

Dietary patterns and stable isotope ecology of sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve

By

Nora W. Sawyer

July 2020

Director of Thesis: Dr. James E. Loudon

Major Department: Anthropology

Primatologists have long been captivated by the study of the inter-relationships between nonhuman primate (NHP) biology, behavior, and ecology. To understand these interplays, primatologists have developed a broad toolkit of methodologies including behavioral observations, controlled studies of diet and physiology, nutritional analyses of NHP food resources, phylogenetic reconstructions, and genetics. Relatively recently, primatologists have begun employing stable isotope analyses to further our understanding of NHPs in free-ranging settings. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values are recorded in the tissues and excreta of animals and reflect their dietary patterns. This study incorporates the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) that inhabited the Beza Mahafaly Special Reserve in southwest Madagascar. The statistical program R was used to measure the impacts of anthropogenic disturbance and season (wet vs. dry) on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of these primates. Furthermore, this project attempted to measure the accuracy of using feeding observations in comparison to stable isotope analysis to infer diet. In order to do so, this project integrated the feeding observations of *L. catta* and *P. verreauxi* with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the plants they ate and compared these values to their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values. Based on feeding observations and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plant values,

an equation was developed to predict the fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the ring-tailed lemurs and Verreaux's sifaka. However, the predicted fecal values did not always align accurately with those that were observed. Nonetheless, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values reflected diverging dietary trends and differences in habitat use patterns among the social groups of the ring-tailed lemurs and Verreaux's sifaka at the reserve. Thus overall, the results of this study demonstrated that both primates partition their resources differently, allowing them to live in sympatric associations. Ultimately, these data are useful for modeling Malagasy lemur behavior, especially those species or populations which are severely impacted by human behavior.

Dietary patterns and stable isotope ecology of sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve

A Thesis Presented to the Faculty of the Department of Anthropology
East Carolina University

In Partial Fulfillment of the Requirements of the Degree of
Master of Arts in Anthropology

By
Nora W. Sawyer
July 2020

© Nora W. Sawyer, 2020

Title: Dietary patterns and stable isotope ecology of sympatric ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) inhabiting the Beza Mahafaly Special Reserve

By
Nora W. Sawyer

APPROVED BY:

DIRECTOR OF THESIS:

James Loudon, PhD

COMMITTEE MEMBER:

Ryan Schacht, PhD

COMMITTEE MEMBER:

Megan Perry, PhD

COMMITTEE MEMBER:

Ariane Peralta, PhD

DEPARTMENT
CHAIRPERSON:

I. Randolph Daniel, Jr., PhD

DEAN OF THE
GRADUATE SCHOOL:

Paul J. Gemperline, PhD

Acknowledgements

The following thesis is the result of my master's degree coursework in anthropology and biology, along with mentorship from my advisor Dr. James Loudon. This work would not be possible without academic advising and support of my committee members: Dr. Loudon, Dr. Ryan Schacht, Dr. Megan Perry, and Dr. Ariane Peralta.

I am grateful to the Beza Mahafaly Special Reserve (BMSR) in southwestern Madagascar, without whom this study would not be possible. I am also grateful for the support of the Mahafaly people and Dr. Loudon's Malagasy colleagues: IAJ Youssouf, Randrianarisoa Jeannicq, Elahavelo, along with the BMSR monitoring team. I also want to thank the Département des Eaux et Forêts, Ecole Supérieur des Sciences Agronomiques, Université d'Antananarivo and The National Association for the Management of Protected Areas in Madagascar (ANGAP) for their support and permissions. I am also grateful for the financial support provided by the National Science Foundation (BCS 0525109). Furthermore, I am also thankful to Drs. Michele Sauter and Matt Sponheimer at the University of Colorado in Boulder for allowing me to conduct this research with them.

I would also like to thank both Dr. Holly Mathews of the Department of Anthropology and Dr. Claudia Jolls of the Department of Biology at East Carolina University for helping me to improve my technical writing skills. As well, I appreciate the guidance of Dr. David Griffith in preparing to write my thesis proposal. Lastly, I want to thank both faculty in the Departments of Biology and Anthropology at East Carolina University for contributing to my growth as a graduate student and researcher.

Table of Contents

List of Tables.....	vi
List of Figures.....	viii
Chapter One: Introduction.....	1
Chapter Two: Background.....	3
Chapter Three: Methods.....	18
Chapter Four: Results.....	28
Chapter Five: Discussion.....	52
Chapter Six: Conclusion.....	62
References.....	66
Appendix A.....	79
Appendix B.....	80

List of Tables

1. Ring-tailed lemur study population (N = 14) depicting individuals, sex, group membership, and habitat.....	22
2. Verreaux's sifaka study population (N = 14) depicting individuals, sex, group membership, and habitat.....	22
3. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard deviations for the BMSR plant organs.....	28
4. Frequency and percentages of feeding intervals for each plant organ part for the BMSR ring-tailed lemurs (<i>Lemur catta</i>).....	29
5. Frequency and percentages of feeding intervals for each plant organ part for the BMSR Verreaux's sifaka (<i>Propithecus verreauxi</i>).....	29
6. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the ring-tailed lemur Green group at BMSR.....	30
7. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the ring-tailed lemur Black group at BMSR.....	30
8. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the Verreaux's sifaka group Vao Vao at BMSR.....	31
9. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the Verreaux's sifaka group Rivotse at BMSR.....	31
10. Mean predicted and observed $\delta^{13}\text{C}$ fecal values and their associated t-test p-values for the BMSR primates and social groups.....	32
11. Mean predicted and observed $\delta^{15}\text{N}$ fecal values and their associated t-test p-values for the BMSR primates and social groups.....	32
12. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs.....	41
13. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs.....	41
14. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka.....	41
15. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka.....	42

16. Pairwise comparisons for the observed $\delta^{13}\text{C}$ fecal values between all social groups at BMSR.....	43
17. Pairwise comparisons for the observed $\delta^{15}\text{N}$ fecal values between all social groups at BMSR.....	44
18. Pairwise comparisons for the observed $\delta^{13}\text{C}$ fecal values grouped by species and season at BMSR.....	45
19. Pairwise comparisons for the observed $\delta^{15}\text{N}$ fecal values grouped by species and season at BMSR.....	46
20. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs, grouped by season.....	47
21. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs, grouped by season.....	47
22. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka, grouped by season.....	48
23. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka, grouped by season.....	48
24. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values with standard deviations for the BMSR ring-tailed lemur and Verreaux's sifaka individuals.....	67

List of Figures

1. Map of the Beza Mahafaly Special Reserve (BMSR) and its location on the island of Madagascar.....	18
2. a. A collared Verreaux's sifaka (<i>Propithecus verreauxi</i>) with an identification tag...21	
b. A collared ring-tailed lemur (<i>Lemur catta</i>) with an identification tag.....	21
3. Median predicted $\delta^{13}\text{C}$ fecal values paired with observed $\delta^{13}\text{C}$ fecal values for the BMSR ring-tailed lemurs across all study months.....	34
4. Median predicted $\delta^{13}\text{C}$ fecal values paired with observed $\delta^{13}\text{C}$ fecal values for the BMSR Verreaux's sifaka across all study months.....	35
5. Median predicted $\delta^{15}\text{N}$ fecal values paired with observed $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs across all study months.....	36
6. Median predicted $\delta^{15}\text{N}$ fecal values paired with observed $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka across all study months.....	37
7. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs and Verreaux's sifaka. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.....	38
8. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemur Black and Green groups. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.....	39
9. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka groups Rivotse and Vao Vao. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.....	40
10. Median observed $\delta^{13}\text{C}$ fecal values for all social groups at BMSR.....	42
11. Median observed $\delta^{15}\text{N}$ fecal values for all social groups at BMSR.....	43
12. Median observed $\delta^{13}\text{C}$ fecal values grouped by species and season at BMSR.....	45
13. Median observed $\delta^{15}\text{N}$ fecal values grouped by species and season at BMSR.....	46

Chapter One - Introduction

The purpose of this study was to understand the dietary patterns of sympatric ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) inhabiting either protected or anthropogenically-disturbed forests at the Beza Mahafaly Special Reserve (BMSR) by comparing their fecal carbon and nitrogen stable isotope values and behavioral feeding observations. To date, only one study has examined the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Verreaux's sifaka from samples collected in the wild (Crowley et al., 2010). Crowley et al. (2010) investigated apparent enrichment (ϵ^*) between several tissue types across the primate order for the purpose of carbon and nitrogen stable isotope analyses. As well, they used collagen samples to estimate keratin (%) and keratin stable isotope values (‰) for Verreaux's sifaka alongside several primate species inhabiting both wild and captive settings. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ collagen values for Verreaux's sifaka (N = 7) were 21.2‰ (± 0.7 SD) and 7.3‰ (± 0.7 SD), respectively (Crowley et al., 2010).

Likewise, only one previous study has reported $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for free-ranging ring-tailed lemurs (Loudon et al., 2007). Loudon et al. (2007) used hair samples to determine the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values for three sympatric ring-tailed lemur groups (N = 30) also inhabiting BMSR. They examined how group membership, sex, health status and migration affected the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of their study population (Loudon et al., 2007). Though sympatric, they observed a uniquely different set of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ isotope values for each group that was attributed feeding behavior, habitat use, and physical health (Loudon et al., 2007).

An important aspect of their study was the use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values coupled with behavioral observations (Loudon et al., 2007). Loudon et al. (2007) suggested that ring-tailed lemurs exploiting disturbed forest areas versus those exploiting protected forest areas

should have distinct isotopic values from each other. Using this approach Loudon et al. (2007) showed that anthropogenic disturbance affected the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of their study subjects. Towards this end, Loudon et al. (2014) used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to estimate the degree to which some South African vervet monkey (*Chlorocebus pygerythrus*) groups were reliant on crops and processed human foods.

This study builds upon these studies and attempting to predict the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs and Verreaux's sifaka by coupling feeding observations with observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values. The predictions were only possible given that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the BMSR plants were known. However, the current study differs from previous isotope studies of nonhuman primates (NHPs) in three primary ways. To begin with, this study used plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to predict the fecal carbon and nitrogen isotope values for the BMSR primates. This differs from most primate isotope studies that primarily use plant stable isotope values as baseline data for interpreting NHP $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Secondly, this study examined monthly and seasonal variations in feeding behavior and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the BMSR primates. Lastly, this study investigates how the BMSR lemurs and sifaka partition their resources allowing for several groups to occupy the same habitat.

Chapter Two - Background

Since the start of the discipline, primatologists have been fascinated by the intersection of nonhuman primate (NHP) biology and behavior (Robbins and Hohmann, 2006). This approach, commonly referred to as “primate behavioral ecology” can be defined as the study of how ecological processes shape primate social dynamics and the evolution of NHP social systems (Janson, 2000). To understand the relationship between dietary patterns and community dynamics, field primatologists record feeding observations of NHPs in the wild. Observational data allowed for them to categorize NHP species into broad dietary groups based on observed focal foods and feeding behaviors in their natural habitat. Generally, these foods are divided into three categories: fruits, leaves, and invertebrates. As well, NHPs rarely hunt and eat vertebrates, but these dietary items do not largely contribute to their diets (Schreier, 2019). NHPs that specialize in feeding on fruits are referred to as *frugivores*. Species that feed primarily on leaves are considered *folivores* and those that primarily consumed invertebrates are labeled *insectivores* (Fleagle, 1988). These classifications have given researchers the opportunity to study relationships between biological, ecological, and behavioral variables among a diverse set of species within the NHP taxon (Fleagle, 1988). This work was largely pioneered by Milton and May (1976), who examined the relationships between diet, body weight, day foraging patterns and home range size by comparing the behavioral ecology of 36 NHP species and found that frugivorous primates typically occupy larger home ranges than folivorous primates.

Comparative socioecology studies of NHPs beginning in the 1960s were also useful in recognizing the types of feeding competition among NHP species and how they affect social relations and social structures (Wrangham, 1980; Harcourt, 1989; van Schaik, 1989; Janson and Goldsmith, 1985; Sterck et al., 1997; Janson, 2000). Wrangham (1980) argued that feeding

competition and the distribution of food resources were among the most important selective pressures impacting primate social systems, philopatry, competition, and dominance hierarchies. Other researchers built upon this dietary model by noting the role that predation (van Schaik, 1989) and female relationships (Isbell and Young, 2002) play key roles in characterizing NHP societies.

Recent developments in primate socioecology

Recent models of primate behavioral ecology and socioecology include considering the role of the NHP consumption of preferred foods and fallback foods (FBFs) (Marshall and Wrangham, 2007; Marshall et al., 2009; Clink et al., 2017), inclusion of data pertaining to group sizes in reference to the social brain hypothesis (Shultz and Dunbar, 2007; Sandel et al., 2016), and a greater resolve to understand the effects of anthropogenic changes on extant NHP populations (Hill, 2017, 2018; Scheun, Greef and Nowack, 2019). Previously, some primatologists hypothesized that FBFs have acted as a selective pressure on primate morphology, ecology, and behavior (Yeager and Kool, 2000; Steenbeek and van Schaik, 2001; Lambert et al., 2004). Marshall and Wrangham (2007) define FBFs as a food source that NHPs exploit when preferred resources are not available to them. Furthermore, they suggest that there are two distinct types of FBFs: i) filler FBFs and ii) staple FBFs. Filler FBFs are consumed on an irregular basis and never account for the entirety of diet. In contrast staple FBFs may account for up to 100% of diet on a seasonal basis and are available throughout the year (Marshall and Wrangham, 2007). According to the authors, NHP taxa that rely on filler FBFs are subject to greater variation in food abundance and resource availability. Whereas those species that primarily consume staple FBFs have access to a more stable food supply (Marshall and Wrangham, 2007). Additionally, long-term research with Bornean white-bearded gibbons

(*Hylobates albibarbis*) and red leaf monkeys (*Presbytis rubicunda*) in Indonesia suggests that FBFs limit carrying capacity in some NHP species (Marshall and Wrangham, 2007; Marshall et al., 2009; Clink et al., 2016).

Since the 2000s, the number of published studies concerning NHPs in anthropogenically-disturbed habitats has greatly increased (McLennan et al., 2017). McLennan et al. (2017) note that anthropogenic habitats are ecosystems that have been altered or monopolized by humans. Human modifications that have impacted primate habitats include de-forestation, agriculture, and urbanization (Estrada et al., 2012; McKinney, 2015). For example, several studies since the late 20th century have noted that elephants and NHPs are considered crop pests among many ethnic groups throughout Africa and Asia (Else, 1991; O’Connell-Rodwell et al., 2000; Strum, 1994). According to Hill (2018), recent studies demonstrate that NHP species of all age and sex classes engage in crop foraging to some extent, despite their risk of being injured or killed by humans (Choudhry, 2004; Katsvanga et al., 2006; McLennan et al., 2012; Priston, 2005; Scheun, Greeff and Nowack, 2019). Based on four years of *ad libitum* observations of the African lesser bush baby (*Galago moholi*) in South Africa, Scheun, Greeff and Nowack (2019) argue that individuals showed behavioral flexibility in response to recent urbanization. Examples include spending time in social groups of 10 individuals rather than moving through their environment in pairs or solitary, and exhibiting a greater frequency of social behaviors such as allo-grooming and sitting in contact and proximity to one another (Scheun, Greeff and Nowack, 2019).

Using conventional ecological sampling methods to determine the abundance and distribution of dietary resources (i.e. edible leaves, flowers, and fruits) has proven difficult for NHPs in free-ranging settings (Vogel and Dominy, 2011). Variables such as food abundance and seasonality are particularly difficult to reliably measure given the dynamic ecological conditions

of each field site and non-uniform methods employed by primatologists to measure ecological variables. Nonetheless, food abundance and seasonality directly impact NHP activity patterns and habitat use throughout the year (Overdorff, 1996). For example, chimpanzees (*Pan troglodytes*) inhabiting Tai National Park in the Ivory Coast spent more of their time feeding on lower quality foods during the dry season when their preferred resources (i.e. fruit) were scarce in comparison to the rainy season when fruits are most abundant (Doran, 1997). This example highlights the direct relationship between NHP primate feeding behaviors and food availability.

There is a rich tradition of watching NHPs and linking their behavioral patterns to the conditions of the ecosystems they inhabit (Janson, 2000). Moreover, these behavioral studies have provided vital data for developing sound conservation initiatives, assisting in the development of nutritional requirements for captive NHPs, and developing testable models to understand the dietary patterns of extinct primates and early hominins (Jolly, 1970; Codron et al., 2018; Ungar and Sponheimer, 2011). However, traditional feeding observations sometimes do not capture the actual foods consumed by animals. This is most notable among ungulate feeding observations which have not always accurately recorded the dietary contributions of grass for “browsing ungulates” (i.e. tree or shrub consumers) or the contributions of browse for “grazing ungulates” (i.e. grass consumers). The relative contributions of browse and graze have been estimated for several species of African ungulates using stable isotope analysis (Cerling et al., 1999; 2003; Codron et al., 2007) which contradict many of the dietary patterns which have been historically reported by researchers using traditional feeding observations.

Stable isotope analyses

One means to quantify dietary behavior as it relates to local and global environmental variables is the use of stable isotopes analyses. Margaret Schoeninger and her colleagues were

among the first anthropologists to use stable isotope analyses to understand NHP diet and habitat use (Schoeninger et al., 1997, 1998, 1999). Before this work, ecologists were primarily using stable isotope ratios to measure plant photosynthetic pathways, trophic positions in food webs, and climatic patterns (Vogel, 1978; Schoeninger and DeNiro, 1984; Rundel et al., 1989; van der Merwe and Medina, 1989, 1991). Schoeninger (1997) suggested that stable isotopes analysis is secondary line of inquiry that can provide biological, behavioral, nutritional, and general ecological information on an organism within their environment. In anthropology, initial stable isotope studies were primarily conducted in archaeology and paleoanthropology (Ambrose and Norr, 1993; Balasse et al., 1999). Most notably paleoanthropologists have used enamel stable carbon isotope analysis of *Paranthropus robustus* and *Australopithecus africanus* to better understand their diet (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 2006a), and their placement in paleo-ecological communities (Lee-Thorp et al., 2003).

Stable isotope analysis is possible because biogeochemical systems and the organisms that live in them are composed of elements including carbon, nitrogen, hydrogen, oxygen, sulfur, fluorine, calcium, phosphorous and strontium (Schoeninger, 1995). These elements occur in multiple atomic forms, referred to as isotopes. Isotopes possess the same number of electrons and protons but vary in their number of neutrons. Atoms with more neutrons are heavier and have slower chemical and physical reactions (Fry, 2006). Stable isotope ratios are expressed as δ values relative to an International standard in parts per thousand (‰) or parts per million (Fry, 2006). For nitrogen, the International standard is atmospheric nitrogen, which is sometimes referred to as the ambient inhalable reservoir (AIR) (Fry, 2006). For carbon, the International standard was PeeDee Belemnite, a Cretaceous marine fossil (*Belemnitella americana*) (Sandberg

et al., 2012). However, recently this source was exhausted and replaced by Vienna PeeDee Belemnite (V-PDB) (Sandberg et al., 2012).

Plants follow three photosynthetic pathways and are referred to as C₃, C₄ and CAM (Crassulacean Acid Metabolism) plants. C₃ plants include trees and shrubs and have $\delta^{13}\text{C}$ values averaging about -28‰ and ranging between -23‰ and -31.5‰ (O’Leary, 1981, 1988). C₄ plants are tropical grasses (and some sedges) and have $\delta^{13}\text{C}$ values that range between -11‰ and -14‰ (O’Leary, 1988). The last group of plants are succulents which are adapted to arid environments and use crassulacean acid metabolism and are referred to as CAM plants (Kluge and Ting, 1978). CAM plants may absorb CO₂ only at night or only during the day. For only nighttime CO₂ absorption, CAM plants will have $\delta^{13}\text{C}$ values averaging approximately -11‰. While for only daytime CO₂ absorption, their $\delta^{13}\text{C}$ values will average approximately -28‰ (O’Leary, 1988). Generally, their $\delta^{13}\text{C}$ values range between -10‰ and -20‰ and often resemble the values of C₄ plants (O’Leary, 1981, 1988; Winter, 1979). Distinctions between CAM and C₄ plants are possible by evaluating physiological characteristics such as succulence and malic acid content during daytime hours (O’Leary, 1988). However, it is largely the different isotopic ratios produced by C₃ and C₄ plants that have allowed scientists to use stable isotope analyses as a proxy for the diet of animals (van der Merwe, 1982).

In the late 1970s, DeNiro and Epstein (1978) conducted a lab experiment which consisted of feeding snails, flies, and mice diets of known isotopic composition. This work demonstrated that the $\delta^{13}\text{C}$ values reflect the foods consumed by an individual animal. Among mice fed Purina Rat Chow, they observed that the carbon dioxide the mice exhaled was depleted by a factor of 1‰ in comparison to the $\delta^{13}\text{C}$ value of the food itself. In contrast, the body tissue and excreta of the mice were positively enriched by 1‰ relative to their food (DeNiro and Epstein 1978). This

demonstrated that different types of animal tissue and excreta vary in their $\delta^{13}\text{C}$ values (van der Merwe, 1982).

