A MULTIFACETED APPROACH FOR ANALYZING PRIMATE DIETARY DIVERSITY AND COMPETITION

A DISSERTATION SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA
BY

TESSA SIERRA CICAK

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF
DOCTOR OF PHILOSOPHY

DR. KIERAN P. MCNULTY

May 2023

Acknowledgements

A dissertation is not created in a vacuum. It is the work and toil of more than one person. I am so grateful for everyone who was involved in this process. Even the seemingly smallest role had an impact on this project's completion. I will try to name and recognize all of those who helped me in the following pages, but please know that if your name is left out, you were not forgotten, and I say "thank you" with all my heart.

First to my advisor Dr. Kieran McNulty. The assistance and mentorship offered by him through this entire process was invaluable. Thank you for believing in answering a difficult research question and helping me when I got too bogged down in the details. The homestretch of a dissertation is never easy and this one was especially challenging. Thank you for your kindness and patience through it all. Additionally, I thank my internal committee members, Dr. Martha Tappen and Dr. Mike Wilson for their feedback and advice along the way. Thank you for bringing in fresh perspectives. A huge thank you goes to Dr. David Fox, my external committee member. Your advice and help throughout this project have been immense. Thank you for getting me started on ecometrics and connecting me with folks who could help with method development.

Thank you to the University of Minnesota Anthropology Department, to the Department Chairs: Dr. Bill Beeman and Dr. Karen Sue Taussig; the Directors of Graduate Studies: Dr. Karen Ho and Dr. David Valentine. Thank you to the front office staff: Marjorie, Kara, Taryn, Megan, Christina, Nora for your help navigating funding, enrollment, and all of the forms.

Data for this dissertation was collected from multiple museums. The permissions and help from the following collections managers made this project possible: Darrin

Lunde from USNM; Marisa Surovy, Sara Ketelsen, and Eleanor Hoeger from the AMNH; Dr. Emmanuel Gillissen from the RMCA (thank you so much for your help getting the hair samples to the Ghent Lab); Adam Ferguson and Lawrence Heaney from the FMNH; Mark Omura from MCZ. Additionally, the museum staff that helped with everything from getting access cards to pointing out where the water fountain was, thank you. Thank you as well to all the National Museum of Kenya staff. Working at your benches and accessing the collections was a dream come true.

This research spanned multiple labs across institutions and continents. Thank you to the lab managers for their unflagging patience and support: Brian Badgely from the UMN XRCT lab; Dr. Jason Curtis and the staff at the University of Florida Isotope Lab; Dr. Samuel Bode and the staff from the Ghent isotope lab. A large thank you is owed to UMN Anthropology Lab Manager, Matt Edling. Thank you for troubleshooting software licensing, helping with new data collection methods, and making sure data was accessible during the pandemic. Thank you to Dr. Samantha Porter of LATIS for your help with all manner of 3D scanner questions, for helping develop post-processing protocols, and for the friendship. I am so excited to work with you and the rest of the LATIS team!

None of the data collection or analyses would have been possible without the support of the following funding agencies and grants: The University of Minnesota Thesis Research Travel Grant; The University of Minnesota Doctoral Dissertation Fellowship; The University of Minnesota Anthropology Department Block Grants; The National Science Foundation Doctoral Dissertation Research Improvement Grant; The Leakey Foundation Research Grant; The Bell Museum Research Grant.

Thank you so much to my UMN friends: Dr. Erin Crowley Champoux, Dr. Caroline Rowe, Dr. Anna Hardin, Dr. Ryan Knigge, Dr. Jason Massey, Dr. Kirsten Jenkins, Dr. Rutger Jansma, Dr. Katrina Yezzi, Dr. Carrie Miller, Dr. Ziane Izri, Zana Sims, Samantha Gogol, Risa Luther, Abbey Hall, Samuel Muteti, Emily Briggs, Annie Melton, Kia Atsales, Kele Missal, Jonathan Keller, and David Birlenbach. You all have been so wonderful and supportive on the most difficult days. Thank you, thank you, thank you.

Thank you to Dan Ehrlich, my constant friend. From late evenings studying osteology as undergrads to endless help in R, you have been a shoulder to cry on and a best friend to laugh with. You've been there for me, always, thanks bffl.

To the rest of my Snakes: Kaity, Elic, Merri and Plekhov. Thank you for the friendship over the last decade, the maps, the memes, the laughs, the advice, and the nonsense; it's been amazing to watch you grow as people and academics and to see the things you've built.

Of note, I would not have finished my dissertation without the never-ending support from my peers and co-workers at Phoenix Flight Studio. The instructors and students showed me what it means to thrive in a supportive learning environment, one where it's okay to make mistakes, to start over, to ask questions, and to be vulnerable. You all kept me going and I can't thank you enough for your constant support, love, and inspiration even when I couldn't tell my right from left. You helped me find strength and courage both in the studio and outside. You also helped me learn the value of rest and knowing and setting my boundaries. If you are a graduate student reading this, please find your community outside of the academia. The world is filled with wonderful and amazing people in the strangest places, don't miss out on meeting them.

Thank you to my grandparents for the support throughout the years, I know you are so proud of me.

Thank you to my sister, Joelle Cicak. You were the best research assistant, and I enjoyed our time spent in museum collections during the day and putting together puzzles in the evenings. Thank you for making me listen to *Stormlight,* without which I would not have processed all my tooth molds. Truly it was the journey before the destination.

And finally, to my mother, Nancy, and father, Joe, to whom this dissertation is dedicated. You fostered creativity and a love of science in every way. Thank you for always encouraging weird experiments in the backyard and helping me with science fair projects. Thank you for all the trips to museums, zoos, and national parks. These experiences were directly impactful to my development as a scientist and researcher. I love you so much.

Dedication

This dissertation is dedicated to my mother, my father and my sister; to the quiet moments we spent in nature.

Abstract

This project tests the hypothesis that primates respond to competition over food resources by focusing their feeding on underutilized resources. This shift in feeding focus is hypothesized to cause change to primates' tooth shape and change their dietary isotopes. Because teeth and isotopes are shown to accurately reflect diet, dental shape analyses were employed to analyze the degree of dental trait variability and isotope analysis examined differences in diet between primate dyads that live together and separately. This project asks three research questions: 1) do closely-related primate species focus their diet on a few key food items when they live together compared to the same species when they occur separately? and 2) do closely-related primate species display morphological traits and isotopic signatures that reflect a focus on fewer key resources when they live together compared to the same species when they occur separately? 3) do the teeth of fossil primates from the Early Miocene display similar dental traits as extant primates which might point to secondary resource use?

TABLE OF CONTENTS

List of Tables

List of Figures

1. Introduction

Species diversify to “better…their chance of succeeding in the battle of life” (Darwin 1859, p. 120). The importance of character divergence was first hypothesized by Darwin to help explain the diversity of life on this planet. He posited that natural selection should drive sympatric species to become more different over time. These differences would, in turn, reduce competition by allowing individual species to occupy separate niches (Pfennig and Pfennig, 2010). The process of morphological change from competition, now termed “character displacement” is evident in many sympatric populations including birds, rodents, lizards, and fish (Brown and Wilson, 1959). The importance of character displacement in species survival has led researchers to examine its effects on morphological traits (*e.g.*, body size, coloration, jaw morphology) as well as ecological traits (*e.g.*, feeding heights and isotopic values) in both extant and extinct populations (Schluter and McPhail, 1992; Crowley *et al.*, 2012; Ruette *et al.*, 2015; Volmer *et al.*, 2016). Among primates, however, rigorous testing of character displacement hypotheses has not been widely pursued. While some studies have examined the effects of competition within extant primate communities (Schreier *et al.*, 2009; Ramdarshan *et al.*, 2011; Stroik, 2014; Berthaume and Schroer, 2017), very few have applied these methods to the primate fossil record (Crowley *et al.*, 2012; Schroer and Wood, 2015).

The studies in this project build upon previous research that sought to understand dietary interactions within and between primate species. They do so by analyzing diet along multiple lines of inquiry comparing closely related species that occur in both sympatric and allopatric contexts. Hence, the impact of potential food competition can be directly assessed. The first study presents a robust literature review and analysis of primate feeding behavior. Next, two methods of dietary analysis are presented for extant primate specimens: 3D dental topographic analysis and stable isotope analysis of primate hair. Lastly, this project examines dental shape in fossil catarrhines to parse out subtle dietary behaviors. By combining multiple datasets in extant primates, this project captures both an adaptive signal (from the teeth) and an in-life signal (from the hair and behavioral studies). By subsequently applying these methods to a diverse set of fossil primate taxa, this project applies a competition-focused lens to interpreting fossil primate diets from a sample of Early Miocene catarrhines from eastern Africa.

The first project in this dissertation asks: Does the presence of a closely related competitor change percentages of primate fruit intake? This question is answered by examining and comparing published field studies of feeding behavior from three families of primarily frugivorous primates.

The second project in this dissertation tests the central hypothesis that primates respond to competition over food resources by feeding on underutilized resources, resulting in character displacement. Tooth shape and dietary isotopes were examined from sympatric and allopatric representatives for the following species comparisons: *Lagothrix lagotricha* and *Ateles belzebul*; *Cercopithecus ascanius* and *Cercopithecus mitis*; *Hylobates lar, Hylobates agilis* and *Symphalangus syndactylus*. These specific comparisons were chosen because they represent closely related taxa that should exhibit food competition when living sympatrically. Comparing their sympatric versus allopatric samples enabled me to test if character displacement was driving shape change in molar shape and across dietary isotopes.

The third project in this dissertation compares molar topography of Early and Middle Miocene eastern African non-cercopithecoid catarrhines to a diverse set of extant frugivores. Because most studies over the last two decades have categorized these fossil catarrhines as general frugivores, my analyses specifically used extant frugivore comparisons to help illuminate subtle differences in feeding strategies among extinct competitors. This project predicts that those fossil catarrhines that were previously posited to have a folivorous component to their diet will have dental shapes which align them with frugivores with a higher leaf intake as part of their fallback dietary strategy.

1.1 OVERVIEW OF DIETARY STUDIES IN THE PRIMATES EXAMINED IN THIS PROJECT

1.1.1 Extant primates

1.1.1.1 Alouatta, Ateles, and Lagothrix

Throughout South America, howler monkeys (*Alouatta*), spider monkeys (*Ateles*), and woolly spider monkeys (*Lagothrix*) appear sympatrically and display a variety of dietary strategies (Iwanaga and Ferreri, 2002; Dew, 2005; Dias and Negrin, 2015). While it was once thought that these three closely related species could coexist due by incorporating different proportions of leaves and invertebrate prey in their diets, observational studies of *Alouatta belzebul*, *Ateles marginates*, and *Lagothrix lagotricha* show high rates of frugivorous dietary overlap for large parts of the year (Peres, 1994; Iwanaga and Ferreri, 2002; Pinto and Setz, 2004; Dew, 2005). There is much observational evidence for territorial guarding of fruiting trees by *Alouatta belzebul,* often intimidating or discouraging *Ateles* and other sympatric primates from feeding locations (Pinto and Setz, 2004). Until recently, *Ateles* and *Lagothrix* species were considered exclusively allopatric due to issues of resource overlap (Peres, 1994). Sites in the western Amazon, however, show sympatry, indicating that *Lagothrix* and *Ateles* share a complex relationship (Peres, 1994; Dew, 2005).

1.1.1.2 Cercopithecus

Cercopithecus taxa are typically frugivorous, equatorial primates. Often, multiple species of *Cercopithecus* are found together in the same group despite extensive overlap in preferred food resources (Cords, 1986; Chapman and Chapman, 1996). These mixed species associations are considered potentially beneficial in predator detection (Chapman and Chapman, 1996). *Cercopithecus mitis* (blue monkeys) and *Cercopithecus ascanius* red tail monkeys) overlap in range and sometimes associate in mixed species groups. In Kibale, Uganda, dietary overlap occurs in 30% of plant species consumed. This contrasts with Kakamega Forest, Kenya, where there is overlap in 70% of food consumed. The difference is likely due to a higher consumption of fruit at Kakamega than at Kibale. At Kakamega, *C. mitis* and *C. ascanius* also differ in their prey capture methods despite consuming similar amounts of insect prey (Cords, 1986). The larger *C. mitis* appears to be more dominant than *C. ascanius* as they often displace *C. ascanius* from feeding in higher parts of the canopy (Houle *et al.*, 2006). At Semleiki Forest, Uganda, however, *C. mitis* is absent and *C. ascanius* has higher population numbers. This is noted as a potential example of competitive release between the two generally sympatric taxa (Struhsaker, 1978).

1.1.1.3 Hylobates and Symphalangus

Most ape species are allopatric, likely as a result – in some cases – of competitive exclusion from feeding competition over ripe fruits. This has been theorized for small-bodied gibbons, but siamangs (*Symphalangus*) and gibbons (*Hylobates*) do live sympatrically in Sumatra and Malaysia (Raemakers, 1978; Reichard and Preuschoft, 2016). Arguments for the cohabitation of these two species build upon divergence in diet, with the siamang thought to be more folivorous and the gibbon more frugivorous. This distinction has become problematic, however, as behavioral observations have revealed greater dietary overlap. Although Malaysian siamangs do consume more leaf matter than sympatric lar gibbons, a high percentage of their diet is composed of ripe figs – an essential food source for sympatric gibbons (Palombit, 1995). Interestingly, siamangs occupy higher canopy levels and exploit larger patches of food in smaller home ranges than do gibbons (Gittens and Raemakers, 1980). Though greater home range and lower canopy level use may be a factor of the lar gibbons' smaller body sizes, allowing them to utilize more flexible supports in smaller trees (Gittens and Raemakers, 1980; MacKinnon and MacKinnon, 1980), Elders (2013) found canopy occupation to be an avoidance strategy. Because there is evidence for ecological divergence within sympatric siamang and gibbon populations, morphological and chemical character displacement also may be expected. Likewise, allopatric gibbons may show evidence of competitive release.

1.1.2 Extinct primates

Early Miocene eastern African stem catarrhines appear at fossil localities in present day Uganda, Kenya, and Ethiopia and likely represent radiations of more primitive Oligocene taxa. While most of these primates are stem catarrhines, some exhibit traits associated with stem hominoids (Harrison, 2002; McNulty, 2010). In addition to being taxonomically important, early Miocene catarrhines display a staggering amount of diversity and regional specificity (Harrison, 2002; Shearer *et al.*, 2015). While there are more than twenty named primate species, these likely represent a small slice of the actual primate diversity in eastern Africa (Harrison, 2002). The large amount of taxonomic and adaptive diversity seen in this group makes understanding ancestor-descendent relationships difficult and causes challenges identifying appropriate extant analogues in comparative studies. For example, early Miocene taxa display similar ranges of molar morphological diversity to extant primates yet have shorter and more rounded cusps (Kay and Ungar, 1997). These primates, some which are posited to be closely related, show large ranges in body sizes: some estimated to be about the size of *Macaca fasciculans* while others are estimated as being as large as a female gorilla. While early Miocene catarrhine teeth display diverse morphology, recent studies (*e.g.*, Shearer *et al.*, 2015) of dental microwear were unable to distinguish diets; instead, microwear signals indicate that these primates were soft-fruit generalists (Shearer *et al.*, 2015). Because many of these primates probably existed within the same geographic and temporal space, frugivory would present issues of feeding competition especially during times of fruit scarcity (Stroik, 2014).

1.2 OVERVIEW OF METHODS

The following methods were used to assess diet in extant primates: 3D topographic analysis of occlusal tooth surfaces and dietary isotopes of primate hair. Tooth morphology is highly dependent on tooth function, and therefore dental adaptations should record the selective pressures that have acted upon a species (Ungar and Kay, 1995; Ungar, 1996; Boyer, 2008; Ungar and Scott, 2009; Bunn *et al*., 2011; Evans, 2013). Further, while differences in resources can have morphological impacts, those changes can take time to manifest. Carbon and oxygen isotope analysis, however, can help parse out subtle dietary behavior within an animal's lifetime and possibly identify differences in vertical niche occupation (Fourie *et al.,* 2008). Fossil primates were only analyzed using 3D topographic analysis.

1.2.1 Overview of 3D Studies of Diet

Mammalian tooth morphology and its correspondence to dietary behavior has a rich research history (Simpson, 1933; Butler, 1983; Kay, 1975; Rosenberger and Kinzey, 1976; Lucas, 2004). Early morphologists often used gross differences in tooth shape to identify dietary behaviors in both living and extinct taxa (Lucas, 2004). Primate dental morphology is no exception, and over the past few decades interest in quantifying the form-function relationship of tooth shape has become ever more refined. Research has supplemented traditional linear measurements of tooth length and width with a suite of metrics that represent the features of the occlusal surface (Jernvall, 1995). These new measures of tooth shape take into account the topography of the entire tooth crown or tooth row (Evans, 2013). Furthermore, these metrics no longer require the identification of homologous features or landmarks, bringing down errors due to interobserver differences (Ungar *et al.*, 2017). While 3D surfaces are required for these analyses, accessibility is increasing due to cost reduction in high-quality scanners, image processing software, as well as open access repositories of 3D data like Morphosource (Locke, 2021).

