Intraspecific Variation in Hair δ^{13}C and δ^{15}N Values of Ring-Tailed Lemurs (*Lemur catta*) With Known Individual Histories, Behavior, and Feeding Ecology

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ABSTRACT   Stable carbon and nitrogen isotope compositions were analyzed from hair samples of 30 sympatric ring-tailed lemurs (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve, Madagascar. All lemurs were known individuals involved in a longitudinal study, which allowed us to explore the degree to which group membership, sex, health status, and migration influenced their stable isotope compositions. The differences in δ^{13}C and δ^{15}N values between groups were small (<1.5‰) but highly significant. In fact, each group was tightly clustered, and discriminant function analysis of the stable isotope data assigned individuals to the group in which they were originally collared with over 90% accuracy. In general, the differences between groups reflected the degree to which they utilized forested versus open habitats. As open habitats at Beza Mahafaly often correspond to areas of anthropogenic disturbance, these data suggest that isotopic data can be useful for addressing questions of lemur conservation. There were few sex differences, but significant differences did occur between individuals of normal and suboptimal health, with those in poor health (especially those in the worst condition) being enriched in ^{15}N and to a lesser degree ^{13}C compared with healthy individuals. Moreover, lemurs that had emigrated between 2003 and 2004 had different δ^{13}C and δ^{15}N compositions than their original groups. Am J Phys Anthropol 133:978–985, 2007.   © 2007 Wiley-Liss, Inc.

Stable isotope analysis has become an important tool for ecologists and has been used to investigate the feeding ecology of diverse fauna including invertebrates, fish, birds, and mammals (e.g., Hobson and Schwarcz, 1986; van der Merwe et al., 1988; Hobson and Clark, 1992; Koch et al., 1995; Abend and Smith, 1997; McIlwee and Johnson, 1998; Fry et al., 1999; Schoeninger et al., 1999; Thompson et al., 1999; Hobson et al., 2000; Harding and Stevens, 2001; Oelbermann and Scheu, 2002; Sponheimer et al., 2003a; Wolf and Martinez del Rio, 2003; Ayliffe et al., 2004). Many of these studies have sought to assign species to broad dietary categories. For instance, several studies have shown that stable isotopes are particularly effective at classifying bovids as grazers, browsers, or mixed feeders (e.g., Tieszen and Imbamba, 1980; Cerling et al., 2003). Such studies tend to be normative in nature, and thus do not emphasize variation within a species, but rather attempt to establish its "typical" dietary behavior. In contrast, others have specifically looked at how a single species alters its diet over time or space. For example, van der Merwe et al. (1988) analyzed bone collagen of elephants (*Loxodonta africana*) from 12 conservation areas and showed that their grass consumption increased as the availability of woody vegetation decreased; others have shown that there can be marked changes in elephant diets seasonally (Cerling et al., 2004; Codron et al., 2006a).

While stable isotopes have proven quite useful for these normative and spatial (environmental) studies, they have been under-utilized to examine how the diets of conspecifics vary within a given area, even though several stable isotope studies suggest that such variation might be significant (e.g., Ben-David et al., 1997; Sze-panski et al., 1999; Sponheimer et al., 2003b; Urton and Hobson, 2005). One reason for this is that most mammalian stable isotope studies have opportunistic sampling strategies, and thus little is known about the ranging behavior, group membership, and health status of individuals that might result in isotopic heterogeneity.

Research question

To date, there have been few published studies of stable isotopes in extant primates (Schoeninger et al., 1997, 1998, 1999; Codron et al., 2006b; Sponheimer et al., 2006a). This is especially true for Madagascar's strepsirrhines (Schoeninger et al., 1998; McGee and Vaughn, 2006), for which more isotopic data have been published for the subfossil extinct lemurs than for extant species

(Schoeninger et al., 1998; Burney et al., 2004; Godfrey et al., 2005, 2006). Here, we begin to address this gap by presenting $\delta^{13}C$ and $\delta^{15}N$ data from the hair of 30 sympatric ring-tailed lemurs (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve, Madagascar (BMSR). These 30 individuals live in three distinct social groups: 1) one, which occupies a primarily undisturbed portion of the BMSR riverine gallery forest; 2) a second group that often sleeps and feeds within the protected reserve, but also regularly exploits resources in areas impacted by human activity; and 3) a third group that primarily lives outside the reserve.