Building upon this work, DeNiro and Epstein (1981) conducted similar laboratory experiments and demonstrated that one can estimate an animal's trophic position in a food web by using the $\delta^{15}\text{N}$ values collected from individual tissues. In a similar vein to their stable carbon isotope study (DeNiro and Epstein, 1978), the study subjects were also snails, flies, and mice provided diets of known ^{15}N -isotopic composition (DeNiro and Epstein, 1981). This study demonstrated that animal tissues are ^{15}N -enriched by $\sim 3\text{-}5\%$ with each step in a trophic food web (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Schoeninger and DeNiro, 1984).

In the natural world, $\delta^{15}\text{N}$ values of soils and plants vary in response to nitrogen cycling, availability of nitrogen, water availability and extent of nitrogen loss within an ecosystem (Amundson et al., 2003). The $\delta^{15}\text{N}$ values of soils are generally higher than atmospheric nitrogen (0‰) given that ^{14}N is preferentially released into the atmosphere through denitrification, leaching, and ammonia volatilization (Sandberg et al., 2012). Regarding plants, $\delta^{15}\text{N}$ values tend to increase as rainfall decreases and temperatures increase indicating that the nitrogen cycle itself is becoming more open (Amundson et al., 2003; Sandberg et al., 2012). High $\delta^{15}\text{N}$ values have also been documented in tropical rainforest ecosystems due to an overabundance of nitrogen (Martinelli et al., 1999). Furthermore, anthropogenic changes to habitat through agriculture, grazing by livestock and fertilizers may increase or decrease the $\delta^{15}\text{N}$ values of soils and hence plants (Aranibar et al., 2008; Bateman and Kelly, 2007).

It is important to note that diet to tissue nitrogen isotope ratios vary to different degrees in response to protein quality (Robbins et al., 2005; Roth and Hobson, 2000; Bearhop et al., 2002; Pearson et al., 2003; Sponheimer et al., 2003b; Vanderklift and Ponsard, 2003). Protein plays an

important role in nitrogen balancing, assimilation, and excretion (Barboza and Parker, 2006; McCutchan et al., 2003; Robbins et al., 2005; Sponheimer et al., 2003b; Vanderklift and Ponsard, 2003). When severely lacking protein, some animals will catabolize their own tissues, and this may result in higher $\delta^{15}\text{N}$ values (Cherel et al., 2005; Hobson and Clark, 1992). Overall, one must recognize that diet, physiology, and environment all interact together in a varied manner to produce the $\delta^{15}\text{N}$ values in animal tissues (Sandberg et al., 2012).

Stable isotope analyses in primatology

Relatively recently, field primatologists began pairing stable isotope analyses with feeding observations to gain a fuller understanding of NHP behavioral ecology. Previous studies have shown that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feces are indicative of diet within the last few days or weeks (Codron et al., 2005; Sponheimer et al., 2003a). The $\delta^{13}\text{C}$ values of NHPs' tissue and excreta provide data regarding their reliance on C_3 , C_4 , and CAM plants and the types of environments they inhabit, and $\delta^{15}\text{N}$ values may provide insights into trophic position. Therefore, analyzing the stable isotope values of these elements can aid in our understanding of NHP behavioral ecology (Crowley, 2012). Furthermore, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of populations or species can be shown in "isotope space" using biplots visually illustrate feeding niches and trophic positions (Newsome et al., 2007).

Stable isotope studies have also revealed the impact of humans on wild NHP populations (Loudon et al., 2007, 2014, 2016). Among the first studies to demonstrate how anthropogenically-disturbed habitats can influence the stable isotope values of NHPs occurred at the Beza Mahafaly Special Reserve (BMSR), Loudon et al. (2007) found that ring-tailed lemurs (*Lemur catta*) that ranged in human altered forests and ate more human foods, exhibited significantly different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ hair values from those that did not. In addition, Schurr et al.

(2012) demonstrated intergroup variation among Barbary macaques (*Macaca sylvanus*) residing in Gibraltar using stable carbon and nitrogen isotope analyses coupled with feeding observations. The macaque group that was isolated from tourists had significantly lower $\delta^{13}\text{C}$ values and significantly higher $\delta^{15}\text{N}$ values in comparison to the groups that interacted with humans. Two of these groups resided at sites that were often frequented by tourists and thus had access to human food. Since 1918, local authorities have provided food and water to the macaques to prevent them from looking for food in urban areas (Schurr et al., 2012). However, at these two sites bus and taxi drivers encouraged the macaques to interact with tourists by feeding them peanuts and uncooked pasta as incentives (Fuentes, 2006). Based on the significant intergroup variation in the stable carbon and nitrogen isotope values between sites, Schurr et al. (2012) data lend support to other research that has demonstrated that the frequency of human exposure through tourism affects macaque dietary patterns and nutrition (Fuentes, 2006).

Stable isotopes analysis is also useful for estimating niche partitioning among sympatric NHP species. One can define sympatric species as taxa that occupy similar ecological niches within the same habitat (Flores-Escobar et al., 2020). To co-exist in the same ecosystem, species should theoretically partition their available resources on temporal and spatial bases (Hutchinson, 1957). Sympatric relationships between two or more NHP species may be achieved via physiological and morphological adaptations or dietary strategies of two or more species (Spencer, 1995). Researchers used stable carbon and nitrogen isotope values to study trophic niches of sympatric mantled (*Alouatta palliata*) and black (*Alouatta pigra*) howler monkeys (Flores-Escobar et al., 2020). The black howler monkey groups displayed a significantly wider isotopic niche and generally higher $\delta^{15}\text{N}$ values (Flores-Escobar et al., 2020). As well, their isotopic niche overlapped with the isotopic niche exhibited by the mantled howler monkeys

(Flores-Escobar et al., 2020). This study demonstrated that sympatric NHP species occupy different isotopic spaces on biplots, and this has also been demonstrated among extant and extinct Malagasy lemur communities (Crowley et al., 2012).

Behavioral ecology of *Lemur catta* and *Propithecus verreauxi*

Ring-tailed lemurs are diurnal strepsirrhine primates that are endemic to the gallery, spiny bush, and dry deciduous forests of the south, southwest, and the interior highlands of Madagascar (Goodman et al., 2006). Average adult body size for ring-tailed lemurs is 2.2 kg (Sussman, 1991). Ring-tailed lemurs have behavioral and biological adaptations for consuming a diet of poor-quality leaves or leaves that contain secondary plant metabolites (Ganzhorn, 1986; Campbell et al., 2000; Simmen et al., 2006a, 2006b). These include an expansive caecum and colon, teeth with pronounced sharp-shearing crests (Kay and Hylander, 1978), and intestinal symbiotic flora that play a role in leaf fermentation (Campbell et al., 2000).

Some primatologists refer to ring-tailed lemurs as opportunistic frugivores/folivores, because of their omnivorous diets and tendency to forage throughout all levels of the forest canopy, including the ground (Rasamimanana and Rafidinarivo, 1993; Sauther, 1994, 1999; Sauther et al., 1999; Simmen et al., 2006a, 2006b). They will feed on fruit, flowers, stems, seeds, leaves, invertebrates, and even soil (Jolly, 1966; Sussman, 1974; Sauther, 1992; Sauther et al., 1999; Yamashita, 2000).

Most studies on ring-tailed lemurs have been conducted at the Berenty Private Reserve and BMSR (Jolly 1966; Goodman et al., 2006; Sauther and Cuzzo, 2009; Yamashita et al., 2016). At BMSR, most food items are only available seasonally (Sauther and Cuzzo, 2009). Previous studies have emphasized the importance of kily or tamarind trees (*Tamarindus indica*) in the ring-tailed lemur diet at BMSR (Sauther, 1998; Yamashita, 2000, 2002). According to

Sauther and Cuzzo (2009), ring-tailed lemurs there feed almost exclusively on kily fruits throughout the year despite the presence of other fruiting species. Sauther and Cuzzo (2009) classified tamarind or kily fruit as an FBF for ring-tailed lemurs living at BMSR, based on the earlier definition from Marshall et al. (2009). On the other hand, they suggested that there is an evolutionary “mismatch” between ring-tailed lemur dentition and their reliance on kily fruits as a FBF based on the particularly high rate of severe tooth wear and antemortem tooth loss among ring-tailed lemurs inhabiting BMSR (Sauther and Cuzzo, 2009). However, studies from wild and captive ring-tailed lemur populations have demonstrated that they have high salivary pH, and this may be an adaption to feeding on particularly acidic food items like tamarind fruits (Sauther and Cuzzo, 2009). In contrast, Sauther and Cuzzo (2009) noted that the BMSR Verreaux’s sifaka have more acidic salivary pH and also ingest much less acidic foods such as leaves. When food resources at BMSR are limited, ring-tailed lemurs will feed on mature leaves from locally cultivated sweet potatoes (*Ipomoea batatas*) and the wild grown Mexican thistle (*Argemone mexicana*) (Sauther and Cuzzo, 2009; LaFleur and Gould, 2009). For example, ring-tailed lemurs sought out these plant species in January 2005 when a cyclone altered the flowering and fruiting season of *T. indica* (LaFleur and Gould, 2009).

Verreaux’s sifaka (*Propithecus verreauxi*) are Malagasy strepsirrhines that are also endemic to the spiny bush and dry deciduous forests of southern/southwestern Madagascar (Louis et al., 2020). *P. verreauxi* are sympatric with *L. catta* at several locations including BMSR, Berenty Reserve, and Kirindy Mitea National Park (KMNP) (Simmen et al., 2003; Loudon et al., 2006; Norscia et al., 2006; Axel and Maurer, 2010). On average, adult Verreaux’s sifaka are 2.8 kg (Richard et al., 2002). Similar to ring-tailed lemurs, Verreaux’s sifaka exhibit numerous morphological and physiological adaptations to a folivorous diet (Norscia et al., 2006).

These adaptations include an enlarged stomach, an elongated caecum and colon, microbial gut flora that likely aid in the detoxification of plant foods (Hill, 1953; Norscia et al., 2006), and molars with pronounced sharp shearing crests suited for breaking down fibrous foods (Kay and Hylander, 1978). As such, *P. verreauxi* spends most of its time in the forest canopy (Loudon and Sauther, 2013). Based on feeding observations of *P. verreauxi* throughout southwestern Madagascar, Richard et al. (2002) recorded dietary differences between the wet and dry seasons with varying reliance on immature leaves, mature leaves, and unripe fruit. At Berenty Private Reserve, Simmen et al. (2003) reported similar findings, and noted that Verreaux's sifaka primarily consumed young and mature leaves but will switch to unripe fruits and flowers when these food sources become seasonally available (Simmen et al., 2003). Verreaux's sifaka may also "fall back" on bark to supplement their diet when preferred food resources are scarce (Richard, 1978; Sussman, 1999).

Field research on *P. verreauxi* has been conducted at BMSR since 1984 (Brockman, 2009; Lawler, 2009) and KMNP since 2006 (Lewis and Rakotondranaivo, 2011). At KMNP, Verreaux's sifaka fed mostly on leaves and flowers during the dry season, but preferentially consumed fruit during the wet season (Norscia et al., 2006). *P. verreauxi* groups at KMNP appeared to prefer plants belonging to the family *Leguminosae* (Norscia et al., 2006). Almost 10 years later, Koch et al. (2016) studied the same population of Verreaux's sifaka at KMNP and found similar results. During the late wet season, *P. verreauxi* individuals spent more time feeding on fruit, relied on flowers during transitional periods, and more frequently fed on mature leaves at the start of the dry season (Koch et al., 2016).

At BMSR, Verreaux's sifaka preferentially fed on the species *Euphorbia tirucalli*, *Acacia bellula*, and *Gonocrypta grevei* (Yamashita, 2002). Yamashita (2002) considers *E. tirucalli* a

staple food for all *P. verreauxi* groups. Unlike ring-tailed lemurs, Verreaux's sifaka almost exclusively feed on the unripe seeds of *T. indica* and rarely consume ripe kily fruit at the site (Yamashita, 2002). In contrast, ring-tailed lemurs rarely feed on unripe kily fruit which is more difficult to process and digest for *L. catta* which has a lower tolerance for tough foods, compared to *P. verreauxi* (Yamashita, 2000, 2002).

According to Amarasekare (2003), sympatry between species often results in feeding competition which may be reduced by dietary shifts resulting in differing feeding niches and trophic positions. Evidence from the studies above indicates that ring-tailed lemurs and Verreaux's sifaka may have achieved sympatry because of different physiological and morphological adaptations and different dietary strategies.

Current Study and Hypotheses

This study investigates the relationship between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the BMSR ring-tailed lemurs and Verreaux's sifaka to observations of their dietary patterns. The dietary patterns of each species were determined by the frequency of intervals that both species were observed consuming various plant organs (i.e. flowers, fruit, leaves and seeds) from the C_3 and CAM plants that grow at the reserve. Over the course of the study, 198 plant samples were collected from BMSR (C_3 plants, $N = 177$; CAM plants, $N = 21$).

H₁: The fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *L. catta* and *P. verreauxi* should accurately reflect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the plant organs they were observed consuming.

The stable carbon and nitrogen isotope values of plants consumed by both primate species at BMSR were used to predict the fecal stable carbon and nitrogen values of the *L. catta* and *P. verreauxi* populations. To account for each species' dependency on plant organs, the frequency of feeding records was included for each plant organ. Given, that the fecal stable

carbon and nitrogen values of each primate reflect the food items they consumed, their predicted fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values should match their feeding observations.

H₂: The BMSR ring-tailed lemurs should exhibit greater stable isotope variation compared to Verreaux's sifaka.

Feeding observations have documented that ring-tailed lemurs are omnivorous and incorporate a greater diversity of plant organs in comparison to their folivorous sifaka counterparts. This greater diversity should be reflected in their fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Towards this end, the BMSR ring-tailed lemurs should occupy a wider isotope space than Verreaux's sifaka when the fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are graphed on biplots for each month.

H₃: During the dry season months (April-July) when preferred ring-tailed lemur foods (i.e. fruits) were not available *L. catta* should shift to alternative dietary resources which should be reflected in their isotope values and identifiable in isotope space.

The plant organs at BMSR have different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Since *L. catta* consume different dietary resources between the wet and dry seasons there should be detectable variation in their fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between seasons. As such, shifts from consuming fruits to alternative foods such as flowers, leaves, and seeds should be detectable in their fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

H₄: Since *P. verreauxi* primarily consumed leaves, their fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values should not significantly change between the wet and dry seasons.

Since leaves are available throughout the year and distributed relatively evenly across space, fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the folivorous *P. verreauxi* should remain homogenous between the wet and dry seasons and from month to month.

H₅: Intragroup comparisons among ring-tailed lemurs and Verreaux's sifaka living in the protected habitat vs. the anthropogenically-disturbed habitat should be reflected in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

There should be observable and statistically significant variation for the fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the social groups for both the BMSR *L. catta* and *P. verreauxi* that occupy drastically different habitats (anthropogenically-disturbed habitat versus protected forest Parcel 1). NHPs that occupy anthropogenically-disturbed habitats frequently exhibit different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values given that they may consume human processed foods (Schurr et al., 2012), human crops (Loudon et al., 2014) or plants growing in open areas that lack a canopy effect (Loudon et al., 2016). Among the BMSR lemurs, it is expected that there will be more variation between groups given that they are omnivorous and readily consume human foods that often exhibit distinctly different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Loudon et al., 2007).

Chapter Three - Materials and Methods

Study Site

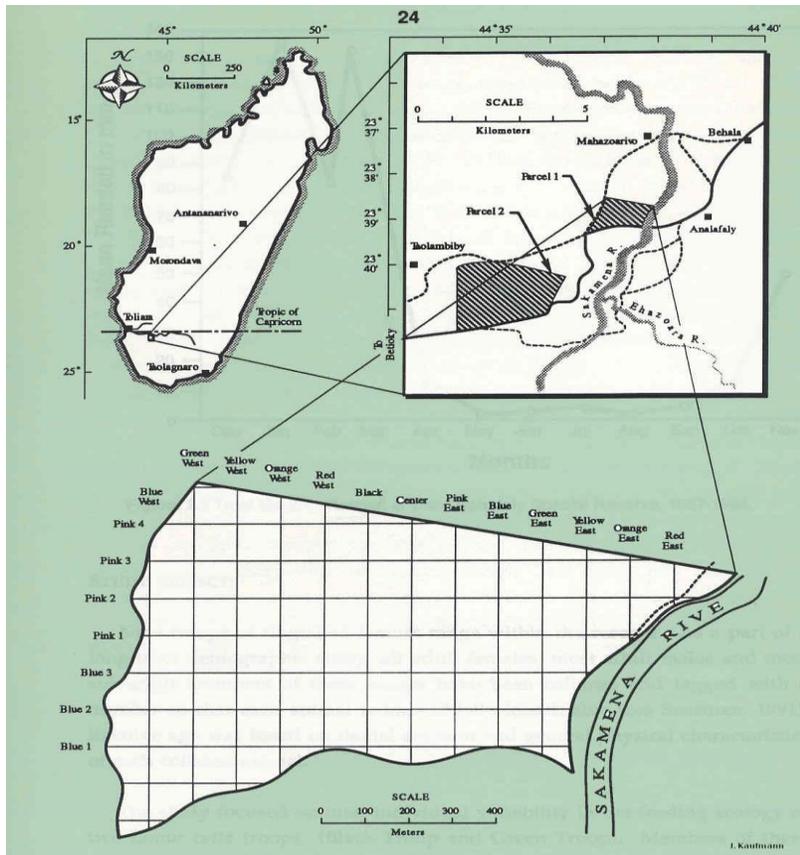


Figure 1. Map of the Beza Mahafaly Special Reserve (BMSR) and its location on the island of Madagascar.

The behavioral data and fecal samples analyzed in this study were collected at the Beza Mahafaly Special Reserve (BMSR) located in southwestern Madagascar (23°30'S latitude, 44 ° 40'E longitude; Fig. 1). The reserve was established on July 4th, 1986 due to a collaboration between the University of Antananarivo (then the University of Madagascar), Yale University, Washington University, and a few non-governmental organizations based in the United States and Madagascar (Ratsirarson, 2003; Sussman and Ratsirarson, 2006). Since its establishment, the reserve has been the site of research, training, and educational projects. In 2004, the management

of BMSR was transferred to the Madagascar National Parks Association which coordinates the network of protected parks and reserves in the country (Loudon, 2009; Sussman et al., 2012).

When data were collected, BMSR consisted of two noncontiguous parcels which were ~10 kilometers apart and totaled to approximately 600 hectares (ha) of land (Sussman and Ratsirarson, 2006; Loudon, 2009). During the mid-2000s the reserve increased to ~4000 ha (Loudon, 2009). At the time of the study, Parcel 1 was approximately 80 ha of fenced and protected gallery forest surrounded by unprotected forests located outside of the parcel. Parcel 1 consists of a layered canopy with dense terrestrial brush and hanging vines (Loudon, 2009). The eastern portion of Parcel 1 borders the Sakamena River. The most dominant tree species in Parcel 1 are kily (*Tamarindus indica*), but acacia (*Acacia royumae*), valiandro (*Quivisanthe papinae*), and sasavy (*Salvadora augustifolia*) are also common tree species (Sussman et al. 2012). Within the parcel, there are at least 49 plant families and 120 plant species (Ratsirarson 2003). In the westward portion, the parcel is characterized by more open areas and fewer tall trees (Loudon, 2009). On the border of the southern midsection of Parcel 1, there is also a research camp for BMSR (Loudon, 2009). It is important to note, that the BMSR ring-tailed lemurs (*Lemur catta*) will range outside of Parcel 1 to consume human food scraps available to them in the camp (Loudon, 2009).

Outside of Parcel 1, the existing forests are significantly fragmented (Whitelaw et al., 2005; Loudon et al., 2006). The unprotected forests outside of Parcel 1 are used by local people to graze livestock including zebu, goats, and sheep (Loudon et al., 2006). As a result of substantial grazing by livestock, the understory has been significantly reduced in the unprotected forests outside of the reserve (Whitelaw et al., 2005; Loudon et al., 2006). The Mahafaly are the dominant ethnic group at BMSR but, the Antandroy and the Tanala peoples also inhabit the area

(Loudon et al., 2006). The Mahafaly people consider ring-tailed lemurs and Verreaux's sifaka as *fady* or taboo to hunt, eat, or kill (Rambelanson, 1988; Loudon et al., 2006). However, in the future local people may be less likely to follow this cultural taboo due to poverty or change in diet (Pettus, 2005).

Southwestern Madagascar is extremely arid, and experiences highly variable climatic conditions. During the dry season (April-November) average rainfall is less than 10 mm per month. In the wet season (December-March), average rainfall is greater than 100 mm per month (Sauther, 1998; Ratsirarson et al., 2001). At BMSR, food availability is highest during the wet season, peaking in February and lowest during the dry season especially in July (Yamashita, 1996; Sauther, 1998). Throughout the duration of this field study, climatological data (i.e. temperature and rainfall) were collected because of this link between resource availability and rainfall. In total, 385.4 mm of rainfall were recorded. While the average annual rainfall at BMSR is about 550 mm (Sauther, 1998; Ratsirarson et al., 2001), only 385.4 mm of rainfall was recorded during the study period, indicating a drier period than average.