Dental topographic analysis (DTA) was developed as a dietary assessment method to circumvent two problems encountered by previous studies: 1) it can be applied successfully to worn and unworn teeth and 2) it can be applied to phylogenetic distant groups (Boyer, 2008; Evans, 2013). These methods take into account the entirety of the occlusal surface shape relying on high-quality three-dimensional laser or micro-CT scans (Winchester, 2014). Boyer *et al.* (2008) used Relief Index (RFI) (a measure of tooth height) and body mass to predict diet in euarchontan taxa. This not only tested RFI's ability to predict diet but examined how tooth shape is affected by phylogeny rather than adaptation. In their phylogenetically disparate sample, RFI was highly predictive of diet category and not affected by phylogeny. Bunn *et al.* (2011) used M_2 mesiodistal length, and a suite of DTA measures to predict diet within strepsirrhines and tarsiers. They found Direchlet Normal Energy (DNE) (a measure of occlusal surface curvature) as a single variable had the highest predictive power (69%) and the combination of DNE, RFI and Orientation Patch Count (OPCR) (a measure of surface complexity) increased diet predictability (78%). Winchester *et al.* (2014) applied RFI, OPCR and DNE to platyrrhine primates. As with previous studies, DNE most strongly predicted diet, classifying at 73%. Furthermore, when combined with measures more susceptible to effects of tooth wear, predictability increased to 85%. (Winchester *et al.,* 2014). Building on this research, Keller *et al.* (2017) further demonstrated that DTA is a powerful tool in predicting dietary behavior. Their study of North American rodent diets was able to glean measures of fallback feeding behavior. This is an important stride to understanding how dietary pressures can shape dental morphology.

This project also computes DNE, RFI, and OPCR in extant and extinct primate teeth. These measurements are be compared against observed dietary behavior to assess their ability to identify intraspecific differences.

1.2.2 Overview of Dietary Isotopes

Stable isotopes have long been used to assess differences in foraging ecology among extant and fossil mammals (Longinelli, 1984; Ayliffe and Chivas, 1990; Sponheimer and Lee-Thorp, 1999; Sponheimer *et al.,* 2009; Sanberg *et al.*, 2012; Crowley, 2014; Carter and Bradbury, 2016). Isotopic analysis can indicate not only dietary categories and but also habitual feeding position in the canopy (Carter, 2001; Krigbaum *et al.*, 2013). To reduce competition, primates will often forage at different levels of the canopy (Krigbaum *et al.,* 2013, Crowley *et al.*, 2016). Vegetation in dense forests shows variability in their isotopic signatures, where plants from the understory are more ^{13}C depleted whereas plants higher in the canopy will have more enriched ^{13}C values. This gradient from lower to higher enrichment is known as the “canopy effect” and is caused by the recycling of CO_2 and low irradiance (Krigbaum *et al.*, 2013). Oxygen isotopes display a similar vertical gradient such that plants lower in the canopy have lower ^{18}O values than those higher up in the canopy. Oxygen also varies with the part of the plant eaten: leaves are more enriched than fruits due to rates of evapotranspiration (Crowley *et al.*, 2016).

Many studies have tested canopy niche occupation within sympatric primate communities (Shoeninger *et al.*, 1997; Shoeninger *et al.*, 1998; Krigbaum *et al.*, 2013; Mancho and Lee-Thorp, 2014; Carter and Bradbury., 2016; Crowley *et al.*, 2016). Within a group of primates at Tai Forest, Cote D'Ivoire, Krigbaum *et al.* (2013) found that while carbon isotopes successfully show differences in feeding behaviors within sympatric species, they do not distinguish niche separation in forest dwelling primates. Oxygen isotopes however can accurately record differences in feeding location (Krigbaum *et al.*, 2013 yet see Carter and Bradbury, 2016 for counterpoint). Stable isotope analysis is still a powerful tool that can parse out feeding ecology as well as trophic level differences in closely related sympatric species (Dammhahn and Kappeler, 2014).

1.3 IMPORTANCE OF RESEARCH

Researchers have long understood the important role of diet in an organism's life and how competition over food resources can shape adaptations (Brown and Wilson, 1956). This project utilizes a holistic approach to quantify competition's effect on dietary behavior in both extant and extinct primates, with important implications for primate ecology as well as paleoanthropology.

This project greatly informs our understanding of extant primate adaptive processes. By applying a suite of ecometrics suitable for detecting subtle differences in dietary behavior and identifying fallback food behavior, this research results in a more detailed quantification of primate diet. Examining how dietary behaviors differ with the presence or absence of certain competitors has important implications for understanding primate behavioral flexibility and thereby one of the proximate causes of adaptive evolution. While many of the methods used here have been applied to other vertebrate groups, this project expands the taxonomic scope of character displacement in primates with the inclusion of platyrrhines who are highly frugivorous and often live in dense primate communities. Further this project examines character displacement on an interspecific level in primates whereas previous research has only looked at character displacement between populations. Through this, important contributions to the field of primate conservation are made. Primate habitats are shrinking from human activity. Widespread habitat loss can cause two results: primates could be forced into closer contact with competitors, or they could be separated entirely. The results of this project can potentially aid in conservation management programs to prevent further primate extinction.

A current theme in paleoanthropological research involves the changing proportions of primate taxa throughout the Neogene. Dozens of primate species existed during the Early Miocene in Africa, most of those recovered represent non-cercopithecoid catarrhines, some likely stem hominoids (McNulty, 2010; Begun, 2015). This distribution changed radically in the Middle Miocene, and some posit that the radiation of cercopithecoid monkeys resulted in competition for fruit resources that ultimately winnowed down the taxonomic diversity in non-cercopithecoid catarrhines (Temerin and Cant, 1983). By identifying subtle dietary specializations within the Early

Miocene sample, this project will directly address questions related to fossil catarrhine extinction and mechanisms of adaptation.

Finally, the methodology of this project, which combines multiple areas of dietary behavior, can readily be applied to the primate and hominin fossil record. *Homo sapiens* stands as the only surviving member of its genus. The fossil record indicates that throughout hominin evolution, this isolation is an exception. Understanding how character displacement operated in human ancestors will help researchers better answer questions about the loss of hominin diversity.

2. Do Primates Vary Food Intake Rates When a Competitor is Present?

2.1 INTRODUCTION

No organism lives in an environment devoid of interaction. Within a given community, *i.e.*, all animal and plant species interacting within an ecosystem, species may compete with each other for resources. As such, competition between organisms is a major force shaping communities by maintaining diversity within an ecosystem (Putnam and Wratten, 1984). Because sharing a resource can reduce the reproductive success of competing species, natural selection will favor adaptations which aid in avoiding interspecific competition, thus reducing competitive overlap (Putnam and Wratten, 1984).

To mitigate competition, sympatric species of the same guild generally diverge in some way to avoid competition, whether by staggering activity time, separating into different vegetation layers, or not eating the same amount of the same resource (Bouliere, 1985; Elder, 2013). Indeed, this behavior follows Gause's (1934) competitive exclusion principle, which states two species living in the same geographic area and occupying the same ecological niche cannot exist: one species must diverge in some way or go locally extinct. The species that survives will be the one with an ecological advantage even if the advantage is very slight (Gause, 1934). When two species diverge in ecology, thus reducing competition and subsequently preventing exclusion, they are said to have gone through "character displacement." Limitations on resources will cause morphological, behavioral, or ecological characters to differentiate. Character displacement can appear in any ecological aspect of a population. Differences in morphology are only one mechanism of facilitating species coexistence (Brown and Wilson, 1956).

Food interactions and competition over food resources are by far the most common biotic relationship (Putnam and Wratten, 1984; Isbell and Young, 2002). This is certainly true in any primate community, as food is almost always a limiting resource. While some sites have higher overall food productivity than others, primates face constraints not only in overall food abundance, but from other vertebrate, and possibly even insect species (Beaudrot *et al.*, 2013). Long-term studies of primate species, indicate that resource partitioning is not simple or straightforward (Stevenson *et al.*, 2000). Because two species cannot coexist in sympatry – *i.e.*, occurring within the same geographic area – without some degree of specialization, interspecific primate competition has long been assessed as an important factor in mammalian community structure. As primates are a large often frugivorous biomass, their presence in forest communities and feeding strategies can influence the available resources for other organisms (Gause, 1934; Isbell and Young, 2002; Dew, 2005; de Almeida Rocha *et al.*, 2015).

While competition is likely greatest between members of the same species, competition between closely related and similarly foraging primate species can cause changes to foraging behavior at best and, at worst, can hamper reproductive success (Stevenson, 1999; Butynski, 2015). As many primate species are frugivorous, forests with less fruit production display a decline in the number of sympatric primate species

(Ganzhorn, 1999; Stevenson, 2001). Furthermore, in environments where fruit productivity is seasonal and there are months of periodic fruit scarcity, frugivorous primate species experience increased pressure from closely related, similarly foraging competitors (Kamilar and Ledogar, 2011). During seasons of scarcity, pressure is exerted on sites with heavy frugivore loads and periodic scarcity may lead to reliance on secondary resources to reduce resource overlap (Marshall and Wrangham, 2007).

Examining how primate species partition limited food resources or rely on less preferred resources is important for identifying how primates cope in ever-shrinking forest habitats. Because shrinking forests cause increased overlap in home ranges, there is potentially more competition over limited food resources. There is concurrence that deforestation is the single biggest threat to primate biodiversity (Marsh, 2003; Chaves *et al.*, 2012). Not only does it decrease the forest size, but logging alters the physical structure of vegetation and ultimately the availability of food resources. These changes may impact primates considerably. Thus, behavioral flexibility would allow a better chance of surviving in altered habitats (Pinto *et al.*, 2003). Further, as forests become more fragmented, loss of both animal and plant species occurs. Primates are important seed dispersers, as the trees they feed from have evolved to be endozoochoric (agents of seed dispersal) and loss of primate diversity can, in turn, further impact forest productivity. Therefore, it is paramount to understand how primates interact with each other and how they behave when a competitor is absent from their territory (Chaves *et al.*, 2012).

This paper seeks to examine whether interspecific competition (competition between species) changes primate feeding behavior by using behavioral observations of primate feeding available in the literature. Understanding intraspecific dietary variation is important when making interspecific comparisons and when relating these differences to niche partitioning, differences in ecology, or differences in dietary adaptations. Further, understanding dietary variability is important to conservation, as it reflects species' flexibility as well as their dependencies (Strushaker, 2017).

2.1.1 Theoretical background on competition in primate taxa

If two species with similar ecological preferences live in the same environment, the overlap will have a direct effect on the each other's free use of available resources. As Putnam and Wratten (1984) summarize, this often manifests as a depressive effect on population growth in one or both species. If competition is particularly intense, one of the species may go locally extinct. Alternatively, one species might be excluded completely or in part from that resource and be forced to change its behavioral ecology (Putnam and Wratten, 1984).

How an organism reacts to competition will affect the breadth of its dietary niche. An organism may respond to competitor pressure by broadening its niche. In other words, it may consume a wide variety of resources to meet its nutritional needs. Intraspecific competition can result in expanded niches, but only in instances when competition with other species is not severe. In those instances, intraspecific competition will force individuals within a population to exploit resources that are underutilized, causing a limiting of resource use at the individual scale but a diversity of resource use on a population scale. Because the population as a whole pursues a wider range of resources, anatomy may become more generalized. (Putman and Wratten, 1984).

On the other hand, an organism might instead narrow its dietary niche by concentrating on a few resources that were under-exploited by other community members (Feinsigner *et al.*, 1981; Chase and Leibold, 2003). Interspecific competition tends to constrain dietary niche breadth. Each species will specialize so that it utilizes the part of its niche not already exploited by a competitor. This change can occur rapidly or slowly (Putnam and Wratten, 1984).

Understanding interspecific competition in primate taxa is complicated. Untangling competition influencing food choice, reproductive success, and biomass from other factors such as rainfall, predator pressure, seasonality, and physiology has proven challenging in many taxa (Morse, 1974; Janson, 1985; Ganzhorn, 1989; Abramsky *et al.*, 1998; Ganzhorn,1999; Morris *et al.*, 2000; Houle *et al.*, 2006). Diamond (1975) proposed that resource competition leads to differences in community assembly and that some species simply could not coexist, creating a checkerboard pattern where one species is absent at one site, present at another, and *vice versa*. Diamond's (1975) assembly rules have been challenged recently (Ulrich 2004 and references therein) in favor of community structure being organized by neutral forces or random abiotic factors (*e.g.*, mean annual temperature, rainfall, elevation) (Urlich, 2004; Buzzard, 2006; Kamilar, 2009; Beaudrot *et al.*, 2013). Most likely, community structure is not the result of one factor and is influenced by both random (*e.g.* abiotic factors) and non-random (*e.g.* competition) processes. Ultimately, when examining hypotheses of community structure, it is important to test multiple lines of evidence (Urlich, 2004)

As with any habitat, forests contain limited resources thus the population of forest inhabitants is expected not to exceed the carrying capacity of forest resources. As part of navigating that process, those inhabitants may diversify into separate niches to mitigate competition and maximize energy return (Gause, 1934). Many observational studies investigate resource overlap and partitioning in primate communities (Gautier-Hion, 1983; Cords, 1987; Guillotin *et al.*, 1994; Peres, 1994; Ganzhorn, 1997; Stevenson *et al.*, 2000). While most of these studies were confined to one site, they demonstrate there is often separation in food resource partitioning. This resource partitioning is not always observed as a redirection of food intake, some of these studies observe differences in canopy level feeding, travel distance to resources, or changes in time of day for feeding (Cords, 1986; Beaudrot *et al.*, 2013).

Even though all primate taxa are burdened to some level by competitive pressure from other primates or vertebrates within its range (Terborgh,1990), this study examines seven genera that are thought to face interspecific pressure from other closely-related primate species.

2.1.2 Dietary Ecology of Alouatta, Ateles, and Lagothrix

Alouatta, *Ateles*, and *Lagothrix* are closely related and often appear sympatrically throughout South America. They display a variety of dietary strategies and coexistence was once thought to be a result of each genus incorporating different proportions of leaves and invertebrates into their diet (Iwanaga and Ferreri, 2002; Dew, 2005; Dias and Negrin, 2015). The relationship between the three is not so straightforward, as observational studies report *Alouatta belzebul*, *Ateles marginates*, and *Lagothrix lagotricha* all display high rates of frugivorous dietary overlap for large parts of the year (Peres, 1994; Iwanaga and Ferreri, 2002; Pinto and Setz, 2004; Dew, 2005). While

Alouatta has many adaptations for efficient folivory, understanding habitat and dietary overlap between *Lagothrix* and *Ateles*, both of which concentrate feeding efforts on ripe fruits, has led researchers to posit various explanations rather than resource partitioning alone (Stevenson *et al.,* 1994; Stevenson *et al.,* 2000; DiFiore and Rodman 2001; Iwanga and Ferrari, 2002; Dew, 2005).

Howler monkeys (*Alouatta* spp.) are the most widely distributed platyrrhine genus, ranging from southeastern Brazil throughout the Amazon Basin, the Guyana Shield, and as far north through Central America as Mexico. *Alouatta* habitats range from *llanos* (*i.e.* a treeless grassy plain) to gallery forests to tropical rainforest (Pinto and Setz, 2004). The twelve howler monkey species exhibit variation in behavior, ecology, and social organization and are, for the most part, allopatric, with a few species sharing contact zones (Pinto and Setz, 2004; Agostini *et al.*, 2010).

They display an energy-minimizing strategy with small day ranges, hind-gut fermentation, and slow food passage rates with extended rest and digestion time (Milton, 1981; Chiarello, 1993). These traits may be an evolutionary strategy to living in dry, seasonal, patchily forested habitats. (Agostini *et al.*, 2010). Originally considered to be folivores, howler monkeys are highly selective foragers, often consuming fruit resources (Dias and Rengel-Negrin, 2015). In their study of all recorded observation of howler monkey diet, Dias and Rengel-Negrin (2015) found that across species, howlers spend nearly 20% of daily activity time feeding from tree resources (leaves, flowers, ripe and unripe fruits). While howler monkeys are best described as folivore-frugivores, in their study, Dias and Rengel-Negrin (2015) found high amounts of both inter-and intraspecific dietary variability (*i.e.*, *Alouatta caraya* was the most folivorous howler monkey while *Al. belzebul* was the most frugivorous). Additionally, Dias and Rengel-Negrin (2015) found fruit intake is correlated with rainfall levels. Dietary range is wider for howlers living in a forest with more variable rainfall, while those living in areas with high mean annual rainfall levels consume the most fruit. Even though forests with higher rainfall may be more productive, they observed that as group size increases, fruit consumption predictably decreases as larger groups deplete fruit patches more rapidly and increase the consumption of alternative food resources (Dias and Rengel-Negrin, 2015).