Schoeninger et al. (1997) demonstrated that $\delta^{13}C$ and $\delta^{15}N$ values among New World Monkeys vary by habitat, by comparing species living in evergreen forests with closed canopies to those inhabiting dry, deciduous forests with open canopies. Preliminary isotopic data for lemurs (i.e., *Propithecus*) from Ranomafana National Park, Madagascar, (McGee and Vaughn, 2006) suggest that $\delta^{13}C$ and $\delta^{15}N$ values differ between areas previously logged and those that have experienced little anthropogenic disturbance. Thus, we would expect lemurs exploiting anthropogencially disturbed areas at BMSR to display different isotopic values than those in more forested areas. The behavior, ecology, and biology of ring-tailed lemurs at BMSR have been studied for many years (see review in Sauther et al., 1999). As a result, we know the group membership, sex, habitat utilization, health, and recent migratory history of each individual included in the current study (e.g., Cuozzo and Sauther, 2006). Hence, we can explore the impact of these variables on stable isotope compositions. We hypothesize that the group living only within the closed canopy, undisturbed gallery forest will be lower in $\delta^{13}C$ (canopy effect: see van der Merwe and Medina, 1991; Schoeninger et al., 1997) and $\delta^{15}N$ values (due to increased reliance on N_2 fixating legumes: see Shearer and Kohl, 1994; Schoeninger et al., 1997) than the two groups that exploit anthropogenically disturbed areas. In addition, we expected that the hair of individuals with suboptimal health values would differ in their isotopic composition, as behavioral and biological data indicate that lemurs in poor health (i.e., severe tooth loss) emphasize different food items in their diet (Sauther et al., 2002; Cuozzo and Sauther, 2006). Finally, given female feeding priority in this species (Sauther, 1993; Sauther et al., 1999), we expected sex differences in isotope values.

MATERIALS AND METHODS
Study site

Research was conducted at the Beza Mahafaly Special Reserve (BMSR) (23°30′S latitude, 44°40′E longitude) in southwestern Madagascar (see Fig. 1). BMSR was established in 1978 and became a special government reserve in 1986 (Sussman, 1991; Ratsirarson, 2003). The reserve has been the focus of long-term studies of ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*), but white-footed sportive lemurs (*Lepilemur leucopus*), gray mouse lemurs (*Microcebus murinus*), and gray brown mouse lemurs (*Microcebus griseorufus*) also live here (Garbutt, 1999; Godfrey and Jungers, 2002; Ratsirarson, 2003; Godfrey and Rasoazanabary, 2004). BMSR is characterized by distinct wet and dry seasons (e.g., Sauther, 1991, 1998; Ratsirarson, 2003) and periodically experiences droughts (e.g., Sauther, 1998; Gould et al., 1999, 2003). The habitat is highly seasonal with
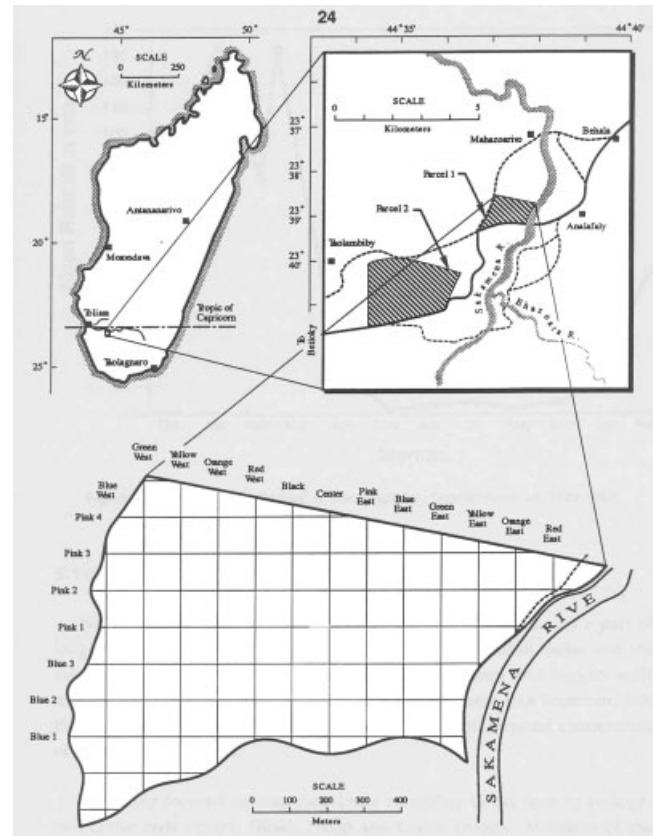