Study Subjects

This study includes two social groups of Verreaux's sifaka (*Propithecus verreauxi*) and two social groups of ring-tailed lemurs (*Lemur catta*). Both species are diurnal. One group from each species inhabited Parcel 1 and the other group inhabited the anthropogenically-disturbed forests outside of Parcel 1. Two species of nocturnal lemurs, the white-footed sportive lemur or lepilemur (*Lepilemur leucopus*) and the grey brown mouse lemur (*Microcebus griseorufus*) also inhabit BMSR (Ratsirarson, 2003; Sussman et al., 2012). The BMSR Verreaux's sifaka population has been studied since the inception of the reserve by Dr. Alison Richard and her colleagues, Drs. Richard Lawler, and Diane Brockman (Richard et al., 1991; 1993; 2002). Adult

Verreaux's sifaka are fitted with collars and numbered identification tags (Fig. 2a). Each tag is unique and is characterized by a specific polygon, color, and number for that group (Richard et al., 2002).

The ring-tailed lemur population at BMSR was studied continuously for decades by Drs. Robert Sussman, Michele L. Sauther and Frank P. Cuzzo (Cuzzo and Sauther, 2004, 2006; Sauther and Cuzzo, 2008). All the ring-tailed lemurs in this study were fitted with a color-coded collar indicating their group membership and numbered identification tags (Loudon, 2009; Figure 2b).



Figure 2. a) A collared Verreaux's sifaka (*Propithecus verreauxi*) with an identification tag. b) A collared ring-tailed lemur (*Lemur catta*) with an identification tag.

All individuals for which behavioral data and fecal samples were collected are shown below along with sex, affiliation, and habitat (Tables 1 and 2). Species are grouped separately. The column heading "Habitat" refers to if the individual inhabited Parcel 1 (Protected) or the anthropogenically-disturbed area outside of Parcel 1 (Disturbed) at BMSR.

Table 1. Ring-tailed lemur study population (N = 14) depicting individuals, sex, group membership, and habitat.

Species	Individual	Sex	Group	Habitat
<i>L. catta</i>	ID #6	Male	Black	Disturbed
<i>L. catta</i>	ID #110	Female	Black	Disturbed
<i>L. catta</i>	ID #116	Female	Black	Disturbed
<i>L. catta</i>	ID #206	Male	Black	Disturbed
<i>L. catta</i>	ID #212	Male	Black	Disturbed
<i>L. catta</i>	ID #226	Male	Black	Disturbed
<i>L. catta</i>	Wyatt	Male	Black	Disturbed
<i>L. catta</i>	ID #9	Female	Green	Protected
<i>L. catta</i>	ID #23	Female	Green	Protected
<i>L. catta</i>	ID #167	Female	Green	Protected
<i>L. catta</i>	ID #175	Male	Green	Protected
<i>L. catta</i>	ID #209	Male	Green	Protected
<i>L. catta</i>	ID #235	Female	Green	Protected
<i>L. catta</i>	BJ	Male	Green	Protected

Table 2. Verreaux's sifaka study population (N = 14) depicting individuals, sex, group membership, and habitat.

Species	Individual	Sex	Group	Habitat
<i>P. verreauxi</i>	ID #111	Female	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #475	Female	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #489	Female	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #492	Female	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #502	Male	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #546	Male	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #567	Female	Rivotse	Disturbed
<i>P. verreauxi</i>	ID #19	Female	Vao Vao	Protected
<i>P. verreauxi</i>	ID #80	Female	Vao Vao	Protected
<i>P. verreauxi</i>	ID #314	Female	Vao Vao	Protected
<i>P. verreauxi</i>	ID #467	Male	Vao Vao	Protected
<i>P. verreauxi</i>	ID #473	Male	Vao Vao	Protected
<i>P. verreauxi</i>	ID #483	Female	Vao Vao	Protected
<i>P. verreauxi</i>	Beta Male	Male	Vao Vao	Protected

Social Groups

There were 14 ring-tailed lemurs affiliated with two social groups, the Black and Green groups. These group names refer to the color of the collar worn by group members (Loudon,

2009). There was a total of 14 Verreaux's sifaka affiliated with two social groups, the Rivotse and Vao Vao groups. In the Mahafaly dialect, Rivotse roughly translates to "river" and this group was sometimes found near the Sakamena riverbed and Vao Vao translates to "news" (Loudon, 2009).

Black Group

The Black group inhabited the anthropogenically-disturbed forests directly south of Parcel 1. Their home range also includes the BMSR research camp. The Black group ranged into the camp each day and would opportunistically eat leftover foods discarded in the camp trash bins. The forest understories that the Black group inhabited were more open compared to those in Parcel 1. In addition, their habitat was accessible to human and ungulate foot traffic. The Black group lemurs preferred to sleep in a forest belt of kily trees next to the Sakamena River (Loudon, 2009). In December of 2005, the Black group was composed of two adult females, four adult males and one natal juvenile named Wyatt (Loudon, 2009; Table 1).

Green Group

The Green group spent much of their time on the eastern side of Parcel 1 directly on the border of the Sakamena River. Three observations were recorded of the Green group crossing the Sakamena River to consume mangoes (*Mangifera indica*) planted by the Mahafaly people (Loudon, 2009). The Green group was generally composed of four adult females, two adult males and one uncollared juvenile named BJ or "Big Juvenile" (Loudon, 2009).

Vao Vao

The Vao Vao group inhabited the eastern side of Parcel 1 nearby the Sakamena River and were sympatric with Green group. Their group was composed of three adult males and four adult females (Loudon, 2009; Table 2). Group composition was stable throughout the study period, but

it was difficult to determine a dominance hierarchy, because there few agonistic interactions between group members. However, it appeared that the oldest female was the highest-ranking individual succeeded by two middle-age females, a younger female, and the adult males of the group (Loudon, 2009). Overall, the Vao Vao group preferred to consume vine leaves which were available to them in the dense understory of the easternmost portion of Parcel 1 (Loudon, 2009).

Rivotse

The Rivotse group was composed of five adult females and two adult males. This group inhabited the anthropogenically-disturbed forests outside of Parcel 1 and were sympatric with the Black group. The Rivotse group ranged from the southern edge of Parcel 1 to the Sakamena River (Loudon, 2009). The southern region of their home range was most severely affected by anthropogenic modifications such as clearing forest for gardens and grazing by livestock. In some areas, the understory was completely absent due to heavy grazing (Loudon, 2009).

Behavioral Data Collection Methods

From December of 2005 to July of 2006, behavioral data were collected on collared sifaka (N = 14 individuals) and lemurs (N = 14 individuals) using 20-minute focal follows with a one-minute interval (Altmann, 1974; Fig. 2). Focal follows and ethograms were constructed based on a pilot study conducted during the previous year. The focal follows were developed to specifically record social and feeding behaviors and behaviors associated with the avoidance, elimination, and acquisition of parasitic infections (Loudon, 2009). During feeding bouts, the plant organ (i.e. bark, flower, fruit, leaf, nut, or seed) and plant species were recorded. *Ad libitum* notes were used to record behaviors that occurred outside or between intervals. All behavioral observations were recorded on a Sony Vaio portable laptop computer (Model VGN-T260P/L) and these data were backed up onto re-writable compact discs each week (Loudon, 2009). For

social interactions, the focal animal follows captured which individuals were initiators or recipients of agonistic affiliative behaviors and the frequency that each animal was in proximity or in contact with others (Loudon, 2009).

Fecal and Plant Sample Collection

Fecal samples were collected in the morning from each sifaka and lemur immediately after defecation (sifaka, N = 112; lemur, N = 112; total, N = 224). Fecal samples were collected from all study subjects at the end of each month (Loudon, 2009). In addition, 198 plant samples were also collected during this period from BMSR (C₃ plants, N = 177; CAM plants, N = 21). Fecal and plant samples were wrapped in foil and desiccated in a sealed camping oven placed in direct sunlight at the BMSR camp.

Lab Preparation

Fecal and plant samples were ground into a fine powder using a mortar and pestle. These samples were then weighed (~2500 µg) and placed in tin capsules. Weights were recorded on individual worksheets noting sample ID along with tray number and cell letter. Capsules were 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). Stable isotope ratios are expressed using the delta (δ) symbol in relation to an international standard in parts per thousand or parts per mill (‰) as in the following example for carbon isotopes:

$$\delta^{13}\text{C} \text{ (‰)} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) * 1000$$

Whereas $R = {}^{13}\text{C}/{}^{12}\text{C}$. The International standard for carbon is the Vienna PDB (V-PDB) and the International standard for nitrogen is atmospheric nitrogen (AIR) for ${}^{15}\text{N}/{}^{14}\text{N}$, respectively. PDB refers to PeeDee Belemnite, a Cretaceous marine fossil (*Belemnitella*

americana), but this source was exhausted and has been replaced by V-PDB standard (Sandberg et al., 2012).

Predicting fecal stable isotope values using feeding observations

Predictions for the observed fecal carbon and nitrogen abundances were calculated using the following equations:

$$\text{Predicted value for carbon} = [\{\Delta p(\% \text{CAM fruit})\} + \{\Delta p(\% \text{CAM leaf})\} + \{\Delta p(\% \text{C}_3 \text{ flower})\} + \{\Delta p(\% \text{C}_3 \text{ fruit})\} + \{\Delta p(\% \text{C}_3 \text{ leaf})\} + \{\Delta p(\% \text{C}_3 \text{ seed})\}] \pm [\text{FF}]$$

$$\text{Predicted value for nitrogen} = [\{\Delta p(\% \text{CAM fruit})\} + \{\Delta p(\% \text{CAM leaf})\} + \{\Delta p(\% \text{C}_3 \text{ flower})\} + \{\Delta p(\% \text{C}_3 \text{ fruit})\} + \{\Delta p(\% \text{C}_3 \text{ leaf})\} + \{\Delta p(\% \text{C}_3 \text{ seed})\}] \pm [\text{FF}]$$

In the above equations, Δp represents the carbon or nitrogen value of the plants which was multiplied by the percentage of each food item and photosynthetic pathway present in the diet of *L. catta* and *P. verreauxi*, respectively. The equation was roughly based on formulas produced by Schwarcz et al. (1985) and later altered by Loudon et al. (2014) to estimate the percentage of C_4 ($\% \text{C}_4$) plant consumption for vervet monkey (*Chlorocebus pygerythrus*) in South Africa. The percentages for each food item were determined by calculating the frequency of intervals that *L. catta* and *P. verreauxi* individuals fed on specific plant organs (i.e. flower, fruit, leaf, or seed). These frequencies were derived from the behavioral feeding observations collected during focal follows. The difference between plant stable isotope values versus those collected from animal fecal matter were accounted for by incorporating a fractionation factor (FF). The FF for carbon was +0.7‰ and for nitrogen was -2.0‰ (Loudon et al., 2019). Predicted

values were calculated for all lemur and sifaka social groups and for each study month (December-July).

Statistical Analysis

Statistical analyses using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the ring-tailed lemur and Verreaux's sifaka were conducted in the statistical program R. Paired t-tests ($N = 12$) were performed to examine the relationship between predicted and observed $\delta^{13}\text{C}$ fecal values, as well as between predicted and observed $\delta^{15}\text{N}$ fecal values. The paired t-tests analyzed predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values by NHP species ($N = 2$) and social group ($N = 4$).

Welch's ANOVA was used for comparisons of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of feces between the two habitats, and the wet and dry seasons. Prior to using Welch's ANOVA, species and habitat were combined into one predictor variable and species and season were combined into another predictor variable. Including more than one variable did not improve the fit of the linear model. As well, Welch's ANOVA accounts for unequal variances. In addition, to each ANOVA, pairwise comparisons were conducted using Tukey's Honestly Significant Difference (HSD) test.

Statistical Figures

All figures were generated in R to visualize the data using the package ggplot2. Individual bi-plots for each month ($N = 8$) were generated to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from Verreaux's sifaka and ring-tailed lemur social groups ($N = 4$) using the packages ggplot2 and ggiraphExtra. This same approach was used for comparisons for each group. Functions used include geom_smooth (method=lm) and stat ellipse () to plot regression lines and 95 percent CI ellipses, respectively.

Chapter Four - Results

The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the plants collected at Beza Mahafaly Special Reserve (BMSR) are presented in Table 3. As expected, the $\delta^{13}\text{C}$ values of the CAM plants were higher than those of the C_3 plants. Among the C_3 plant organs, seeds exhibited the highest $\delta^{13}\text{C}$ values followed by flowers and fruits. While leaves were the most depleted in ^{13}C . For $\delta^{15}\text{N}$, fruits exhibited the highest values while flowers exhibited the lowest values.

Table 3. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard deviations for the BMSR plant organs.

Pathway and Plant Part	$\delta^{13}\text{C}$ (‰)	N	$\delta^{15}\text{N}$ (‰)	N
C_3 flower	-27.4 ± 1.8	14	3.7 ± 4.4	14
C_3 fruit	-27.4 ± 2.1	29	5.2 ± 3.3	29
C_3 leaf	-28.9 ± 1.7	130	4.7 ± 3.3	130
C_3 seed	-26.0 ± 1.5	4	5.0 ± 3.3	4
CAM flower	-14.5 ± 1.0	5	5.4 ± 3.3	5
CAM leaf	-15.3 ± 1.8	16	5.2 ± 2.4	16

The feeding observations for the BMSR ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) are presented in Tables 4 and 5. Throughout the study, the ring-tailed lemurs primarily consumed C_3 fruits (64.8%) followed by C_3 leaves (27.2%). Overall, the BMSR ring-tailed lemurs were omnivorous in comparison to their sympatric sifaka counterparts (Tables 4 and 5). The BMSR Verreaux's sifaka predominantly consumed C_3 leaves (58.7%) followed by C_3 fruits (35.2%). Both primates at BMSR largely ignored CAM plants and CAM leaves only accounted for 1.1% of the ring-tailed lemur diet and 1.8% of the sifaka diet. Sifaka were not observed consuming any CAM fruits during the entire study and CAM fruits only accounted for 0.4% of the ring-tailed lemur diet. No C_4 plants were included in this study because they are rarely found throughout southern Madagascar and no studies have observed extant lemurs consuming them (Crowley and Godfrey, 2013).

Table 4. Frequency and percentages of feeding intervals for each plant organ part for the BMSR ring-tailed lemurs (*Lemur catta*).

Month	CAM fruit	CAM leaf	C ₃ flower	C ₃ fruit	C ₃ leaf	C ₃ seed	Total Intervals
December (wet)	0 (0%)	0 (0%)	6 (3.2%)	95 (50.8%)	49 (26.6%)	37 (19.8%)	187
January (wet)	0 (0%)	0 (0%)	0 (0%)	327 (65.8%)	170 (34.2%)	0 (0%)	497
February (wet)	0 (0%)	0 (0%)	85 (16.5%)	86 (16.7%)	344 (66.8%)	0 (0%)	515
March (wet)	0 (0%)	0 (0%)	43 (21.4%)	143 (71.1%)	15 (7.5%)	0 (0%)	201
April (dry)	13 (2.3%)	28 (5.0%)	18 (3.2%)	429 (76.5%)	73 (13.0%)	0 (0%)	561
May (dry)	0 (0%)	0 (0%)	32 (5.4%)	508 (86.0%)	51 (8.6%)	0 (0%)	591
June (dry)	0 (0%)	0 (0%)	0 (0%)	419 (79.4%)	109 (20.6%)	0 (0%)	528
July (dry)	0 (0%)	10 (3.1%)	0 (0%)	200 (61.7%)	114 (35.2%)	0 (0%)	324
Total	13 (0.4 %)	38 (1.1%)	184 (5.4%)	2207 (64.8%)	925 (27.2%)	37 (1.1%)	3404

Table 5. Frequency and percentages of feeding intervals for each plant organ part for the BMSR Verreaux's sifaka (*Propithecus verreauxi*).

Month	CAM fruit	CAM leaf	C ₃ flower	C ₃ fruit	C ₃ leaf	C ₃ seed	Total Intervals
December (wet)	0 (0%)	0 (0%)	21 (7.0%)	11 (3.7%)	267 (89.3%)	0 (0%)	299
January (wet)	0 (0%)	8 (1.3%)	1 (0.2%)	172 (27.3%)	450 (71.3%)	0 (0%)	631
February (wet)	0 (0%)	4 (0.8%)	0 (0%)	67 (13.3%)	423 (83.8%)	11 (2.2%)	505
March (wet)	0 (0%)	2 (0.5%)	77 (19.9%)	97 (25.1%)	210 (54.4%)	0 (0%)	386
April (dry)	0 (0%)	35 (9.3%)	36 (9.6%)	65 (17.3%)	235 (62.5%)	5 (1.3%)	376
May (dry)	0 (0%)	3 (0.6%)	17 (3.4%)	198 (40.1%)	276 (55.9%)	0 (0%)	494
June (dry)	0 (0%)	13 (1.6%)	0 (0%)	541 (65.0%)	278 (33.4%)	0 (0%)	832
July (dry)	0 (0%)	5 (1.4%)	0 (0%)	216 (59.3%)	143 (39.3%)	0 (0%)	364
Total	0 (0%)	70 (1.8%)	152 (3.9%)	1367 (35.2%)	2282 (58.7%)	16 (0.4%)	3887

H₁: The observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for *L. catta* and *P. verreauxi* should accurately reflect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the plant organs they were observed consuming during the study period.

To test H₁, the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for *L. catta* and *P. verreauxi* were compared to predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values. These predicted values were determined by calculating the frequency of behavioral intervals that each primate species was observed consuming each plant organ (see Methods). The observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values and the predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for each group on a monthly basis are presented in Tables 6-9. Isotopically speaking, the observed and predicted $\delta^{13}\text{C}$ fecal values for both the BMSR lemurs and sifakas aligned better than the observed and predicted $\delta^{15}\text{N}$ fecal values for both primate species. Comparisons between the two BMSR primates suggest that the predicted and observed $\delta^{13}\text{C}$ fecal values were more accurate for the ring-tailed lemurs. Overall, the months of

May-July were especially problematic for predicting the $\delta^{13}\text{C}$ fecal values for the sifaka and this may be linked to phenological leaf cycles at the site.

Table 6. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the ring-tailed lemur Green group at BMSR.

Month	Predicted $\delta^{13}\text{C}$	Observed $\delta^{13}\text{C}$	Predicted $\delta^{15}\text{N}$	Observed $\delta^{15}\text{N}$
December (wet)	-28.3	-27.1	4.5	3.0
January (wet)	-26.5	-27.1	4.8	3.1
February (wet)	-28.6	-27.7	3.8	2.7
March (wet)	-27.8	-26.9	4.2	2.6
April (dry)	-28.4	-26.8	4.2	3.1
May (dry)	-28.6	-26.9	4.3	3.1
June (dry)	-29.1	-27.2	5.2	3.0
July (dry)	-29.5	-26.5	6.3	3.1
Total	-28.4	-27.0	4.7	3.0

Table 7. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the ring-tailed lemur Black group at BMSR.

Month	Predicted $\delta^{13}\text{C}$	Observed $\delta^{13}\text{C}$	Predicted $\delta^{15}\text{N}$	Observed $\delta^{15}\text{N}$
December (wet)	-26.6	-26.4	4.8	3.0
January (wet)	-27.4	-27.4	4.6	2.9
February (wet)	-28.2	-28.6	4.6	2.7
March (wet)	-27.2	-26.7	5.3	3.2
April (dry)	not measured*	-28.1	not measured*	4.8
May (dry)	-26.6	-26.8	4.7	3.0
June (dry)	-28.0	-26.8	4.7	3.2
July (dry)	-28.0	-27.5	5.3	2.9
Total	-27.4	-27.3	4.8	3.2

*Ring-tailed lemurs in the Black group were observed feeding on CAM fruit during the month of April. Predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for April were not measured, because mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for CAM fruit were not available.

Table 8. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the Verreaux's sifaka group Vao Vao at BMSR.

Month	Predicted $\delta^{13}\text{C}$	Observed $\delta^{13}\text{C}$	Predicted $\delta^{15}\text{N}$	Observed $\delta^{15}\text{N}$
December (wet)	-28.5	-27.8	4.5	2.6
January (wet)	-27.9	-27.4	4.0	2.9
February (wet)	-29.9	-28.1	3.5	2.7
March (wet)	-28.1	-27.3	4.1	2.6
April (dry)	-29.2	-27.7	4.1	2.6
May (dry)	-29.2	-27.8	5.0	2.8
June (dry)	-28.6	-27.0	4.0	3.1
July (dry)	-29.1	-27.4	3.0	5.6
Total	-28.7	-27.6	4.0	3.1

Table 9. Monthly mean predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the Verreaux's sifaka group Rivotse at BMSR.