While all parts of the leaf are usually consumed, howler monkeys consume more young leaves than mature leaves (Dias and Rengel-Negrin, 2015). Howlers also supplement their diet with bark, gums, decaying wood, pinecones, roots, eggs, insects, nectar, flowers, and termites. Insect consumption may be an important vitamin and mineral source, but much consumption is likely accidental (Bovicino, 1989; Bicca-Marques, 1992; Chiarello, 1994; Bravo and Zunio ,1999; Mendes, 1999; Bravo and Sallenave, 2000; DeSouza *et al.*, 2002; Pinto *et al.*, 2003; Almeida-Silva *et al.*, 2005; Ludwig *et al.*, 2008; Carmego *et al.*, 2008; Martins, 2008; Prates and Bicca-Marques, 2008; Bicca-Marques *et al.*, 2009; Pave *et al.*, 2009; Fernandez *et al.*, 2017).

Unequivocally, howler monkey teeth display adaptations for eating leaves. They have thin enamel and high shearing crests as well as small incisors (Cristobal-Azkarate *et al.*, 2015). Their intestinal anatomy shows an enlarged caecum and proximal colon as well as gut bacteria beneficial in processing large amounts of vegetation (Dias and Rengel-Negrin, 2015). Milton (1981) points out that howler monkeys may have to eat leaves due to slow gut passage rates, making them unable to extract large amounts of protein from fruit sources alone. They have fewer adaptations for effective fruit processing despite observed fruit eating. In *Alouatta* this has been hypothesized to be an ancestral condition as all other Atelidae consume primarily fruit resources. This greater reliance on leaves may have come from selective pressure with other fruit eating primates in Neotropical forests (Rosenberger, 2011).

While variation exists, howler monkeys spend most of their time in the middle and upper forest strata (Bravo and Sellenave, 2003). The middle stratum is used for feeding and resting while the upper stratum is used mostly for resting. Where howler monkey species do overlap, food competition does not seem to be a driving factor in forest strata usage. However, studies show that during lean periods when food is extremely scarce, howler monkeys do exhibit some vertical niche stratification (Agostini *et al.,* 2010).

Interactions with sympatric primates range from aggressive to friendly (Cristóbal-Azkarate *et. al*., 2015). Howler monkeys are frequently harassed and attacked by white-faced capuchins in Santa Rosa National Park, Costa Rica, often resulting in *Alouatta* leaving feeding trees (Rose *et al*., 2003). While howler withdrawal from feeding patches is observed, mantled howler monkeys sometimes display aggressive behaviors to capuchins in return (Fedigan and Jack, 2012). On many occasions, howler monkeys have been observed to feed with spider monkeys (*Ateles* spp.) (Klein and Klein, 1973; Mendes-Pontes, 1997). Though co-feeding occurs, spider monkeys have been observed to supplant howlers from feeding trees and howlers are observed waiting until spider monkeys are done feeding before entering a feeding tree (Simmen, 1992). At other sites, spider monkeys avoid howler monkeys (Dias and Rangel-Negrín 2015). There are no published studies describing interactions between *Alouatta* and *Lagothrix*. Studies of fruit availability of *Lagothrix* agonistic behavior, however, does indicate there is some aggression towards other primates when feeding in proximity (Cavalcante *et al.,* 2021).

Spider monkeys (*Ateles* spp.) are the largest platyrrhine species and range from southern Mexico, through Central America, and into Brazil. Based on analysis of DNA, there are four distinct species of spider monkey each divided into subspecies (Celeria de Lima *et al.*, 2007; Collins, 2008). All subspecies are strictly arboreal and their post-cranial anatomy aids in fruit seeking behaviors (Dew, 2005). Their long, lithe bodies and extremely dexterous prehensile tail aids in semi-brachiation through the rain forest canopy (DiFiore and Link, 2008). This rapid, efficient movement helps them access widely dispersed food patches (Dew, 2005).

Spider monkeys are a classic example of a ripe fruit specialist, as 55%-90% of their overall diet consists of ripe fruit (DiFiore and Link, 2008). Their dental anatomy reflects this fruit-seeking behavior, with incisors that are quite developed while their molars are small but have wide crushing basins. The small size of their molars is consistent with expected frugivore dentition but might be related to their absolutely smaller face when compared with other atelines (Rosenberger *et al.*, 2008). Spider monkey molar topography is quite simple as they do not crush seeds and instead swallow them whole (Link and DiFiore, 2006). Because of this seed swallowing strategy, they are considered to be important seed dispersers (Dew, 2005; Link and DiFiore, 2006). While ripe fruits comprise the bulk of their diet, spider monkeys often supplement their diet with unripe fruit and animal resources, though this can vary from site to site (Wallace, 2005).

An example of dietary variance between sites is at Yasuni National Park, Ecuador. There, *Ateles* consumes more than 250 plant species, whereas at Santa Rosa National Park, Costa Rica, they only consume 30-40 species. Indeed, at some sites, leaf resources seem to be seasonally important, comprising up to 36% of *Ateles belzebuth chamek* in Bolivia during the dry season (Wallace, 2005). Insectivory and consumption of other animal prey is limited. While it does occur, it is only is reported consistently during caterpillar blooms. During these blooms, feeding bouts are long and spider monkeys actively search for caterpillars and caterpillar larvae (van Roosmalan, 1988).

At most sites, *Ateles* foraging behavior, ranging behavior, and group size are driven by fruit availability (Wallace, 2008). While often moving quickly through the canopy, *Ateles* will stay longer in larger fruiting trees and fruit patches likely to maximize energy from fruit abundance. *Ateles* lives in multi-male, multi-female fission-fusion societies with group composition changing throughout the day. Often, they forage in small parties that are a subset of the larger group (DiFiore and Link, 2008).

Woolly monkeys are a large bodied, critically endangered ateline (Defler and Stevenson, 2014). Their current range consists of largely undisturbed central and western Amazonian rainforest, yet they are also found in the highlands of the Andes of Venezuela, Peru, Colombia, and Ecuador (Mantilla-Meluk, 2013). *Lagothrix* is especially sensitive to hunting pressures and has been driven locally extinct in many areas with higher human activity (Defler and Defler 1996). Current locales for undisturbed populations are difficult to access and as such they remain poorly studied (Peres 1994) and much of the literature focuses on populations within Colombia (Defler and Stevenson, 2014). There are two recognized species of wooly monkey: yellow woolly monkey (*Lagothrix flauvacauda*) and Humboldt's woolly monkey (*Lagothrix lagotricha*). The latter is more widespread and divided into four allopatric subspecies. Both live in *terra firme* forest, away from large rivers that are susceptible to seasonal flooding (Stevenson *et al.,* 1994).

Lagothrix is a large-bodied primate and ranges in weight from 6.5 to 12 kg, putting it in the same body size category as *Ateles* and *Brachyteles* (Peres, 1994). *Lagothrix* is unique in that it lives in large groups ranging from 35-70 individuals. Their large size coupled with large group membership makes them the largest primate biomass in areas where they are not sympatric with *Ateles* (Peres, 1994). Group home range size varies between 250 and 760 ha and, unlike *Ateles*, woolly monkeys move as a group. Though subgroupings are not uncommon, they maintain auditory contact during travel and feeding (Stevenson *et al.,* 1994). Cohesive group movement is often slow, moving quadrupedally through the canopy, searching for food as they travel. They do not often travel long distances, yet much of their time is spent moving in search of food (Dew, 2005; Ange-van Heugten, 2014).

Their diet consists of ripe fleshy fruits and is supplemented by young leaves and insects (DiFiore and Rodman, 2001; Dew, 2005). Often, they choose fruits which are lower in fat and higher in total sugars and water. Fruit consumption is not necessarily correlated with fruit availability and in some communities, fruit consumption is highest during periods of lowest fruit availability (DiFiore, 2004; Ange-van Heugten, 2014). However, other studies rank them as opportunistic frugivores since, during periods of scarcity, insect and leaf consumption was higher (Gonzalez *et al.,* 2016). Dietary variation is common across subspecies and across seasons. They have been observed to consume large amounts of insects perhaps indicating different protein requirements than other ateline primates (Ange-van Heugten, 2014). It is postulated that woolly monkeys may have physiological constraints that prevent them from ingesting large amounts of foods with secondary compounds or higher levels of fat, but more research is needed to confirm this (Stevenson, 2001; Dew, 2005). Like spider monkeys, woolly monkeys ingest large seeds and are important seed dispersers and agents of forest regeneration (Gonzalez *et al.,* 2016).

2.1.3 Dietary Ecology of Cercopithecus ascanius and Cercopithecus mitis

Cercopithecus mitis (blue monkeys) and *Cercopithecus ascanius* (red-tailed monkeys) are two guenon species endemic to central Africa (Butynski, 2015). While both species range in habitat from dry costal forest to lowland rain forest, (Cords, 1987), *C. mitis* is more ecologically diverse than *C. ascanius* and is found in riparian, gallery, and swamp forests as well as lowland and montane forests (Butynski and de Jong, 2020). While they share large ranges of overlap, zones of allopatry exist for both species. For example, *C. ascanius* is absent from forests on Mt. Elgon, Kenya and *C. mitis* is absent from the forests of Lake Victoria, Kenya (Cords, 1987). Despite *C. mitis* being more widely distributed than *C. ascanius*, *C. mitis* has a more fragmented distribution which may explain the high amount of variation within the species coloration and pelage patterns (Lawes *et al*., 1990).

Both *C. mitis* and *C. ascanius* have multiple subspecies assigned within each species however, subspecies of guenon show very little genetic differentiation despite differentiation in body size, pelage patterns, and coloration (Else *et al*., 1985; Butynski and de Jong, 2020). Subspecies differentiation is likely the result of allopatric speciation from climatically driven forest isolation (Turner *et al*., 1988). Despite being from different groups within the genus *Cercopithecus,* hybrids of red-tailed and blue monkeys have been identified in Gombe, Budongo, and Kibale National Parks. In some instances, female hybrids were fertile and produced offspring of their own (Detwiler, 2002).

While the subspecies taxonomy of *C. ascanius* and *C. mitis* is extensively debated (Butynski and de Jong, 2020 and references therein), they are both classified as members of the subfamily Cercopithecinae due to their cheek pouches, lack of enamel on their lower incisors, elongated cranial bones, flattened cranial vault and lack of a hypoconulid on the third molar (Butynski, 2015).

Both taxa are predominantly frugivorous and often co-occur in forests and forage in close association (Cords, 1987; Detwiler, 2010). For example, in Kenya these two species often associate within foraging areas while displaying up to 70% of overlap of dietary items (Cords, 1990). Multiple studies have sought to understand the social dynamics that drive these mixed species groupings and the ecological dynamics that allow for the sharing of resources (Gathua, 1999; Cords, 1987; Chapman and Chapman, 2000). Mixed association tends to increase competition among members, but this is only an issue if the resources are limiting; this drives questions of whether red-tailed and blue monkeys are truly competitors and, if they are, what are the costs of mixed species associations (Cords, 1990).

For example, at Kibale, Uganda, red-tailed and blue monkeys associate 27.6% of the time and have considerable dietary overlap (Bryer *et al*., 2013). In the Kibale forest, fruit is most dense in upper levels of the canopy. This is likely not site specific because lower canopy levels receive less sunlight and therefore produce fruit less densely in these conditions (Houle *et al.*, 2007; Houle *et al.*, 2010). At this site, interspecific dominance hierarchies seem to determine foraging height. While *C. ascanius* has large group sizes (14-50 individuals), they are submissive to blue monkeys, mangabeys, and chimpanzees (Strushaker, 2017). This is measured via outcomes of aggressive interactions over fruit (Bryer *et al*., 2013). When feeding in a single-species group, *C. ascanius* fed higher in the canopy but was often displaced by other primate species if feeding was interrupted (Cords, 1990). Houle *et al.,* (2010) found that *C. ascanius* consumed foods more quickly when feeding in polyspecific associations but that dominant species never adjusted their feeding height or feeding rate. It is also possible that subordinate species feed faster on foods of lower nutritional quality, thus more dominant species also benefit from the ability to forage at higher canopy due to the higher nutritional quality of the ripe fruit (Houle *et al.,* 2010).

At Kakamega Forest, Kenya, Cords (1990) found that red-tailed and blue monkeys often foraged together but redtails were, again, often displaced by the larger blue monkeys. She concluded that the mixed species association seemed to be preferred and not random as they often lasted 4-6 hours on average. Furthermore, during these associations, red-tailed monkeys often fed briefly or waited for blue monkeys to be finished. Cords (1990) noted a potential temporal niche separation between the two species as *C. ascanius* were more active towards the end of the day and at that time were able to feed uninterrupted by blue monkeys as *C. mitis* was resting during this time. While food consumption did not vary strongly between the sympatric associates at

Kakmega, female red-tailed monkeys seem to take in more insects, though this could be a need for more protein during pregnancy or lactation (Cords, 1986; Cords, 1990).

Bryer *et al.,* (2013) found red-tailed monkeys at Kibale foraged closer to blue monkeys when feeding on fruit resources, indicating that the clumped nature of the food resource may be a factor determining association since they found that the monkeys were more widely dispersed when feeding on leaf resources. In the same study, they found that *C. ascanius* consumed more fruit items when associating with mangabeys (which have a higher proportion of fruit resources in their diet compared to red-tailed monkeys) than leaves. Bryer *et al.,* (2013) concluded that despite the potential competition cost incurred to red-tailed monkeys, feeding in mixed species associations provided benefits in terms of predator detection. Furthermore, while the subordinate status of red-tailed monkeys in mixed species associations may cause competition over fruit resources, they may not cause a nutritional trade-off as red-tailed monkeys can effectively fall back on insect resources if other food resources are being exploited by heterospecific competitors (Bryer *et al.,* 2013).

Cercopithecus mitis has a more varied diet than other guenon species and while they still consume much fruit, they incorporate comparatively more plant matter (Lawes *et al.,* 1990). Lawes *et al*. (1990) have suggested that ingesting more leaf matter is a strategy by *C. mitis* to mitigate competition with more specialized sympatric primates or with congeners. However, whereas the lack of a frugivorous competitor at Cape Vidal, South Africa should result in more fruit consumption, the *C. mitis* community there instead shows a high proportion of leaf-eating (Lawes *et al.,* 1990). *C. mitis* seems to concentrate its feeding efforts on a small number of food items despite being recognized as less of a specialist than other guenon species (Lawes *et al.,* 1991).

2.1.4 Dietary Ecology of Hylobates and Symphalangus

Hylobatids display a range of interspecific body size variation that is rare among extant anthropoids, the reasons for which are not well understood. While most species in the gibbon group (*Hylobates*, *Nomascus*, *Hoolock)* are small (between 5.3 and 7.8 kg), the closely related siamang (*Symphalangus*) is 1.5-2 times larger (Reichard and Preuschoft, 2016). The difference in body size becomes more interesting when patterns of resource use are examined.

Most gibbon species are allopatric, likely to reduce feeding competition over ripe fruits (Elders, 2013). Siamangs and gibbons, however, live sympatrically in Sumatra and in Malaysia (Raemakers, 1979; Reichard and Preuschoft, 2016). Most arguments for the coexistence of these two species build upon divergence in diet with the siamang thought to be more folivorous and the gibbon more frugivorous (Raemakers, 1984; Elders, 2013). Reichard and Prueschoft (2016) point out that the increased gut length in the siamang corresponds with adaptations to folivory and would aid in leaf digestion. Furthermore, folivory is associated with the ability to grow to a larger body size (Reichard and Preuschoft, 2016). The distinction between gibbon and siamang diets, however, has become problematic as more behavioral observations reveal higher degrees of dietary overlap than once thought (Raemakers, 1977; McKinnon and McKinnon, 1980; Palombit, 1995). While Malaysian siamangs do take in more leaf matter than sympatric lar gibbons, they are definitive “fig seekers” . A high percentage of siamang diet is composed of ripe figs and is comparable to the percentage of figs eaten by small-bodied gibbons (Palombit, 1995). While small-bodied gibbons do consume more non-fig fruits than siamangs, there are still high degrees of dietary overlap between sympatric siamangs and gibbons (Elder, 2009).