Fig. 1. Map of Madagascar indicating the location of the Beza Mahafaly Special Reserve.

~99% of the annual rainfall occurring between November and April (Sauther, 1998). The reserve consists of 4,000 ha, and includes two forests types, riverine and spiny forest, as well as a research camp.

The original protected and fenced riverine forest parcel was ~80 ha, and is located on the Sakamena River (see Fig. 2). This area of forest is dominated by kily trees (*Tamarindus indica*) and exhibits a high closed canopy (Sussman and Rakotozafy, 1994). This parcel is protected from grazing by livestock by a barbed wire fence and consists of a rich understory of saplings, lianas, and terrestrial herbs (Sauther, 1991). The camp habitat includes both the reserve camp and disturbed and degraded forest (see Fig. 3). The understory here has been removed by heavy grazing (Whitelaw et al., 2005).

Study population

Ring-tailed lemurs (*Lemur catta*) are best characterized as omnivores, existing in a wide range of habitats that are geographically distributed throughout the southern regions of Madagascar (e.g., Sauther et al., 1999; Sussman, 1999; Jolly, 2003). Of all the extant strepsirrhines, they are the most terrestrial and reflect a generalist pattern observed in some Old World Monkeys (e.g., Sauther et al., 1999; however, see Wright, 1999 for distinctions between lemurs and haplorrhine primates). Their diet is dominated by leaves and fruits, with flowers and occasionally insects also consumed, all based on seasonal availability (Sauther et al., 1999; Jolly, 2003).

Fig. 2. Image of the protected riverine gallery forest at Beza Mahafaly Special Reserve, used by Teal Group.

Fig. 3. Image of the degraded forest outside of the protected reserve used by the Orange and Blue Groups.

This generalist approach, coupled with an omnivorous diet, allows them to colonize and exploit a broad spectrum of ecotones, many of which are difficult for other Malagasy lemurid species. These habitats include anthropogenically-disturbed environments, as is the case at BMSR (Ratsirarson, 2003; Cuozzo and Sauther, 2004; Sauther et al., 2004; Whitelaw et al., 2005). We focused on three groups for this study: 1) Teal Group, which occupies the original protected and fenced riverine forest; 2) Blue Group, which has the largest home range and primarily lives outside the reserve in anthropogenically disturbed habitat; and 3) Orange Group, which of-

ten sleeps and feeds within the protected reserve, but also regularly exploits resources in areas impacted by human activity including the camp.

Field and lab methods

Data for our analysis were collected from 30 ring-tailed lemurs (five males and five females from each group) at BMSR in 2004. Hair samples from each of the 30 individuals studied were collected during routine health inspections of anesthetized animals. Individual lemurs were captured using a Telinject blow dart system and a drug mixture of Ketamine and Diazepam, based on protocols developed over the past 17 years and 360 captures of ring-tailed lemurs at BMSR (Sauther et al., 2006). After examination and the collection of biological samples, individuals were released in the area where they were originally captured (normally within 6 h). We followed all IACUC guidelines for these captures.