Month	Predicted $\delta^{13}\text{C}$	Observed $\delta^{13}\text{C}$	Predicted $\delta^{15}\text{N}$	Observed $\delta^{15}\text{N}$
December (wet)	-27.7	-28.2	3.0	2.7
January (wet)	-27.0	-27.7	2.7	2.8
February (wet)	-28.4	-25.8	3.5	2.8
March (wet)	-29.2	-27.6	3.5	2.7
April (dry)	-29.5	-30.0	3.9	2.8
May (dry)	-28.9	-26.9	3.2	3.0
June (dry)	-29.0	-27.0	3.4	3.0
July (dry)	-29.4	-26.7	4.4	3.0
Total	-28.6	-27.5	3.4	2.8

In total, six paired t-tests were performed between the predicted and observed $\delta^{13}\text{C}$ fecal values. These analyses included comparisons for the BMSR ring-tailed lemurs, the BMSR Verreaux's sifaka, and also for the two lemur groups, the Green group and the Black group, and the sifaka groups, Vao Vao and Rivotse. The mean predicted and observed $\delta^{13}\text{C}$ fecal values, and the associated p-values are presented in Table 10. As well, six paired t-tests were performed between the predicted and observed $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs, BMSR Verreaux's sifaka, and all four social groups. The mean predicted and observed $\delta^{15}\text{N}$ fecal values, and the associated p-values are presented in Table 11.

Most of the paired t-tests in Table 10 show that the predicted $\delta^{13}\text{C}$ values were significantly greater than the observed $\delta^{13}\text{C}$ fecal values for both the BMSR ring-tailed lemur and Verreaux's sifaka. However, the predicted $\delta^{13}\text{C}$ values were generally similar when compared to the observed $\delta^{13}\text{C}$ fecal values for the Black group. Overall, these results show that the predicted $\delta^{13}\text{C}$ values did not closely match with the observed $\delta^{13}\text{C}$ fecal values.

All the paired t-tests in Table 11 demonstrate that the predicted $\delta^{15}\text{N}$ values were significantly greater than the observed $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemur and Verreaux's sifaka. In contrast to the results shown in Table 10, the predicted $\delta^{15}\text{N}$ values were also significantly greater than the observed $\delta^{15}\text{N}$ fecal values for the Black group ($p = 0.000002889$). Generally, the predicted $\delta^{15}\text{N}$ values did not match well with the observed $\delta^{15}\text{N}$ fecal values.

Table 10. Mean predicted and observed $\delta^{13}\text{C}$ fecal values and their associated t-test p-values for the BMSR primates and social groups.

Species	Group	Mean Predicted $\delta^{13}\text{C}$	Mean Observed $\delta^{13}\text{C}$	p-value
<i>L. catta</i>	Green & Black	-27.9	-27.2	*0.005808
<i>P. verreauxi</i>	Vao Vao & Rivotse	-28.7	-27.5	*0.0005599
<i>L. catta</i>	Green	-28.4	-27.0	*0.007643
<i>L. catta</i>	Black	-27.4	-27.3	0.2833
<i>P. verreauxi</i>	Vao Vao	-28.7	-27.6	*0.000244
<i>P. verreauxi</i>	Rivotse	-28.6	-27.5	*0.06199

*Indicates significant p-values.

Table 11. Mean predicted and observed $\delta^{15}\text{N}$ fecal values and their associated t-test p-values for the BMSR primates and social groups.

Species	Group	Mean Predicted $\delta^{15}\text{N}$	Mean Observed $\delta^{15}\text{N}$	p-value
<i>L. catta</i>	Green & Black	4.8	3.1	*0.00000004896
<i>P. verreauxi</i>	Vao Vao & Rivotse	3.7	3.0	*0.00003953
<i>L. catta</i>	Green	4.7	3.0	*0.0002639
<i>L. catta</i>	Black	4.8	3.2	*0.00002889
<i>P. verreauxi</i>	Vao Vao	4.0	3.1	*0.0002547
<i>P. verreauxi</i>	Rivotse	3.4	2.8	*0.01054

*Indicates significant p-values.

Figure 3 shows median predicted and observed $\delta^{13}\text{C}$ fecal values for the BMSR ring-tailed lemurs. While Figure 4 depicts median predicted and observed $\delta^{13}\text{C}$ fecal values that were paired for the BMSR Verreaux's sifaka. For the BMSR ring-tailed lemurs, the majority of the observed $\delta^{13}\text{C}$ fecal values were less than the predicted $\delta^{13}\text{C}$ values (Fig. 3). Similarly, most of the observed $\delta^{13}\text{C}$ fecal values were lower than the predicted $\delta^{13}\text{C}$ values for the BMSR Verreaux's sifaka (Fig. 4). As well, median predicted $\delta^{13}\text{C}$ values appeared to match with median observed $\delta^{13}\text{C}$ fecal values more closely for the BMSR Verreaux's sifaka in comparison to the BMSR ring-tailed lemurs. It is important to note, Tables 6 and 7 suggest that the monthly mean predicted and observed $\delta^{13}\text{C}$ fecal values were a closer match for the BMSR ring-tailed lemur Black and Green groups than the sifaka social groups.

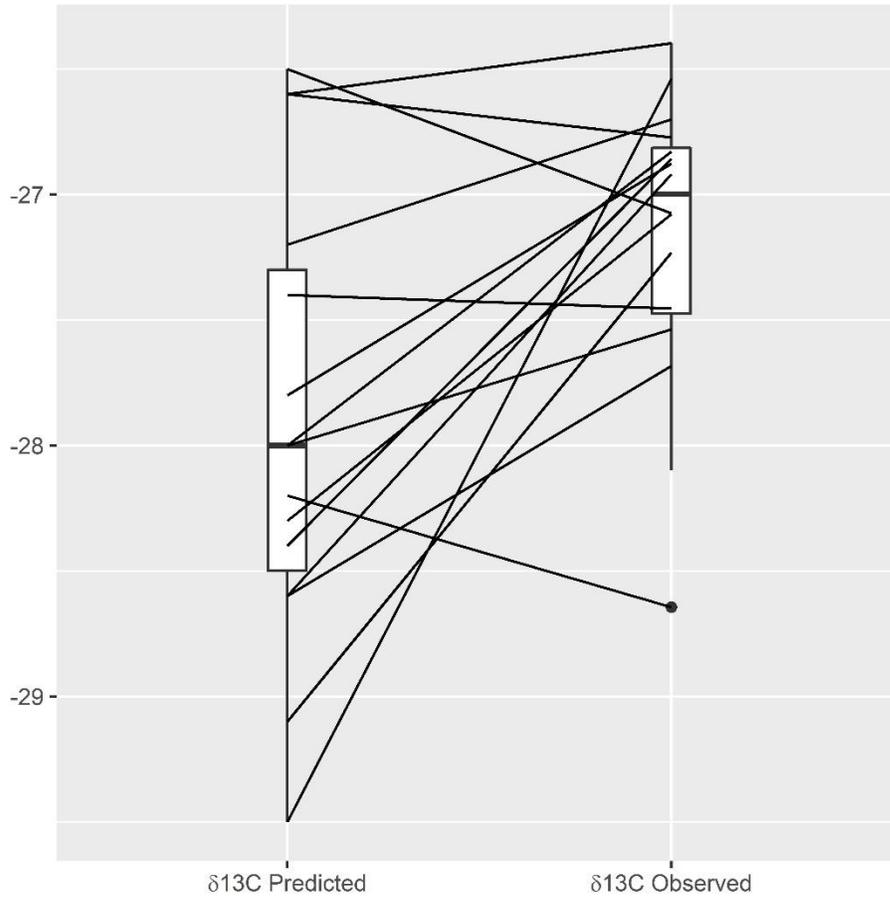


Figure 3. Median predicted $\delta^{13}\text{C}$ fecal values and observed $\delta^{13}\text{C}$ fecal values for the BMSR ring-tailed lemurs across all study months.

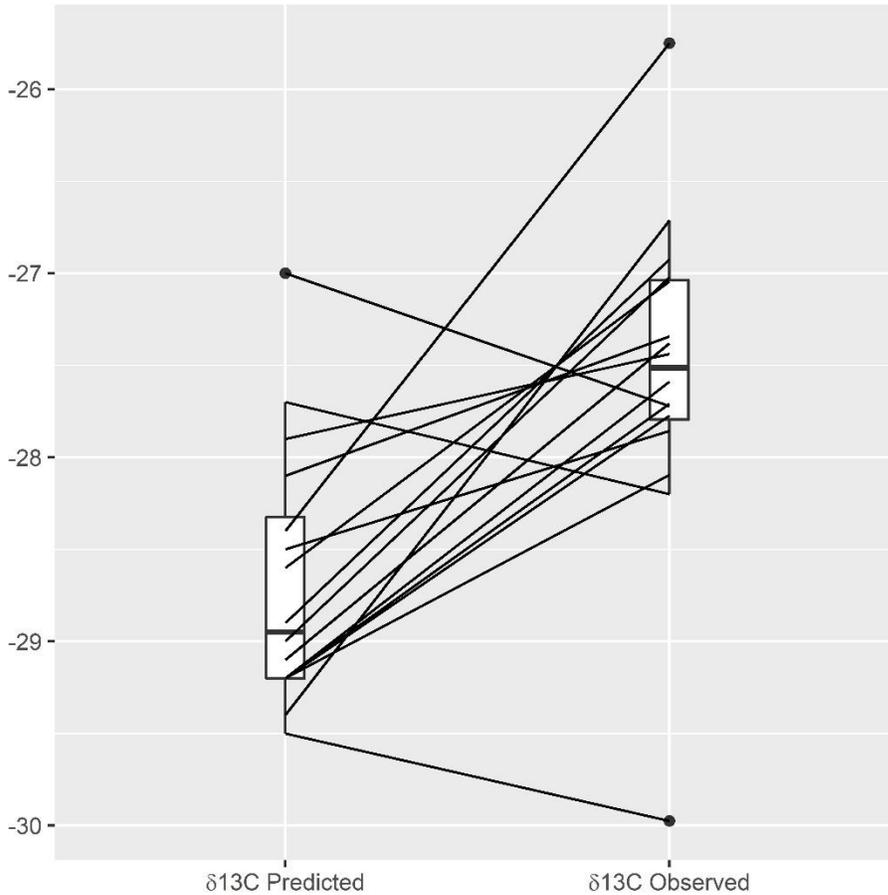


Figure 4. Median predicted $\delta^{13}\text{C}$ fecal values and observed $\delta^{13}\text{C}$ fecal values for the BMSR Verreaux's sifaka across all study months.

Median predicted and observed $\delta^{15}\text{N}$ fecal data for the BMSR ring-tailed lemurs are presented in Figure 5. Figure 6 depicts median predicted and observed $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka. For both BMSR primates, the median predicted $\delta^{15}\text{N}$ values were generally greater than the median observed $\delta^{15}\text{N}$ fecal values. As well, both Figures 5 and 6 demonstrate that the median predicted $\delta^{15}\text{N}$ values matched poorly with the median $\delta^{15}\text{N}$ observed fecal values for both species.

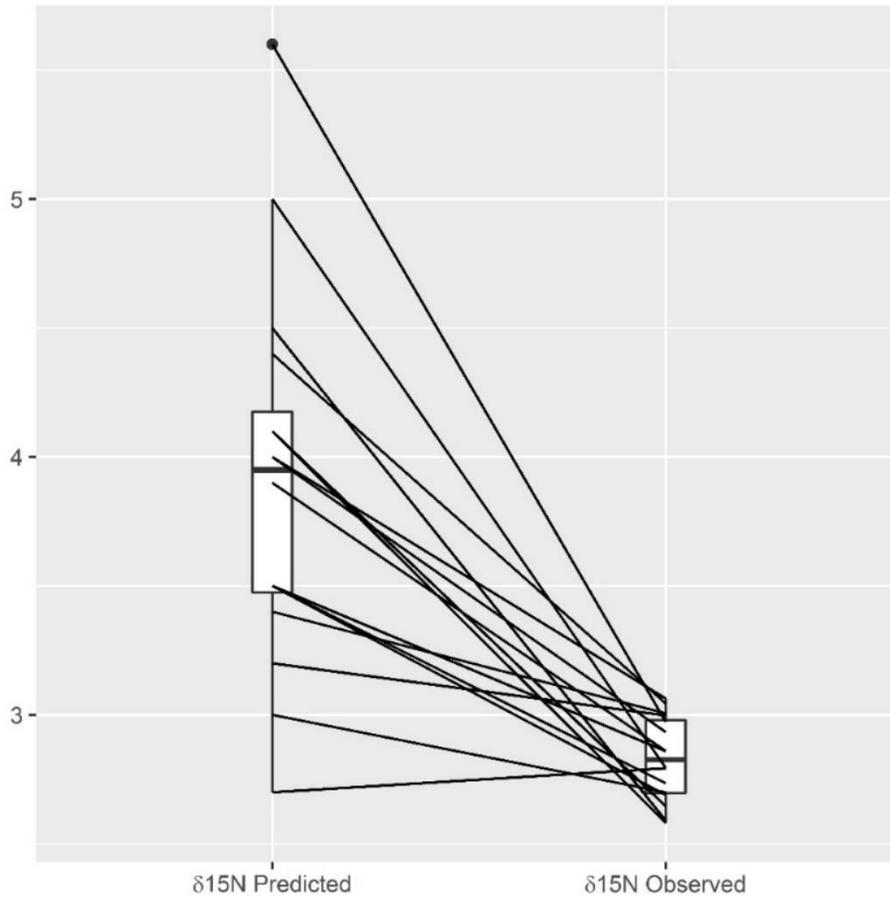


Figure 5. Median predicted $\delta^{15}\text{N}$ fecal values and observed $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs across all study months.

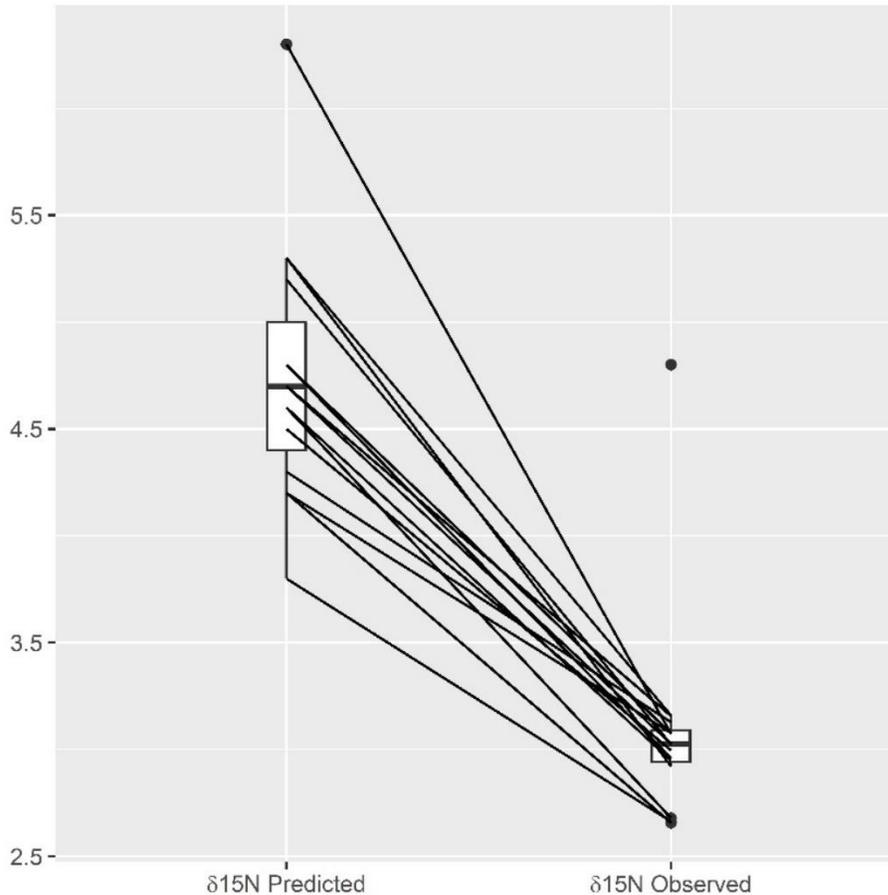


Figure 6. Median predicted $\delta^{15}\text{N}$ fecal values and observed $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka across all study months.

H₂: The BMSR ring-tailed lemurs should exhibit greater stable isotope variation when compared to the BMSR Verreaux's sifaka.

Among the BMSR ring-tailed lemurs, the $\delta^{13}\text{C}$ fecal values ranged between -26.3‰ and -28.6‰, while their $\delta^{15}\text{N}$ fecal values ranged between 2.6‰ and 4.8‰. Figure 7 shows that the BMSR ring-tailed lemurs generally occupied a greater isotope space when plotted using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes in comparison to the sifaka (Fig. 7). This was particularly true for the months of December, February, and July when the ring-tailed lemur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space was larger or encapsulated the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space of the sifaka.

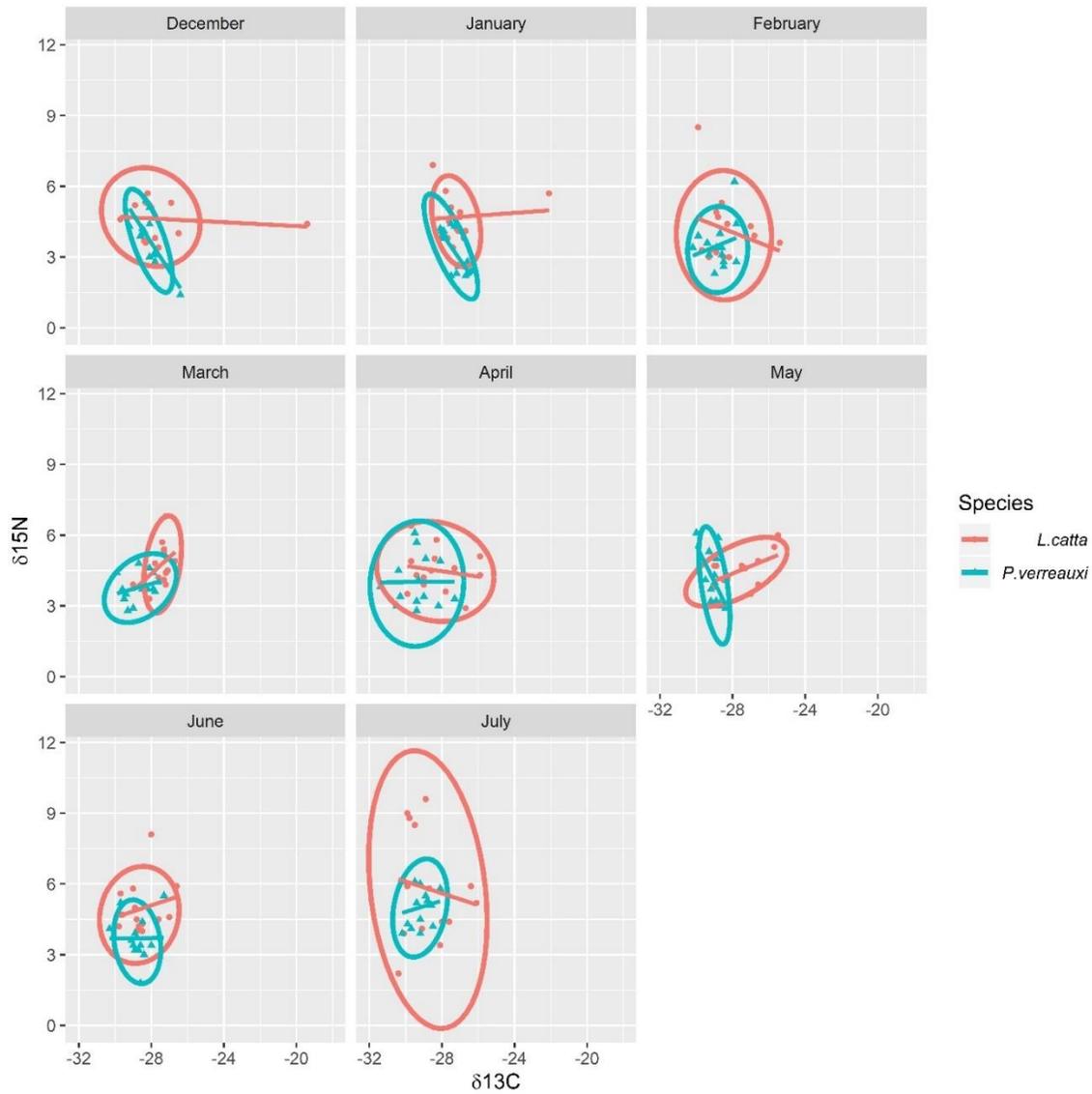


Figure 7. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs and Verreaux's sifaka. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.

Intergroup comparisons depicting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space for the BMSR ring-tailed lemurs and Verreaux's sifaka groups are presented in Figures 8 and 9.