While siamangs and small-bodied gibbons may overlap in food, they do diverge in other ecological aspects. Gittens and Raemakers (1980) found that siamangs prefer higher canopy levels and therefore feed higher up. Siamangs also exploit larger patches of food in a smaller home range, whereas small-bodied gibbons utilize greater home ranges. The greater home range may be a function of lar and agile gibbon smaller body size, as they can more easily navigate through the dense forest (Gittens and Raemakers, 1980; MacKinnon and MacKinnon, 1980). The use of lower canopy levels may be a function of competition as Elders (2013) found siamangs often displaced gibbons from productive feeding patches, which often occur higher up in the canopy. In the same study, Elders (2013) found canopy occupation may be an avoidance strategy by small-bodied gibbons as siamangs at the site of Way Canguk, Sumatra, often displaced gibbons from feeding trees. Furthermore, gibbons at this site were observed to have faster feeding times and larger ranges to account for the competitor pressure (Elders, 2013).

2.2 STUDY DESIGN

The aim of this paper is to investigate whether primates vary their diets based on the presence of closely related competitors. As explained above, the primates investigated here are mostly frugivorous, or at least will prefer ripe fruits when foraging. Because fruit is considered to be a more limited resource, this paper hypothesizes that fruit intake will primarily be affected by sympatry or allopatry with respect to closely related competitors. This study does acknowledge that other factors not necessarily related to feeding competition may contribute to differences in fruit intake across sites. Hence, the second aim of this paper is to investigate whether two factors unrelated to competition (rainfall and body mass) more accurately predict dietary behavior than the presence or absence of a competitor. To that end, the following hypotheses are tested:

1. Percentage of feeding time devoted to limited food items (*e.g.*, fruit and flowers) is lower when primates live in sympatry and higher when they are allopatric.
2. More evenly dispersed food items (i.e., leaves) show higher feeding percentages when closely related species are sympatric.
3. Larger body size is positively correlated with higher leaf intake.
4. Higher rainfall is positively correlated with fruit and flower intake.

2.3 METHODS

2.3.1 Data Collection

Percentage of feeding time devoted to each food category was extracted from observational studies and compilations of feeding data (Table 2.1). Studies were included if the duration was longer than nine months. Although this lower boundary potentially obscured seasonal variation in diet, the majority of dietary data came from studies 12 months or longer, with 9-12-month studies included to increase the number of allopatric samples. Most behavioral observations were compiled via scan sampling or focal follows. While differences in sampling methods could generate biases in feeding category recorded, sampling method differences were not associated with individual species. Thus, errors do due different behavioral observation methods are expected to be random rather than biased.

First, feeding time was extracted from each study, then the proportion of time spent feeding on different food resources was calculated as a percentage of total feeding time. The following dietary categories were used: fruit, leaves, flowers, animal prey, other. The "fruit" category consisted of both ripe and unripe fruit and fruit parts. "Leaves" included young leaves and mature leaves as well as petioles, stems, and other fibrous items. "Animal Prey" consisted of vertebrate and invertebrate species. "Flowers" included buds. "Other" included any food item reported which did not fit into other categories (*e.g*., gums, fungi, galls) as well as items placed in "Other" by the original authors. Thus, the category "Other" could potentially include items like stems or buds if these were specified in the cited studies. Finer-scale food categories could potentially result in better diet classifications, but such resolution is not possible from the current literature.

Feeding percentages in each study were totaled to confirm observations added up to 100%. Any studies whose total feeding data summed to less than 98% or more than 102% were removed.

Average rainfall was also taken from site reports. Average female body mass was taken from Smith and Jungers (1997). Female body mass instead of species body mass was used to mitigate effects of sexual dimorphism in males. While Smith and Jungers (1997) report body weights for most species analyzed here, there might be discrepancies in taxonomic designation between the behavioral studies and assigned body mass. All body mass was recorded at the species level and then averaged to get the genus body weight average used in the Ordinary Least Squares regression.

2.3.2 Dietary Comparisons

First, averages for each feeding category were calculated for each species and each genus, regardless of sympatry or allopatry (Table 2.1). Next, feeding averages were calculated for each species when in sympatry or allopatry (Table 2.2).

To test whether percentage of feeding time devoted to limited food items (*e.g*., fruit and flowers) is lower when primates live in sympatry and higher when they are allopatric (Hypothesis 1), Mann-Whitney U tests were used to determine whether average feeding percentages differed between taxa in sympatry with competitors and the same taxa in places where competitors are absent. Next, to test whether average feeding percentages of more evenly dispersed food items (i.e. leaves) show higher feeding percentages when closely related species are sympatric (Hypothesis 2), Mann-Whitney U tests were again employed.

Regressions were calculated to determine whether female body mass (Hypothesis 3) or rainfall (Hypothesis 4) predicted food consumption in each category.

2.4 RESULTS

2.4.1 Feeding Averages

Results are reported, first, by looking at overall dietary behavior for each genus sampled. Average feeding values for each species and for each genera are compiled in

Table 2.1. Next, average percentage of feeding time devoted to each food category is examined by competitor presence or absence, reported in Table 2.2.

Ateles consumed the most fruit resources of any of the primates included in this study. Across spider monkey species, *Ateles* averaged 79.42% of it diet from fruit resources, 10.73% on leaf resources, 4.39% on flowers, 0.58 on animal prey, and 5.38% on other resources. *Lagothrix* spent the second highest amount of time consuming fruit resources (65.44%). *Lagothrix* concentrated more on animal prey (16.26%) than leaves (14.27%) as its secondary diet choice. *Alouatta*, examined as a genus, had the lowest average time spent on fruit resources (27.72%); notably the species *Alouatta macconelli* spent more time eating fruit resources than did *Lagothrix* spp.

C. ascanius and *C. mitis* had nearly identical feeding averages for fruit (47.96%, 47.49%), leaves (22.59%, 22.55%), and flowers (7.08%, 7.86%). *C. ascanius* spent more time on average consuming seeds (25.2%) than did *C. mitis* (19.17%).

Hylobates consumed more fruit resources than *Symphalangus* (44.04%, 30.16%). These averages may be skewed as studies differed on whether they included figs in the "Fruit" category the "Other" category. *Hylobates* consumed fewer leaf resources than *Symphalangus* (27.05%, 32.73%).

Table 2.1: Feeding averages of all species sampled in this study for the diet categories "Fruit," "Leaves," "Flowers," "Seeds," "Animal Prey," and "Other".

Feeding averages							
Averages	Fruit	Leaves	Flowers	Seeds	Animal Prey	Other	Citation
Ateles belzebuth	80.59	9.60	4.08	NR	0.26	6.62	1-8
Ateles chamek	80.83	13.44	3.21	NR	0.33	0.53	9-11
Ateles geofferyi	69.50	14.93	7.10	NR	1.53	7.26	12-15
Ateles pansicus	79.80	7.90	6.40	NR	1.00	5.60	16
Ateles hybridus	92.40	3.10	0.30	NR	NR	4.20	17
Average all *Ateles*	79.47	10.73	4.39	NR	0.58	5.38	-
Average all *Lagothrix*	65.44	14.27	2.27	NR	16.26	3.22	18-29
Alouatta bezebul	42.64	38.10	12.12	NR	NR	4.60	30-34
Alouatta caraya	26.6	64.57	6.56	NR	NR	3.50	35-46
Alouatta palliata	26.93	54.85	17.06	NR	NR	2.20	47-55
Alouatta guariba	22.52	66.25	9.18	NR	NR	4.30	56-60
Alouatta macconelli	69.00	28.60	2.40	NR	NR	NR	62
Alouatta seniculus	31.68	57.56	6.86	NR	NR	7.14	62
Average all *Alouatta*	27.72	59.64	10.35	NR	NR	4.44	-
Cercopithecus ascanius	47.96	22.59	7.08	25.20	6.47	2.99	63-74
Cercopithecus mitis	47.49	22.55	7.86	19.17	4.83	4.60	75-85
Average all *Symphalangus*	30.16	32.73	6.06	NR	7.76	27.8	86-92
Average all *Hylobates*	44.04	27.05	3.63	NR	5.65	23.99	86-92

1. Dew 2005; 2. Suarez 2006; 3. DiFiore *et al.,* 2008; 4. Nunes, 1998; 5. Pontes, 1997; 6. Russo *et al.,* 2005; 7. DiFiore *et al.,* 2008; 8. Klein and Klein, 1977; 9. Felton *et al.,* 2008; 10. Wallace, 2005; 11.Symington, 1987; 12. Chapman and Chapman, 1991;13. Chapman, 1987; 14. Campbell, 2000; 15. van Roosamalen, 1988; 16. Mittermeier and van Roosmalen, 1981; 17. Link *et al.,* 2012; 18. Peres,1993, 19. Peres, 1994; 20. Stevenson *et al*., 1994; 21. Stevenson, 2006; 22. Stevenson *et al*., 2000; 23. DiFiore and Rodman, 2001; 24. Dew, 2005; 25. Defler and Defler, 1996; 26. Gonzales *et al*., 2016; 2,7. Neville *et al*., 1976; 28. Zarare and Stevenson, 2014; 29. Cifuentes *et al.,* 2013; 30. Bonvicino, 1989; 31. Carmargo *et al*., 2008; 32. de Souza *et al*., 2002; 33. Pinto and Setz, 2004; 34. Pinto *et al*., 2003; 35. Alves and Guix, 1992; 36. Rumiz *et al*., 1986; 37. Agostini *et al*., 2010; 38. Prates, 2007; 39. Prates and Bicca Marques, 2008; 40. Bicca-Marques and Calegaro-Marques, 1994; 41. Bravo and Sellenave, 2003; 42. Ludwig *et al*., 2008; 43. Rimoli et *al*., 2008; 44. Zunino 1986; 45. Arditit 1992; 46. Muhle 2008; 47. Asensio-Herrero *et al*., 2007; 48. Chapman, 1987a; 49. Chapman 1987b; 50. Glander, 1981; 51. Martínez-Esquivel, 2010; 52. Milton, 1980; 53. Rodríguez-Luna, 2003; 54. Serio-Silva, 1995; 55. Serio-Silva, 2002; 56. Mendes, 1989; 57. Silva, 1981; 58. Chiarello, 1994; 59. Chiarello, 1995; 60. Almeida-Silva et al 2005; 61. Martins, 2008; 62. Dias and Rangel-Negrin, 2015; 63. Bryer *et al*., 2013; 64. Strushaker, 2017; 65. Tweheyo and Obua, 2001; 66. Lambert, 2001; 67. Chapman and Champman, 2000; 68. Strushaker, 1980; 69. Cords, 1986; 70. Cords, 1987; 71. Byers *et al*., 2015; 72. Gathua, 2000; 73. Strushaker, 1978; 74. Sheppard, 2000; 75. Butynski, 1990; 76. Gautier-Hion, 1980; 77. Kaplin and Moermond, 1998; 78. Kaplin and Moermond, 1998; 79. Lawes *et al*., 1991; 80. Beeson *et al*., 1996; 81. Lawes *et al*., 1990; 82. Schlichte, 1978; 83. Fairgrieve 1995; 84. Rudran, 1978; 85. Tashiro, 2006; 86. Elders, 2008; 87. Elders, 2013; 88. Palombit, 1995; 89. Raemakers, 1979; 90. Raemakers and Chivers, 1980; 91. Reichard and Preuschoft, 2016; 92. Gittens and Raemakers, 1980

Considering whether a competitor was present at each site (Table 2.2), *Alouatta* did not spend less time on average consuming fruit resources when sympatric with *Ateles*, *Lagothrix*, or other *Alouatta* species. Not so of *Ateles* and *Lagothrix* which both followed the predicted pattern and spent less time consuming fruit resources when sympatric with closely related primates. For example, *Lagothrix* higher average consumption in all non-fruit categories when sympatric with *Ateles* when compared to its allopatric averages. Notably, *Lagothrix* had a higher average time spent consuming animal prey when sympatric with *Ateles*. Because there was only one study able to be included where *Lagothrix* and *Ateles* had feeding observations from sites where either species was allopatric from *Alouatta*, averages for sympatry and allopatry with *Alouatta* were not generated.

Similarly, only one study was identified where *C. ascanius* was allopatric from *C. mitis*. Once again, averages were not calculated for sympatry or allopatry for *C. ascanius* data. When examining *C. mitis* feeding averages, *C. mitis* spent more time consuming fruit and flower resources when allopatric from *C. ascanius*.

Because no studies were identified where *Symphalangus* was allopatric from *Hylobates*, averages were not calculated for *Symphalangus*. When allopatric from *Symphalangus*, *Hylobates* consumed more fruit resources than when in sympatry. *Hylobates* also consumed more leaf resources when allopatric. All statistical tests were conducted in R (Version 4.2.1).

Table 2.2: Feeding averages by genus based on sympatry or allopatry.

Averages	Fruit	Leaves	Flowers	Seeds	Animal Prey	Other
Alouatta						
Sympatric w *Ateles*	32.36	50.58	8.26	NR	NR	3.27
Allopatric w *Ateles*	28.05	60.73	13.79	NR	NR	2.46
Sympatric w *Lagothrix*	39.50	52.00	5.00	NR	NR	3.50
Allopatric w *Lagothrix*	29.08	57.66	10.26	NR	NR	2.69
Sympatric w *Alouatta*	36.40	50.72	6.40	NR	NR	6.10
Allopatric w *Alouatta*	28.79	58.09	10.42	NR	NR	2.41
Ateles						
Sympatric w *Lagothrix*	78.42	11.21	3.84	NR	0.26	6.53
Allopatric w *Lagothrix*	80.88	10.31	4.4	NR	0.73	3.9
Lagothrix						
Sympatric w *Ateles*	59.91	13.12	2.2	NR	22.46	2.86
Allopatric w *Ateles*	79.9	12.65	0.82	NR	4.47	2.15
C. mitis						
Sympatric w *C. ascanius*	47.12	20.84	6.00	20.47	2.07	3.33
Allopatric w *C. ascanius*	58.33	18.95	11.43	2.95	1.45	6.87
Hylobates						
Sympatric w *Symphalangus*	32.87	25.57	3.87	NR	15.03	22.33
Allopatric w *Symphalangus*	46.14	26.33	3.59	NR	3.93	17.68
Averages	Fruit	Leaves	Flowers	Seeds	Animal Prey	Other

2.4.2 Mann Whitney U-tests

To assess whether percentage of feeding time devoted to limited food items (*e.g.*, fruit and flowers) is significantly lower when primates live in sympatry and higher when they are allopatric (Hypothesis 1) and whether more evenly dispersed food items (i.e. leaves) show higher feeding percentages when closely related species are sympatric (Hypothesis 2), Mann-Whitney U statistics were calculated to test the null-hypothesis that there is no difference in feeding percentages regardless of sympatry or allopatry. (Table 2.3).

Table 2.3: Results of Mann-Whitney U tests on feeding percentages. Significance notated in bold.

Species	Fruit	Leaves	Flowers	Seeds	Animal Prey	Other
			Alouatta			
Sympatric w *Ateles*	0.4034	**0.00464**	0.0991	NA	NA	0.6267
Sympatric w *Lagothrix*	0.1734	0.3678	0.5086	NA	NA	0.8256
Sympatric w *Alouatta*	0.2762	0.3691	0.5984	NA	NA	0.0858
			Ateles			
Sympatric w *Lagothrix*	0.2766	0.9232	0.8849	NA	0.2150	0.0914
			Lagothrix			
Sympatric w *Ateles*	**0.0161**	1	0.2602	NA	**0.0214**	0.7946
			C. mitis			
Sympatric w *C. ascanius*	0.5209	1	0.1628	0.0579	0.5473	0.2454
			Hylobates			
Sympatric w *Symphalangus*	0.3400	0.4217	**0.03221**	NA	0.1991	0.9598

Ateles species showed no dietary categories to differ significantly regardless of whether they were allopatric or sympatric with any species of *Lagothrix*. *Lagothrix* species, however, showed significant differences in consumption of “Animal Prey” (p = 0.0214) and “Fruit” (p = 0.0161) when sympatric with *Ateles*. There was only one occurrence where either *Ateles* or *Lagothrix* was allopatric with *Alouatta*, and therefore these were not included.

Alouatta consumed a significantly higher amount of leaves when sympatric with *Ateles* (p > 0.00464). Differences in “Fruit” and “Flowers” consumption were not significant. No categories were significant when *Alouatta* was in allopatry or sympatry with *Lagothrix* or with other *Alouatta* species.

There was only one instance where *C. ascanius* was allopatric from *C. mitis,* so a statistical test was not run. A difference in seed consumption when *C. ascanius* was sympatric with *C. mitis* is notable (p = 0.0579) given the small samples available for this type of rigorous analysis, but is not here considered significant. No other categories showed differences in consumption when allopatric or sympatric.

Only flower consumption was found to differ significantly (p = 0.0322) in cases where *Hylobates* and *Symphalangus* were sympatric.