During examination, the health status of each animal was determined. Variables used to assess health status were: noticeable areas of hair loss (possibly a result of mange), open wounds (with evidence of infection), dental abscesses, decayed teeth (tooth is soft and rotting), high white blood cell counts (indicative of infection), anemia (based on clinically low hematocrit levels), and low body weight relative to the norm for this population. Lemurs were placed in one of two health categories: 1) normal health (none of the above variables present) and 2) sub-optimal health (the presence of one or more of the above variables). All behavior and feeding ecology data were collected using focal animal scan sampling (Altmann, 1974).

For each animal, hair collection followed a standard protocol and was cut from near the end of the tail as close to the skin as possible. Each hair sample was placed in a plastic bag with the proximal end (that nearest to the skin) down. Ring-tailed lemur tail hair is grown continuously at a rate of ~ 1 cm per month (Loudon, personal observations), and does not molt (Lent, personal communications). Hair was collected on all individuals within the same 3 week period, thus all samples represent the same time period, and thus diet.

Hair samples were cleaned with ethyl alcohol and cut with a razor blade, weighed (~ 700 micrograms), placed in tin capsules, and combusted in an elemental analyzer (Carlo-Erba, Milan, Italy) and analyzed for stable carbon and nitrogen isotope abundances using a flow-through inlet system on a continuous flow isotope ratio mass spectrometer (Finnigan, Bremen, Germany). $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed in delta (δ) notation in parts per thousand or per mil (‰) relative to the PeeDee Belemite (PDB) and atmospheric N_2 standards. All samples for this study were analyzed during one analytical run for which standard deviations of replicate measurements of internal standards (protein and yeast) were <0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Controlled feeding studies of multiple mammalian taxa have demonstrated that hair $\delta^{13}C$ and $\delta^{15}N$ values tend to be enriched by about 3‰ and 2.8–6.0‰ compared with dietary values, respectively (Roth and Hobson, 2000; Sponheimer et al., 2003c). Group and life history data for each individual were unknown at the time of isotopic analyses, thereby providing a blind test. We tested for isotopic differences between groups (Teal, Blue, and Orange) using analysis of variance (ANOVA) and the conservative Scheffé test. Health status and sex differences were investigated

TABLE 1. Lemur group affiliation, sex, health, δ^{13}C, δ^{15}N as well as results of the discriminant function analysis [squared distance to group centroid (DIST), predicted group membership (PRED), and posterior probability of belonging to that group (PROB)]