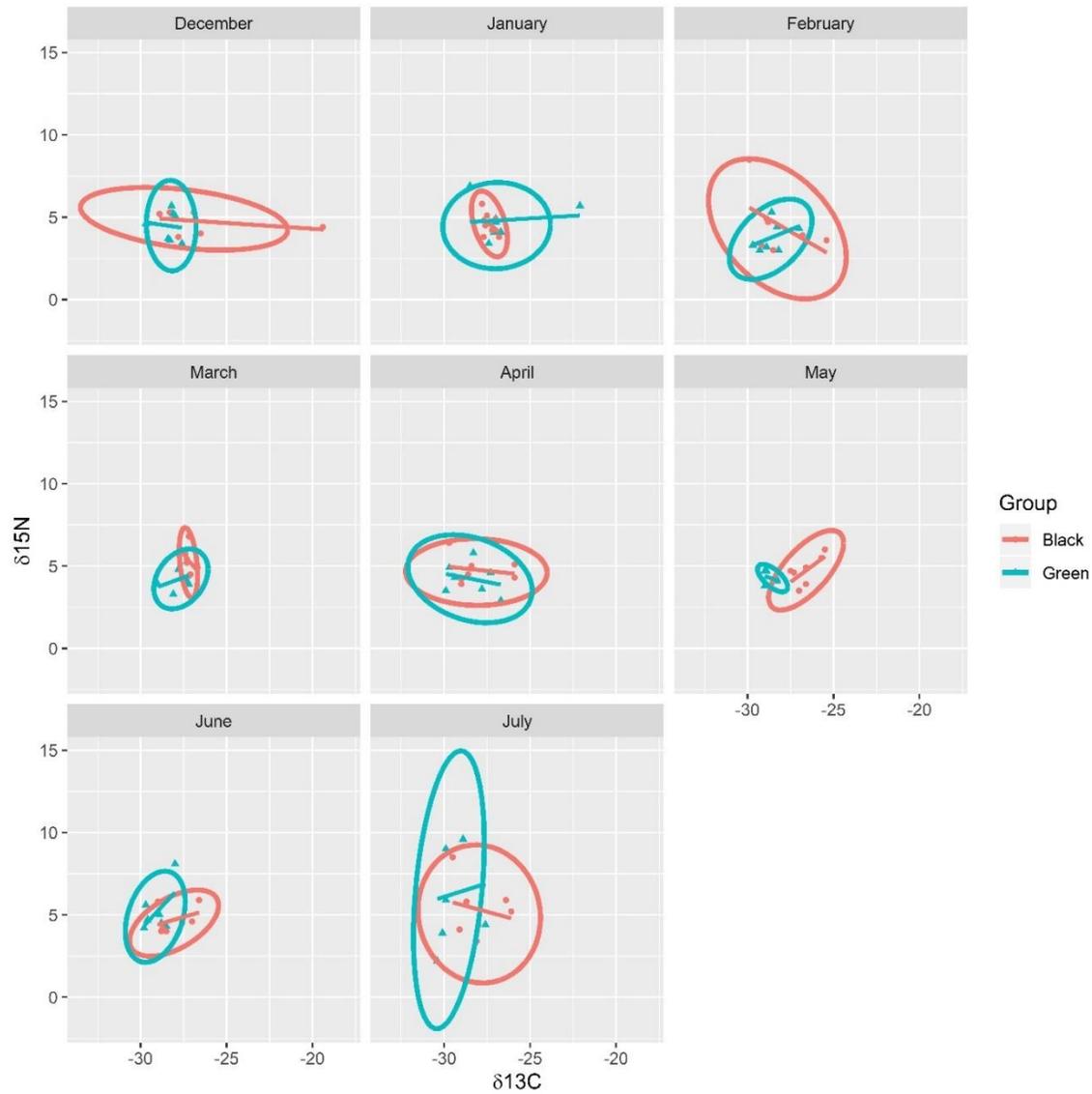


Figure 8. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemur Black and Green groups. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.

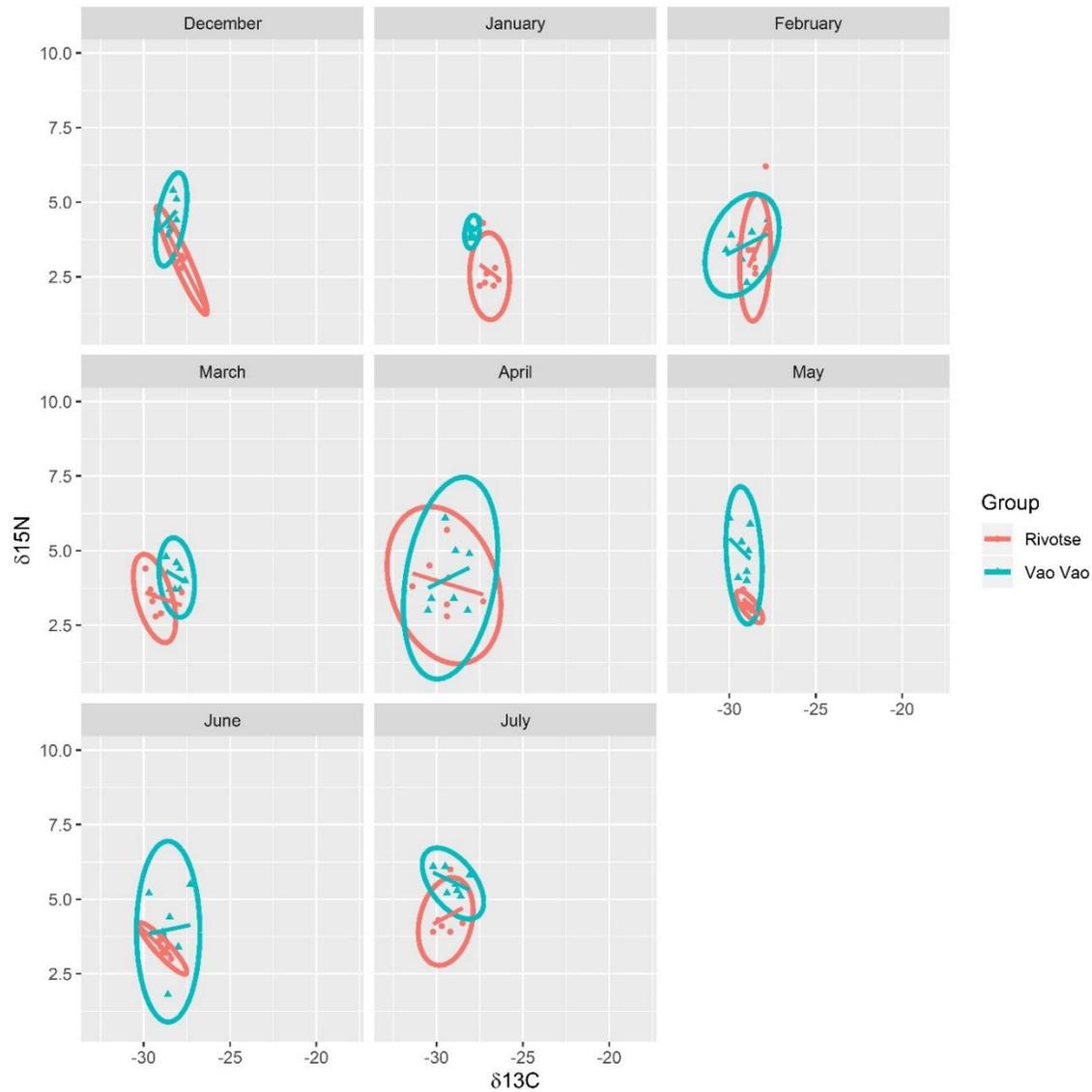


Figure 9. Monthly biplots showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka groups Rivotse and Vao Vao. Symbols represent individuals, lines show regressions, and ellipses are 95% confidence intervals.

Tables 12 and 13 show mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values with standard deviations and coefficients of variation for the BMSR ring-tailed lemurs. The Black and Green groups have similar mean $\delta^{15}\text{N}$ fecal values (Table 13), but dissimilar mean $\delta^{13}\text{C}$ fecal values (Table 12). Comparable standard deviations indicate that these both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values are relatively close together in isotope space. However, high coefficients of variation reveal that the $\delta^{15}\text{N}$ fecal

values are likely further apart in isotope space and more variable than the $\delta^{13}\text{C}$ fecal values.

Overall, ring-tailed lemurs have much lower coefficients of variation for their $\delta^{13}\text{C}$ fecal values (Table 12).

Table 12. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs.

Species	Group	Mean $\delta^{13}\text{C}$ (‰)	CV (%)
<i>L. catta</i>	Green & Black	-27.9 ± 1.5	5.3
<i>L. catta</i>	Green	-28.4 ± 1.3	4.6
<i>L. catta</i>	Black	-27.5 ± 1.6	5.7

Table 13. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs.

Species	Group	Mean $\delta^{15}\text{N}$ (‰)	CV (%)
<i>L. catta</i>	Green & Black	4.8 ± 1.3	27.1
<i>L. catta</i>	Green	4.7 ± 1.5	31.5
<i>L. catta</i>	Black	4.8 ± 1.1	22.4

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values with standard deviations and coefficients of variation for the BMSR Verreaux's sifaka are presented in Tables 14 and 15. Vao Vao and Rivotse have similar mean $\delta^{13}\text{C}$ fecal values, but less similar mean $\delta^{15}\text{N}$ fecal values. Based on similar standard deviations from the mean, both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values are relatively close together in isotope space. However, due to the high coefficients of variation it is probable that the $\delta^{15}\text{N}$ fecal values are oriented farther apart from each other than the $\delta^{13}\text{C}$ fecal values (Table 15). Table 14 shows that the $\delta^{13}\text{C}$ fecal values generally have lower coefficients of variation and thus are likely oriented closer together in isotope space.

Table 14. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka.

Species	Group	Mean $\delta^{13}\text{C}$ (‰)	CV (%)
<i>P. verreauxi</i>	Vao Vao & Rivotse	-28.7 ± 0.9	3.2
<i>P. verreauxi</i>	Vao Vao	-28.7 ± 0.8	2.7
<i>P. verreauxi</i>	Rivotse	-28.6 ± 1.0	3.6

Table 15. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka.

Species	Group	Mean $\delta^{15}\text{N}$ (‰)	CV (%)
<i>P. verreauxi</i>	Vao Vao & Rivotse	3.9 ± 1.0	26.3
<i>P. verreauxi</i>	Vao Vao	4.4 ± 1.0	21.9
<i>P. verreauxi</i>	Rivotse	3.4 ± 0.9	25.6

Figure 10 depicts median observed $\delta^{13}\text{C}$ fecal values for all the social groups of *L. catta* and *P. verreauxi*. Among the four social groups, there were significant differences in the $\delta^{13}\text{C}$ fecal values (Welch's ANOVA $F_{3,27} = 4.37$, $p = 0.01$). Pairwise comparisons using Tukey's HSD test showed that the $\delta^{13}\text{C}$ fecal values for the Black group were significantly higher compared to the Rivotse group ($p = 0.02$) and Vao Vao group ($p = 0.02$). All other pairwise comparisons were nonsignificant (Table 16).

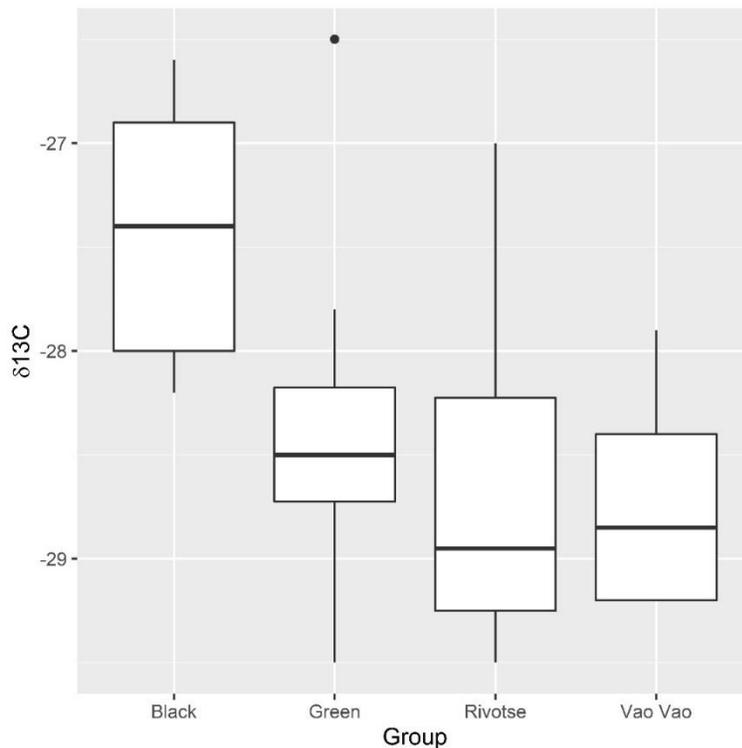


Figure 10. Median observed $\delta^{13}\text{C}$ fecal values for all social groups at BMSR.

Table 16. Pairwise comparisons for the observed $\delta^{13}\text{C}$ fecal values between all social groups at BMSR.

Intergroup comparisons	p-value
Green group vs. Black group	0.12
Rivotse vs. Black group	0.02
Vao Vao vs. Black group	0.01
Rivotse vs. Green group	0.90
Vao Vao vs. Green group	0.80
Vao Vao vs. Rivotse	1.00

Figure 11 shows median observed $\delta^{15}\text{N}$ fecal values across all four social groups. Among the BMSR lemur and sifaka social groups there were significant differences (Welch's ANOVA $F_{3,27}=8.17, p=0.0004$). Pairwise comparisons for the $\delta^{15}\text{N}$ fecal values between the four groups using Tukey's HSD test are presented in Table 17. The $\delta^{15}\text{N}$ fecal values for Rivotse were significantly lower than the $\delta^{15}\text{N}$ fecal values for all other groups. All other pairwise comparisons were nonsignificant (Table 17).

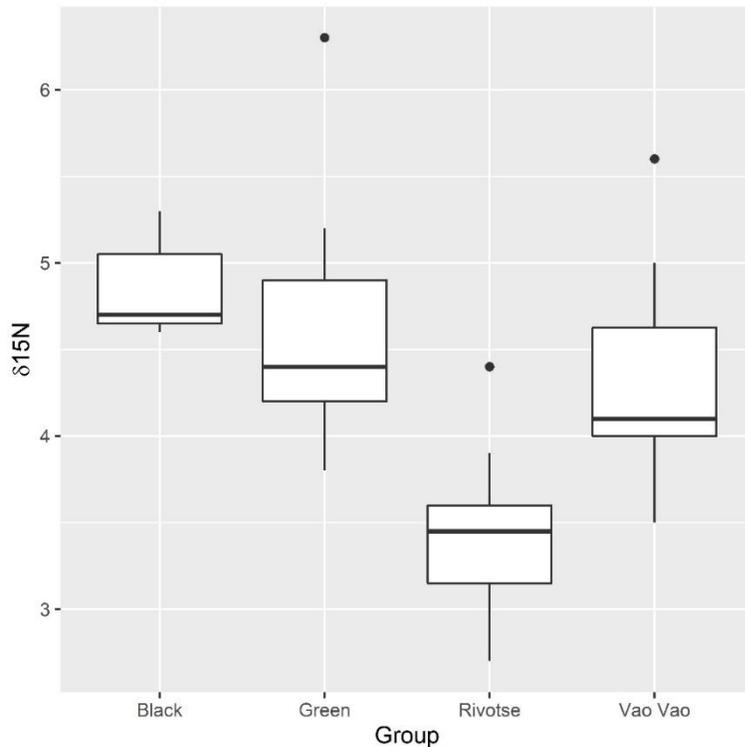


Figure 11. Median observed $\delta^{15}\text{N}$ fecal values for all social groups at BMSR.

Table 17. Pairwise comparisons for the observed $\delta^{15}\text{N}$ fecal values between all social groups at BMSR.

Intergroup comparisons	p-value
Green group vs. Black group	0.92
Rivotse vs. Black group	0.0007
Vao Vao vs. Black group	0.39
Rivotse vs. Green group	0.002
Vao Vao vs. Green group	0.73
Vao Vao vs. Rivotse	0.03

Figure 12 depicts the median observed $\delta^{13}\text{C}$ fecal values across species (lemur or sifaka) and season (wet or dry). When grouped by species and season, there were significant differences among the four groups (Welch's ANOVA $F_{3, 27} = 6.10$, $p = 0.003$). Pairwise comparisons for the $\delta^{13}\text{C}$ fecal values grouped by species and season using Tukey's HSD test are shown in Table 18. The majority of pairwise comparisons for the $\delta^{13}\text{C}$ fecal values were not significant (Table 18). Only the $\delta^{13}\text{C}$ fecal values for *P. verreauxi* during the dry season were significantly different when compared to the $\delta^{13}\text{C}$ fecal values of *L. catta* during the wet season.

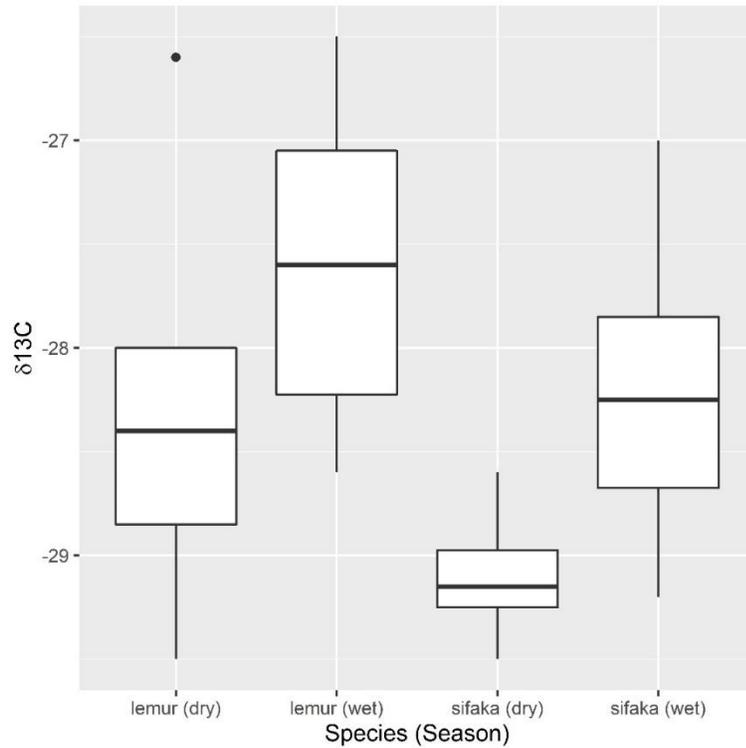


Figure 12. Median observed $\delta^{13}\text{C}$ fecal values grouped by species and season at BMSR.

Table 18. Pairwise comparisons for the observed $\delta^{13}\text{C}$ fecal values grouped by species and season at BMSR.

Species and Season	p-value
lemur, wet season vs. lemur, dry season	0.22
sifaka, dry season vs. lemur, dry season	0.16
sifaka, wet season vs. lemur, dry season	1.00
sifaka, dry season vs. lemur, wet season	0.001
sifaka, wet season vs. lemur, wet season	0.26
sifaka, wet season vs. sifaka, dry season	0.10

Figure 13 shows median observed $\delta^{15}\text{N}$ fecal values grouped by species and season. There were significant differences among the $\delta^{15}\text{N}$ fecal values when grouped by species and season (Welch's ANOVA $F_{3, 27} = 6.05$, $p = 0.003$). Pairwise comparisons for the $\delta^{15}\text{N}$ fecal values grouped by species and season using Tukey's HSD test are shown in Table 19. Two of six pairwise comparisons were statistically significant (Table 19). During the wet season, the $\delta^{15}\text{N}$

fecal values for sifaka groups were significantly lower than the $\delta^{15}\text{N}$ fecal values for lemur groups ($p = 0.03$). As expected, the $\delta^{15}\text{N}$ fecal values for sifaka groups during the wet season were also significantly lower than the $\delta^{15}\text{N}$ fecal values for lemur groups during the dry season ($p = 0.002$).

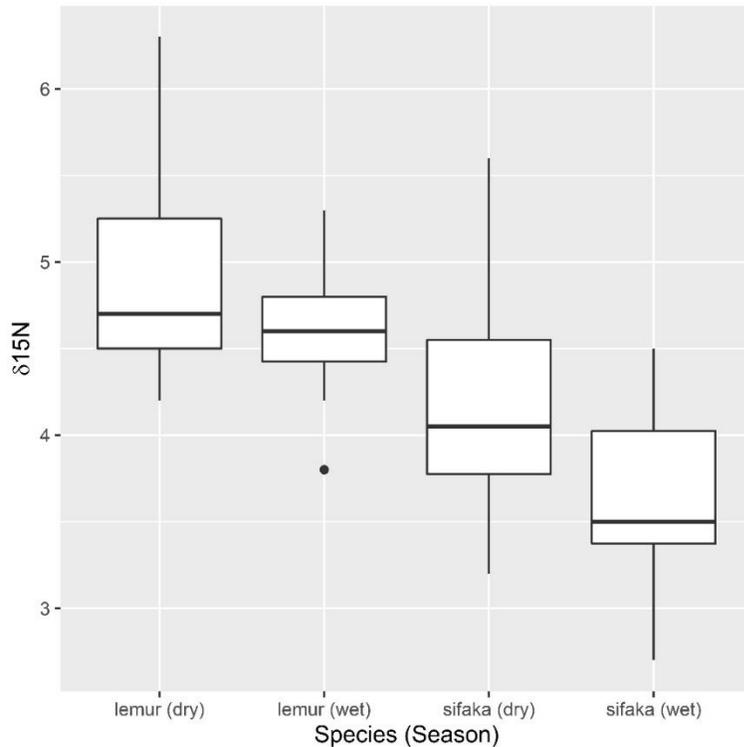


Figure 13. Median observed $\delta^{15}\text{N}$ fecal values grouped by species and season at BMSR.

