could complement behavioral data in assessing diet (Stewart et al., 2003; Symes et al., 2013). Whereas observational data can identify individual dietary items and track daily diets, isotopes can provide a more integrated signal of bulk dietary intake over time. Stable carbon and nitrogen isotope values reflect ingested and assimilated dietary material and can be obtained from a large proportion of the population. Isotopic data have been used previously to interpret dietary differences among sympatric mouse lemur species and among populations of mouse lemurs inhabiting different localities (Dammhahn and Kappeler, 2010; Crowley et al., 2011; Crowley et al., 2013; Dammhahn and Kappeler, 2014). However, questions remain: To what extent do observational and isotopic data yield the same dietary signal? Can field researchers benefit by collecting both? In this article we explore the match or mismatch between observational and isotopic data and the degree to which these data provide insights into the future of *M. griseorufus*. We test the following hypotheses:

1. The diets of reddish-gray mouse lemurs vary among sexes, seasons, and habitats at Beza Mahafaly.
2. Observational and isotopic data are complementary. Observed differences in diet among localities, seasons, and sexes are also recorded in the isotope values of mouse lemur fur.
3. Observational and isotopic data can identify the types of resources that are critical for survival and reproduction. *Microcebus griseorufus*, which normally lives in habitats that have sparse fruit production, can adapt to living in moist habitats that offer more fruit, but it will be challenged by continued loss of sugar-rich foods in dry habitats.

Using stable isotopes to infer diet

Isotope values for an animal's fur can reveal what it eats as well as the environment it inhabits. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for an animal's fur incorporate the carbon and nitrogen from the food it ingests, but predominantly reflect dietary protein (O'Connell and Hedges, 1999; Jim, 2004). Carbon and nitrogen from consumed plants and animal prey are incorporated into an animal's tissues with some fractionation. This fractionation is predictably passed up the food chain; herbivores have higher $\delta^{13}C$ and $\delta^{15}N$ values than those in consumed plants, and faunivores have higher $\delta^{13}C$ and $\delta^{15}N$ values than herbivores (DeNiro, 1978; DeNiro and Epstein, 1981; Hyodo et al., 2010; Dammhahn et al., 2013; Symes et al., 2013).

Isotope values for consumed plants are affected by plant physiology as well as external abiotic and biotic variables. Trees, shrubs, and herbs that use the Calvin cycle (C_3 photosynthetic pathway) have lower $\delta^{13}C$ values than grasses that use the Hatch-Slack (C_4) photosynthetic pathway or succulents that use Crassulacean acid metabolism (CAM) (Kluge et al., 1995; Muzuka, 1999; Codron et al., 2007). Most plants acquire nitrogen from soil nitrate and ammonium, and their $\delta^{15}N$ values can be quite variable (Martinelli et al., 1999; Schmidt and Stewart, 2003; Crowley et al., 2011). However, some plants, including many legumes (Fabaceae), are able to obtain nitrogen directly from the atmosphere because they have symbiotic nitrogen-fixing bacteria. These plants typically have $\delta^{15}N$ values that are close to 0‰ (Schmidt and Stewart, 2003).

Plant parts may also differ isotopically. Fruits can have slightly higher $\delta^{13}C$ values than leaves, but the two are often isotopically indistinguishable (Cernusak et al., 2002; Dammhahn, 2008; Crowley et al., 2011). The $\delta^{13}C$ value of phloem (which is the precursor to exuded gum) fluctuates temporally (Pate and Arthur, 1998; Gessler et al., 2008). However, on average, gum has $\delta^{13}C$ values that are slightly higher than those in leaves and fruits (Cernusak et al., 2002; Dammhahn, 2008). These differences are particularly pronounced at night and during the dry season (Gessler et al., 2008). Measured $\delta^{15}N$ values for exudates are also variable, but in general exudates tend to be enriched in ^{15}N compared to leaves (Cernusak et al., 2002; Dammhahn, 2008). Arthropods have higher $\delta^{13}C$ and $\delta^{15}N$ values than plant material (Kupfer et al., 2006; Dammhahn and Kappeler, 2010; Hyodo et al., 2010).

Isotope values for plants are further affected by environmental variables such as temperature, relative humidity, soil moisture, and degree of solar insolation (Handley et al., 1999; Heaton, 1999; Kohn, 2010). Plants growing in cool, moist habitats with thicker canopies tend to have lower $\delta^{13}C$ and $\delta^{15}N$ values than those growing in hot, dry habitats with open canopies (van der Merwe and Medina, 1991; Martinelli et al., 1999; Amundson et al., 2003; Schmidt and Stewart, 2003; Crowley et al., 2011). Consequently, a mouse lemur living in a moist forested environment is also expected to have lower $\delta^{13}C$ and $\delta^{15}N$ values than an individual living in an open, arid environment. Anthropogenic disturbance (i.e., logging and cattle grazing) can modify sun exposure, relative humidity, and soil characteristics. These impacts may result in increased $\delta^{13}C$ and $\delta^{15}N$ values for plant tissues and animal consumers (e.g., France, 1996; Evans and Belnap, 1999; Nakagawa et al., 2007).

Because isotope values for mouse lemurs are affected by both diet and environmental conditions, it is crucial to account for isotopic differences among localities before assessing dietary differences among allopatric populations (e.g., Post, 2002; Crowley et al., 2013). Isotope values for plants provide an isotopic environmental baseline for the habitat in which they live. Here, we use the differences in carbon and nitrogen isotope values between lemurs and leaves from non-leguminous C_3 plants (called apparent fractionation) to control for baseline environmental isotopic variation among localities. We use non-leguminous C_3 plants because they account for the majority of lemur diet and are the dominant type of plant at all of the localities we studied. Apparent fractionation values are denoted as $\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$. We calculated these values by taking the difference between the carbon or nitrogen isotope value

TABLE 1. Summary of expected apparent fractionation (Δ) values between lemur fur and leaves from non-leguminous C_3 plants for animals with different diets

Diet	Expected $\Delta^{13}C_{Lemur\text{-}plant}$	Expected $\Delta^{15}N_{Lemur\text{-}plant}$	Notes
Plant-based diet	2.4‰	2.1‰	$\Delta^{13}C$ will be slightly larger if animals consume substantial amounts of CAM plants. $\Delta^{15}N$ will be slightly smaller if animals rely extensively on legumes. $\Delta^{13}C$ and $\Delta^{15}N$ may be slightly larger if animals consume substantial amounts of exudates or fruit.
Mix of plants and arthropods	5.4‰	3.3‰	Both $\Delta^{13}C$ and $\Delta^{15}N$ can distinguish omnivores from animals that consume mostly plants.
Predominantly arthropods	5.4‰	6.4‰	$\Delta^{15}N$ is a strong indicator of trophic level, being well-correlated with degree of faunivory. $\Delta^{13}C$ cannot distinguish relative amounts of arthropods in the diet of omnivores.

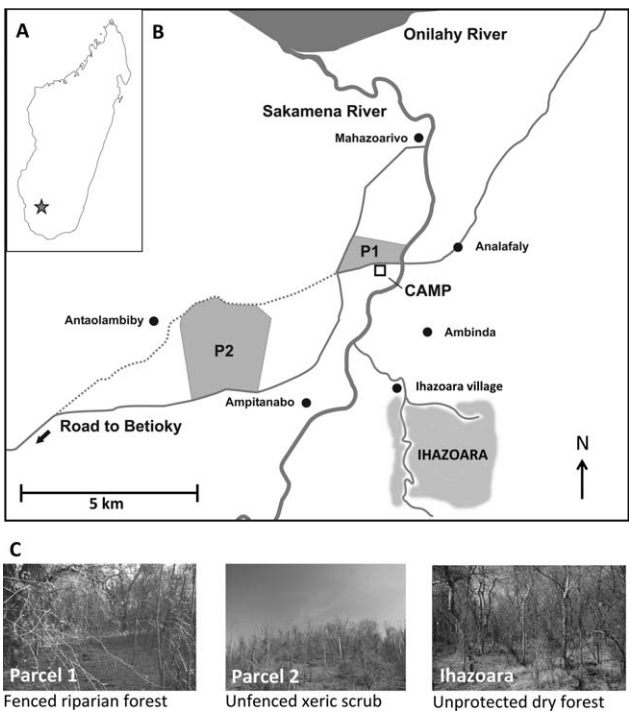

Fig. 1. Map of Madagascar with BMSR demarcated by a star (**A**), blowup map of the three study areas (**B**), and photos of the three study areas during the dry season (**C**). Photo credits B.E.C. and E.R. Map adapted from original drawn by Darren Godfrey.

for each lemur and the mean isotope values for leaves from non-leguminous C_3 plants from each location.