Individual	Group	Sex	Health	δ^{13}C	δ^{15}N	DIST	PRED	PROB
127	Blue	Male	Suboptimal	−23.9	7.0	0.289	Blue	0.935
133	Blue	Male	Normal	−23.9	7.0	0.289	Blue	0.935
136	Blue	Male	Normal	−24.0	7.0	1.170	Blue	0.798
140	Blue	Male	Suboptimal	−23.9	6.8	0.138	Blue	0.970
263	Blue	Male	Normal	−24.0	6.7	0.245	Blue	0.942
Blue males				*−23.9 ± 0.1*	*6.9 ± 0.1*			
126	Blue	Female	Normal	−23.9	6.9	0.038	Blue	0.958
132	Blue	Female	Suboptimal	−23.5	7.5	1.095	Blue	0.983
135	Blue	Female	Normal	−23.9	6.5	2.537	Blue	0.987
137	Blue	Female	Normal	−24.1	6.6	0.486	Blue	0.889
139	Blue	Female	Suboptimal	−23.2	7.6	2.601	Blue	0.999
Blue females				*−23.7 ± 0.4*	*7.0 ± 0.5*			
Blue group				*−23.8 ± 0.3[T]*	*7.0 ± 0.4[T]*			
143	Teal	Male	Normal	−23.6	7.7	12.418	Orange[M]	0.549
145	Teal	Male	Normal	−24.9	5.7	0.458	Teal	0.964
146	Teal	Male	Normal	−25.1	5.7	0.312	Teal	0.989
151	Teal	Male	Normal	−25.3	5.4	0.938	Teal	0.997
160	Teal	Male	Suboptimal	−25.1	6.0	2.635	Teal	0.860
Teal males				*−24.8 ± 0.7*	*6.1 ± 0.9*			
142	Teal	Female	Suboptimal	−24.4	6.2	2.646	Blue[M]	0.559
144	Teal	Female	Normal	−25.3	5.1	2.468	Teal	0.996
148	Teal	Female	Suboptimal	−25.1	5.7	0.312	Teal	0.989
158	Teal	Female	Normal	−25.2	5.3	1.306	Teal	0.994
162	Teal	Female	Suboptimal	−25.1	5.7	0.312	Teal	0.989
Teal females				*−25.0 ± 0.4*	*5.6 ± 0.4*			
Teal group				*−24.9 ± 0.5[BO]*	*5.9 ± 0.2[BO]*			
153	Orange	Male	Suboptimal	−24.3	7.5	1.736	Orange	0.999
274	Orange	Male	Normal	−24.4	7.2	0.544	Orange	0.996
166	Orange	Male	Suboptimal	−24.2	7.7	2.685	Orange	0.999
170	Orange	Male	Suboptimal	−23.4	8.0	4.858	Orange	0.663
269	Orange	Male	Normal	−24.3	7.6	2.990	Orange	0.999
Orange males				*−24.1 ± 0.4*	*7.6 ± 0.3*			
156	Orange	Female	Suboptimal	−23.9	7.2	4.186	Blue*	0.718
154	Orange	Female	Suboptimal	−23.9	7.5	0.954	Orange	0.940
171	Orange	Female	Normal	−24.6	6.8	1.068	Orange	0.940
174	Orange	Female	Normal	−24.6	6.6	2.065	Orange	0.628
168	Orange	Female	Normal	−24.3	7.1	0.222	Orange	0.964
Orange females				*−24.3 ± 0.4*	*7.0 ± 0.4[S]*			
Orange group				*−24.2 ± 0.4[T]*	*7.3 ± 0.4[T]*			

In the δ^{13}C and δ^{15}N columns a superscripts B, O, or T indicates that the group's mean value is different from that of Blue, Orange, or Teal group respectively, while an superscript S indicates that the mean value for the group's females differs from the mean value of the group's males ($P < 0.05$). In the PRED column, a superscript M indicates that the individual migrated from its natal group (and should therefore not be classified with it), while a superscript * indicates that the individual was misclassified.

using the student's t test. Statistical analyses were performed using SPSS 14.0, with significance set at $P = 0.05$.

RESULTS

See Table 1 and Figure 4 for the δ^{13}C and δ^{15}N values of each lemur, group, and for the sexes of each group. There were highly significant differences between groups for both δ^{13}C and δ^{15}N values ($P < 0.0001$). Pairwise comparisons demonstrate that δ^{13}C values for Teal Group were significantly lower compared with Blue group ($P < 0.0001$) and Orange Group ($P < 0.01$), while Teal Group had significantly lower δ^{15}N values than Blue Group ($P < 0.0001$) and Orange Group ($P < 0.0001$).

The stable isotope values of individuals within groups cluster together (see Fig. 4), indicating that group membership could be determined via stable isotope analysis. To test this hypothesis, we performed a discriminant function analysis (DFA) using δ^{13}C and δ^{15}N values and were able to correctly predict group membership for 27

of the 30 individuals (see Table 1 for DFA results). While this correct classification rate of 90% is quite good, it actually underestimates our classificatory success, for as will be discussed in the following sections, two of the individuals that were "misclassified" had emigrated from their original group (Teal Group). Thus, when the emigrants are excluded, our classification success jumps to 27 out of 28 (96%). We further evaluated this finding using leave-one-out cross-validation, where 28 separate DFAs were performed with each sample left out of the training dataset once to serve as an "unknown" (emigrants were excluded). The DFAs attributed these "unknowns" to their actual groups 93% of the time, suggesting that for these ring-tailed lemurs, group membership can be quite accurately predicted using stable isotope data. Similarly, others have found that stable isotopes in hair and feathers can provide information about where an individual came from and its habitat utilization (e.g., Hobson, 1999; Bowen et al., 2005).