Table 19. Pairwise comparisons for the observed $\delta^{15}\text{N}$ fecal values grouped by species and season at BMSR.

Species and Season	p-value
lemur, wet season vs. lemur, dry season	0.67
sifaka, dry season vs. lemur, dry season	0.13
sifaka, wet season vs. lemur, dry season	0.002
sifaka, dry season vs. lemur, wet season	0.66
sifaka, wet season vs. lemur, wet season	0.03
sifaka, wet season vs. sifaka, dry season	0.27

Tables 20 and 21 show mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values with standard deviations, and coefficient of variation percentages for the BMSR ring-tailed lemurs, grouped by season. Mean

$\delta^{13}\text{C}$ fecal values for the dry season are dissimilar between the Green and Black groups, but similar for the wet season. For the Green and Black groups, mean $\delta^{15}\text{N}$ fecal values are relatively comparable across both the wet and dry seasons. Overall, the coefficients of variation are relatively low for the $\delta^{13}\text{C}$ fecal values and relatively high for the $\delta^{15}\text{N}$ fecal values across both seasons. During the dry season, the Green group has a particularly high coefficient of variation (36.1%) based on its $\delta^{15}\text{N}$ fecal values. However, based on its $\delta^{13}\text{C}$ fecal values during the dry season, the Green group also has the lowest coefficient of variation (3.2%). This indicates that generally $\delta^{13}\text{C}$ fecal values are clustered relatively close together while $\delta^{15}\text{N}$ fecal values exhibit more variation.

Table 20. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs, grouped by season.

Species	Group	Season	Mean $\delta^{13}\text{C}$ (‰)	CV (%)
<i>L. catta</i>	Green & Black	dry	-28.3 ± 1.3	4.5
<i>L. catta</i>	Green	dry	-28.9 ± 0.9	3.2
<i>L. catta</i>	Black	dry	-27.7 ± 1.3	4.6
<i>L. catta</i>	Green & Black	wet	-27.6 ± 1.6	5.9
<i>L. catta</i>	Green	wet	-27.8 ± 1.4	5.0
<i>L. catta</i>	Black	wet	-27.3 ± 1.8	6.7

Table 21. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR ring-tailed lemurs, grouped by season.

Species	Group	Season	Mean $\delta^{15}\text{N}$ (‰)	CV (%)
<i>L. catta</i>	Green & Black	dry	4.9 ± 1.5	29.8
<i>L. catta</i>	Green	dry	5.0 ± 1.8	36.1
<i>L. catta</i>	Black	dry	4.9 ± 1.1	22.0
<i>L. catta</i>	Green & Black	wet	4.6 ± 1.0	23.1
<i>L. catta</i>	Green	wet	4.3 ± 1.0	22.0
<i>L. catta</i>	Black	wet	4.8 ± 1.1	23.2

Tables 22 and 23 present mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values, standard deviations, and coefficient of variation percentages for the BMSR Verreaux's sifaka, grouped by season. Table 22 shows that Rivotse and Vao Vao have similar mean $\delta^{13}\text{C}$ fecal values for both the wet and dry

seasons. On the other hand, their mean $\delta^{15}\text{N}$ fecal values are dissimilar across both seasons. Based on analogous standard deviations, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values are both clustered similarly close together isotopically. On the contrary, the generally high coefficients of variation for the $\delta^{15}\text{N}$ fecal values indicate that these values are not closely oriented to each other for either season. However, it is important to note that during the wet season based on $\delta^{15}\text{N}$ fecal values, Vao Vao had the lowest coefficient of variation (14.7%). Comparably, the much lower coefficients of variation for the $\delta^{13}\text{C}$ fecal values show that these values are oriented closely isotopically during both the wet and dry seasons.

Table 22. Mean $\delta^{13}\text{C}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka, grouped by season.

Species	Group	Season	Mean $\delta^{13}\text{C}$ (‰)	CV (%)
<i>P. verreauxi</i>	Vao Vao & Rivotse	dry	-29.1 ± 0.8	2.6
<i>P. verreauxi</i>	Vao Vao	dry	-29.0 ± 0.7	2.5
<i>P. verreauxi</i>	Rivotse	dry	-29.2 ± 0.8	2.6
<i>P. verreauxi</i>	Vao Vao & Rivotse	wet	-28.2 ± 0.8	3.1
<i>P. verreauxi</i>	Vao Vao	wet	-28.4 ± 0.7	2.4
<i>P. verreauxi</i>	Rivotse	wet	-28.1 ± 1.0	3.5

Table 23. Mean $\delta^{15}\text{N}$ fecal values with standard deviations and coefficient of variation (CV) percentages for the BMSR Verreaux's sifaka, grouped by season.

Species	Group	Season	Mean $\delta^{15}\text{N}$ (‰)	CV (%)
<i>P. verreauxi</i>	Vao Vao & Rivotse	dry	4.2 ± 1.1	25.7
<i>P. verreauxi</i>	Vao Vao	dry	4.7 ± 1.1	24.5
<i>P. verreauxi</i>	Rivotse	dry	3.7 ± 0.8	21.0
<i>P. verreauxi</i>	Vao Vao & Rivotse	wet	3.6 ± 0.9	24.4
<i>P. verreauxi</i>	Vao Vao	wet	4.0 ± 0.6	14.7
<i>P. verreauxi</i>	Rivotse	wet	3.1 ± 0.9	28.2

H₃: During the dry season months (April-July) when preferred ring-tailed lemur foods (i.e. fruits) were not available, *L. catta* should shift to alternative dietary resources which should be reflected in their stable isotope values and identifiable in isotopic space.

During the dry season months (April-July), it was expected that the BMSR ring-tailed lemurs should switch from preferred fruits to fewer desirable foods: leaves, seeds, and CAM

resources (Table 4). However, feeding observations (Table 4) show that they consumed mostly fruit resources during the dry season. As well, Figures 7 and 8 (above) demonstrate that there were few changes in their $\delta^{13}\text{C}$ fecal values between the dry and wet seasons. During June and July, the lemurs consumed foods with highly variable $\delta^{15}\text{N}$ fecal values (Fig. 7 and Fig. 8). Low coefficients of variation for ring-tailed lemurs (Table 12) show that their $\delta^{13}\text{C}$ fecal values were more closely clustered and much less variable than their $\delta^{15}\text{N}$ fecal values (Table 13).

Particularly low (3.2%) and high (36.1%) coefficients of variation for the Green group during the dry season demonstrate that this group may have been more affected by seasonal shifts than the Black group. Overall, the data provided here does not support H₃.

H₄: Since *P. verreauxi* primarily consumed leaves, their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values should not significantly change between the wet and dry seasons.

It was expected that the BMSR sifaka $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values would not significantly differ between the wet and dry seasons. Among the BMSR Verreaux's sifaka, the $\delta^{13}\text{C}$ fecal values ranged between -25.7‰ and -29.9‰. While their $\delta^{15}\text{N}$ fecal values ranged between 2.5‰ and 3.0‰. According to the pairwise comparisons using Tukey's HSD test, the BMSR sifaka $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values were similar between the wet and dry seasons (Table 14, $\delta^{13}\text{C}$: $p = 0.10$; Table 15, $\delta^{15}\text{N}$: $p = 0.27$). Figures 12 and 13 correspond to Tables 14 and 15, respectively. Figure 12 illustrates that the BMSR sifaka $\delta^{13}\text{C}$ fecal values were generally lower during the wet season in comparison to the dry season when fruit was less available. As shown in Figure 13, the BMSR sifaka $\delta^{15}\text{N}$ fecal values were slightly lower during the wet season in comparison to the dry season.

In contrast, the feeding observations revealed that leaves accounted for 74.1% of wet season feeding and 45.1% of dry season feeding (Table 5). As well, Figures 7 and 9 show dynamic shifts in the BMSR sifaka $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values as they followed changes in

feeding patterns from month to month. This is best illustrated by the changes in isotopic niche space for Vao Vao from December to February and then again from March to May (Fig. 9). While the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of *P. verreauxi* were overall similar between the dry and wet seasons, there were changes in their feeding behaviors and isotopic niche space from month to month and between seasons. As well, a relatively low coefficient of variation (14.7%) for $\delta^{15}\text{N}$ during the wet season indicates that Vao Vao was likely consuming a much less variable diet than Rivotse. In comparison, Rivotse during the wet season had a much higher coefficient of variation (28.2%) However, there is still a lack of statistical support for H_4 .

H₅: Intragroup comparisons among ring-tailed lemurs and Verreaux's sifaka living in the protected habitat vs. the anthropogenically-disturbed habitat should be reflected in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values.

In general, there is some variation for the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values between the sifaka and lemur groups living in protected and anthropogenically-disturbed habitats. In Figure 8, there is observable variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space between the ring-tailed lemur Green and Black groups. There is also observable variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niche space between the Verreaux's sifaka Vao Vao and Rivotse (Fig. 9).

The $\delta^{15}\text{N}$ fecal values of Rivotse were significantly lower than the $\delta^{15}\text{N}$ fecal values of Vao Vao, the Green group, and the Black group (Fig. 11; Welch's ANOVA $F_{3, 27} = 8.17, p = 0.0004$). Tukey's HSD test shows that the $\delta^{15}\text{N}$ fecal values of Rivotse while living in the anthropogenically-disturbed habitat were significantly less than the $\delta^{15}\text{N}$ fecal values of Vao Vao (Fig. 11; Table 13, $\delta^{15}\text{N}$: $p = 0.03$) which inhabited protected Parcel 1. However, Tukey's HSD test also demonstrates that the $\delta^{13}\text{C}$ fecal values for the Black group residing in the anthropogenically-disturbed habitat were generally similar when compared to the $\delta^{13}\text{C}$ fecal values for the Green group which inhabited protected Parcel 1 (Fig. 10; Table 12). For the

sifaka groups, Rivotse and Vao Vao, it appears that habitat type (protected versus disturbed) may have affected their $\delta^{15}\text{N}$ fecal values and resulted in significantly different values between the two groups. However, it appears that habitat type had little to no effect on the $\delta^{13}\text{C}$ fecal values for the ring-tailed lemurs (Fig. 10; Table 12).

Chapter Five - Discussion

Predicting the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values

H_1 put forth the expectation that the predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values would largely match the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*). This was expected, because measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for BMSR plant organs coupled with feeding intervals for each plant organ were used to determine predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for both primate species. However, the results did not support this hypothesis. For $\delta^{13}\text{C}$, predicted and observed values appear to match most closely for the Black group, while for $\delta^{15}\text{N}$, predicted and observed values appear to match best for Rivotse. On the other hand, paired t-tests show that for most groups predicted and observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values were significantly different and therefore do not match well. However, for the Black group, predicted and observed $\delta^{13}\text{C}$ fecal values were overall similar. This indicates that predicted $\delta^{13}\text{C}$ fecal values for the Black group are likely more reliable than predicted $\delta^{13}\text{C}$ fecal values for any of the other groups that were tested at BMSR.

Past studies have demonstrated that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values reveal diet within days or weeks (Codron et al., 2005; Sponheimer et al., 2003a). Therefore, it is possible that the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values were more indicative of recently consumed food items, rather than all resources consumed throughout the month. Furthermore, monthly feeding intervals were used with plant isotope values to determine the predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values. Predicted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values may be more representative of monthly dietary composition, whereas the observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values may be more indicative of dietary composition just days or weeks before a fecal sample was collected in the field.

In the case of the Black group, predicted and observed $\delta^{13}\text{C}$ fecal values may have been more accurate if their diet were less varied than that of the other groups. Loudon et al. (2009) and Whitelaw et al. (2005) note the lack of an understory in some areas of the unprotected forest outside of Parcel 1 and that the forests were extremely fragmented due to livestock grazing. Previous studies on tropical forest systematics have shown that $\delta^{13}\text{C}$ values are highest at the top of the canopy and lowest in the understory due to a “canopy effect” (van der Merwe and Medina, 1991; Broadmeadow et al., 1992; Broadmeadow and Griffiths, 1993; Heaton, 1999). However, the unprotected forests at BMSR were more open due to livestock grazing and this results in higher $\delta^{13}\text{C}$ fecal values given the lack of a canopy effect as has been documented in chimpanzees (*Pan troglodytes*) living in open environments (Sponheimer et al., 2006b; Loudon et al., 2016).

For the BMSR ring-tailed lemurs and Verreaux’s sifaka, all paired t-tests performed between the predicted and observed $\delta^{15}\text{N}$ fecal values were significantly different. This suggests that the predicted and observed $\delta^{15}\text{N}$ fecal values matched relatively poorly. This is not surprising, given that the $\delta^{15}\text{N}$ values of plants and soils often vary in response to nitrogen cycling, water availability and nitrogen loss. Sandberg et al. (2012) note that aside from diet, physiology and the environment also play crucial roles in the $\delta^{15}\text{N}$ values of animals. Furthermore, several studies note that diet to tissue nitrogen ratios exhibit variability in response to protein quality (Robbins et al., 2005; Roth and Hobson, 2000; Bearhop et al., 2002; Pearson et al., 2003; Sponheimer et al., 2003b; Vanderklift and Ponsard, 2003). If lacking protein, animals may catabolize their own tissue, and this results in higher $\delta^{15}\text{N}$ values (Hobson et al., 1993). However, to determine if the BMSR primates are lacking macronutrients or in poor health, physical examinations would be required.

One must also take into consideration that the biological and behavioral differences between ring-tailed lemurs and Verreaux's sifaka may have affected the accuracy of the predicted fecal stable isotopes values. Members of the genus *Propithecus*, exhibit much greater vascularization of the colon and caecum when compared other lemur species (Campbell et al., 2004). As a result, the gut morphology of sifakas are particularly well-suited for digesting plant matter and they are often referred to as "seed predators" since they produce fecal pellets with fully digested seeds, fruits, flowers, and leaves (Loudon, 2009). Sifaka also exhibit a gut transit time of between 24 and 48 hours (Campbell et al., 2004). In contrast, ring-tailed lemurs do not fully digest the plants they consume, and their gut transit times have yet to be determined in free-ranging settings. Thus, predictions for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values may have been inaccurate due to the differences in gut morphology and the gut transit times between the two primate species analyzed in this study.

While the equation used in this study not be not be accurate for predicting the fecal stable isotope values of the BMSR ring-tailed lemurs and Verreaux's sifaka, it does have heuristic value in that no previous studies have used feeding observations to predict stable isotope values. There is no doubt that stable isotope analyses are useful for making inferences about NHP diet, habitat use and anthropogenic impacts. However, it is important to assess the accuracy of both stable isotopes analyses and feeding observations alike, because both are widely used methodologies in the fields of primate behavioral ecology and paleo-anthropology (Pollock, 1979; Balasse et al., 1999; Janson, 2000; Blumenthal et al., 2012; Reitsema, 2012; Flores-Escobar et al., 2020).

Niche partitioning between the BMSR ring-tailed lemurs and Verreaux's sifaka

According to H₂, it was expected that the ring-tailed lemur groups would exhibit greater variation in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values and occupy a wider isotopic space in comparison to Verreaux's sifaka groups. This was expected, because ring-tailed lemurs generally consume a greater variety of food items (i.e. flowers, fruits, stems, seeds, leaves, and invertebrates) and are characterized as "omnivorous" (Jolly, 1966; Sussman, 1974; Sauther, 1992; Sauther et al., 1999). In contrast, Verreaux's sifaka primarily consume leaves and are referred to as "folivores" (Yamashita, 2000). Given the greater dietary breadth of *L. catta*, the BMSR ring-tailed lemurs should exhibit a greater degree of variation in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values compared to the BMSR Verreaux's sifaka.

Figure 7 demonstrates that the ring-tailed lemur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space is greater than that of the Verreaux's sifaka for the months of December, February, and July. For the months of February and July, the ring-tailed lemur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space visually enveloped the Verreaux's sifaka $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space (Fig. 7).

Intraspecific comparisons between the ring-tailed lemur Black and Green groups demonstrated monthly variations in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space (Fig. 8). In June and April, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space of the Green and Black groups were similar in size (Fig. 8). In contrast, the Black group $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space was greater than or almost fully encapsulated that of the Green group in the months of December, February, and May (Fig. 8). January was the only month during which the Green group $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope space encapsulated that of the Black group. Overall, Figure 8 demonstrates that the Black group is primarily responsible for driving the stable isotope variation exhibited by the BMSR ring-tailed lemurs.

Verreaux's sifaka intraspecific comparisons also revealed variation in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values throughout the study. However, the coefficients of variation of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the BMSR ring-tailed lemurs were generally higher than those of the BMSR Verreaux's sifaka (Tables 12-15). This indicates that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values for the omnivorous ring-tailed lemurs in comparison to the folivorous Verreaux's sifaka were more variable (Tables 12-15). In sum, these data support H₂, which hypothesized that ring-tailed lemurs would exhibit greater variation in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values in comparison to Verreaux's sifaka.

Tukey's HSD test also identified significant pairwise comparisons for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values between the Black group and Rivotse, and the Green group and Vao Vao, respectively (Tables 16 and 17). Significant differences between sympatric social groups of the ring-tailed lemurs and Verreaux's sifaka (i.e. the Black group and Rivotse, the Green group and Vao Vao) demonstrate that species-specific feeding preferences and dietary adaptations largely determined the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values we found. Feeding studies at BMSR by Yamashita (2000, 2002) noted that ring-tailed lemurs preferred ripe kily fruit and had lower tolerance for tough foods in comparison to Verreaux's sifaka. Moreover, ring-tailed lemurs spend significantly more time on the ground and will eat foods from each level of the sifaka are generally restrained to the canopy.

The results of this study also demonstrated that niche partitioning occurred between the BMSR ring-tailed lemur and Verreaux's sifaka and thereby has allowed the two species to exist in sympatric associations (Hutchinson, 1957; Spencer, 1995). Examples of niche partitioning are abundant among animal communities, but difficult to quantify. Since stable isotopes provide comparable feeding data between two or more species, this technique shows great promise for

addressing surround niche partitioning, feeding niches, trophic positions, and community ecology (Newsome et al., 2007). In this study, the differences in the BMSR primate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values were driven primarily by the diets of the BMSR primates, and to a lesser degree by the environments each species inhabits. This is evident from the feeding observations among the BMSR primates which showed that the Verreaux's sifaka mostly consumed C_3 leaves (58.7%) whereas ring-tailed lemurs mostly consumed C_3 fruits (64.8%) during the study period (Tables 4 and 5).

The data from this study may also contribute to our understanding of extinct lemur communities. Using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots, Crowley et al. (2012) showed that extant and extinct Malagasy lemur communities occupied distinct isotopic spaces indicative of niche partitioning through both time and space. This study analyzed the bone collagen stable isotope values which have slower turnover than feces and cannot capture dietary changes over short periods of time, but are able to provide a glimpse into the potential habitats used by extinct lemurs before the impact of humans.

The effect of seasonality on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values

H₃ suggested that there would be a detectable shift in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the BMSR ring-tailed lemurs as they transitioned from eating fruits in the wet seasons to leaves in the dry season. The feeding observations in Table 4 demonstrate that the ring-tailed lemurs fed on C_3 fruits throughout the year. Unexpectedly, in some dry season months ring-tailed lemurs consumed a greater percentage of C_3 fruits than during some wet season months. For example, in July (dry season) C_3 fruits accounted for 86.0% of their diet in contrast to February (wet season) when C_3 fruits composed only 16.7% of their diet. At BMSR, ring-tailed lemurs have been observed consuming kily fruits year-round (Sauter and Cuzzo, 2009) as a fallback food (FBF).

Lafleur and Gould (2009) note that in January of 2005 a cyclone near BMSR altered the flowering and fruiting cycles of *T. indica*. The data collected for this study began in December of 2005 and it is likely that extreme weather associated with the cyclone caused kily fruits to be unavailable for that year. The BMSR ring-tailed lemurs relied more heavily on C₃ leaves (66.8%) in the month of February during the wet season of 2006, while during the dry season of 2006, it is unlikely any extreme weather event impacted the availability of kily fruits given that ring-tailed lemurs consumed C₃ fruits in such high quantities during the dry season months (Table 4). Pairwise comparisons of the ring-tailed lemur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values generated no significant p-values when comparing ring-tailed lemur isotopic values between the wet and dry seasons and this probably linked to their fluid dietary patterns throughout the year that may have been impacted by climatic conditions.

H₄ expected that *P. verreauxi* groups would exhibit lower variation in their fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the dry and wet seasons given that they are folivorous and leaves are abundant throughout the year. The stable isotope data suggest there were no significant differences in diet between the wet and dry season for Verreaux's sifaka. However, there were observable differences in their feeding behaviors between the wet and dry seasons (Table 5; Fig. 7 and Fig. 9). For example, in February (wet season) C₃ leaves composed 83.8% of their diet (Table 5). Whereas, in May (dry season) C₃ leaves accounted for 55.9% of the Verreaux's sifaka diet (Table 5). Figure 7 shows that the isotopic niche space for Verreaux's sifaka visibly increased from March to April. In particular, the isotopic niche space for Vao Vao also dramatically increased from March to April (Fig. 9). The discrepancies between the isotope data and feeding data may be attributed to the limitations of behavioral observations. The BMSR

sifaka may have consumed foods that were not easily observed, consumed at night, or consumed during a period of a particular month or season that no feeding observations were recorded.