After accounting for isotope values for plants, it is possible to assess diet-driven isotopic differences among mouse lemur populations (Codron et al., 2007; Nakagawa et al., 2007; Dammhahn and Kappeler, 2010). Based on recent work conducted on a small mammal community in Malaysia (Hyodo et al., 2010), we would expect $\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$ values for a mouse lemur that consumes mostly plant material to be about 2.4 and 2.1‰, respectively (Table 1). For a mouse lemur that consumes a mixture of plant and arthropod material, carbon and nitrogen apparent fractionation values should be about 5.4 and 3.3‰, respectively. If arthropods provide the majority of dietary protein, then $\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$ values should be about 5.4 and 6.4‰, respectively (Hyodo et al., 2010).

METHODS

BMSR is located in the Spiny Thicket Ecoregion of southwestern Madagascar (Fig. 1). The climate is highly seasonal, and characterized by a prolonged dry season and a brief rainy season (Sussman and Ratsirarson, 2006). The reserve is divided into Parcel 1 (P1), an 80 hectare remnant of deciduous riparian forest protected by a barbed wire fence, and Parcel 2 (P2), 520 hectares of unfenced xeric scrub dominated by succulents and dry, spiny shrubs (Sussman and Ratsirarson, 2006; Axel and Maurer, 2011). *Microcebus griseorufus* is found in both parcels. The species also lives in a nearby, unprotected dry deciduous forest bordering a village called Ihazoara (Fig. 1). Floral composition, species diversity, and degree of human disturbance differ among these three localities. P1 is characterized by large trees with a relatively continuous canopy at 15–20 m. P2 and Ihazoara are both characterized by shorter scrub with a discontinuous canopy (Sussman and Ratsirarson, 2006). Parcel 1 is regularly used as a cattle enclosure by local villagers. Clear cutting for corn cultivation and harvesting of trees is prevalent at P2. In the vicinity of the village at Ihazoara, all large trees have been removed and the presence of people and cows is ubiquitous throughout (ER personal observation). In effect, all three of these forests can be characterized as "disturbed," but because of its proximity to a village, Ihazoara is considered to be the most disturbed of the three. Unlike mouse lemurs in the riparian and xeric forests, no individuals at Ihazoara were observed to enter seasonal torpor during the harsh dry season, and there were indicators of high mouse lemur mortality (Rasoazanabary, 2011; Godfrey and Rasoazanabary, 2012).

Focal observational data (instantaneous point samples) for the lemurs at BMSR were collected by one of us (ER) on 57 focal individuals (29 males and 28 females). These individuals were radio-collared and tracked for varying lengths of time between November 22, 2006 and August 26, 2007. On the basis of monthly rainfall, we designated the rainy season as November through April, and the dry season as May through October. Focal individuals were sampled virtually equally from each of the three habitats (20 from P1, 18 from Ihazoara, and 19 from P2), and during both wet (24 individuals) and dry (33 individuals) seasons. Focal-individual-follows were

conducted simultaneously by teams of three people working in each forest. Because the radio collars (TW4-button cell tags, Biotrack, Wareham, UK) only last up to 3 months, the capture and fitting of individuals for focal individual sampling was conducted twice, once in November, 2006, and a second time in May, 2007. Radio-collared individuals were followed using a portable TR-4 receiver (Telonics, Impala, AZ). Focal observations were recorded every 2 min for a total of 788 h during the rainy season and 1,129 h during the dry season. In total, we collected 2,749 focal individual dietary observations (1,046 at P1, 483 at Ihazoara, and 1,220 at P2). Feeding observations were designated as follows: arthropods (including homopteran secretions), fruit, plant exudates (or gums), leaves, or flowers. Homopteran secretions were included in the arthropod category because when observing mouse lemurs in the high canopy, it was often difficult to distinguish between the two. For every feeding observation, the tree species at which feeding occurred was also recorded. Feeding observations were analyzed using Pearson chi-square analysis to test for the significance of differences in the frequency distributions for feeding on different resources by locality, sex, and season (and combinations thereof).

We built diet profiles based on observations of instances of dietary choice (i.e., feeding on fruit, insects or insect secretions, exudates, leaves or flowers). These observations are for randomly caught and radio-collared animals observed essentially at random times. We did not fit a full random effects model (accounting for individual differences) because of the sampling imbalance in our data. Some individuals have low representation; under such conditions, random effects models exhaust the existing degrees of freedom, and the error terms cannot be statistically justified. However, we checked for the potential negative influence of pseudoreplication (i.e., disproportional sampling of individuals) by recalculating the dietary profile distributions using a per-animal level of data aggregation before averaging to the subgroup distributions. Animal level data aggregation, which gives pseudoreplication its best opportunity to express itself, gave distributions that were not statistically different from the instantaneous dietary choice distributions. There was no evidence of distortion from pseudoreplication. Both levels of aggregation point to a common underlying proportional structure, which we used to create the expectations in our Pearson chi-squares, and to look for associations between site, sex, season, and diet. We also checked that no single animal or small subgroup of animals dominated the overall proportions; the best represented animal accounted for only 6% of the observations and the percentages represented by other single individuals quickly died off in a classic negative exponential curve.

In addition to analyzing focal individual data, we analyzed stable carbon and nitrogen isotope values from 322 mouse lemur fur samples collected by ER between September 2004 and October 2008. In total we analyzed: 144 samples from P1, 96 samples from P2 and 82 samples from Ihazoara; 154 samples from females and 163 from males; 219 dry season samples and 103 rainy season samples. Data for lemur fur from Parcels 1 and 2 are previously published (Crowley et al., 2011). Here we present new isotope data for lemur fur from Ihazoara (raw isotope data provided in Supporting Information Table S1). Lemurs were captured in Sherman traps overnight and released at their sites of capture at dusk the following evening. Males and females were both trapped during the rainy and dry seasons. Fur samples were collected from the lower back near the base of the tail using tweezers and stored at room temperature in plastic bags. Samples were collected in accordance with University of Massachusetts, Amherst IACUC Protocol No. 27-17-01 to E.R., and imported to the US under CITES permit No 08US158368.

We also analyzed isotope data from plants to control for isotopic variability relating to baseline environmental differences among localities (raw isotope data provided in Supporting Information Table S2). Leaf samples were collected during January 2009 from the same areas where lemurs were captured. Samples were collected from a range of frequently encountered species from each locality (listed in Table 2). All of these species are consumed by mouse lemurs at BMSR. Leaf samples were dried thoroughly and shipped to the US by the Missouri Botanical Garden.

In the lab, fur samples were cleaned using methanol and dried. Plant samples were ground using an agate mortar and pestle. Plant ($\sim$5 mg) and fur samples ($\sim$0.7 mg) were added to tin capsules, and analyzed for carbon and nitrogen isotope values on a Finnigan ThermoElectron Delta+XP continuous flow system connected to a Carlo Erba elemental analyzer at the Stable Isotope Laboratory, University of California, Santa Cruz. Analytical precision based on 49 replicates of the standard IAEA Acetanilide was $\pm 0.2‰$ for carbon and $\pm 0.1‰$ for nitrogen. The average isotopic difference between duplicate analyses for seven fur samples was $\pm 0.1‰$ for both isotopes.