Comparisons between the sexes in each group revealed no significant differences in δ^{13}C values. However, in Orange Group, males had higher δ^{15}N values compared

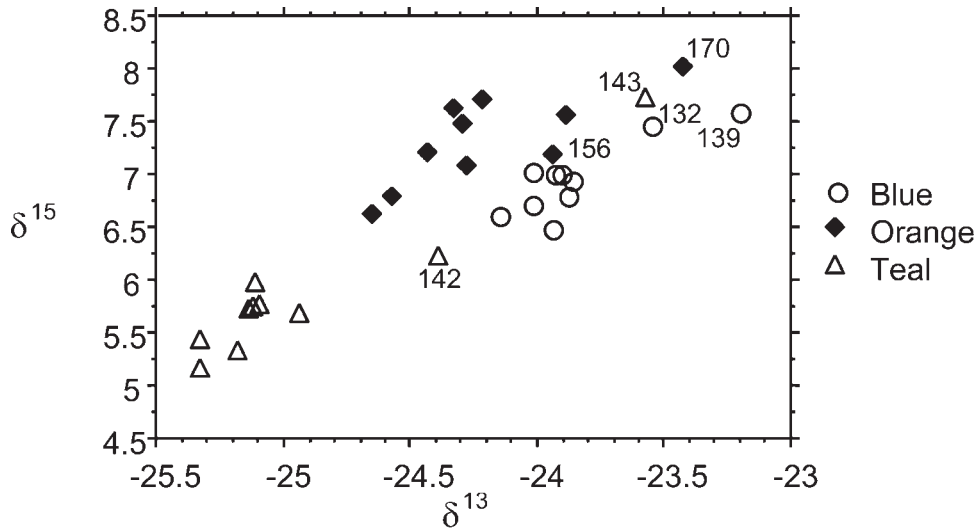**Fig. 4.** δ^{13}C and δ^{15}N of all the specimens analyzed in this study. The greatest outliers (Teal 143 and Teal 142) reflect the fact that these individuals recently emigrated. Individuals that are in the poorest health (Orange 170 and Blue 139 are mentioned in the text) tend to be enriched in ^{13}C and most especially in ^{15}N. Teal, the only group that is restricted to pristine forest areas, is significantly depleted in both ^{13}C and ^{15}N compared with other groups.

to females ($P < 0.01$). To investigate the degree to which health status affects stable isotope composition, we normalized the δ^{13}C and δ^{15}N value of each individual to its group mean so that all three groups could function as a single analytical unit. This was necessary because the number of individuals in each group with suboptimal health was too small for meaningful intragroup statistical analysis. When comparing individuals to normalized group means and excluding the two emigrants, individuals with suboptimal health (δ^{13}C = 0.1 $\pm$ 0.4‰; δ^{15}N = 0.2 $\pm$ 0.3‰ n = 11) were shown to be significantly enriched in ^{13}C and ^{15}N compared with healthy individuals (δ^{13}C = $-0.2 \pm$ 0.2‰; δ^{15}N = 0.1 $\pm$ 0.3‰ n = 17) by about 0.3‰ and 0.5‰, respectively ($P < 0.01$). In contrast, this method revealed no significant sex differences in δ^{13}C or δ^{15}N values ($P > 0.10$).