2.4.3 Regressions of female body mass on fruit consumption and rain fall on fruit consumption

Regressions were performed to examine the extent to which fruit consumption is predicted by rainfall (Table 2.4) and female body mass (Table 2.5).

Ordinary least-squares regression was used to test whether rainfall significantly predicted fruit consumption. The fitted regression model was: Fruit consumption= 0.38465*Rainfall + 29.26345. The overall regression was statistically significant (R^2 = 0.1652, F(1, 150) = 29.69, p < 2.035e-07). When each genus is examined individually, only fruit consumption in *Alouatta* was significantly predicted by rainfall, and in both instances R^2 values were small, demonstrating a significant but weak correlation.

OLS regression to assess whether female body mass significantly predicted leaf consumption resulted in a model of: Leaf consumption= -4.2508 *BodyMass+ 59.8597. While the overall regression was statistically significant (R^2 = 0.1154, F(1, 150) = 19.58, p < 1.85e-05) higher female body mass was associated with less leaf consumption among all genera in this study. Results are reported in Table 2.5. Looking within each family, only platyrrhines had a statistically significant relationship between body mass and leaf consumption (R^2 = 0. 0.7284, F(1, 86) = 230.6, p < 2.2e-16). Once again, the regression revealed a negative relationship between body mass and leaf consumption.

Table 2.4: Regression results of fruit consumption compared to average rainfall. Significance notated in bold.

Fruit by rainfall	**Df**	**Estimate**	**Std. Error**	**Pr(>|t|)**	**F**	**R^2**
All	150	0.38465	0.07059	**2.03e-07**	29.69	0.1652
Alouatta	57	0.5035	0.1808	**0.00727**	7.751	0.1197
Ateles	15	0.7305	0.5522	0.206	1.75	0.1045
Lagothrix	10	2.360	2.171	0.302366	1.182	0.1057
C. ascanius	14	0.01546	0.01776	0.399	0.7577	0.05134
C. mitis	14	-0.9345	1.6646	0.583407	0.3152	0.02202
Hylobates	12	0.005379	0.003998	0.2034	1.81	0.1311
Symphalangus	4	-0.000467	0.0065008	0.946	0.00516	0.00129

Table 2.5: Regression results of leaf consumption compared to average body mass. Significance notated in bold.

Leaves by body mass	**Df**	**Estimate**	**Std. Error**	**Pr(>|t|)**	**F**	**R^2**
All	150	-4.2508	0.9608	**1.85e-05**	19.58	0.1154
Platyrrhine	86	-13.5268	0.8907	**<2e-16**	230.6	0.7284
Cercopithecus	30	-2.813	3.562	0.4359	0.6236	0.02036
Hylobatids	23	2.370	1.481	0.123	2.56	0.1001

2.5 DISCUSSION

2.5.1 Competition Pressure on Feeding Rates

Hypothesis 1 posited that percentage of feeding time devoted to limited food items is lower when primates live in sympatry and higher when they are allopatric. Relatedly, Hypothesis 2 posited that more evenly dispersed food items show higher feeding percentages when closely related species are sympatric. While this sample broadly followed the expected patterns when simple feeding category averages were considered only a few species showed significant differences in their feeding behavior when allopatric.

2.5.2 Platyrrhines

Out of all three platyrrhine genera, *Ateles* consumed the most fruit resources followed by *Lagothrix*. *Alouatta* consumed the fewest fruit resources. When sympatric, *Ateles* and *Lagothrix* both had lower fruit averages than when allopatric. Both also had slightly higher average leaf consumption when allopatric though fruit comprised the bulk of both diets. For *Ateles*, differences in fruit consumption were not considered significantly different, whereas for *Lagothrix,* the Mann Whitney U tests showed significant differences in fruit consumption. Interestingly, *Lagothrix* had much higher rates of animal prey intake when sympatric with *Ateles*. While both *Ateles* and *Lagothrix* do consume animal prey when the opportunity arises, *Lagothrix* is observed to frequently seek out animal prey, especially during periods of fruit scarcity (Gonzalez *et al.,* 2016). Because most studies spanned a year or more, therefore capturing most or all seasons, it is unlikely that this is simply an artifact of seasonal data capture. While the high percentage of Animal Prey counts could be an artifact of sampling bias as Animal Prey counts are difficult to capture from an observational point, across studies *Lagothrix* did consume more animal prey consistently where it was sympatric with *Ateles.* The observed increase in animal prey consumption by *Lagothrix* may indicate a strategy to buffer against competition from sharing feeding ranges with a similarly large bodied frugivore.

Within the platyrrhine sample, fruit percentages for *Alouatta* were unexpected. It was predicted that *Alouatta* would focus more on leaf resources when sympatric with *Ateles or Lagothrix*. Instead, *Alouatta* consumed more fruit when in sympatry with the other two platyrrhine species. It should be noted that in most *Alouatta* species examined, the majority of their diet was composed of leaf resources (except for *Alouatta belzebuth* and *Alouatta macconnelli*). While fruit consumption was higher when sympatric, fruit was a secondary resource for the majority of *Alouatta* species included in this dataset. A few potential reasons could explain higher fruit consumption when sympatric. The first could be that forests able to host both *Alouatta* and *Ateles* and/or *Lagothrix* have higher overall fruit production, therefore lessening the effects of competition. The second potential reason that *Alouatta* had high levels of fruit consumption when living in sympatry with other Atelines is that within this study, unripe fruit consumption was combined within "Fruit." Howler monkeys have special adaptations that allow them to consume higher levels of unripe fruit without facing ill effects from toxins and tannins than *Ateles* or *Lagothrix* (Righini *et al*., 2015). Therefore, *Alouatta* may not eat more *ripe* fruit resources when sympatric but may shift their attention to *unripe* fruit resources rather than expanding their range. Further examining the pattern of *Alouatta* concentrating on higher levels of fruit resources when in sympatry and future lines of research into abiotic factors that allow for higher primate loads could help untangle whether fruit feeding is a competitive strategy or a consequence of living in a more productive forest habitat.

2.5.3 Cercopithecus

The results from the two guenon species included here follow a similar pattern as the platyrrhine sample. Both guenons had very similar average values for each dietary category. *C. ascanius* did consume slightly more seeds on average than *C. mitis*, which could be a buffering behavior to mitigate feeding competition. *C. mitis* follows the expected pattern of higher fruit consumption at sites when allopatric from *C. ascanius* and lower average fruit consumption and higher leaf and seed consumption when *C. mitis* was sympatric with *C. ascanius*. This may be a strategy to mitigate competition and specialize on alternative resources. While the Mann-Whitney U tests did not indicate that dietary differences were significantly different, there was a suggested relationship within the Seed category. Likely, these dietary behaviors are borne out of a need to buffer competitive interactions, but it may not be competition with red-tails that is driving the dietary changes.

Despite associating in large groups, guenons are generally not considered to be a large frugivorous biomass and often are competing with chimpanzees and baboons for fruit resources. Recently, Frogge *et al*. (2022) observed that that *C. mitis* may be more affected by competition with grey cheeked mangabeys than with red-tails. They found that at sites with large mangabey populations, like Kibale Forest in Uganda, blue monkeys have significantly lower population densities, which they linked to competition pressure with grey cheeked mangabeys. Red-tailed monkeys did not seem to be as affected by the presence of mangabeys despite more observed antagonistic interactions (Frogge *et al*., 2022).

2.5.4 Hylobatids

Symphalangus and *Hylobates* are considered to share a complex relationship in terms of range overlap. Similar to *Ateles* and *Lagothrix*, most *Hylobates* species do not currently overlap ranges with each other (Elder 2009). Ranges do overlap in some areas with the closely related *Symphalangus*. This relationship is posited to be stable because *Symphalangus* consumes more leaf resources than *Hylobates* and therefore is able to better circumvent competition over limited fruit resources (Reichard Holger Preuschoft 2016). In this study, *Symphalangus* did consume more leaves and *Hylobates* consumed more fruits, but neither of these values was significantly different. Interestingly, *Hylobates* was found to consume more flowers when sympatric, which may be a competition-mitigating strategy: *Hylobates* has been observed being displaced from fruit trees by *Symphalangus (*O'Brien and Kinnaird, 2011). Potentially obscuring the results for the hylobatid group may be the placement of figs in the "Other" dietary category within many studies while others included figs as fruit resources. Despite best efforts, untangling figs from other food items was not always possible in the published literature and therefore results based on those potentially conflicting allocations are not easily interpreted. Figs are an important keystone resource and often are available when other fruits are not, thereby mitigating pressure brought on by fruit scarcity during less productive seasons (Elder 2009).

2.5.5 Rainfall and Body Mass as dietary predictors

Hypothesis 3 and Hypothesis 4 investigate how biotic and abiotic factors may contribute to differences in primate diet. Hypothesis 3 states that different levels of rainfall may cause increases in fruit consumption as areas with more rainfall are thought to have higher forest productivity. Hypothesis 4 investigates whether body mass significantly predicts leaf consumption. Larger primates are observed to consume more leaf resources and larger body size has been linked with higher levels of folivory (Reichard and Prueschoft 2016).

Rainfall significantly but weakly predicted fruit consumption when all primate datapoints were considered. When individual genera were examined, only *Alouatta* had a significant relationship between fruit consumption and site rainfall levels. This is in line with the findings of Dias and Rangel-Negrín (2015). They found that howler monkey diet is strongly predicted by rainfall levels and that frugivory increases significantly as rainfall increases.

Body mass should predict leaf consumption (Rosenberger *et al*., 2011). Larger body size is posited as one reason siamangs consume more leaf resources than gibbons (Reichard and Prueschoft, 2016). While overall the regression indicated a significant relationship across all species represented, the relationship indicated larger body size correlated with less leaf consumption. Likely this negative relationship was caused by an uneven sample of folivores to frugivores. Within the platyrrhines, while *Alouatta* definitively consumes more leaf resources than either *Ateles* or *Lagothrix*, *Alouatta* has an average female body mass of 4.69 kg. This is in contrast to *Atele*s (8.07kg) and *Lagothrix* (7.24kg). While not significant, *Hylobates* and *Symphalangus* were the only family with a positive relationship between body size and leaf consumption. Recently, it has been argued that leaf consumption is not an adequate explanation for the larger body size of the siamang, as they are observed to eat as much fruit as the smaller bodied gibbon (Elder 2009).

2.6 CONCLUSION

This broad investigation of the feeding literature for seven genera of primates provides an interesting path forward in examining resource use and diet breadth in these primate taxa. Given that the data came from many different studies that employed differences in data capture, it is wise to be cautious in interpreting these results. Authors have pointed out that relying on behavioral studies alone may not paint a full picture of dietary behavior in a species (Struhsaker, 2017). When studying rainforest primates who have diverse food sources, tree communities may be heterogenous over short distances and patterns of phenology may be unsynchronized. Therefore, average values may not capture similarities or differences between species or populations (Raemakers and Chivers, 1980; Struhsaker, 2017). Furthermore, when large amounts of food items are available, it may be difficult to assess actual abundance. Marshall and Wrangham (2007) pointed out that many preferred items are also rare. They further pointed out that food selection is assessed from a large number of independent feeding samples from a representative set of individuals, not all individuals in the group (Marshall and Wrangham, 2007). Depending on the length of time of each data point, full temporal variation may not be captured even when sample sizes are large enough, or study periods span multiple seasons (Marshall and Wrangham, 2007). Cords (1990) concluded that dietary flexibility blurs traditional trophic categories and assessment of a single group in a single habitat at a single time may not represent the actual diet of the species. Competition has long been considered a driving force in primate food selection. By examining a wide array of studies from a wide geographic area across multiple primate families, this study hoped to circumvent some of the issues from using limited amounts of data. While the studies examined here do present only a snapshot into each primate community studied, it offers a representative survey of dietary behavior across different levels of competitive pressure. While no hypothesis was conclusively supported by the data, overall trends indicate that competition may have some effect on dietary composition among these primates.

3. Assessing dietary behavior through dental shape and dietary isotopes in extant primates

In the previous chapter, an analysis of observation based studies of primate food intake was examined to answer the question: Do primates vary their feeding behavior when a competitor is present? The results imply a trend indicating that primates with the ability to have greater dietary variability such as *Lagothrix*, will consume more non-fruit resources when they are sympatric with a large bodied frugivore like *Ateles* or *Alouatta*. Even primates with more rigorous dietary requirements like *Ateles* exhibit some behavioral flexibility when facing competitor pressure from large frugivorous biomasses like certain subspecies of *Alouatta*.

Within the guenon and hylobatid sample, results were less clear. While there is variability in the fruit intake of *C. mitis* when sympatric with *C. ascanius*, the guenon data may be confounded slightly as both are small-bodied primates when compared to other frugivorus primates that may overlap with them (*i.e.* chimpanzees and baboons). *Hylobates* and *Symphalangus* did not show a clear trend in response to potential increased competition. This may be an issue with sampling in that figs were considered "other" by multiple studies rather than included in fruit feeding counts while in other studies figs were included in fruit intake rates.

What the results of the previous chapter do indicate is that there is variability in dietary behavior. Because that variability in feeding behavior exists, it might be enough pressure to cause changes to feeding morphology, specifically tooth shape within sympatric species. This phenomenon is termed "character displacement" and is explored in the following chapter.

The theory of character displacement was first posited by Brown and Wilson (1956). At its simplest, when two similarly adapted species find themselves in an area where a resource is limited two outcomes might occur. The first is that of "competitive exclusion," which states that the better adapted individual will thrive and the less well adapted individual will go locally extinct. A second option is that each species with diverge slightly in their morphology to allow for a wider range of resource use. This will cause some aspect of each individual species to be more different in areas where they are sympatric compared to allopatric counterparts (Brown and Wilson, 1956).

While character displacement is hard to discern from random chance and thus from the 1970s-1980s it was highly criticized as supporting "just so stories" rather than critical evaluations of testable hypotheses (Gould and Lewontin 1979; Losos 2000). Recently, a resurgence in the study of adaptation shaping populations has made a comeback but this time multiple lines of evidence are critically evaluated in order to evaluate the extent to which competition may be acting on traits between two sympatric species (Schluter and McPhail, 1992; Adams and Rohlf, 2000).

Therefore, the next chapter employs dental topographic analysis (DTA) and stable isotope analysis to test the **central hypothesis that primates respond to competition over food resources by feeding on underutilized resources, resulting in character displacement.**

The next chapter examines three primate dyads: *Ateles* and *Lagothrix*; *C. mitis* and *C. ascanius*; and *Symphalangus* and *Hylobates*. *Alouatta* was dropped from the analysis as their evolutionary adaptations to folivory make comparisons difficult. DTA was employed to quantify change along the lower molar row for the six primate species. The magnitude of DTA difference was then analyzed using a general linear model: the displacement statistic.

In addition to DTA and overall dental shape, isotope for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ were analyzed from hair collected from a sample of the individuals from the DTA analysis. While competition might not be strong enough to warrant change in the physical shape of the tooth, isotope analysis might indicate differences in foraging height or plant part consumption when primate dyads are sympatric as opposed to when they are allopatric.

4. Examining the role of competition in primate dietary morphology and isotopes

4.1 INTRODUCTION

Sympatry of closely-related species has sparked persistent questions in the field of ecology regarding how organisms with similar requirements partition available resources (e.g. Brown and Wilson, 1956; Hutchinson, 1959; Yom Tov, 1991; Schluter and McPhail, 1992; Racz and Demeter, 1998; Hertler and Volmer, 2008). Broadly, it is expected that niche overlap should not be complete among closely related species (De Leon *et al.,* 2014). Although many studies have measured niche divergence, most often focusing on the degree of dietary overlap between species, results vary between species: some showing strong niche divergence (Herrera, 1978; Hogstad, 1978; Alatalo *et al*., 1986) where others show broad dietary overlap (*e.g*., Lister, 1976; Wiens, 1989; Hickey *et al.,* 1996; Martin & Genner, 2009). If competition occurs between two species, and if it is strong enough to limit resources for one or both at a given location, two possible outcomes are predicted: one competitor will evolve an advantage causing the other to become locally extinct, or both taxa will evolve to occupy non-competing niches and remain sympatric (Gause, 1934; Pfennig and Pfennig, 2010; Schroer and Wood, 2015). The latter often produces a change in morphology that enables one or both species to better exploit under-utilized resources and is termed “character displacement” (Brown and Wilson, 1956). This process has been documented in many sympatric populations including birds, rodents, carnivores, lizards, and fish (Dayan and Simberloff, 2005 and references therein). Likewise, the importance of character displacement for species survival has led researchers to examine its effects on anatomical (e.g., body size, coloration, jaw morphology) and ecological (e.g., feeding heights and isotopic values) traits in both extant and extinct populations (Schluter and McPhail, 1992; Crowley *et al.,* 2012; Ruette *et al.,* 2015; Volmer 2016). Among primates rigorous testing of character displacement hypotheses has been infrequent (for examples, see Schreier *et al.,* 2009; Ramdarshan *et al.,* 2011; Stroik 2014; Berthaume and Schroer 2017). Furthermore, many studies look for evidence of character displacement only as specialized adaptive change resulting in more restricted resource exploitation (as reviewed in De Leon *et al.,* 2014). Important factors such as character release (*i.e.,* relaxation of morphological characters) allowing for the widening of niche breadth are frequently ignored.