We verified normality and confirmed homogeneity of variances using Bartlett tests. We used student t-tests to compare isotope values for CAM and C_3 plants, and to compare legumes and nonlegumes. We used one-way Analysis of Variance (ANOVA) coupled with Tukey's post hoc tests for honestly significant differences (Tukey's HSD) to compare isotopic differences among plants from the three localities.

Mouse lemur fur is short ($\leq$1 cm) and is thought to grow throughout the year. We anticipate that any given fur sample will represent the previous 1–2 months of dietary intake (see Caut et al., 2008). Therefore, we considered fur collected in June–November to represent dry season diet and December-May to represent rainy season diet (see Rakotondranary et al., 2011 for a similar approach).

We calculated apparent fractionation values between each lemur and the mean carbon and nitrogen isotope values for leaves from non-leguminous C_3 plants ($\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$) at each site to control for baseline isotopic variability among localities. Mean isotope values for non-leguminous C_3 plants provide a systematic estimate of baseline isotope values for each locality. They also make up the majority of resources consumed by mouse lemurs at each locality (Table 3). By calculating the apparent fractionation between lemurs and the mean isotope values for non-leguminous C_3 plants at each locality, we can account for these baseline differences. Differences in apparent fractionation values among localities should reflect dietary differences rather than environmental differences. We verified that isotopic differences among years are minimal ($<1‰$). We then used multifactor ANOVA to test for differences in apparent fractionation values among lemur sexes, localities, and seasons, as well as interactions among these variables. Controlling for other variables, we then used Tukey's HSD tests to compare groups within each

TABLE 2. Summary isotopic and elemental data for each plant species from each locality

Locality	Family	Genus	Species	Plant type	*N*	Mean $\delta^{13}C \pm 1\sigma$	Mean $\delta^{15}N \pm 1\sigma$
P1	Mimosaceae	*Alantsilodendron*	*humbertii*	Legume	5	-28.2 ± 0.3	2.8 ± 1.5
	Euphorbiaceae	*Euphorbia*	*tirucalli*	CAM	5	-14.8 ± 0.8	3.0 ± 1.8
	Combretaceae	*Terminalia*	*fatraea*	C_3	5	-27.6 ± 0.8	2.7 ± 2.0
	Meliaceae	*Cedrelopsis*	*grevei*	C_3	5	-28.5 ± 0.5	2.7 ± 0.6
	Cesapliniaceae	*Tamarindus*	*indica*	Legume	5	-28.2 ± 0.7	0.5 ± 1.1
	Malvaceae	*Grewia*	*grevei*	C_3	5	-29.7 ± 1.4	2.4 ± 1.9
	Combretaceae	*Terminalia*	*seyrigii*	C_3	5	-27.7 ± 0.5	2.4 ± 1.4
	Apocynaceae	*Pentopetia*	*androsaemifolia*	C_3	5	-28.4 ± 1.3	4.4 ± 0.6
				All P1 Species	40	-26.6 ± 4.6	2.6 ± 1.7
				All C_3	35	-28.3 ± 1.0	2.5 ± 1.7
				All CAM	5	-14.8 ± 0.8	3.0 ± 1.8
				All Non-legumes	30	-26.1 ± 5.3	2.9 ± 1.5
				All Legumes	10	-28.2 ± 0.5	1.6 ± 1.7
P2	Mimosaceae	*Alantsilodendron*	*humbertii*	Legume	5	-26.6 ± 0.4	2.2 ± 1.0
	Euphorbiaceae	*Euphorbia*	*tirucalli*	CAM	5	-14.3 ± 0.6	4.7 ± 0.2
	Didieraceae	*Alluaudia*	*procera*	CAM	5	-14.2 ± 0.1	5.2 ± 1.1
	Combretaceae	*Terminalia*	*fatraea*	C_3	5	-25.9 ± 0.5	3.3 ± 0.7
	Phyllanthaceae	*Phyllanthus*	*decaryanus*	C_3	5	-25.6 ± 0.6	3.9 ± 1.0
	Meliaceae	*Cedrelopsis*	*grevei*	C_3	5	-27.1 ± 0.3	4.9 ± 0.9
	Malvaceae	*Grewia*	*grevei*	C_3	5	-27.6 ± 0.9	5.1 ± 1.0
	Combretaceae	*Terminalia*	*seyrigii*	C_3	4	-26.3 ± 1.0	4.7 ± 0.5
	Cucurbitatceae	*Xerosicyos*	*danguyi*	CAM	5	-16.3 ± 1.4	3.7 ± 1.2
	Apocynaceae	*Pentopetia*	*androsaemifolia*	C_3	1	-28.3	2.7
				All Species	45	-22.8 ± 5.5	4.3 ± 1.5
				All C_3	30	-26.6 ± 1.0	4.0 ± 1.3
				All CAM	15	-15.3 ± 1.2	5.0 ± 1.5
				All Non-legumes	40	-22.4 ± 5.7	4.5 ± 1.3
				All Legumes	5	-26.6 ± 0.4	2.2 ± 1.0
Ihazoara	Mimosaceae	*Alantsilodendron*	*humbertii*	Legume	5	-27.4 ± 0.5	3.2 ± 1.4
	Combretaceae	*Terminalia*	*fatraea*	C_3	5	-26.3 ± 0.3	5.2 ± 1.7
	Phyllanthaceae	*Phyllanthus*	*decaryanus*	C_3	5	-26.2 ± 0.7	6.0 ± 1.3
	Meliaceae	*Cedrelopsis*	*grevei*	C_3	5	-27.4 ± 0.5	5.8 ± 1.3
	Malvaceae	*Grewia*	*grevei*	C_3	5	-27.9 ± 0.6	7.2 ± 1.1
	Cucurbitatceae	*Xerosicyos*	*danguyi*	CAM	3	-14.1 ± 0.3	4.9 ± 0.9
	Apocynaceae	*Pentopetia*	*androsaemifolia*	C_3	5	-28.2 ± 1.0	4.8 ± 1.6
				All species	33	-26.0 ± 3.9	5.3 ± 1.7
				All C_3	30	-27.2 ± 1.0	5.4 ± 1.8
				All CAM	3	-14.1 ± 0.3	4.9 ± 0.9
				All non-legumes	28	-25.8 ± 4.2	5.7 ± 1.5
				All legumes	5	$-27.4 \pm$	3.2 ± 1.4

Data for non-leguminous C_3 and CAM plants are lumped in the "non-legume" category.

category. All analyses were conducted using SPSS 21 or JMP 5.0. All tests were two-tailed with significance set at $\alpha = 0.05$.

RESULTS

Baseline environmental information from plant isotope data

Raw isotope data for plants collected at BMSR are provided in Supporting Information Table S2. CAM plants have significantly higher $\delta^{13}C$ values than C_3 plants ($T = -44.18$, df = 116, $P < 0.0001$), but there are no differences in $\delta^{15}N$ values between these two groups ($T = -1.42$, df = 116, $P = 0.16$). High $\delta^{13}C$ values for CAM succulents suggest that the species sampled use CAM photosynthesis exclusively (Kluge et al., 1995). We find no difference in $\delta^{13}C$ values between leguminous and non-leguminous C_3 plants ($T = 0.71$, df = 93, $P = 0.74$). However, legumes have significantly lower $\delta^{15}N$ values ($T = 4.88$, df = 93, $P < 0.0001$). These values indicate that legumes obtain some, but not all, of their nitrogen from symbiotic nitrogen-fixing bacteria. There are small (<2‰) isotopic differences among C_3 species at each locality (Table 2).

Non-leguminous C_3 plants differ significantly in $\delta^{13}C$ and $\delta^{15}N$ values among localities (Carbon: $F_{2,74} = 17.15$, $P < 0.0001$; Nitrogen: $F_{2,74} = 26.75$, $P < 0.0001$). Tukey's post hoc HSD tests reveal that plants from P1 have significantly lower $\delta^{13}C$ values than those from P2 and Ihazoara ($P < 0.05$). Nitrogen isotope values are unique for each site. Plants from Ihazoara have the highest $\delta^{15}N$ values, plants from P2 are intermediate, and plants from P1 have the lowest $\delta^{15}N$ values ($P < 0.05$ for all post hoc comparisons; Fig. 3).