The effect of anthropogenic disturbance on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values

H₅ posited that there should be observable and significant variation between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of anthropogenically-disturbed groups versus groups inhabiting the protected forests at BMSR. Ring-tailed lemurs and Verreaux's sifaka groups in the disturbed forests had access to human foods not available to the groups that inhabited the protected Parcel 1. It was expected that the presence of human foods in their diet would be reflected as observable and significant variation in their isotopic values based on previous stable isotope research on NHPs living among humans (Loudon et al., 2007, Schurr et al., 2012). At BMSR, Loudon et al. (2007) found that ring-tailed lemur groups that inhabited the camp and consumed human foods exhibited different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This is less of an issue for the BMSR sifaka that have never been observed consuming human foods. In addition, the BMSR sifaka and ring-tailed lemurs inhabiting the anthropogenically-disturbed forests consumed foods from more open canopies. Therefore, their $\delta^{13}\text{C}$ values should be higher due to the lack of a canopy effect than groups that lived in the protected habitat at BMSR (Sponheimer et al., 2006b; Loudon et al., 2016).

In this study, the differences between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the BMSR ring-tailed lemur groups living in the anthropogenically-disturbed (Black) versus protected (Green) habitats were nonsignificant (Table 16). However, Figure 10 shows that the confidence intervals of the median $\delta^{13}\text{C}$ fecal values for the Black and Green groups do not overlap. As well, Figure 8 demonstrates observable variation in the isotopic niche space between the ring-tailed lemur Black and Green groups. This indicates that anthropogenic disturbance likely influenced the $\delta^{13}\text{C}$

fecal values of the Black and Green groups, but that Tukey's HSD test was unable to identify such an effect, because the sample size was too small ($N = 14$). It is also worth noting that the Green group inhabited the protected forests at BMSR, but on few occasions was observed crossing the Sakamena River to feed on mangoes (*Mangifera indica*) cultivated by the local Mahafaly people (Loudon, 2009).

For the BMSR Verreaux's sifaka, the groups living in the anthropogenically-disturbed habitat (Rivotse) and the group in the protected parcel (Vao Vao) had significantly different $\delta^{15}\text{N}$ fecal values ($p = 0.03$, Table 17). Figure 9 also shows observable variation in the isotopic niche space between the Verreaux's sifaka Rivotse and Vao Vao. These results demonstrate that habitat type did affect the $\delta^{15}\text{N}$ fecal values for the BMSR Verreaux's sifaka. Contrary to these findings, Tukey's HSD test identified the pairwise comparison for the mean $\delta^{13}\text{C}$ fecal values between Rivotse and Vao Vao were generally similar. It is also plausible that the effect of habitat type (i.e. level of anthropogenic disturbance) on the $\delta^{13}\text{C}$ fecal values of the BMSR Verreaux's sifaka was not apparent because the sample size was too small ($N = 14$).

Recent studies have also provided new insights on how captivity or anthropogenic disturbance affects the gut microbiome of the Malagasy primates (Bennett et al., 2016; Greene et al., 2018, 2019). Green et al. (2019) found that among specialist lemurs (i.e. sifaka) the "effects" of captivity were more apparent in the gut microbiome than among generalist species such as ring-tailed lemurs. In contrast, Bennett et al. (2016) observed among the BMSR ring-tailed lemurs that habitat or anthropogenic disturbance did affect gut microbiota composition. However, they also observed lower interindividual variability in general gut microbiome composition between groups that inhabited anthropogenically-altered environments. As well, Bennett et al. (2016) employed a larger sample size ($N = 45$ ring-tailed lemurs) for their study

which may have caused the effect of anthropogenic disturbance affects on diet and therefore the gut microbiome to be more apparent.

Perofsky et al. (2017) found that among wild Verreaux's sifaka, group membership was the most accurate predictor of gut microbiome similarity and diversity between individuals, even after controlling for other variables. These studies show the value of microbial data for investigating dietary patterns among wild ring-tailed lemurs and Verreaux's sifaka. It would be helpful to compare microbial data with feeding observations and stable isotopes analyses presented here in order to gain a more comprehensive picture of how diet was affected by anthropogenic disturbance and or seasonality. Furthermore, microbial data could be used along with stable isotopes analyses to assess the overall accuracy of feeding observations.

Chapter Six - Conclusion

Study Limitations and Improvements

The results of this study did not support all my expectations. While the attempt to predict the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values using feeding observations and plant isotopes was unsuccessful, it does highlight the inherent variability of stable isotope analyses and feeding observations. Therefore, I think it is important to use both stable isotope analyses and feeding observations when studying the dietary patterns of wild NHPs, because this will provide a more comprehensive understanding of their behavior and habitat use patterns. The dataset used for this study was larger than most published stable isotope studies for NHPs and the publication of these data can contribute to the current primatological literature. The data used here were also from feces and to date there are relatively few studies that have concentrated on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of NHPs. Given that this study concentrated on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal data, it was difficult to make direct comparisons to most stable isotope studies that generally utilize bone, collagen, hair, or enamel values (Sandberg et al., 2012). Furthermore, as noted previously, fecal stable isotope values provide feeding and habitat utilization data based on days or weeks and represent the undigested portion of diets. In contrast, bone, collagen, and hair stable isotope values provided data on the order of weeks or months and enamel stable isotope values represent feeding and/or habitat utilization date of infant, juvenile, or subadult stages of a NHP's life (Sponheimer et al., 2009; Crowley et al., 2012).

There are a variety of methodological approaches that could be employed to improve on this study. One improvement would include providing captive ring-tailed lemurs and Verreaux's sifaka experimental diets to get a better understanding of their gut transit times and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fractionation offsets of the values of the foods they ingest and the values that are exhibited in their feces. Another improvement would include focusing on behavioral observations that

attempted to better capture the stable isotope ecology of the BMSR ring-tailed lemurs and sifaka. This would include more precise data collection on ecological variables at the site, geographic locations, canopy positions, and inter and intragroup competition. This dataset could also be expanded to include the nocturnal NHPs at BMSR which include the understudied white-footed sportive lemur or lepilemur (*Lepilemur leucopus*) and the gray brown mouse lemur (*Microcebus griseorufus*).

Despite the shortcomings of this study, these data documented that anthropogenic disturbance affected the BMSR ring-tailed lemur and Verreaux's sifaka in different ways. It would be helpful to collect more data to represent how these patterns have changed since the original study period. As well, a larger sample size may better illustrate the effect of anthropogenic disturbance. It was clear that anthropogenic disturbance affected the $\delta^{15}\text{N}$ fecal values of the BMSR Verreaux's sifaka, but there was no observable effect on their $\delta^{13}\text{C}$ fecal values. By using a larger sample size, an observable effect on the $\delta^{13}\text{C}$ fecal values of the BMSR Verreaux's sifaka may become visible. As well, a significant effect on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ fecal values of the BMSR ring-tailed lemurs may be identifiable with a larger sample set.

Broader Impacts and Future Directions

It will be important for future studies to assess the impact of anthropogenic disturbance on primate populations at BMSR and throughout Madagascar. Given that anthropogenic activities such as livestock grazing have been shown to alter the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of soils and plants (Aranibar et al., 2008) it is likely that these practices contributed to the presence of an anthropogenic effect on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the ring-tailed lemurs and Verreaux's sifaka residing at BMSR. Furthermore, understanding the effects of anthropogenic disturbance on their

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values will help us to determine the specific human activities that are influencing their feeding patterns.

Measuring the impact of anthropogenic activities on our NHP relatives is especially important given that human economic policies and practices have led to significant habitat loss (Estrada et al., 2017). Other factors that have negatively impacted NHPs are bushmeat hunting, the illegal pet trade, climate change and the spread of anthroponotic diseases (Estrada et al., 2017). All of these factors combined have caused severe harm to NHP populations worldwide such that 60% of primate species are at risk of becoming extinct and 75% are experiencing decreasing population numbers (Estrada et al., 2017). *Lemur catta* and *Propithecus verreauxi*, are both at risk of becoming extinct (IUCN, 2008).

The Malagasy primates account for 20% of all NHP species, make-up 30% family-level diversity and among mammals are the most at-risk group for becoming extinct (Schwitzer et al., 2014). Recent phylogenetic analyses resulted in a large increase in the number of recognized extant lemur taxa, from 43 to 101 species (Schwitzer et al., 2014). These 101 species are found only in Madagascar and 94% of these species are threatened with extinction (Schwitzer et al., 2014). The extinction crisis in Madagascar is the result of fragmentation, alteration, and loss of Madagascar's forests (Schwitzer et al., 2014). Although, increased bushmeat hunting in response to political instability since 2009 has also contributed to the problem.

According to Schwitzer et al. (2014), only 10 to 20% of the island's original forest cover still exists. Furthermore, many Malagasy strepsirrhines are seed dispersers for many of Madagascar's large seed-producing trees, including kily or tamarind trees, *Tamarindus indica* (Federman et al., 2016). Their role as seed dispersers is one aspect of the complex and

interdependent relationship lemurs have with Madagascar's forests. As such, the extinction of lemurs would likely set off extinction cascades of other species on Madagascar.

The negative impact of anthropogenic activity on Madagascar's five endemic lemur families is stressed here to emphasize the conservation implications of this study and the study subjects. This study demonstrates the ecological importance of *Lemur catta* and *Propithecus verreauxi*, given that each occupy a distinct ecological niche in their habitat. Therefore, the extinction of one or both species would negatively affect the unique flora and fauna communities of southwest Madagascar. Understanding the dietary preferences of these primates within the context of their changing environment will help us react and respond to the impending extinction crisis of Madagascar's lemurs and these two sympatric species.

References

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecol Lett* 6:1109-1122.
- Ambrose S.H. and Norr L. 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB and Grupe G, editors. *Prehistoric human bone: archaeology at the molecular level*. Berlin: Springer-Verlag. P 1-37.
- Amundson R, Austin AT, Schuur EAG, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D and Baisden WT. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochemistry Cycles* 17:1-10.
- Aranibar JN, Anderson IC, Epstein HE, Feral CJW, Swap RJ, Ramontsho J and Macko SA. 2008. Nitrogen isotope composition of soils, C₃ and C₄ plants along land use gradients in southern Africa. *J Arid Environ* 72:326-337.
- Axel AC and Maurer BA. 2010. Lemurs in a complex landscape: mapping species density in subtropical dry forests of southwestern Madagascar using data at multiple levels. *Am J Primatol* 73:38-52.
- Bateman AS and Kelly SD. 2007. Fertilizer nitrogen isotope signatures. *Isotopes in Environ and Health Stud* 43:237-247.
- Balasse M, Bocherens H and Mariotti A. 1999. Intra-bone variability of collagen and apatite isotopic composition used as evidence of a change of diet. *J Archaeol Sci* 26:593-598.
- Barboza PS and Parker KL. 2006. Body protein stores and isotopic indicators of N balance in female reindeer (*Rangifer tarandus*) during winter. *Phys Biochem Zool* 79:628-644.
- Bearhop S, Waldron S, Votier SC and Furness RW. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon isotopes in avian blood and feathers. *Physiol Biochem Zool* 75:451-458.
- Bennett G, Malone M, Sauter ML, Cuozzo FP, White B, Nelson KE and Amato KR 2016. Host age, social group, and habitat type influence the gut microbiota of wild ring-tailed lemurs (*Lemur catta*). *Am J Primatol* 78: 883-892.
- Blumenthal SA, Chritz KL, Rothman JM and Cerling TH. Detecting intrannual dietary variability in wild mountain gorillas by stable isotope analysis of feces. 2012. *Proc Nat Acad Sci USA* 109:21277-21282.
- Broadmeadow MSJ, Griffiths H, Maxwell C and Borland AM. 1992. The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO₂, within tropical forests formation. *Acta Oecol* 89:35-441.

- Broadmeadow MSJ and Griffiths H. 1993. Carbon isotope discrimination and the coupling of CO₂ fluxes within forest canopies. In: Ehleringer JR, Hall AE and Farquhar GD, editors. *Stable Isotopes and Plant Carbon-Water Relations*. San Diego: Academic Press. p 109-130.
- Brockman DK, Cobden AK and Whitten PL. 2009. Birth season glucocorticoids are related to the presence of infants in sifaka (*Propithecus verreauxi*). *Proc Biol Sci* 276:1855-1863.
- Campbell J, Williams C and Eisemann J. 2004. Characterizing gastrointestinal transit time in four lemur species using barium- impregnated polyethylene spheres (BIPS). *Am J Primatol* 64:309-321.
- Campbell JL, Eisemann JH, Williams CV and Glenn KM. 2000. Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Hapalemur griseus*, and *Lemur catta*. *Am J Primatol* 52:133-142.
- Cerling TE, Harris JM and Leakey MG. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Acta Oecol* 120:364-374.
- Cerling TE, Harris JM and Passey BH. 2003. Diets of east African Bovidae based on stable isotope analysis. *J Mammal* 84:456-470.
- Cherel Y, Hobson KA and Hassani S. 2005. Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol Biochem Zool* 78:106-115
- Choudhury A. 2004. Human-elephant conflicts in Northeast India. *Hum Dimens Wildl* 9:261-70.
- Clink DJ, Dillis C, Feinlen KL, Beaudrot L and Marshall AJ. 2017. Dietary diversity, feeding selectivity, and responses to fruit scarcity of two sympatric Bornean primates (*Hylobates albibarbis* and *Presbytis rubicunda rubida*). *PLoS One* 12: e0173369.doi:10.1371/journal.pone.0173369.
- Clutton-Brock TH and Harvey PH. 1977. Primate ecology and social organization. *J Zool* 183:1-39.
- Codron D, Lee-Thorp JA, Sponheimer M and Codron J. 2007. Stable carbon isotope reconstruction of ungulate diet changes through the seasonal cycle. *S Afr J Wildl Res* 37:117-125.
- Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D and Codron J. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation. *Int J Primatol* 29:757-772.
- Codron D, Codron J, Sponheimer M, Lee-Thorp JA, Robinson T, Grant CC, and De Ruiter D. 2005. Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces. *Koedoe* 48:115-124.
- Crowley BE, Carter ML, Karpanty SM, Zihlman AL, Koch PL and Dominy NJ. 2010. Stable carbon and nitrogen isotope enrichment in primate tissues. *Acta Oecol* 164:611-626.

- Crowley BE. 2012. Stable isotope techniques and applications for primatologists. *Int J Primatol* 33:673-701.
- Crowley BE and Godfrey LR. 2013. Why all those spines? Anachronistic defenses in the Didiereoideae against now extinct lemurs. *S Afr J Sci* 109:1-7.
- Cuozzo FP and Sauther ML. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids. *J Hum Evol* 46:623-631.
- Cuozzo FP and Sauther ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *J Hum Evol* 51:490-505.
- DeNiro MJ and Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495-506.
- DeNiro MJ and Epstein S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341-351.
- Doran D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging and grouping patterns in Tai Chimpanzees. *Int J Primatol* 18: 183-206.
- Else JG. 1991. Nonhuman primates as pests. In Box HO, editors. *Primate responses to environmental change*. Dordrecht: Springer. p 155-165.
- Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KA, Nijman V, Heymann EW, Lambert JE, Rovero F, Barelli C, Setchell JM, Gillespie TR, Mittermeier RA, Arregoitia LV, de Guinea M, Gouveia S, Dobrovolski R, Shanee S, Shanee N, Boyle SA, Fuentes A, MacKinnon KC, Amato KR, Meyer ALS, Wich S, Sussman RW, Pan R, Kone I and Li B. 2017. Impending extinction crisis of the world's primates: Why primates matter. *Sci Adv* 3:e1600946.
- Estrada A, Raboy BE and Oliveira LC. 2012. Agroecosystems and primate conservation in the tropics: a review. *Ame J Primatol* 74:696-711.
- Federman S, Dornburg A, Daly DC, Downie A, Perry GH, Yoder AD, Sargis EJ, Richard A, Donoghue MJ and Baden AL. 2016. Implications of lemuriform extinctions for the Malagasy flora. *Proc Natl Acad Sci USA* 113:5041-5046.
- Fleagle JG. 1988. *Primate Adaption and Evolution*. New York: Academic Press.
- Flores-Escobar E, Sanpera C, Jover L, Cortés-Ortiz L, Rangel-Negrín A, Canales-Espinosa D and Dias PAD. 2020. Isotopic niche partitioning in two sympatric howler monkey species. *Am J Phys Anthropol*:1-9.
- Fry, B. 2006. *Stable isotope ecology*. New York: Springer-Verlag.

- Fuentes A. 2006. Patterns and context of human-macaque interactions in Gibraltar. In: Hodges K, Cortes J, editors. *The Barbary macaque*. Nottingham: University of Nottingham Press. p 169-184.
- Ganzhorn JU. 1986. Feeding behavior of *Lemur catta* and *Lemur fulvus*. *Int J Primatol* 7:17-30.
- Gartlan JS and Struhsaker TT. 1972. Polyspecific associations and niche separation of rainforest anthropoids in Cameroon, West Africa. *J Zool* 168:221-266.
- Goodman SM, Rakotoarisoa SV and Wilmé L. 2006. The distribution and biogeography of the ring-tailed lemur (*Lemur catta*) in Madagascar. In: Jolly A, Sussman R, Koyama N and Rasamimanana H, editors. *Ring-tailed lemur biology: Lemur catta in Madagascar*. New York: Springer. p 3-15.
- Greene LK, McKenney EA, O'Connell TM, Drea CM. 2018. The critical role of dietary foliage in maintaining the gut microbiome and metabolome of folivorous sifakas. *Sci Rep* 8:14482.
- Greene LK, Bornbusch SL, McKenney EA, Harris RL, Gorvetzian SR, Yoder AD and Drea CM. 2019. The importance of scale in comparative microbiome research: New insights from the gut and glands of captive and wild lemurs. *Am J Primatol* 81:e22974.
- Harcourt AH. 1989. Environment, competition and reproductive performance of female monkeys. *Trends Ecol Evol* 4:101-105.
- Heaton THE. 1999. Spatial, species, and temporal variations in the $^{13}\text{C}/^{12}\text{C}$ ratios of C_3 plants: implications for palaeodiet studies. *J Archaeol Sci* 26:637-649.
- Hill CM. 2017. Primate crop feeding behavior, crop protection, and conservation. *Int J Primat* 38:385-400.
- Hill CM. 2018. Crop foraging, crop losses and crop raiding. *Ann Rev Anthropol* 47:377-394.
- Hill WCO. 1953. *Primates: comparative anatomy and taxonomy 1: Strepsirrhini*. Edinburgh, UK: The University Press.
- Hladik CM and Charles-Dominique P. 1974. The behavior and ecology of the sportive lemur (*Lepilemur mustelinus*) in relation to its dietary peculiarities. In: Martin RD, Doyle GA and Walker AC, editors. *Prosimian biology*. London: Duckworth. p 25-37.
- Hobson KA and Clark RG. 1992. Assessing avian diets using stable isotopes. II. Factors influencing diet-tissue fractionation. *Condor* 94:189-197
- Hunt Curtin S. 1976. Niche differentiation and social organization in sympatric and Malaysian colobines. Ph.D. Dissertation, University of California Berkeley.
- Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427.

- Isbell LA and Young TP. 2002. Ecological models of social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* 139:177-202.
- Janson CH. 2000. Primate socio-ecology: the end of a golden age. *Evol Anthropol* 9:73-86.
- Janson CH and Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326-336.
- Jolly A. 1966. *Lemur behavior*. Chicago: University of Chicago Press.
- Jolly A. 1970. Malagasy lemurs--clues to our past. *Animal Kingdom* 70: 66-75.
- Katsvanga CAST, Mudyiwa SM and Gwenzi D. 2006. Bark stripping and population dynamics of baboon troops after chemical control in pine plantations of Zimbabwe. *Afr J Ecol* 44:413-16.
- Kay RF and Hylander WL. 1978. The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In Montgomery GG, editors. *The Ecology of Arboreal Folivores*. Washington, DC: Smithsonian Institution Press. p 173-191.
- Kluge M. and Ting I. 1978. *Crassulacean Acid Metabolism: Analysis of an Ecological Adaptation*. Berlin: Springer-Verlag.
- Koch F, Ganzhorn JU, Rothman JM, Chapman CA and Fitchel C. 2017. Sex and seasonal differences in diet and nutrient intake in Verreaux's sifaka (*Propithecus verreauxi*). *Am J Primatol* 79:1-10.
- LaFleur M and Gould L. 2009. Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatol* 80:233-246.
- Lambert JE, Chapman CA, Wrangham RW and Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *Am J of Phys Anthropol* 125:363-368.
- Lawler RR, Caswell H, Richard AF, Ratsirarson J, Dewar RE and Schwartz M. 2009. Demography of Verreaux's sifaka in a stochastic rainfall environment. *Acta Oecol* 161:491-504.
- Lee-Thorp JA, van der Merwe NJ and Brain CK. 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotope analysis. *J Hum Evol* 27:361-372
- Lee-Thorp JA, Sponheimer M and van der Merwe NJ. 2003. What do stable isotopes tell us about hominid dietary and ecological niches in the Pliocene? *Int J Osteoarchaeol* 13:104-113.
- Lewis RJ and Rakotonranaivo F. 2011. The impact of cyclone Fanele on sifaka body condition and reproduction in the tropical dry forest of western Madagascar. *J Trop Ecol* 27:429-432.