DISCUSSION

In this study, we document significant differences in the stable isotopic compositions of three sympatric groups of ring-tailed lemurs (*Lemur catta*). Teal Group was never observed outside of the fenced portion of the gallery forest, and this group's diet consisted completely of naturally occurring foods. This part of the reserve is characterized by continuous forest canopy and a thick understory, likely resulting in a "canopy effect" producing plants that are relatively depleted in ^{13}C (Vogel, 1978; Schleser and Jayasekera, 1985; van der Merwe and Medina, 1991). The exclusive utilization of this heavily forested habitat probably explains Teal Group's lower δ^{13}C value compared with the other groups. Teal Group also exhibits the lowest δ^{15}N values of the three groups. Throughout the reserve, *T. indica* is prevalent and is an important resource for this population throughout the year (Sauther, 1998). *T. indica* is a member of the Leguminosae family, whose members have a symbiotic relationship with nitrogen-fixing bacteria, often resulting in reduced δ^{15}N values (e.g., Virginia and Delwiche, 1982; Shearer et al., 1983; Schulze et al., 1991). All three groups consume this species, but Teal Group's diet is dominated by this fruit, which likely accounts for its depletion in ^{15}N. Planned isotopic analyses of recently collected samples of BMSR vegetation will allow us to test this hypothesis.

In contrast, Blue Group exhibited the highest mean δ^{13}C value. Blue Group had the largest group membership and concomitantly the largest day range (Sauther and Cuozzo, unpublished data). Blue Group primarily utilizes anthropogenically altered habitats characterized by arid, open areas of disturbed forest with broken canopy and an understory that is denuded of saplings and terrestrial herbaceous plants (Whitelaw et al., 2005). Blue Group's regular exploitation of this environment is likely reflected in its higher mean δ^{13}C value. Similarly, Orange Group leaves the fenced portion of reserve daily and ranges in the disturbed forests, although it returns to the protected reserve at night, which at least partially explains its enrichment in ^{13}C compared with Teal Group. In addition like Blue or Teal Group, Orange Group regularly ranges into the research camp. Consequently, human foods (i.e., discarded fruit and vegetable scraps) are available, which might explain to some extent their higher δ^{13}C values. Perhaps more significantly, a Mahafaly taboo prohibits the use of in-ground latrines (Ratsirarson, 2003), and thus feces from open-air latrines were consumed by Orange Group (Fish et al., 2007). It is possible that this contributed to the ^{13}C-enrichment of Orange Group compared with Teal Group, and quite likely contributed to Orange Group having the highest δ^{15}N values of the three groups in this study, as fecal δ^{15}N is enriched by about 3‰ compared with most plant foods (Sponheimer et al., 2003d). Nevertheless, Blue Group's δ^{15}N values are similar to those of Orange, despite a lack of coprophagy, suggesting that the high δ^{15}N and δ^{13}C values of Blue and Orange Groups largely reflect the utilization of areas where human activity has reduced the forest canopy and eliminated the understory (Whitelaw et al., 2005). Preliminary data from Ranamafana National Park indicate that the isotopic values of lemurs (i.e., *Propithecus edwardsi*) living in recently logged and nonlogged habitats significantly differ (McGee and Vaughn, 2006). Together these data illustrate the potential of using isotopes as a tool to evaluate anthropogenic change.

In general, animals in suboptimal health exhibited slightly elevated δ^{13}C, and more consistently, higher δ^{15}N values. For instance, Orange 170 was the most enriched in both ^{13}C and ^{15}N of the entire male population and was arguably in the poorest health. This lemur