Reconstructing mouse lemur diets from observational data

There are differences in the plant species consumed by mouse lemurs at each locality. Whereas mouse lemurs from P1 consume more *Rhopalocarpus, Acacia, Grewia*, and *Bridelia*, individuals from P2 and Ihazoara consume more *Terminalia, Alantsilodendron*, and *Operculariacarya* (Table 3). Non-leguminous C_3 plants are the most

TABLE 3. Plant species that were consumed 10 or more times at each locality (data from Rasoazanabary, 2011)

Family	Genus and species	Vernacular name	CAM or C_3?	Legume?	No. of feeding records P1	No. of feeding records P2	No. of feeding records Ihazoara
Mimosaceae	*Acacia bellula*	Tratsiotse	C_3	Yes	171		
Mimosaceae	*Alantsilodendron humbertii*	Avoha	C_3	Yes		210	93
Phyllanthaceae	*Bridelia* sp.	Tsikidrakatse	C_3	No	128	19	
Burseraceae	*Commiphora aprevalii*	Daro	C_3	No		14	
Burseraceae	*Commiphora brevicalyx*	Taraby	C_3	No		14	30
Euphorbiaceae	*Euphorbia tirucalli*	Famata	CAM	No	21		
Malvaceae	*Grewia leucophylla*	Tratramborondreo	C_3	No	135		
Mimosaceae	*Mimosa delicatula*	Kirava	C_3	Yes		47	
Anacardiaceae	*Operculicarya decaryi*	Jabihy	C_3	No		44	
Cactaceae	*Opuntia dilleri*	Raketa	CAM	No		17	
Sphaerosepalaceae	*Rhopalocarpus lucidus*	Tsiongake	C_3	No	197		
Salvadoraceae	*Salvadora angustifolia*	Sasavy	C_3	No	19		
Rhamnaceae	*Scutia myrtina*	Roiombilahy	C_3	No	34		
Cesapliniaceae	*Tamarindus indica*	Kily	C_3	Yes	10		
Combretaceae	*Terminalia fatraea*	Fatra	C_3	No	26	359	97
Combretaceae	*Terminalia seyrigii*	Taly	C_3	No	19	23	
Combretaceae	*Terminalia tricristata*	Talifalike	C_3	No	11		
	Unknown	Maragnatolaka				13	

Observations include feeding on leaves, flowers, fruit and exudates.

TABLE 4. Comparisons of dietary intake from focal individual sampling for seasons, localities, and sexes, with chi square tests of the significance of differences in frequency distribution

Comparison	X^2	df	P	Focal individual observations
Diet × season localities and sexes pooled	785.59	4	<0.001	Gum exudates are main staple during the dry season; arthropods and fruit are more important during the rainy season.
Diet × locality seasons and sexes pooled	197.46	8	<0.001	At P1, fruit consumption is relatively high (29.3% of diet versus 13.7% for Ihazoara and 11.5% for P2), and arthropod consumption is relatively low (26.6% of diet versus 42.0% at Ihazoara and 35.7% at P2); At P2, gum consumption is especially high (52.6% of diet versus ~ 40% at the two other sites) and fruit consumption is much lower than at other sites. At Ihazoara, arthropod consumption is relatively high, and fruit and gum consumption relatively low.
Diet × locality; dry season; sexes pooled	73.77	8	<0.001	Gum is the staple during the dry season at all localities, but gum consumption is relatively low at Ihazoara (64.8% vs. 79.2% at P1, 78.8% at P2). Arthropod consumption is higher at Ihazoara (28.9%) but comparable at P1 and P2 (~20% of the diet, sexes pooled).
Diet × locality rainy season; sexes pooled	199.16	8	<0.001	Fruit consumption is more important at P1 than at P2 or Ihazoara in the rainy season. Arthropod consumption is higher at Ihazoara and at P2 than at P1.
Diet × sex; seasons and localities pooled	29.59	4	<0.001	Both sexes consume more gum than arthropods and more arthropods than fruit (plus trivial amounts of leaves and flowers). However, fruit consumption is higher than expected in females (20.6% of diet versus 15.9% of diet of males); gum consumption is higher than expected in males (51.8% of diet versus 42.8% of diet of females).
Diet × sex; dry season; localities pooled	29.45	4	<0.001	Gum is the primary staple for both males and females (>75% of dietary observations). However, males consume relatively more arthropods (24.7%) than females (16.7%), and females consume relatively more gum (80.2% of diet) than males (75.3%).
Diet × sex; rainy season localities pooled	42.48	4	<0.001	Arthropods are the primary staple for both males and females (~40% of the diet). There is no difference in arthropod consumption by sex. Males consume relatively more fruit (40.0%) than do females (29.4%).

important dietary items, although mouse lemurs consume some legumes at all three localities, and a small amount of CAM plants at P1 and P2 (Table 3).

The main findings on the feeding budgets of both sexes in both seasons and across sites are summarized in Tables 4 and 5. Plant exudates (46.5% of all feeding observations) and arthropods (33.4% of all feeding observations) are the most important dietary items for the mouse lemurs at all three localities. However, the relative proportions of these items differ among localities, seasons and sexes (Tables 4 and 5, Fig. 2). Exudates are the most important food item at all three localities during the dry season (Tables 4 and 5; Fig. 2). During the rainy season, fruit is the most important component of the diet at P1, and arthropods are the most important food item at P2 and Ihazoara, where little or no fruit is available.

TABLE 5. Comparisons of observed dietary differences among sexes for each season in each locality, with chi square tests of the significance of differences in frequency distribution

Comparison	X^2	df	P	Focal individual observations
Diet × sex; dry season; P1	8.46	2	0.015	Gum is the primary resource for both sexes, but females consume more than expected (84.2% of diet) and males less than expected (75.6% of diet). Males consume more arthropods than expected (24.4% vs. 14.6% of diet for females).
Diet × sex; dry season; Ihazoara	13.45	2	0.001	Gum is the primary resource for both sexes, but females consume more than expected (70.1%) and males less than expected (56.4%). Males consume more arthropods than expected (43.6% vs. 19.5% of diet for females).
Diet × sex; dry season; P2	6.11	2	0.047	Gum is the primary resource for both sexes, but females consume more than expected (81.3%) and males less than expected (77.8%). Males consume more arthropods than expected (22.2% vs. 17.5% of diet for females).
Diet × sex; rainy season; P1	19.45	4	0.001	Fruit is the primary resource for both sexes, followed by arthropods. Males consume more fruit than expected (at 54.2% vs. 44.2% for females), while females consume more arthropods (34.3%) than males (25.8%). Both sexes consume slightly <20% gum.
Diet × sex; rainy season; Ihazoara	26.78	4	<0.001	Arthropods are the primary resource for both sexes, but males consume more than expected (64.5%) while females consume less than expected (43.7%). Females consume more gum than expected (33.7% of diet versus only 11.3% for males). Both sexes consume <20% fruit and leaves.
Diet × sex; rainy season; P2	30.77	4	<0.001	Arthropods are the primary resource for both sexes, but males consume more than expected (66.4%) while females consume less than expected (44.2%). Females consume more gum than expected (35.4% of diet versus only 10.1% for males). Both sexes consume slightly more than 20% fruit.