- Loudon JE. 2009. The parasite ecology and socioecology of ring-tailed lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) inhabiting the Beza Mahafaly Special Reserve. Unpubl. Ph.D. Dissertation, University of Colorado Boulder.
- Loudon JE and Sauter ML. 2013. Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Beza Mahafaly Special Reserve. *Madag Conserv Dev* 8:21-28.
- Loudon JE, Sauter ML, Fish KD, Hunter-Ishikawa M and Ibrahim YK. 2006. One reserve, three primates: applying a holistic approach to understand the interconnections among ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), and humans (*Homo sapiens*) at Beza Mahafaly Special Reserve, Madagascar. *Ecological & Environmental Anthropology* 2:54-74.
- Loudon JE, Sponheimer M, Sauter ML and Cuzzo FP. 2007. Intraspecific variation in hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of ring-tailed lemurs (*Lemur catta*) with known individual histories, behavior and feeding ecology. *Am J Phys Anthropol* 133:978-985.
- Loudon JE, Grobler JP, Sponheimer M, Moyer K, Lorenz JG and Turner TR. 2014. Using the stable carbon and nitrogen isotope compositions of vervet monkeys (*Chlorocebus pygerythrus*) to examine questions in ethnoprimateology. *PLoS One* 9:e100758.
- Loudon JE, Sandberg PA, Wrangham RW, Fahey B and Sponheimer M. 2016. The stable isotope ecology of Pan in Uganda and beyond. *Am J Primatol* 78:1070-1085.
- Loudon JE, Wakefield ML, Kimel HM, Waller MT, Hickmott AJ, White FJ and Sponheimer M. 2019. Stable isotope data from bonobo (*Pan paniscus*) faecal samples from the Lomako Forest Reserve, Democratic Republic of the Congo. *Afr J Ecol* 57:437-442
- Louis EE, Sefczek TM, Bailey CA, Raharivololona B, Lewis R and Rakotomalala, EJ. 2020. *Propithecus verreauxi*. *The IUCN Red List of Threatened Species* 2020: e.T18354A115572044. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T18354A115572044.en>. Accessed on 16 July 2020.
- Marshall AJ and Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1219-1235.
- Marshall AJ, Boyko CM, Feilen KL, Boyko RH and Leighton M. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. *Am J Anthropol* 140:603-614.
- Martinelli LA, Piccolo MC and Townsend AR. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* 46:45-65.
- McCutchan Jr JH, Lewis Jr WM, Kendall C and McGrath CC. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378-390.

- McGee E and Vaughn S. 2006. Stable isotope analysis: a technique for evaluating ecological change in disturbed habitats. *Int J Primatol* 27 Supplement 1:499.
- McKinney T. 2015. A classification system for describing anthropogenic influence on nonhuman primate populations. *Am J Primatol* 77:715-726.
- McLennan MR, Hyeroba D, Asiimwe C, Reynolds V and Wallis J. Chimpanzees in mantraps: lethal crop protection and conservation in Uganda. *Oryx* 46:598-603.
- McLennan MR, Spagnoletti N and Hockings KJ. 2017. The implications of primate behavioral flexibility for sustainable human-primate coexistence in anthropogenic habitats. *Int J Primatol* 38:105-121.
- Milton K and May ML. 1976. Body weight, diet and home range area in primates. *Nature* 259:459-462.
- Minagawa M and Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135-1140.
- Newsome SD, del Rio CM, Bearhop S and Philips DL. 2007. A niche for isotopic ecology. *Front Ecol Environ* 5:429-436.
- Norscia I, Carrai V, Borgognini-Tarli SM (2006) Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *Int J Primatol* 27:1001-1022.
- Nowak K, Wimberger K, Richards SA, Hill RA and Le Roux A. 2017. Samango monkeys (*Cercopithecus albogularis labiatus*) manage risk in a highly seasonal, human-modified landscape in Amathole Mountains, South Africa. *Int J Primatol* 38:194-206.
- O'Connell-Rodwell CE, Rodwell T, Rice M and Hart LA. 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biol Conserv* 93:381-391.
- O'Leary M.H. 1988. Carbon isotopes in photosynthesis. *BioScience* 38:328-336.
- O'Leary M.H. 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20:553-567.
- Overdorff DJ. 1996. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *Am J Primatol* 40:327-342.
- Pearson SF, Levey DJ, Greenberg CH, Martinez del Rio C. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Acta Oecol* 135:516-523.
- Perofsky AC, Lewis RJ, Abondano LA, Di Fiore A and Meyers LA. 2017. Hierarchical social networks shape gut microbial composition in wild Verreaux's sifaka. *Proc Biol Sci* 284:20172274.
- Pettus A. 2005. Wild Harvest: A Taste for Extinction. *Harvard Magazine* 107. Online publication: <http://www.harvardmagazine.com/on-line>.

- Pollock JJ. 1979. Spatial distributions and ranging behavior of lemurs. In Doyle GA and Martin RD, editors. *The Study of Prosimian Behavior*. New York: Academic Press. p 359-09.
- Priston NEC. 2005. Crop-Raiding by *Macaca ochreata brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation. Ph.D. Dissertation, University of Cambridge.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rambeloson FR. 1988. Contribution à l'étude de l'utilisation des ressources forestieres aux environs de la Reserve Special de Beza Mahafaly (Cas du village Analafaly) Mémoire de fin d'études, Establissement d'Enseignement Supérieur des Sciences Agronomiques, Université d'Antananarivo.
- Rasamimanana H and Rafidinarivo E. 1993. Feeding behaviour of *Lemur catta* females in relation to their physiological state. In: Kappeler P and Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 271-295.
- Ratsirarson J. 2003. Réserve Spéciale de Beza Mahafaly. In: Goodman SM, Benstead JP, editors. *The natural history of Madagascar*. Chicago: University of Chicago Press. p 1520-1525.
- Ratsirarson J, Randrianarisoa J, Ellis E, Emady RJ, Efitroarany RJ, Razanajaonarivalona EH, and Richard AF. 2001. Beza Mahafaly: écologie et réalités socio-économiques. *Research Development Biology* 18:1-104.
- Reitsema LJ. 2012. Introducing fecal stable isotope analysis in primate weaning studies. *Am J Primatol* 74:926-939.
- Reitsema LJ, Patrick KA and Muir AB. 2016. Inter-individual variation in weaning among rhesus macaques (*Macaca mulatta*): serum stable isotope indicators of suckling duration and lactation. *Am J Primatol* 78:1113-1134.
- Richard AF. 1978. Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes. In: Montgomery GG, editors. *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, DC: Smithsonian Institution Press. p 519-533.
- Richard AF, Rakotomanga P and Schwartz M. 1991. Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984-1988. *Am J Phys Anthropol* 84:307-322.
- Richard AF, Rakotomanga P and Schwartz M. 1993. Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984-1991. *Am J Primatol* 30:1-20.
- Richard AF, Dewar RE, Schwartz M and Ratsirarson J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *J Zool* 256:421-436.

- Robbins CT, Felicetti LA and Sponheimer M. 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Acta Oecol* 144:534-540.
- Robbins MM and Hohmann G. 2006. Primate feeding ecology: an integrative approach. In: Hohmann G, Robbins MM and Boesch C, editors. *Feeding ecology in apes and other primates*. New York: Cambridge University Press. p 1-15.
- Rodrigues MA. 2017. Female spider monkeys (*Ateles geoffroyi*) cope with anthropogenic disturbance through fission-fusion dynamics. *Int J Primatol* 38:838-855.
- Roth JD and Hobson KA. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Can J Zool* 78:848-852.
- Rundel PW, Ehleringer JR, and Nagy KA. 1989. *Stable Isotopes in Ecological Research*. New York: Springer-Verlag. p 525.
- Sandberg PA, Loudon JE and Sponheimer M. 2012. Stable isotope analysis in primatology: a critical review. *Am J Primatol* 74:969-989.
- Sandel AA, Miller JA, Mitani JC, Nuun CL, Patterson SK and Garamszegi LZ. 2016. Assessing sources of error in comparative analyses of primate behavior: Intraspecific variation in group size and the social brain hypothesis. *J Hum Evol* 94:126-133.
- Sauther ML. 1991. Reproductive behaviour of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 84:463-477.
- Sauther ML. 1992. Effect of reproductive state, social rank and group size on resource use among free-ranging ring-tailed lemurs (*Lemur catta*) of Madagascar. Ph.D. Dissertation, Washington University.
- Sauther ML. 1994. Wild plant use by pregnant and lactating ring-tailed lemurs, with implications for early hominid foraging. In: Etkin N, editors. *Eating on the wild side*. Tucson, AZ: University of Arizona Press. p 240-256.
- Sauther ML. 1998. The interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. *Folia Primatol Supplement* 69:309-320.
- Sauther ML and Cuzzo FP. 2008. Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). *Folia Primatologica* 79:55-78.
- Sauther ML and Cuzzo FP. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitats. *Am J Phys Anthropol* 140:671-686.
- Sauther ML, Sussman RW and Gould L. 1999. The socioecology of the ring-tailed lemur: thirty-five years of research. *Evol Anthropol* 8:120-132.

- Scheun J, Greeff D and Nowack J. 2019. Urbanization as an important driver of nocturnal primate sociality. *Primates* 60:375-381.
- Schoeninger MJ. 1995. Stable isotope studies in human evolution. *Evol Anthropol* 4:83-98.
- Schoeninger MJ. 2010. Diet reconstruction and ecology using stable isotope ratios. In: Larsen CS, editor. *A companion to biological anthropology*. Chichester, UK: John Wiley & Sons, Ltd. p 445-464.
- Schoeninger MJ and DeNiro MJ. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim Cosmochim Acta* 48:625-639.
- Schoeninger MJ, Iwaniec UT and Glander KE. 1997. Stable isotope ratios indicated diet and habitat use in New World monkeys. *Am J Phys Anthropol* 103:69-83.
- Schoeninger MJ, Iwaniec UT and Nash LT. 1998. Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Acta Oecol* 113:222-230.
- Schoeninger MJ, Moore J and Sept JE. 1999. Subsistence strategies of two savanna chimpanzee populations: the stable isotope evidence. *Am J Primatol* 49:297-314.
- Schreier AL, Schlaht RM and Swedell L. 2019. Meat eating in wild hamadryas baboons: Opportunistic trade-offs between insects and vertebrates. *Am J Primatol* 81:e23029.
- Schurr MR, Fuentes A, Luecke E, Cortes J and Shaw E. 2012. Intergroup variation in stable isotope ratios reflects anthropogenic impact on the Barbary macaques (*Macaca sylvanus*) of Gibraltar. *Primates* 53:31-40.
- Schwarcz HP, Melbye J, Katzenberg MA and Knyf M. 1985. Stable isotopes in human skeletons of southern Ontario: reconstructing palaeodiet. *J Archaeol Sci* 12:187-206.
- Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, Peacock H, Ratsimbazafy, Razafindramanana J, Louis Jr EE, Chikhi L, Colquhoun IC, Tinsman J, Dolch R, LaFleur M, Nash S, Patel E, Randrianambinina B, Rasolofoharivelo T and Wright PC. 2014. Averting lemur extinctions and Madagascar's political crisis. *Sci* 343:842-843.
- Shultz S and Dunbar RIM. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 274:2429-2436.
- Simmen B, Hladik A and Ramasiarisoa P. 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. *Int J Primatol* 24:949-968.
- Simmen B, Peronny S and Jeanson M, 2006a. Diet quality and taste perception of plant secondary metabolites by *Lemur catta*. In: Jolly A, Sussman RW, Koyama N,

- Rasamimanana H, editors. Ringtailed Lemur Biology: *Lemur catta* in Madagascar. New York: Springer. p 160-184.
- Simmen B, Sauther ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L and Hladik A. 2006b. Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Jolly A, Sussman RW, Koyama N and Rasamimanana H, editors. Ring-tailed lemur biology: *Lemur catta* in Madagascar. New York: Springer. p 55-68.
- Shultz S and RIM Dunbar. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proc Biol Sci* 274:2429-2436.
- Sponheimer M, Codron D, Passey BH and de Ruiter DJ. 2009. Using carbon isotopes to track dietary change in modern, historical, and ancient primates. *Am J Phys Anthropol* 140:661-670.
- Sponheimer M and Lee-Thorp JA. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Sci* 283:368-370.
- Sponheimer M, Loudon JE, Codron D, Howells ME, Pruett JD, Codron J, De Ruiter DJ and Lee-Thorp JA. 2006b. Do “savanna” chimpanzees consume C4 resources? *J Hum Evol* 51:128-133.
- Sponheimer M, Passey BH, de Ruiter DJ, Guatelli-Steinberg D, Cerling TE and Lee-Thorp JA. 2006a. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science* 314:980-982.
- Sponheimer M, Robinson T, Ayliffe L, Passey B, Roeder B, Shiplay L, Lopez E, Cerling T, Dearing D and Ehleringer J. 2003a. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Can J Zool* 81:871-876.
- Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D and Ehleringer J. 2003b. Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}\text{N}$ values from controlled feeding study. *Int J Osteoarchaeol* 13:80-87.
- Spencer LM. 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. *J Mammal* 76:448-471.
- Sussman RW. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am J Phys Anthropol* 84:43-58.
- Sussman RW. 1974. Ecological distinctions in sympatric species of *Lemur*. In: Martin RD, Doyle GA and Walker AC, editors. *Prosimian Biology*. London: Duckworth. p 75-108.

- Sussman RW and Ratsirarson J. 2006. Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana HR, editors. Ringtailed lemur biology. New York: Springer p 43-51.
- Sussman RW, Richard AF, Ratsirarson J and Sauter ML. 2012. Beza Mahafaly Special Reserve: long-term research on lemurs in southwestern Madagascar. In: Kappeler P and Watts D, editors. Long-term field studies of primates. Berlin Heidelberg: Springer-Verlag. p 45-66.
- Steenbeek R and van Schaik CP. 2001. Competition and group size in Thomas langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behav Ecol Sociobiol* 49:100-110.
- Sterck EHM, Watts DP and van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291-309.
- Strum SC. 1994. Prospects for management of primate pests. *Revue Ecologie (Terre Vie)* 49:295-306.
- Tattersall I. 1982. *The Primates of Madagascar*. New York: Columbia Press.
- Ungar PS and Sponheimer M. 2011. The diets of early hominins. *Science* 334:190-193.
- Vanderklift MA and Ponsard S. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Acta Oecol* 136:169-182.
- van der Merwe NJ. Carbon isotopes, photosynthesis, and archaeology. 1982. *Am Sci* 70:596-606
- van der Merwe NJ and Medina E. 1989. Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rain forests. *Geochim Cosmochim Acta* 53:1091-1094.
- van der Merwe NJ and Medina E. 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *J Archeol Sci* 18:249-259.
- van Schaik CP. 1983. Why are diurnal primates living in groups? *Behaviour* 87:91-117.
- van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V and Foley R, editors. *Comparative socio-ecology of mammals and humans*. Oxford, UK: Blackwell Publications. p 195-218.
- Vogel E.R., Dominy N.J. 2011. Measuring ecological variables for primate field studies. In Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK and Stumpf RM, editors. *Primates in Perspective*. Oxford, UK: Oxford University Press. p 367-377.
- Vogel JC. 1978. Isotopic assessment of the dietary habits of ungulates. *S Afr J Sci* 74:298-301.

- Whitelaw DC, Sauther ML, Loudon JE and Cuzzo F. 2005. Anthropogenic change in and around Beza Mahafaly Reserve: methodology and results. *Am J Phys Anthropol*. Supplement 40:227.
- Winter K. 1979. Effect of different CO₂ regimes on the induction of crassulacean acid metabolism in *Mesembryanthemum crystallinum*. *Aust J Plant Physiol* 6:589-594.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.
- Yamashita N. 1996. Seasonal and site specificity of mechanical dietary patterns in two Malagasy lemur families (*Lemuridae* and *Indriidae*). *Int J Primatol* 17:355-387.
- Yamashita N. 2000. Mechanical thresholds as a criterion for food selection in two prosimian primate species. In: Spatz HC and Speck T, editors. *Proceedings of the 3rd Plant Biomechanics Conference, Freiburg-Badenweiler August 27th to September 2nd*. Stuttgart: Thieme Verlag. p 590-595.
- Yamashita N. 2002. Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *Int J Primatol* 23:1025-1051.
- Yamashita N, Cuzzo FP, Sauther ML, Fitzgerald E, Riemenschneider A and Ungar PS. 2016. Mechanical food properties and dental topography differentiate three populations of *Lemur catta* in southwest Madagascar. *J Hum Evol* 98:66-75.
- Yeager CP and Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF and Jolly CJ, editors. *Old world monkeys*. Cambridge, UK: Cambridge University Press. p 496-521.

Appendix A

IACUC Approval Letter

MEMORANDUM

To: James E. Loudon – Anthropology
From: Silvia N. Iorio – Lab Animal Program Coordinator
Date: June 24, 2005
Re: Animal Protocol Approval

The Institutional Animal Care and Use Committee has reviewed your Category A animal protocol entitled "The Parasite Ecology and Sociology of Ring-Tailed Lemurs and Verreaux's Sifaka at Beza Mahafaly, Madagascar" and has determined that it is in accord with the Public Health Service Policy on the humane care and use of laboratory animals used in research and teaching.

The committee has approved your proposed use of animals at its June 22, 2005 meeting. Since you have provided the requested permits, nothing more is required from you. This approval will be valid for three years and will expire in 2008. An annual Protocol Update Sheet will be sent to you on a yearly basis.

A signed copy of the approved protocol is attached for your files and for use by laboratory personnel. If a verification letter to a funding agency is required, it is your responsibility to provide this office with the correct mailing address as soon as it becomes available.

Thank you for your concern for animal welfare and your patience and willingness to work with the policies and procedures of the IACUC.

C/ M. Sauther, Anthropology
Office of Contracts and Grants

Appendix B

Table 24. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values with standard deviations for the BMSR ring-tailed lemur and Verreaux's sifaka individuals.

Species	Individual	Group	Mean $\delta^{13}\text{C}\text{‰}$	SD	N	Mean $\delta^{15}\text{N}\text{‰}$	SD	N
<i>L. catta</i>	ID #6	Black	-28.3	1.2	8	5.9	1.6	8
<i>L. catta</i>	ID #110	Black	-27.5	0.9	8	4.6	1.0	8
<i>L. catta</i>	ID #116	Black	-26.4	2.9	8	4.6	0.5	8
<i>L. catta</i>	ID #206	Black	-27.7	1.3	8	4.7	0.7	8
<i>L. catta</i>	ID #212	Black	-28.3	1.0	8	5.0	0.9	8
<i>L. catta</i>	ID #226	Black	-26.7	1.0	8	4.8	1.2	8
<i>L. catta</i>	Wyatt	Black	-27.6	1.0	8	4.3	0.8	8
<i>L. catta</i>	ID #9	Green	-28.0	2.5	8	4.8	1.0	8
<i>L. catta</i>	ID #23	Green	-28.7	0.8	8	4.5	1.3	8
<i>L. catta</i>	ID #167	Green	-29.0	1.1	8	3.9	0.9	8
<i>L. catta</i>	ID #175	Green	-28.0	1.0	8	4.6	1.7	8
<i>L. catta</i>	ID #209	Green	-28.3	0.7	8	5.3	2.3	8
<i>L. catta</i>	ID #235	Green	-28.5	1.2	8	5.3	1.7	8
<i>L. catta</i>	BJ	Green	-28.0	1.0	8	4.3	0.8	8
<i>P. verreauxi</i>	ID #111	Rivotse	-28.3	1.2	8	3.4	1.3	8
<i>P. verreauxi</i>	ID #475	Rivotse	-29.0	1.1	8	3.5	0.7	8
<i>P. verreauxi</i>	ID #489	Rivotse	-28.8	0.7	8	3.4	0.6	8
<i>P. verreauxi</i>	ID #492	Rivotse	-28.2	1.0	8	3.7	1.2	8
<i>P. verreauxi</i>	ID #502	Rivotse	-28.7	1.4	8	3.4	1.1	8
<i>P. verreauxi</i>	ID #546	Rivotse	-28.8	0.9	8	3.5	0.7	8
<i>P. verreauxi</i>	ID #567	Rivotse	-28.6	0.9	8	3.1	0.5	8
<i>P. verreauxi</i>	ID #19	Vao Vao	-28.5	1.0	8	4.8	1.0	8
<i>P. verreauxi</i>	ID #80	Vao Vao	-29.0	0.8	8	4.2	1.4	8
<i>P. verreauxi</i>	ID #314	Vao Vao	-28.6	0.6	8	4.5	0.5	8
<i>P. verreauxi</i>	ID #467	Vao Vao	-28.6	0.8	8	4.4	0.8	8
<i>P. verreauxi</i>	ID #473	Vao Vao	-28.7	0.7	8	4.0	0.6	8
<i>P. verreauxi</i>	ID #483	Vao Vao	-28.8	0.7	8	4.3	0.9	8
<i>P. verreauxi</i>	Beta Male	Vao Vao	-28.7	0.9	8	4.1	1.3	8