suffered from hair loss and severe antemortem tooth loss (81% tooth loss, see description in Cuozzo and Sauther 2004, 2006) and he was frequently observed sitting below trees eating partially chewed *T. indica* fruits that had been dropped by other group members (Cuozzo and Sauther, 2006). He also commonly engaged in coprophagy (Fish et al., 2007). It is likely that this animal's extensive tooth loss (including all six mandibular molars, as well as four of six maxillary molars) inhibited his ability to mechanically break down the fruit's hard surface, making partially chewed fruit and human feces important food resources. The same trend is seen in females, such as Orange 156, whose biomedical values indicate hepatic inflammation (Miller et al., in press), and Blue 139, who is the most enriched in both δ^{13}C and δ^{15}N of the entire female population, and who has lost 39% of her dentition (Cuozzo and Sauther, 2004). This trend of individuals in poor health being enriched in ^{13}C and ^{15}N is found in all groups and sexes, and not surprisingly, is most pronounced in individuals in the poorest condition (e.g., Blue 132, Blue 139, Orange 156, Orange 170). One possible explanation for the enrichment in individuals with poor health is that they have inadequate diets, forcing them to catabolize their tissues for use as energy and amino acid sources as demonstrated in birds (Hobson et al., 1993). It has been suggested that high δ^{15}N values in whales may be a response to catabolizing tissues during periods when feeding ceased or was reduced (Best and Schell, 1996; Hobson and Schell, 1998). A similar mechanism might be responsible for the high δ^{15}N values of the lemurs in poor health, as many of the lemurs had either severe tooth loss or low body weight, likely indicating poor diets. Yet, several lab and field studies have not found conclusive links between body weight and stable isotope compositions (e.g., Ben-David et al., 1997, 1999; Frazer et al., 1997; Schmidt et al., 1999), and we therefore feel it premature to confidently ascribe the observed enrichment to this mechanism rather than ecological factors.

Migratory behavior is also readily apparent in the stable isotope data. The two conspicuous outliers in this dataset (Teal 142 and Teal 143 see Fig. 4) had recently left Teal Group to join a smaller group (Pink Group) that forages to the west of Teal Group's home range. This migration occurred between July 2003 and May 2004. We do not have stable isotope composition data for the remainder of Pink Group, thus we cannot determine the degree to which their hair has been equilibrated with their new diets. Nevertheless, their disparate δ^{13}C and δ^{15}N values from that of Teal Group's mean values, and their classification as non-Teals using discriminant function analysis, suggests that stable isotope analysis can be used for tracking population movements and changes in group membership in Malagasy lemurs.

The mean δ^{13}C and δ^{15}N values of this ring-tailed lemur population ($n = 30$) are -24.3‰ and $+6.7$‰, respectively, while white-footed sportive lemurs (*Lepilemur leucopus*) in the same reserve are relatively depleted in ^{15}N (-1.2‰) and enriched in ^{13}C ($+3.0$‰) by comparison (Schoeninger et al., 1998). Schoeninger et al. (1998) noted that *L. leucopus* consumes high quantities of CAM plants that are enriched in ^{13}C compared with available C_3 vegetation at BMSR. In fact, they also found a strong positive correlation between time spent feeding on CAM plants and δ^{13}C values. At present, it is unknown to what degree ring-tailed lemurs utilize CAM plants at Beza, although this study suggests that they

are not consumed to any significant degree, as their hair δ^{13}C values are typical of pure C_3-consuming forest primates (Schoeninger et al., 1997, 1999). Hence, it is likely that differential CAM plant consumption substantially accounts for the divergent δ^{13}C values of these lemur species. Because the only ring-tailed lemur group similar in its δ^{15}N signature to the lepilemurs stayed exclusively in the most pristine, protected forest environments (Teal), it is likely that the general enrichment in ^{15}N composition of the ring-tailed lemurs reflects their ability to utilize a wide variety of environments, including those that have been highly disturbed.

CONCLUSION

We investigated variations in stable isotope compositions in three sympatric groups of ring-tailed lemurs (*Lemur catta*). Each group exhibited a distinctly different δ^{13}C or δ^{15}N signature, which likely reflects differences in habitat utilization. We also found significant differences in the δ^{13}C and δ^{15}N values of individuals with different health profiles, and between sexes in one of the three study groups. This study also demonstrates that δ^{13}C and δ^{15}N data can be used to assign group membership and document migration history in ring-tailed lemurs from the Beza Mahafaly Special Reserve. In short, this study illustrates the benefits of fusing intensive long-term ecological and behavioral field analyses with stable isotopic studies.

ACKNOWLEDGMENTS

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