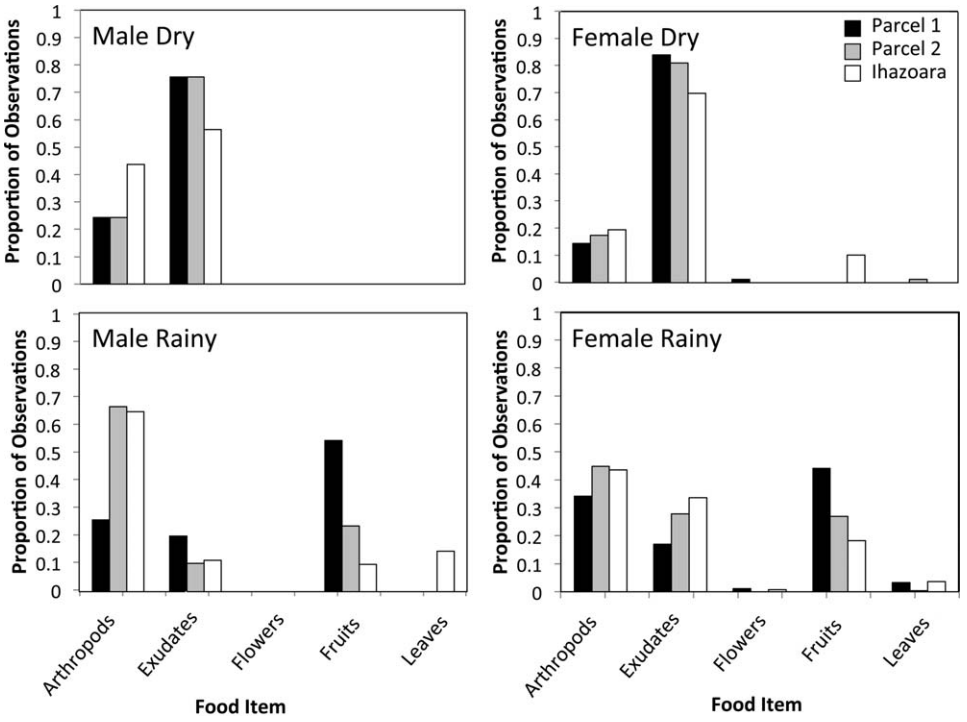

Fig. 2. Feeding observations for radio-collared individuals from each of the three forest habitats at Beza Mahafaly (Adapted from Rasoazanabary, 2011). Number of feeding observations (N) are as follows: Dry Season Males: P1 = 242, P2 = 387, Ihazoara = 55. Dry Season Females: P1 = 177, P2 = 166, Ihazoara = 87. Rainy Wet Season Males: P1 = 271, P2 = 119, Ihazoara = 62. Rainy Season Females: P1 = 361, P2 = 548, Ihazoara = 279.

At all localities, both males and females depend heavily on gum during the dry season and arthropods during the rainy season (Table 4). However, the relative proportions of each food source differ between the sexes (Table 5). During the dry season, females consume more exudates and less arthropods than males at all three localities (Tables 4 and 5; Fig. 2). During the rainy season, males continue to consume more arthropods and less exudates than females at P2 and Ihazoara, but females consume more arthropods than males at P1 (Table 5; Fig. 2).

Reconstructing mouse lemur diets from isotope data

Raw isotope data for lemurs are provided in Supporting Information Table S1. Apparent fractionation values between lemurs and non-leguminous C_3 plants are

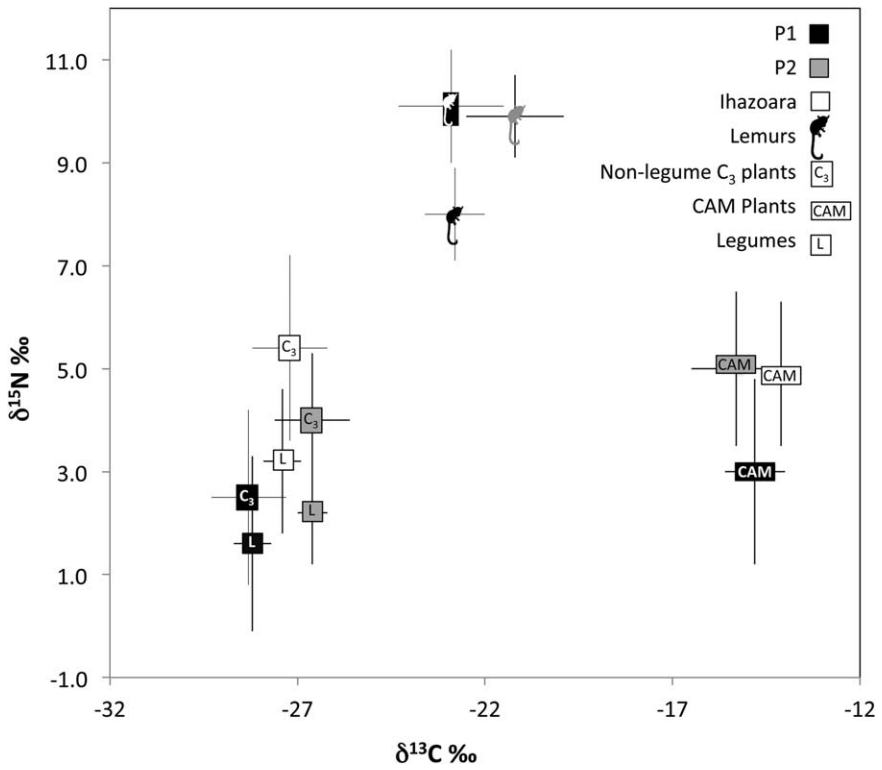

Fig. 3. Carbon and nitrogen isotope data (mean ± 1σ) for lemurs and plants from each locality.

variable, but consistent with trophic omnivory at all three localities (Tables 1 and 6; Hyodo et al., 2010). On average, lemurs have $\delta^{13}C$ values that are 4.6–5.6‰ and $\delta^{15}N$ that are 4.2–6.3‰ higher than those in plants (Table 6; Fig. 3).

Mean apparent fractionation values for carbon and nitrogen are remarkably similar for P1 and P2, and consistent with those expected for omnivores whose dietary protein comes predominantly from animal matter (Tables 1 and 6; Hyodo et al., 2010). At Ihazoara, mean apparent fractionation values are slightly smaller, which suggests less reliance on animal matter (Tables 1 and 6).

There are no significant differences in $\Delta^{13}C_{lemur\text{-}plant}$ values among localities, sexes or seasons (Table 7), a result that is rather unsurprising since mouse lemurs are omnivores and carbon is relatively ineffective at distinguishing different amounts of consumed animal matter. There is a significant interaction between season and locality ($P = 0.0002$). Controlling for other variables, post hoc tests indicate that $\Delta^{13}C_{lemur\text{-}plant}$ values are indistinguishable for P1 and P2 ($P > 0.05$), but significantly smaller for mouse lemurs from Ihazoara ($P < 0.05$; Table 6; Fig. 4). During the rainy season, apparent fractionation values for Ihazoara are similar to those for P1 and P2 ($P > 0.05$). However,

TABLE 6. Mean apparent fractionation (Δ) between lemurs and non-leguminous C_3 plants at each locality

Locality	Season	Sex	Lemur N	$\Delta^{13}C_{Lemur\text{-}plant}$	±1σ	$\Delta^{15}N_{Lemur\text{-}plant}$	±1σ
P1							
	Rainy	Male	25	5.1	0.7	5.2	0.7
	Rainy	Female	35	5.5	0.9	5.2	0.6
	Dry	Male	47	5.4	0.8	5.9	0.9
	Dry	Female	33	5.6	0.8	5.3	0.9
P2							
	Rainy	Male	23	5.1	1.1	6.3	0.9
	Rainy	Female	19	5.5	1.8	6.1	0.9
	Dry	Male	23	5.6	0.7	5.9	0.7
	Dry	Female	31	5.2	1.5	5.6	0.6
Ihazoara							
	Rainy	Male	19	4.5	1.3	4.8	0.9
	Rainy	Female	24	5.0	0.7	5.1	1.2
	Dry	Male	26	3.8	1.4	4.6	1.0
	Dry	Female	12	3.6	2.1	4.2	1.0

Error is propagated in quadrature.

TABLE 7. Results from multifactor ANOVA for $\Delta^{13}C_{lemur\text{-}plant}$ values

Variable	df	Adjusted r^2	SS	*F*	*P*
Season			3.96	3.11	0.079
Locality			79.33	72.07	**<0.0001**
Sex			4.49	3.52	0.062
Season × locality			23.03	9.03	**0.0002**
Season × sex			1.03	0.81	0.37
Sex × locality			0.96	0.38	0.69
Season × locality × sex			1.2	0.47	0.62
Whole model	**11,316**[a]	**0.20**	**112.83**	**8.04**	**<0.0001**

Significant results ($\alpha = 0.05$) are presented in bold.
[a] Model and total degrees of freedom are reported.