4.1.1 Character displacement

Character displacement occurs when species overlap in habitat and resource use and resource limitations cause morphological characters to differentiate (Brown and Wilson, 1956). These characters are not limited to morphology, but can be ecological, behavioral, or physiological (Brown and Wilson, 1956). Closely related species are predicted to be more heavily affected by character displacement since they typically have similar resource requirements (Dayan and Simberloff ,2005; Pfennig and Pfennig, 2010). Reliance on similar resources causes rapid depletion, potentially limiting reproductive success. Hence, a population may exploit under-utilized resources to mitigate competition. This can lead to character displacement as the group adapts to more effectively exploit the novel resources, with the result that competing species exhibit more divergent morphology when they occur together (Ramdarshan *et al.* 2011). Competition mitigation is not limited solely to differential food consumption, and observations of behavioral changes in the presence of a competitor species have included altered feeding times, durations, or location (Cords, 1986; Beaudrot *et al.* 2013), any of which can lead to anatomical changes.

Character displacement can be difficult to detect and linking morphological change to specific behavioral differences is challenging in any study. Over the last three decades, studies of character displacement both at the species scale as well as the community-wide scale have examined dozens of extant and extinct taxa including mammals, birds, reptiles, amphibians, insects, other invertebrates, and plants (Dayan and Simberloff, 2005). While early studies of character displacement often used the term as a loose synonym for resource partitioning or dietary specializations, more recent studies have focused on characters that actually show a relationship between morphology and diet (Dayan and Simberloff, 2005).

The most comprehensive way to test character displacement is to document the degree of divergence in extant taxa by comparing allopatric species to the same taxa in a sympatric setting (Schluter and McPhail, 1992; Ruette *et al.* 2015). This has been done in multiple empirical studies. Notably, Dayan *et al.* (1989) and Dayan & Simberloff (2005) demonstrated in carnivore dentition that the maximum diameter of the upper canine reflected preferred prey size and was affected by competition when other members of the carnivore guild overlapped in hunting range. Schluter and McPhail (1992) investigated character displacement in the three-spined stickleback. They found sympatric species show distinct differences in scale color and feeding anatomy, whereas allopatric populations display morphological traits intermediate between the sympatric extremes. They concluded that since the allopatric populations are not competing with a closely related fish species for food, they are able to pursue more general feeding strategies instead of becoming specialists (Schluter and McPhail, 1992). Similar empirical studies in lizards, finches, rodents, and mustelids have found evidence for competition-induced trait divergence (Brown and Wilson, 1956; Schluter and McPhail, 1992; Pfennig and Phennig, 2010; Bol'shakov *et al.* 2015; Ruette *et al.* 2015).

4.1.2 Competition studies in primates

As food is almost always a limiting resource in primate communities, competition over food and food interactions are by far the most common biotic relationship (Putnam and Wratten 1984; Isbell and Young, 2002). The manner in which primates partition resources is not simple or straightforward. Primates compete not only with members of their own species but with closely related primate species and other mammal and bird species as well (Beaudrot *et al.* 2013). While competition from other species within a primate's range certainly can affect foraging behavior, often competition is greatest between closely related, similarly foraging species (Stevenson, 1999; Butynski, 2015). It is often observed that as fruit production declines, the number of primate species present declines as well (Ganzhorn, 1999; Stevenson, 2001). When fruit production is seasonal, resulting in months of fruit scarcity, frugivorous primates experience increases in pressure from closely related, similarly foraging competitors. Forest sites with heavy frugivore loads experience the most pressure during these periods of scarcity. However, long periods of scarcity and increased competition may cause some primates to rely on secondary resources in order to reduce resource overlap (Marshall and Wrangham, 2007; Kalimer and Ledogar 2011; Neha *et al.,* 2021; Fonesca *et al*., 2022).

4.1.3 Measuring changes in diet using tooth shape

Understanding the relationship between diet and tooth form has a rich history within comparative anatomy (Kay, 1975, and references therein). Linking phenotype to ecological context is important not only for understanding how behaviors manifest in extant primates, but it can also illuminate feeding behaviors in fossil species (Scott *et al.,* 2018). For decades, debates on the relationship between molar size and shape and food breakdown have persisted in the literature. This has led to the development of a plethora of methods for quantifying the relationship between molar shape and dietary behavior. Early quantification methods included linear measurements (Kay, 1975), ratios of crest length to tooth length, and ratios of crest length to body size (Kay and Hylander, 1978), but these relied on landmarks of the tooth surface. Since dietary wear can obliterate landmarks, a suite of quantification methods termed dental topographic analysis (DTA) were developed to facilitate larger sample sizes and the inclusion of worn teeth, (Jernvall, 1995). Dental topographic analysis represents a method for finding subtle dietary differences by quantifying the tooth surface and takes into account the entirety of the molar occlusal surface and quantifies differences in tooth shape across specimens (Berthaume *et al*., 2020). Changes and/or differences in molar shape affect molar occlusion and therefore impact how effectively food items are processed by the organism's teeth (Berthaume *et al*., 2020).

DTA has been applied across a wide array of research questions (Winchester *et al.* 2014; Pampush *et al.* 2016; Berthaume and Schroer, 2017) and almost all DTA analyses follow a similar protocol: digitization of a tooth surface, digital processing, and finally shape quantification (Berthuame *et al*., 2020). Most pertinent to this project are three DTA measures – Relief Index (RFI), Orientation Patch Count Rotated (OPCR), and Dirichlet Normal Energy (DNE) – that reliably identify dietary category membership as well as correlate to mechanical properties of food items (Boyer, 2008; Bunn *et al.*, 2011; Evans, 2013; Winchester *et al.*, 2014).

Relief Index (RFI) is a ratio of the surface area of a tooth's crown and the area of the tooth's planometric footprint. As occlusal relief increases, so too will the value of the index (Allen *et al*., 2015). This measure can be applied to the entire tooth crown (e.g., Boyer, 2008) or restricted to the occlusal basin (Ungar and M'Kirera, 2003) if one wants to limit the study to only the mastication area of the tooth. Generally, teeth with taller crowns and longer crests have higher RFI values (Boyer, 2008). Within primates, high RFI correlates with taller cusps often associated with folivores or insectivores. Primates with lower RFI scores are often frugivores or hard object feeders (Berthaume et al 2020).

Orientation Patch Count (OPC) was first employed by Evans *et al*. (2007). This shape descriptor examines the "tools" present on a tooth surface. If teeth evolve to most efficiently break down food, then as the difficulty of mechanical breakdown increases so too should the processing capability of the tooth. Adding features (*i.e.,* crenulations, cingula, beading) to the tooth surface is an effective way to increase this processing capability as more food can be processed with each stroke (Evans *et al*., 2007). OPC measures each separately oriented area (or "patch") on the occlusal surface. The tooth surface is treated as a circle and the surface is first assigned to one of 8 X-Y plane directional categories. Each X-Y plane portion comprises 45° of 360° total tooth surface. Orientation Patch Count Rotated (OPCR) is a derivative of OPC. It was developed as concerns arose over OPC's sensitivity to user defined orientations. To reduce the potential for user generated error, OPCR involves rotating specimens eight times in the xy-plane, by 5.625° each time, for a total rotation of 45°. After each rotation, OPC is measured, and the OPCR value is the average of the eight OPC values (Wilson *et al*., 2012). Continuous areas of a tooth that point the same direction are considered "patches." As the number of "patches" increases, so too does surface complexity.

Dirichlet Normal Energy (DNE) measures the variability of a tooth surface. As a tooth increases in curvature and deviates away from a flat surface, the surface will be calculated as having more Dirichlet Normal energy. DNE increases for teeth with many cusps, multiple crests, crenulations, or enamel wrinkling. Primates with higher DNE scores often have taller, sharper cusps associated with folivory, whereas primates with lower-cusped molars, and thus lower DNE scores, are associated with frugivory (Berthaume *et al*., 2020). Curvature added by enamel crenulations or deep creases between crests can confound DNE scores, as those taxa will have higher DNE scores but may not be folivorous (Allen *et al*., 2015).

Further, there is ample evidence that combining DTA measures in a single analysis allows for more accurate identification of dietary category membership across phylogenetically disparate groups (Winchester *et al.* 2014). Keller *et al.* (2017) have demonstrated DTA's accuracy in predicting dietary behavior and have further shown its use in identifying fallback feeding behaviors among distantly related rodent taxa. Thus, these methods have the potential to detect subtle differences in dietary preferences and thereby measure levels of competition among both living and fossil primate communities.

4.1.4 Measuring changes in diet using dietary isotopes

Stable isotopes have long been used to assess differences in foraging ecology among extant and fossil mammals (Longinelli ,1984; Sponheimer and Lee-Thorp, 1999; Sponheimer *et al*., 2009; Sanberg *et al*., 2012; Crowley, 2014; Carter and Bradbury, 2016). Put simply, stable isotopes are versions of an element that have different atomic masses due to their complement of neutrons. All elemental atomic numbers are derived from their unique number of protons, but the element's atomic mass is derived from summing its protons and neutrons (Carter, 2001). For example, carbon has six protons and six neutrons making its atomic mass 12. This mass is notated in superscript before the symbol for the element (e.g., ^{12}C). An isotope is produced if the element gains one or more neutrons and therefore becomes heavier (Sulzman, 2007). Heavier isotopes always have more neutrons (e.g., ^{13}C,^{15}N, ^{18}O) while lighter always have fewer neutrons (e.g., ^{12}C, ^{14}N, ^{16}O). Different isotopes of the same element do not differ in their chemical behaviors but do differ in their thermodynamic and kinetic reactions (Sulzman, 2007; Carter, 2001; Crowley, 2012).

During physical and chemical reactions, the differences in mass cause changes to the proportion of the heavier to lighter isotopes. This process called fractionization

(Carter, 2001). Thus, the ratios of stable isotopes within biological samples will vary due to differences in habitat, physiology, and dietary behavior; by measuring how different stable isotopes are incorporated into an organism's different tissues, diet and niche partitioning can be assessed (Crowley, 2012). Because the heavier stable isotope has at least one additional neutron, its weight affects the rate that it enters into a chemical reaction. Therefore, chemical bonds are less easily broken in the heavier isotope than in the lighter isotope (Sulzman, 2007). The resulting different proportions of the same element can be measured in the form of a ratio which reflects the amount of heavier and lighter isotopes (generally noted as parts per thousand, called "per mil") and the difference is notated with the delta (δ) symbol (Crowley, 2012). The ratio of the heavy to light isotope is compared to an internationally recognized standard for each element (Sulzman, 2007). Carbon is compared to the reference standard Pee Dee Belemnite (PDB) which contains a higher percentage of ^{13}C to ^{12}C (Carter, 2001). Oxygen isotopes are compared to Standard Mean Ocean Water (V-SMOW) (Crowley, 2012). Nitrogen is compared to the international standard: Ambient Inhalable Reservoir (AIR) (Crowley, 2012).

Because stable isotopes do not decay, their total abundance is fixed in the biosphere. These proportions can be changed as both biotic and abiotic processes preferentially utilize some versions of isotopes over others, thereby enriching or depleting samples (Carter, 2001).

Carbon isotopes reflect plant physiology (Crowley, 2012). Plants have evolved three different photosynthetic pathways: C_3, C_4, and crassulacean acid metabolism (CAM). Typically, C_3 plants are trees, shrubs, and grasses from regions with cool growing seasons, while C_4 are typically tropical grasses. Succulents, epiphytic orchids, and bromeliads utilize the CAM pathway (Crowley, 2012). The main difference between these pathways is based on the enzyme used to fix carbon during photosynthesis. In C_3 plants, the enzyme ribulose bisphosphate carboxylase/oxygenase ("RuBisCO") fixes one molecule of CO_2 to synthesize three molecules of 3-phosphoglyceric acid (Sulzman, 2007). This results in a $\delta^{13}C$ depletion of -38‰ to -22‰ (Crowley, 2012). In C_4 plants, carbon is fixed using the enzyme phosopheneno pyruvate (PEP) carboxylase. Because of this different pathway, C_4 plants discriminate less against ^{13}C and are thus less depleted compared to C_3 plants with a range of -21‰ to -9‰ (Carter, 2001). CAM plants are those that experience extreme water stress and have adapted to switch between C_3 and C_4 photosynthetic pathways leading to intermediate $\delta^{13}C$ values between -30‰ to -9‰ (Carter, 2001).

Nitrogen isotopes are most indicative of protein consumption (Carter, 2001), but values can also reflect plant physiology and microbial associations as well as nutrient availability (Crowley, 2012). Most nitrogen comes from the atmosphere which has a fairly consistent ratio of $^{15}N/^{14}N$ (Mariotti, 1983; Carter, 2001). Nitrogen is fixed by bacteria and algae into ammonia and nitrates which can then be used by plants and animals (Carter, 2001).

Plants obtain nitrogen from soil nitrate and ammonium and generally their $\delta^{15}N$ values is greater than 0‰. Plants in moist forest have $\delta^{15}N$ values <0‰. The ratio of $\delta^{15}N$ is also used to measure the amount of protein present in an animal's diet and while it has traditionally been used to assign trophic levels to secondary consumers (i.e faunivores are more $\delta^{15}N$ enriched than the frugivores they consume), ^{15}N depletion can also indicate feeding on legumes (Oelze *et al.*, 2014).

Using oxygen isotope ratios can aid in understanding subtle climatic and biogeochemical influences on body water composition and can be useful in detecting dietary specializations among herbivorous animals (O'Grady *et al.*, 2012; Carter and Bradbury, 2016). Oxygen should reflect different water sources including both surface water from local precipitation as well as groundwater (Crowley, 2012). The ratio of ^{18}O to ^{16}O is most commonly measured as $\delta^{18}O$ because that isotope is most common in the atmosphere and relatively constant (Carter, 2001). Groundwater and rainwater can have differing ^{18}O ratios depending on fluctuation in mean annual temperature, average rainfall, and proximity to the ocean. Oxygen is incorporated into animal tissue in multiple ways: animals obtain oxygen through respiration, drinking and eating food with high water content (Crowley, 2012). Animals that are obligate drinkers will have $\delta^{18}O$ values depleted in ^{18}O compared to animals that get most of their water from plant sources since those sources are evaporated compared to water (Cerling *et al.*, 2004). While plants' roots and stems are not enriched in ^{18}O when compared to source water, the amount of evapotranspiration occurring can increase $\delta^{18}O$ values in leaves as the lighter ^{16}O evaporates more readily (Barbour, 2007). Because oxygen isotope ratios are altered by evapotranspiration, leaves are higher in $\delta^{18}O$ than other parts of the same plant, such as fruits (Marshall *et al.*, 2007). This is because leaves have a higher surface area/volume ratio in contrast with fruits which have a low surface area/high volume ratio (Carter and Bradbury, 2016).

Stable isotopes have been used to investigate various aspects of primate feeding ecology ranging from weaning studies (Reitsema, 2012), levels of meat or protein consumption (Oelze *et al*., 2011), amount of leaves and vertical stratification (Carter and Bradbury, 2016), and paleohabitat reconstruction (Lee-Thorp *et al*., 1989). Pertinent to this project is the use of stable isotopes to demonstrate niche partitioning in environments where multiple taxa overlap.

One of the first studies to address questions about primate ecology using dietary isotopes was Lee-Thorp *et al*. (1989). In this paper, they investigated the dietary ecology of extinct non-human primates: *Papio robinsoni* and *Theopithecus oswaldi* from Swartkrans in South Africa. Using $\delta^{13}C$ values to reconstruct diet they found that *T. oswaldi* had a diet with a higher component of C_4 grasses while the sympatric *Papio robinsoni* consumed more C_3 vegetation. Similarly, dietary isotopes were used by Codron *et al*. (2007) to investigate differences between dietary niches of extant and fossil taxa. Using, $\delta\ ^{15}N$ and $\delta^{13}C$ stable isotope analysis of baboon fecal, hair, and tooth enamel samples, they compared results to fossil hominin and fossil *Papio* isotope data. They found that while both the fossil sample and extant sample likely both lived on the African savanna and thus consumed substantial C_4 resources, there is less variation in modern *Papio* taxa than in the fossil *Papio* or hominin sample. They concluded that it is unlikely that hominins specialized on any one food item and instead pursued a strategy of ecological generalist (Codron *et al.,* 2007).