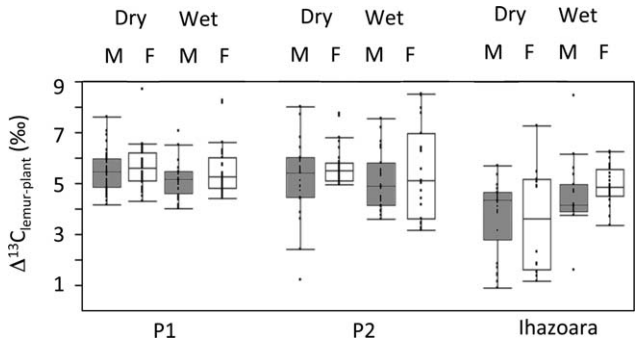

Fig. 4. Box-and-whisker plots of apparent carbon fractionation values ($\Delta^{13}C_{lemur\text{-}plant}$) for male and female lemurs from each locality during each season. For each group, boxes include median, 1st and 3rd quartiles and whiskers extend 1.5× the interquartile range from the box. During the dry season, $\Delta^{13}C_{lemur\text{-}plant}$ values are larger at P1 and P2 than at Ihazoara (Tukey's post hoc HSD $P < 0.05$). Otherwise there are no differences among localities, sexes or seasons (Tukey's post hoc HSD $P > 0.05$).

TABLE 8. Results from multifactor ANOVA for mouse lemur $\Delta^{15}N_{lemur\text{-}plant}$ values

Variable	df	Adjusted r^2	SS	*F*	*P*
Season			2.70	3.62	0.058
Locality			71.76	48.18	**<0.0001**
Sex			3.15	4.23	**0.04**
Season × locality			14.31	9.61	**<0.0001**
Season × sex			4.10	5.51	**0.02**
Sex × locality			0.70	0.47	0.63
Season × locality × sex			1.17	0.78	0.46
Whole Model	**11,316**[a]	**0.27**	**93.44**	**11.40**	**<0.0001**

Significant results ($\alpha = 0.05$) are presented in bold.
[a] Model and total degrees of freedom are reported.

during the dry season, lemurs from Ihazoara have significantly smaller $\Delta^{13}C_{lemur\text{-}plant}$ values than lemurs from any of the other localities or seasons, including the rainy season at Ihazoara ($P < 0.05$; Table 6; Fig. 4).

There are significant differences in $\Delta^{15}N_{lemur\text{-}plant}$ values among localities ($P < 0.0001$) and between sexes ($P = 0.04$; Table 8). There are also significant interactions between locality and season ($P < 0.0001$) as well as between sex and season ($P = 0.02$; Table 8). Controlling for other variables, post hoc tests indicate that during the rainy season, $\Delta^{15}N_{lemur\text{-}plant}$ values are largest at P2, intermediate at P1, and smallest at Ihazoara ($P < 0.05$ for all pairwise comparisons; Fig. 5). During the dry season, $\Delta^{15}N_{lemur\text{-}plant}$ values for P1 and P2 are indistinguishable but they are significantly smaller at Ihazoara ($P < 0.05$; Table 6; Fig. 5). Post hoc tests also indicate that overall, apparent fractionation values for males are similar among seasons ($P > 0.05$). Female mouse lemurs have smaller $\Delta^{15}N_{lemur\text{-}plant}$ values than males during the dry season ($P < 0.05$), but there are no differences between the sexes during the rainy season ($P > 0.05$; Table 6; Fig. 5).

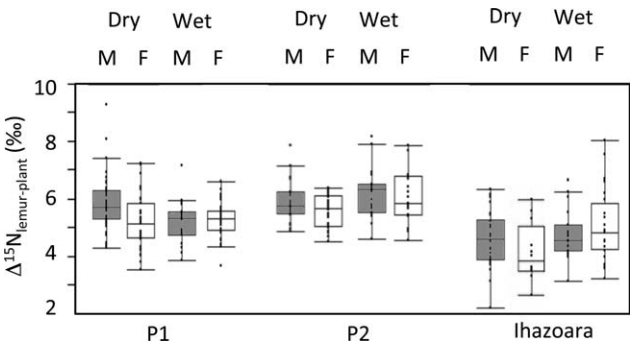

Fig. 5. Box-and-whisker plots for nitrogen apparent fractionation values ($\Delta^{15}N_{lemur\text{-}plant}$) for male and female lemurs from each locality during each season. For each group, boxes include median, 1st and 3rd quartiles and whiskers extend 1.5× the interquartile range from the box. Accounting for other variables, males have larger $\Delta^{15}N_{lemur\text{-}plant}$ values during the dry season (Tukey's post hoc HSD $P < 0.05$) but there are no isotopic differences between sexes during the rainy season. During the dry season, $\Delta^{15}N_{lemur\text{-}plant}$ values are larger at P2 and P1 than at Ihazoara (Tukey's post hoc HSD $P < 0.05$). During the rainy season, $\Delta^{15}N_{lemur\text{-}plant}$ values are largest at P2, intermediate at P1, and smallest at Ihazoara (Tukey's post hoc HSD $P < 0.05$).

We acknowledge that despite the significance of the multifactor ANOVA tests, these models are only able to explain 20 and 27% of the variation in apparent fractionation in carbon and nitrogen, respectively (Tables 7 and 8). Additional variables, such as differences in which plant species are favored by mouse lemurs at each locality, may also be responsible for isotopic differences among populations. Although there are only small isotopic differences among C_3 plants at each locality, isotope values for C_3, CAM, and leguminous species can differ substantially (Table 2).

DISCUSSION

Quantifying background isotopic variability among habitats using plant isotope data

Small differences in $\delta^{13}C$ values among nonleguminous C_3 plants from the three localities likely reflect differences in canopy density and soil moisture. Plants from P1 have the lowest $\delta^{13}C$ and $\delta^{15}N$ values, which is consistent with the relatively dense canopy at this locality. Canopy cover increases relative humidity and soil moisture and decreases sun exposure to understory leaves (Ehleringer et al., 1986; van der Merwe and Medina, 1991). C_3 plants from P2 have the highest $\delta^{13}C$ values, which is consistent with lower relative

humidity and more sun exposure at this locality (Ehleringer et al., 1986). However, $\delta^{15}N$ values for plants from P2 are not exceptionally high. Despite the arid conditions at this locality, the soils are moist, even during the dry season (BEC personal observation). Therefore, plants growing at P2 may not be particularly water stressed. Relatively low $\delta^{13}C$ values for C_3 plants from all three localities provide additional evidence that in general, plants at BMSR have adequate access to water. High $\delta^{15}N$ values for C_3 plants from Ihazoara could result from aridity or disturbance. Based on the degree of anthropogenic activity at this locality, we expect that increased $\delta^{15}N$ values reflect disturbance. This forest is regularly visited by people as well as cattle, and most large trees have been removed (ER personal observation). These activities have undoubtedly compacted the soil, which can increase denitrification rates and gaseous loss of ^{14}N (Nadelhoffer and Fry, 1994; Evans and Belnap, 1999; Aranibar et al., 2008). Isotopic differences among localities may also partially result from differences in which plant species were sampled at each site (Heaton, 1999). However, we would expect these differences to be small (Table 2).

In summary, CAM species consistently have higher $\delta^{13}C$ values than other plant groups and legumes have lower $\delta^{15}N$ values than other groups (Fig. 2). Small isotopic differences among non-leguminous C_3 plants from each locality likely reflect differences in biotic and abiotic factors. Lower isotope values at P1 are consistent with the and cooler conditions at this locality. Higher $\delta^{15}N$ values for plants from Ihazoara may result from disturbance. We can account for this background isotopic variability among localities using apparent fractionation values.