Dammhahn and Kappeler (2014) used carbon and nitrogen isotopes to assess whether trophic patterns overlapped in communities of sympatric lemurs. They found lemurs separated into different trophic niches and ranged over two trophic levels. They posited that competition had been a major structuring force in the dry forest lemur community as there is pronounced trophic differentiation among species (Dammhahn and Kappeler 2014). Using isotopes to assess dietary differences and understand potential competitive strategies was also examined by Flores-Escobar *et al*. (2020). In their study of niche partitioning in sympatric black howler monkeys and mantled howler monkeys, $\delta^{13}C$ and $\delta^{15}N$ isotopes and compared them to allopatric samples. They found that in allopatry, black howler monkeys had a broader niche determined by high $\delta^{15}N$ values, but they found no difference in the mantled howler monkeys' niche when sympatric or allopatric. Thus, it may be that one species is able to adjust its dietary behavior to accommodate overlapping territory with another closely related species (Flores-Escobar *et al*., 2020).

Carter and Bradbury (2016) investigated oxygen isotopes in the bone carbonate of five primate species and four ungulate species from Kibale National Forest, Uganda. While $\delta^{13}C$ results showed that the animals were feeding in a closed forest habitat and did not indicate niche partitioning, the results from the $\delta^{18}O$ values clustered by species and tracked with the proportion of leaves in each species' diet. Additionally, Carter and Bradbury (2016) found evidence that $\delta^{18}O$ values were further modified by vertical niche partitioning. While vertical niche partitioning may explain some variation within the diets of the different taxa studied, the authors posit that it is the amount of leaves vs. fruits in the diet that lead to a greater source of isotopic variation (Carter and Bradbury, 2016).

While vertical niche partitioning may not have been the main driver in the differences of $\delta^{18}O$ values in Carter and Bradbury (2016), investigating the variation in stable isotopes at different levels of the forest can be a powerful approach to examine differences in vertical niche occupation as a means to avoid competitive interactions (Krigbaum, 2013; Crowley, 2014; Lowry *et al*., 2021). Within a closed canopy forest, there can be high levels of variation in the stable isotope ratios of leaves and fruits from the same tree but growing at different heights. Commonly referred to as the "canopy effect," it can affect stable isotope ratios of carbon ($\delta^{13}C$), oxygen($\delta^{18}O$), and to a small degree, nitrogen ($\delta^{15}N$) (Lowry et al 2021 and references therein). The canopy effect is the result of vertical gradients in sunlight, humidity, source water, and photosynthetic rates. The effects of these gradients are described for the isotopes measured in this dissertation.

Plants following the C_3 photosynthetic pathway show a gradient in ^{13}C depletion (Lowry *et al*., 2021). Within closed canopy forests, the understory has CO_2 which is reduced in ^{13}C due to the carbon recycling of decomposing of leaf litter. Additionally, closed canopy forests show gradients in the photosynthetically available radiation (PAR) at different levels in the canopy (van der Merwe and Medina, 1991). Because dense canopies can block 95-99% of light from reaching the forest floor, in lower canopy levels the reduced light and temperature reduce transpiration rates (Lowry *et al*., 2021). Because of this, plants will preferentially fix $^{12}CO_2$ and discriminate against $^{13}CO_2$, causing leaves in the understory to have more negative $\delta^{13}C$ values. As $\delta^{13}C$ is measured farther up in the canopy leaves will have higher $\delta^{13}C$ values. This is because leaves will preferentially fix $^{13}CO_2$ at a higher rate due to higher evapotranspiration (van der Merwe and Medina, 1991; Krigbaum *et al*., 2013; Lowry *et al*., 2021).

A similar gradient exists in ^{18}O isotope ratios due to differences in humidity and evapotranspiration. Within the upper canopy there is relatively lower humidity and thus higher rates of evapotranspiration and therefore preferential loss of lighter $H_2{}^{16}O$, leaving leaves and fruits enriched in ^{18}O (Krigbaum *et al*., 2013; Lowry *et al*., 2021).

Because $\delta^{15}N$ values are driven mostly by the isotopic composition of the source soil, vertical stratification has been rarely documented. Recently Lowery *et al*. (2021) found a significant correlation between PAR and $\delta^{15}N$, but not a correlation in overall height.

These gradients can be reflected in primate isotope ratios and indicate habitual forest stratum usage. The occupation of lower canopy layers has implications for foods available to competing primate species, i.e., fruits may be more abundant at higher levels in the canopy (Houle et al. 2006). Identifying differences in habitual canopy-level occupation can further our understanding of primate niche partitioning within rainforests (Krigbaum, 2013). It is expected that primate species that have been identified as less dominant will be feeding lower in the canopy and therefore have lower $\delta^{13}C$ and $\delta^{18}O$ values.

While dietary isotopes can be assessed from a multitude of body tissues, this project focuses on primate hair. Hair is easy to harvest, and collection is minimally destructive as only small amounts are needed for analysis (Oelze, 2016).

Hair is a hard keratin that develops within the hair follicle in the dermis of an organism and each hair follicle is connected to a blood supply (Oelze, 2016). Hair keratin is comprised of polypeptides which form a matrix of cysteine and glycine-tyrosince-rich proteins (Marshall *et al*., 1991). Because hair grows incrementally, it can retain a dietary signal over time until it ceases growing or is shed. Hair forms much more quickly (at a rate of approximately 1 cm per month) and has a higher turnover rate than other tissues used in isotope analysis, like bone and teeth (Oelze, 2016). Because each hair follicle is connected to the blood stream, the isotopic signatures of the amino acids within the blood stream will be the same as those in the forming hair shaft (O'Grady *et al*., 2012; Oelze, 2016).While there may be some temporal delay in the signature of the hair shaft relative to shifts in diet (as seen in horse studies, cow studies, and rat studies) there is no comprehensive data on non-human primate turnover rates (Oelzle, 2016). Hair grows in three phases: the anlagen phase (growth phase), catagen phase (regression phase), and telogen (rest phase), until it is shed (Carter, 2001). Hair is only metabolically active during the anlagen phase. Once hair is no longer metabolically active, it enters the telogen stage and may stay adhered to the body for 10 weeks. During these 10 weeks, the hair will not absorb any recent dietary isotope signal. Therefore, it is important that hairs are only used that were in the active growth phase in isotope studies (Oelze, 2016).

4.1.5 Ateles and Lagothrix

Spider monkeys (*Ateles* spp.) and woolly monkeys (*Lagothrix* spp.) are closely related, ecologically similar platyrrhines (Dew, 2005). Both are similar in body size (6-8kg), forage in the canopy, and seek out ripe fruits (Dew, 2001). Previously, researchers hypothesized that *Ateles* and *Lagothrix* were unable to coexist due to their ecological similarity (Hernimdez-Camacho and Cooper, 1976). This was reinforced by considerable range overlap (Figure 4.1) but, at many study sites, either one species is absent, or if both are present, they inhabit different areas (*i.e.*, higher elevation) or are separated by geographic barriers (Klein and Klein 1976; Terborgh, 1983). More recently multiple studies have observed *Ateles* and *Lagothrix* foraging nearby in the rainforest (Iwanga and Ferrari, 2001; Dew, 2005; Snodderly *et al*., 2019).

While both genera focus primarily on ripe fruits, they diverge in several aspects of their behavior and morphology which hint at potential niche partitioning. Group size, ranging behavior, and foraging behavior is driven by fruit availability for *Ateles* (Wallace, 2008). Their long lithe bodies aid them in quickly moving through the canopy using semi-brachiation. Observations show that *Ateles* will stay longer in larger fruiting trees and fruit patches likely to maximize energy from fruit abundance. *Ateles* group composition changes throughout the day and they are characterized as living in multi-male, multi-female fission-fusion societies. Often, they forage in small parties that are a subset of the larger group (DiFiore and Link, 2008).

While foraging subgroups are not uncommon for *Lagothrix*, generally they move as a large, cohesive group through the canopy (membership ranges from 35-70 individuals) (Stevenson *et al*., 1994). *Lagothrix* is characterized by slow, quadrupedal movement through the canopy. Additionally, day ranges are smaller than that of *Ateles* (Dew, 2005; Ange-van Heugten, 2014).

Both *Ateles* and *Lagothrix* display dental morphology consistent with frugivory. *Ateles* displays large spatulate incisors and molars with reduced shearing crests and wide crushing basins (Rosenberger *et al.*, 2008). Spider monkey molar topography is quite simple as they do not crush seeds and instead swallow seeds whole (Link and DiFiore, 2006). Overall, their molars are small, but their size is consistent with expected frugivore dentition (Rosenberger *et al*., 2008). While *Lagothrix* also displays incisors that are well developed and large compared to body size, investigations of molar shearing quotient reveal that *Lagothrix* molars are not as reduced in shearing crest height as *Ateles* (Anthony and Kay, 1993).

While primarily frugivorous, dietary variability occurs in both genera (as reviewed in Chapter 2). Flexibility in diet may have direct effects on dental morphology if preferred resources are scarce due to higher competition. While *Lagothrix* displays dental morphology that enables better processing of more tough or fibrous items, observational studies have not been able to identify a shift to tougher object consumption at sites where it is sympatric with *Ateles* (Dew 2005).

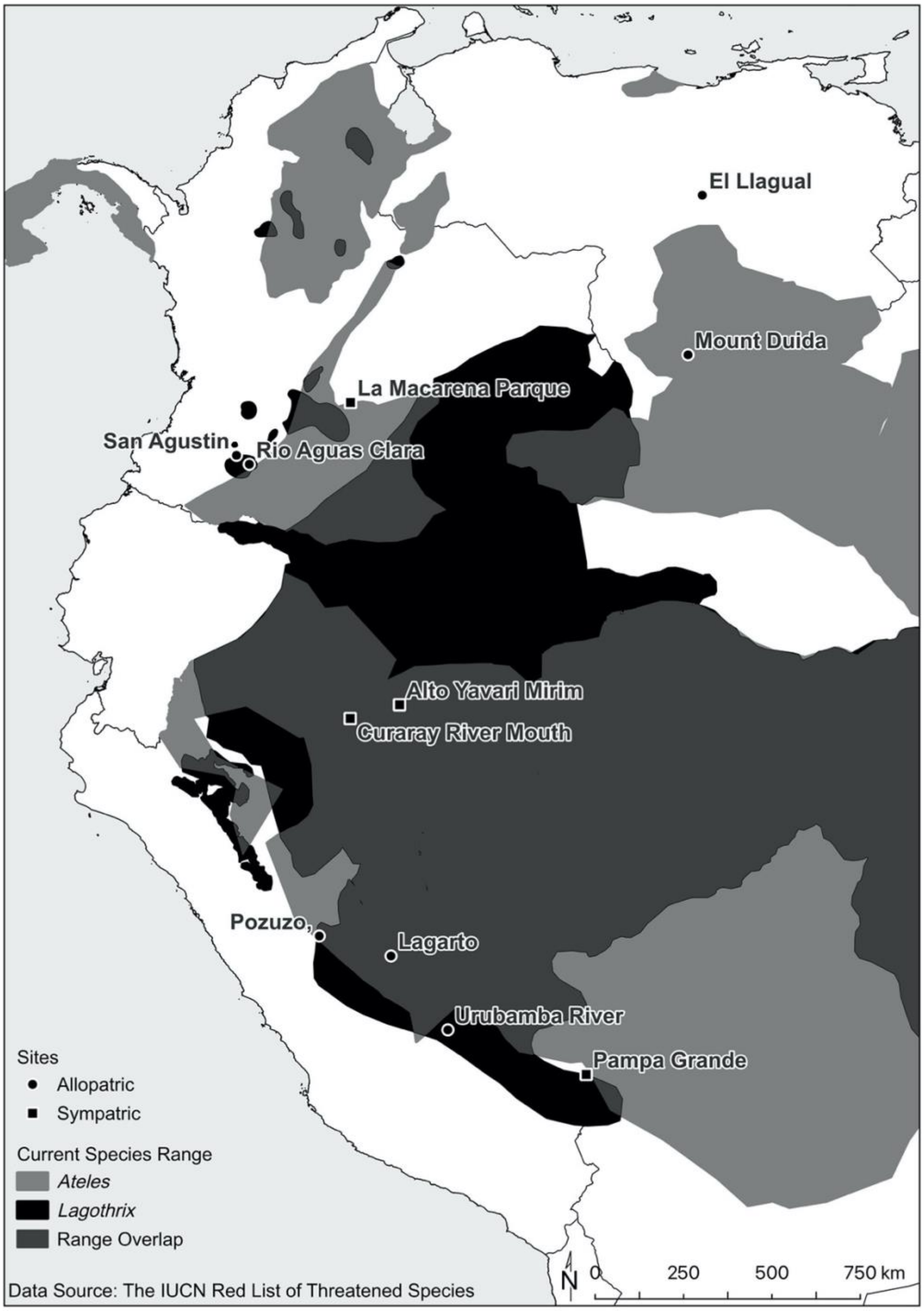

Figure 4.1: Map listing locations of *Ateles* spp. and *Lagothrix* spp. samples as well as overlap of ranges

4.1.6 Cercopithecus ascanius and Cercopithecus mitis

Cercopithecus mitis (blue monkeys) and *Cercopithecus ascanius* (red-tailed monkeys) are two guenon species found throughout dry coastal forests and lowland rainforests of central Africa (Figure 4.2) (Cords, 1987; Butynski, 2015). While there are pockets of allopatry for both species, much of their range overlaps (Cords, 1987; Lawes *et al*., 1990; Butynski and de Jong, 2020). When they do co-occur in forests, they often forage in close association (Cords, 1987; Detwiler, 2010). While the social dynamics that drive these mixed species groupings are well researched, the ecological consequences of resource sharing are less well understood (Cords, 1987; Gathua, 1999; Chapman and Chapman, 2000). Mixed association tends to increase competition among members, but this is only an issue if the resources are limiting; this drives questions of whether red-tailed and blue monkeys are truly competitors and, if they are, what are the costs of mixed species associations (Cords, 1990).

While sometimes categorized as generalists due to differences in the proportion of leaves, insects, and other non-fruit resources at various sites (Lambert, 1997), *C. mitis* and *C. ascanius* predominantly seek out fruit (as reviewed in Chapter 2). Cercopithecines are unique in their treatment of fruit resources: unlike colobines and pitheciines, they lack the ability to digest crushed seeds and they do not often swallow fruit seeds whole as seen in many platyrrhines and apes (Lambert, 1997). Instead, they are categorized as "seed spitters" (Corlett and Lucas, 1990) Indeed, when fruit is consumed much of the processing to extract pulp takes place by dexterous oral manipulation by use of the cheek teeth and cheek pouches (Lambert, 1997). While most primate frugivores follow the pattern of large anterior teeth and small cheek teeth, cercopithecines have both large anterior teeth and large cheek teeth (Lucas, 1994). Furthermore, cercopithecine cheek teeth (and those of all extant cercopithecoids) are highly specialized and characterized by a bilophodont pattern with tall cusps and sharp crests, though guenons have slightly more bunodont molars (Lambert, 1997).

Both *C. mitis* and *C. ascanius* are observed to consume highly varied diets as a possible response to increased competition. Lawes *et al*. (1990) have suggested that ingesting more leaf matter is a strategy by *C. mitis* to mitigate competition with more specialized sympatric primates or with congeners. Lambert (2002) reports that *C. ascanius* may have a highly diverse diet at Kibale National Park, Uganda in order to mitigate competition from other primate species.