The diets of reddish-gray mouse lemurs vary among sexes, seasons, and habitats at Beza Mahafaly

According to focal follow data, mouse lemur diet at BMSR is dominated by exudates during the dry season. Females consume more exudates and less arthropod matter than males at all three localities (Tables 4 and 5; Fig. 2). During the rainy season, observed diets are more variable. Arthropods are the primary resource for mouse lemurs at P2 and Ihazoara, and fruit is the primary resource for lemurs at P1 (Tables 4 and 5; Fig. 2). Females consume fewer arthropods and more exudates than males at P2 and Ihazoara, but more arthropods than males at P1 (Table 4). These locality differences likely relate to fruiting phenology or availability of food items in each habitat.

Observed differences in diet among localities, seasons, and sexes are also recorded in the isotope values of mouse lemur fur

On the basis of focal follow data, we have clear expectations about how isotope values should differ among seasons, localities, and sexes:

1. During the rainy season, apparent fractionation values should be larger at P2 and Ihazoara, where more arthropods are consumed, and smaller at P1, where more fruit is consumed.
2. During the dry season, observations suggest that exudates account for the majority of mouse lemur diets. Arthropod consumption is comparable at P1 and P2 and higher at Ihazoara. Therefore, apparent fractionation values should be comparable at all three localities, and lower than during the rainy season.
3. Male mouse lemurs should have larger apparent fractionation values than females during the dry season because they consume more arthropods (Table 4; Fig. 4).

We find mixed support for these expectations. In agreement with the observations from focal individual sampling, $\Delta^{15}N_{lemur\text{-}plant}$ values are larger at P2 than at P1 during the rainy season and similar at the two localities during the dry season (Fig. 5). There are no differences in $\Delta^{13}C_{lemur\text{-}plant}$ values between P1 and P2 during either season (Fig. 4). We suspect that the reason we do not see any differences in $\Delta^{13}C_{lemur\text{-}plant}$ values between P1 and P2 is that fruit does not contribute much protein to the diet of mouse lemurs (Ganzhorn et al., 2009). The isotope values of fur predominantly reflect consumption of arthropods, and carbon is only effective at distinguishing omnivores from herbivores (Table 1).

Unexpectedly, mouse lemurs from Ihazoara have the smallest mean apparent fractionation values for both carbon and nitrogen, particularly during the dry season (Table 6), although there is considerable spread in $\Delta^{15}N_{lemur\text{-}plant}$ and $\Delta^{13}C_{lemur\text{-}plant}$ values, especially for females (Figs. 4 and 5). Small $\Delta^{15}N_{lemur\text{-}plant}$ and $\Delta^{13}C_{lemur\text{-}plant}$ values may reflect lower arthropod consumption for most of the individuals sampled at this locality. However, this is in contrast to focal individual observations, which suggest that arthropod consumption at Ihazoara is comparable to or higher than that observed at P2 (Tables 4 and 5; Fig. 2). It is possible that focal observations may have overestimated actual ingestion of arthropods at Ihazoara. Because it is difficult to differentiate consumption of arthropods and consumption of homopteran secretions, these two foods were lumped for focal individual sampling. Because homopteran secretions are a sugary material derived from plant sap (Dammhahn, 2008; Crowley unpublished data), nitrogen isotope values can easily distinguish between these two types of foods. Lower $\Delta^{15}N_{lemur\text{-}plant}$ and possibly lower $\Delta^{13}C_{lemur\text{-}plant}$ values at Ihazoara suggest that some observed feeding records on arthropods were instead homopteran secretions. Abundance of homopterans might be higher at Ihazoara, which is arid and has less canopy cover than the other two localities (Gorham et al., 2002). Smaller $\Delta^{15}N_{lemur\text{-}plant}$ values at Ihazoara could also result from heavy reliance on legumes. Among the plant species consumed >10 times, legumes accounted for 40% of the focal feeding observations at Ihazoara, but only 24% and 34% of the observations at P1 and P2, respectively (Table 3). Reliance on exudates from *Alantsilodendron humbertii* may be particularly important for females during the dry season (Rasoazanabary, 2011); Fig. 2). It is also possible that available observational data do not capture the full array of mouse lemur dietary items at this locality. Overall, fewer observational data exist for Ihazoara compared to the other localities (Table 3) and we do not have any behavioral observations for the last 2 months of the dry season or the first 2 months of the rainy season (Rasoazanabary, 2011).

In addition to indicating lower consumption of arthropods, smaller apparent fractionation values at Ihazoara might reflect less consumption of plant exudates by lemurs at this locality during the dry season. Because

gum tends to have higher $\delta^{13}C$ and $\delta^{15}N$ values than other plant parts, less reliance on exudates could result in slightly smaller apparent fractionation values (Table 1). Smaller $\Delta^{13}C_{lemur\text{-}plant}$ values at Ihazoara might also reflect consumption of leaves. In general, we would expect leaves to have slightly lower $\delta^{13}C$ and $\delta^{15}N$ values than other plant parts (Pate and Arthur, 1998; Cernusak et al., 2002; Dammhahn and Kappeler, 2010). Although leaf eating observations are very rare (Fig. 2), young leaves may be an important resource during the rainy season for Ihazoara males (Rasoazanabary, 2011). Finally, smaller $\Delta^{13}C_{lemur\text{-}plant}$ values might reflect exclusive consumption of C_3 plants at Ihazoara, particularly during the dry season. There have been no observations of CAM consumption at Ihazoara, but small amounts of CAM resources are consumed at P1 and P2 (Table 3; (Crowley et al., 2011; Rasoazanabary, 2011).

To summarize, isotope data are largely consistent with observational data. Apparent fractionation values for nitrogen are smaller at P1 than P2 during the rainy season, which likely reflects less reliance on arthropods and more reliance on fruit. Unexpectedly, $\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$ values are smallest at Ihazoara, particularly during the dry season. Small $\Delta^{15}N_{lemur\text{-}plant}$ values suggest observations may have overestimated arthropod consumption, and that a portion of the observed records of feeding on arthropods were instead homopteran secretions. Less reliance on exudates, combined with consumption of leaves, CAM plants or legumes could also contribute to smaller $\Delta^{13}C_{lemur\text{-}plant}$ and $\Delta^{15}N_{lemur\text{-}plant}$ values at this site.

On the basis of focal follow data, we would expect male mouse lemurs to have larger apparent fractionation values than females during the dry season because they consume more arthropods (Tables 1, 4, and 5). We find mixed support for this expectation. Overall, $\Delta^{15}N_{lemur\text{-}plant}$ values for males and females are indistinguishable during the rainy season, but during the dry season, males have larger apparent fractionation values than females (Table 6; Fig. 5). At P2 and Ihazoara, this pattern most likely reflects less arthropod consumption by females during the dry season (Fig 2; Tables 4 and 5).

However, inferences drawn from focal follow and isotopic data conflict slightly at P1. Observational data suggest that males at P1 consume more arthropods than females during the dry season and arthropods and more fruit than females during the rainy season (Fig. 2, Table 5). The observed proportion of arthropods consumed by males at this locality is comparable during both seasons (ca. 25%). In agreement with these focal observations, males have larger apparent fractionation values during the dry season (Table 6). However, males and females have comparable $\Delta^{15}N_{lemur\text{-}plant}$ values during the rainy season and $\Delta^{15}N_{lemur\text{-}plant}$ values for males are substantially higher during the dry season than the wet season (Table 6; Fig. 5). Fruit is the main dietary source for males and females during the rainy season. Because fruits can have lower $\delta^{13}C$ and $\delta^{15}N$ values than arthropods, it is possible that heavy reliance on fruit during the rainy season is partially responsible for our results, particularly for nitrogen. As discussed above, it is also possible that some records of feeding on arthropods during the rainy season were instead observations of feeding on homopteran secretions or that observational data do not capture the full dietary breadth of male mouse lemurs at Parcel 1.

Unfortunately, we do not have focal individual sampling data for a full annual cycle for males or females. No focal observation data are available for September–November at any of the localities, which comprise the last 2 months of the dry season and the first month of the rainy season. During the dry season, male mouse lemurs might consume more arthropods than focal observations suggest, or they could eat additional dietary items, such as vertebrate matter, that was not observed. Alternatively, males could consume fewer legumes than females during the dry season (Rasoazanabary, 2011).

Overall, it is most likely that isotopic differences between sexes primarily reflect differential consumption of arthropods. However, several additional factors could potentially contribute to these measured differences that are worthy of consideration. As mentioned above, heavy reliance on exudates could result in increased apparent fractionation values. During the dry season, female mouse lemurs consume more gum than males at all three localities (Tables 4 and 5), yet females have smaller $\Delta^{15}N_{lemur\text{-}plant}$ values than males and $\Delta^{13}C_{lemur\text{-}plant}$ values do not differ between the sexes (Tables (6–8); Figs. 4 and 5). Many of the exudates targeted by mouse lemurs at BMSR are produced by legumes (i.e., *Alantsilodendron humbertii* and *Acacia bellula*), which have lower $\delta^{15}N$ values than non-leguminous C_3 plants. If males consume fewer exudates derived from legumes than females during the dry season (as suggested by focal observational data; Rasoazanabary, 2011), then this could also contribute to the larger $\Delta^{15}N_{lemur\text{-}plant}$ values for males.

However, we suspect that like fruits, exudates account for only a small amount of mouse lemur dietary protein. Gum primarily consists of complex branched polysaccharides (Nash, 1986; Ushida et al., 2006; Nussinovitch, 2010), and with the exception of some legumes, it contains little protein (Garber, 1993; Nussinovitch, 2010). Mouse lemurs may derive energy from gum polysaccharides, which would help them build fat reserves for torpor. However, there would be little isotopic evidence for this in fur keratin because carbon and nitrogen isotope values for fur primarily reflect dietary protein, which is most likely derived from arthropods, and possibly leaves.

Smaller $\Delta^{15}N_{lemur\text{-}plant}$ values for females could also result from reduced activity levels (and greater use of seasonal torpor) during the dry season (Rasoazanabary, 2011). Metabolic changes associated with reduced activity levels could have an isotopic effect (Dammhahn and Kappeler, 2010; Lee et al., 2012). Such an inference is supported by two factors: 1) Capture rates are lower for females during the dry season at P1 and P2; and 2) At all three sites, males travel greater distances than females (i.e., the greatest distance between capture locations is consistently larger in males than in females), and have higher apparent mortality rates than females (often associated with greater activity levels; Rasoazanabary 2011). However, if reduced activity levels result in low $\Delta^{15}N_{lemur\text{-}plant}$ values, we might expect to see minimal isotopic differences between males and females at Ihazoara, where neither sex was observed to undergo seasonal torpor (Rasoazanabary, 2011). This is not what we observe. Apparent fractionation values for nitrogen are smaller for females at all localities, including Ihazoara (Fig. 4). Because lipids have lower $\delta^{13}C$ values than protein (Jim et al., 2004), we might also expect females to have smaller $\Delta^{13}C_{lemur\text{-}plant}$ values than males during the dry season (assuming torpor involves catabolism of fat reserves). Again, this is not what we observe.

Average $\Delta^{13}C_{lemur\text{-}plant}$ values are smaller for females at P2 and Ihazoara. However, females have larger $\Delta^{13}C_{lemur\text{-}plant}$ values than males at P1 (Fig. 4), and controlling for locality, there is no significant difference in $\Delta^{13}C_{lemur\text{-}plant}$ values between sexes or seasons (Table 7). It would, therefore, appear that seasonal torpor does not have a significant impact on fur isotope values.

To summarize, isotope data corroborate observed dietary differences between males and females. Males have higher $\Delta^{15}N_{lemur\text{-}plant}$ values than females, which predominantly reflects differential consumption of arthropods, particularly during the dry season. Apparent fractionation values for carbon appear to be poorly suited to distinguish between more and less faunivory or differentiate consumption of different sugar-rich foods (e.g., exudates or fruit).

Can behavioral information inferred from isotopic and observational data be used to predict the resilience of reddish-grey mouse lemurs to future environmental change?

Both focal follow and isotopic data indicate that *Microcebus griseorufus* has a flexible diet at Beza Mahafaly. That flexibility, however, does not guarantee that this species will successfully cope with future environmental change. *Microcebus griseorufus* is well adapted to living in some of the most seasonal and arid environments in Madagascar—habitats in which fruit is available for only a limited time of year and in which exudates become an essential, sugar-rich resource during the dry season. In such environments, the ability to build sufficient fat reserves to enter seasonal torpor may be challenging (Kobbe et al., 2011; Vuarin et al., 2013). The inability to exercise seasonal torpor likely reduces the ability of individuals to cope with seasonal shortages in food supply (Canale and Henry, 2010).

It is not typical for *M. griseorufus* to occupy riparian forests such as P1, and our data indicate this species' diet is very different in this habitat than in other forests. Both males and females at P1 consume a lot of fruit in the wet season and both are able to access sufficient exudates during the dry season. Females, in particular, eat more fruit in the wet season and more exudates during the dry season at P1 than at other localities (Table 5; Fig. 2). Increased reliance on fruit does not adversely affect these individuals; they have heavier average body masses, and relatively more of them undergo seasonal torpor than at the other localities (Rasoazanabary, 2011). The population at P1 also appears to be growing; recapture rates are relatively high (Rasoazanabary, 2011). Our data thus suggest that this species is quite capable of substituting fruit for other sugar-rich foods such as exudates. Essentially, when in gallery forests, the diet of *M. griseorufus* converges on that of other mouse lemurs, such as *M. murinus*, that depend on high fruit production to build their fat reserves (e.g., Dammhahn and Kappeler, 2008).

In contrast, focal observations and isotope data suggest that females at Ihazoara consume the least amount of fruit during the wet season and the lowest proportion of plant exudates during the dry season (Fig. 2). Neither male nor female mouse lemurs undergo seasonal torpor at Ihazoara, which is the most degraded of the three forests at Beza Mahafaly. Population turnover is high (and recapture rates very low) at all three localities, but it is highest at Ihazoara (Rasoazanabary, 2011; Godfrey and Rasoazanabary, 2012). Sugar-rich foods may be even more important for mouse lemurs in extremely arid environments than focal individual sampling indicates. Isotope data, which can distinguish the consumption of homopteran secretions from the consumption of arthropods, suggest that mouse lemurs at Ihazoara may be targeting homopteran secretions to make up for insufficient fruit and/or exudates in their diets. To understand why individuals from Ihazoara do not enter seasonal torpor, more research should be done on what these individuals are nutritionally lacking that cannot be compensated for by access to arthropod secretions.

CONCLUSIONS

Focal observations suggest that mouse lemur diets are variable at Beza Mahafaly Special Reserve. After accounting for baseline isotopic variability among localities, stable isotope values for mouse lemur fur are broadly consistent with observed differences in diet among localities, sexes, and seasons. Isotopic and observational data are largely complementary but differ in several important ways. Focal follow data are usually only available for a small number of individuals, and cannot distinguish between orally processed material and ingested material. It may be particularly challenging to identify consumption of arthropods versus homopteran secretions when dealing with small, nocturnal primates high in the canopy. On the other hand, stable isotope data can be obtained from a larger number of individuals and may be particularly useful for quantifying ingestion of animal matter. However, they may be less effective at identifying consumption of sugar-rich materials, such as fruits and plant exudates, which contribute minimally to dietary protein. Collecting both isotopic and observational data provides a more robust estimate of diet than either can offer when used alone. Our results underscore the importance of sugar-rich foods to mouse lemurs, particularly in the dry season, when the ability to enter seasonal torpor offers metabolic advantages (Kobbe and Dausmann, 2009; Vuarin et al., 2013). These ecological constraints may increase the vulnerability of mouse lemurs that are already living in arid habitats to future anthropogenic or climate-induced habitat change.

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