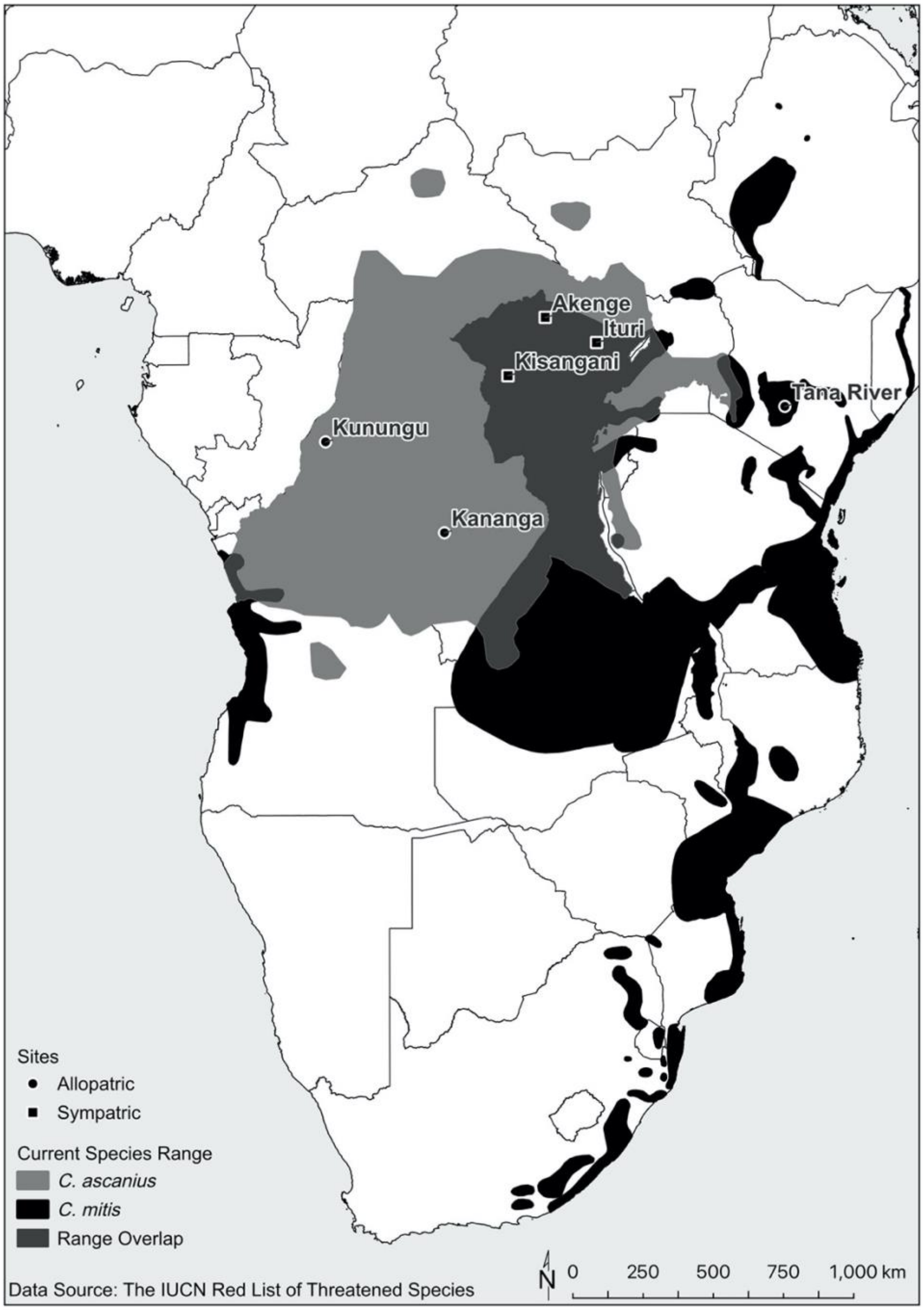

Figure 4.2: A map of *Cercopithecus mitis* and *Cercopithecus ascanius* sample locations and area of range overlap.

4.1.7 Hylobates and Symphalangus

Siamangs (*Symphalangus syndactylus*) and gibbons (*Hylobates* spp.) are two small-bodied apes that live sympatrically in Sumatra and in Malaysia (Figure 4.3) (Raemakers, 1979; Reichard and Preuschoft, 2016). Their coexistence was once thought to be a function of niche specialization: gibbons consuming fruit resources and siamangs consuming more leaf resources. Recent observational studies (Raemaekers, 1979), however, indicate that siamangs are just as frugivorous as gibbons and actively seek out fruit resources (Elder, 2009). This drives questions of hylobatid coexistence as most gibbon species are exclusively allopatric (as reviewed in Chapter 2).

While both siamangs and gibbons may actively seek out fruit resources, they diverge in their morphology in a variety of ways, most notably in their body size. Gibbons weigh about 50% less than siamangs, but their arms are not proportionally shorter (Gittens and Raemaekers, 1980). Therefore, gibbons are thought to be able to travel greater distances while expending less energy than the siamang. This is reflected in their foraging ranges as gibbons travel about two times further in a day than do siamangs (MacKinnon, 1977; Gittens and Raemaekers, 1980). In both species, travel is limited to some extent by their rigidly defended territories (MacKinnon, 1977). Within each territory both species employ different foraging strategies: gibbons are more likely to travel to disparate fruit patches and consume foods from a wider variety of tree species, while siamangs seek out more highly concentrated sources, like figs (MacKinnon, 1977; Palombit, 1995).

Siamangs and gibbons also diverge in their molar morphology. Gibbons display molars similar in shape to other frugivores: gibbons display low bunodont cusps and wide basins, while siamangs have sharper shearing crests which aid in the shearing of fibrous vegetation (Gittens and Raemaekers, 1980; Kay, 1984). In addition to teeth adapted to better process more fibrous food resources, siamangs have a larger colon which is thought to aid in digestion of more plant cellulose (Gittens and Raemaekers, 1980).

Due to the smaller overall size of the gibbon compared to the siamang, it is posited that gibbons do not pose a great competitive threat to siamangs in terms of feeding competition (MacKinnon, 1977). Siamangs do pose a competitive threat to gibbons, however, and are observed both passively and actively outcompeting gibbons for fruit resources (O'Brein and Kinnard 2011). Observational studies reveal that the presence of siamangs within a gibbon group territory significantly reduced gibbon fruit intake (43% when sympatric vs 62% when allopatric) even within the same study site, potentially causing a depressive effect on *Hylobates* population densities (MacKinnon, 1977).

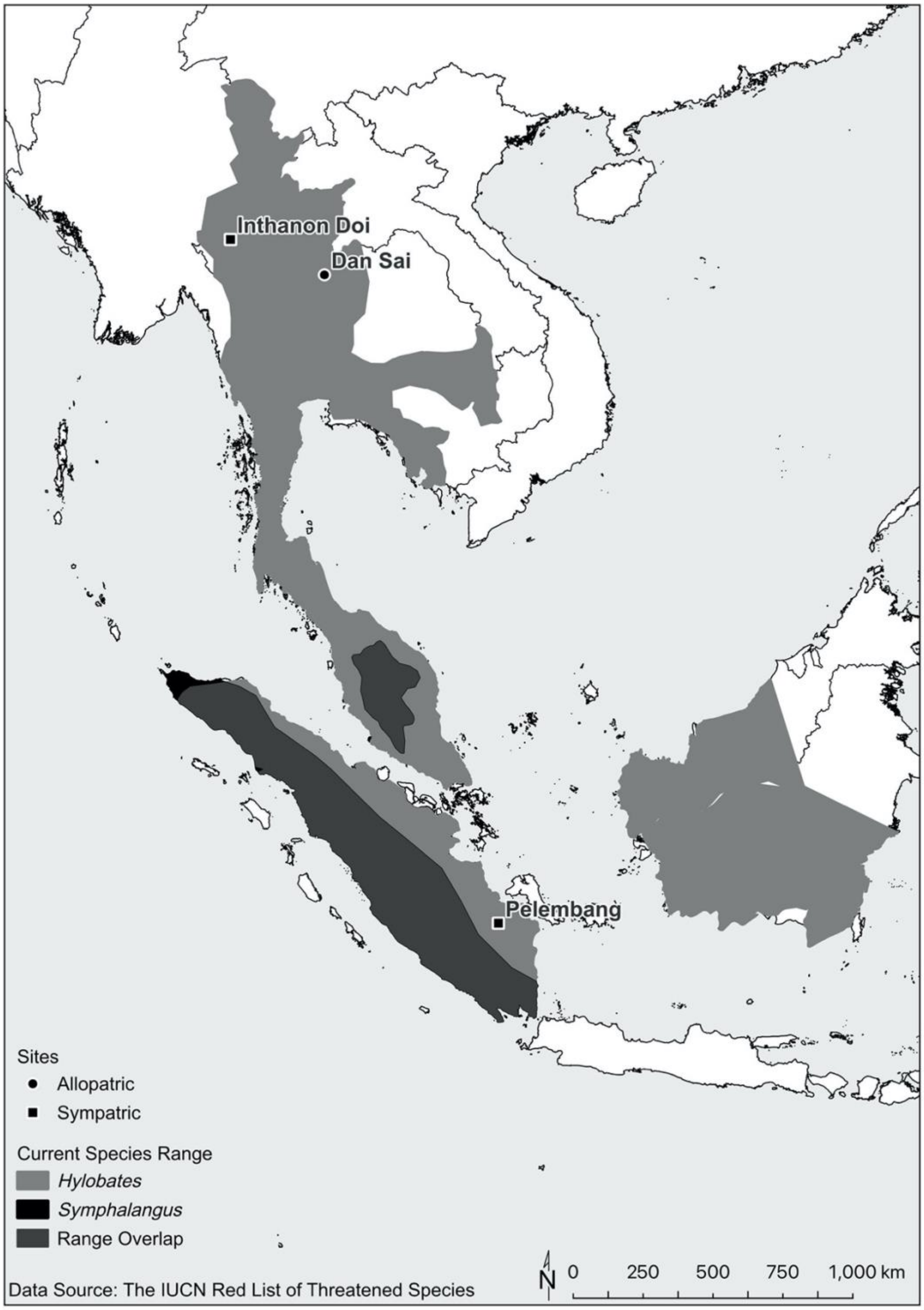

Figure 4.3: A map showing location data for *Hylobates* and Symphalangus samples as well as range extents.

4.2 STUDY DESIGN

4.2.1 Hypotheses and Predictions

Although we have the tools to identify the effects of competition on the anatomy, few studies have specifically examined this in sympatric primate communities (Ramdarshan *et al.*, 2011; Stroik, 2014), and rigorous testing across sympatric and allopatric populations is entirely lacking (Schreier *et al.*, 2009). The few studies that have examined character displacement in primates have looked within a single taxon or used coarsely defined ranges of sympatry and allopatry (Schroer and Wood, 2015; Berthaume and Schroer, 2017). These studies indicate that character displacement may be occurring within primate communities, but more rigorous testing is needed to demonstrate the scope and nature of the phenomenon.

Here I propose employing dental topographic analysis and stable isotope analysis to assess the **central hypothesis that primates respond to competition over food resources by feeding on underutilized resources, resulting in character displacement**. Although we expect primates to employ a variety of behaviors to mitigate pressures from competitor taxa, including differentiating diet and canopy-level occupation (Beaudrot *et al.*, 2013; Stroik, 2014; Carter and Bradbury, 2016), the *effects* of competition reduction strategies on morphological adaptation are not well documented.

To that end, this project tests the **specific hypothesis that closely-related sympatric primates display morphological traits and isotopic signatures that reflect focus on fewer key resources compared to their allopatric counterparts.** This is tested through specifically comparing dental and isotopic traits under conditions of both sympatry and allopatry. The following predictions are made:

Prediction a: Variables extracted from dental topographic analysis (DTA) will be more divergent in sympatric primate dyads, whereas DTA values will show more overlap between allopatric populations of those same species.

Prediction b: $\delta^{13}C$ and $\delta^{18}O$ will show evidence of vertical displacement when primate dyads occur sympatrically.

4.3 MATERIALS

4.3.1 Specimen selection

Specimens were sampled from the following museums: Smithsonian Museum of Natural History (Washington, D.C.), American Museum of Natural History (New York City, N.Y), Field Museum of Natural History (Chicago, I.L), Royal Museum for Central Africa (Turvuren, Belgium), Harvard Museum of Comparative Zoology (Cambridge, M.A).

Museum databases were mined for specimens with metadata attached, prioritizing location data. All specimens had documented country of origin, state, province, and specific location. While it was most desirable if specimens had geographic coordinates for collection site as well, the age of some collections meant these specific data were not available. In the case of old specimens, field logs and maps were examined in order to confirm locations that may have had spelling changes or name changes. IUCN red list species range data were incorporated to confirm areas of species sympatry or allopatry. Attempts to confirm sympatry or allopatry were also made by reading behavioral studies as well as expedition journals, and collection logs.

4.3.2 Ateles and Lagothrix Sympatric sites

Curaray River Mouth, Peru

Ateles and *Lagothrix* specimens came from the area of Curaray River Mouth in Loreto, Peru. Specimens were collected from expeditions in the 1920s by Carlos Olalla and his sons (Wiley 2010). Likely the specimen collections came from areas that are now included in the Pacaya Samiria National Reserve, Peru. In their survey of the monkeys of Pacaya Samiria, Allgas et al (2018) report that the reserve encompasses 2,080,000 ha and is the second largest reserve in Peru. The environment around the area consists of *terre firme* and *varzea* (or seasonally flooded forest) habitats. The mean annual temperature is 27°C. The area receives high levels of rainfall with an average of 2500 mm per year. The area is lower lying than the other specimen sites, with an elevation of only 93 meters. Canopy height ranges between 30 and 40 m. This area is home to 11 species of sympatric primate, making it one of the highest areas of primate biodiversity in the world (Allgas et al. 2018).

Pampa Grande, below San Ignacio, Peru

Ateles and *Lagothrix* specimens were collected from the Pampa Grande area (14°00"S 69°00"W) of Peru near the present day Bahuaja-Sonene National Park. Specimens were collected in 1951 by Hilda Heller. The temperature and rainfall in the region is typical of the Peruvian Amazon with an average temperature of 26° C and average annual rainfall of 1600-2400mm. The climate is categorized as humid sub-tropical forest and humid cloud forest (Shoobridge, 2002).

Alto Yavari Mirim, boca Rio Yaquerana, Peru

Ateles and *Lagothrix* specimens from the site of Alto Yavari from Loreto, Peru were collected in the 1950s. The collection area is near the present day Tamishiyacu Tahuayo Regional Conservation Area (TTRCA). The area around the collection site lies within the Amazon basin and is considered to have a sub-tropical climate with a distinct wet and dry season. Average rainfall is around 3000mm and mean annual temperature ranges are 25 °C to 33 °C. The region consists of seasonally flooded and upland forests. Researchers have noted the high biodiversity of this region (Puertas and Bodmar, 1993; Santillan *et al*., 2015)

While this area is very close to the Curaray collection site, I have made a distinction between these two sites as the Amazon River and its subsequent split into the Ucayali and Maranon Rivers would create a dispersal barrier for the primates within this region (Puertas and Bodmar, 1993).

La Macarena Parque, Rio Sansa, Colombia

Ateles and *Lagothrix* specimens came from La Macarena Parque in Colombia. In their survey of the park, Klein and Klein (1976) report that La Macarena is located at 3° 00” N, 73° 00” W and encompasses 4,250 sq miles. The park has mountain terrain, foothills, and floodplains and a diverse array of habitat types, ranging from mixed forests to swamps. The maximum elevation in the park is 3,000 meters (Klein and Klein, 1976). The park gets around 2,600 mm of precipitation annually (Matsuda and Izawa, 2008) Multiple species of monkeys inhabit the park area as well as a variety of other mammals and birds (Klein and Klein, 1976).

4.3.3 Ateles allopatric locations

Ateles specimens from the El Llagual area of Venezuela were collected in 1909 by M.A. Carriker Jr. for the American Museum of Natural History (Allen *et al.*, 1910). Specimens were collected around 7° 25” N, 65 10”W and areas near the present-day Cuara National Park. The area is classified as a tropical hill forest characterized by seasonal variation in rainfall with a dry season in February and March. The area receives an average of 2, 974mm of rain each year. The average temperature ranges from 21°C - 31°C (Castellanos, 1998).

Mount Duida, Valle de los Monos Cerro Duida, Venezuela

Ateles specimens from the Mt. Duida area of Venezuela were collected in 1928 by George H.H. Tate for the American Museum of Natural History. Specimens were collected around 3°30'48.0"N 65°37'34.0"W near present day Duida National Park (Tate and Hitchcock, 1930). The vegetation of the park is comprised of lower montane forests as well as shrubland and meadows along the tepuis slopes. Despite the high elevation, floristic and ecological diversity is very rich (Huber, 2001). The mean annual temperature for the area is around 27°C. However, due to changes in elevation, the average temperature can range 5-10 degrees depending on elevation within the park (Tate and

Hitchcock, 1930). The average rainfall is 2,700mm and the region is characterized by high daily humidity (Anhuf and Winkler, 1999).

4.3.4 Lagothrix allopatric locations

San Agustin, Colombia

Allopatric *Lagothrix* specimens came from the site of San Agustin, Huila, Colombia. The mean annual temperature 18.6°C. The mean annual precipitation of the area is 2075mm/year. The general elevation is 1,730 meters above sea level (Hernandez-Camacho and Cooper, 1976).

Pozuzo, Peru

Primates from Pozuzo come from the Pasco region of Peru. This area is located in the micro-basin of the Río Santa Cruz. The area is inhabited by humans and in the last few decades deforestation due to ranching and farming has decreased forest diversity. Interviews with locals report that *Ateles* was once commonly hunted in the area. However, *Ateles* is no longer present in the region due to lack of suitable habitat. Woolly monkeys remain in the area. The mean annual temperature 17°C -28 °C. Average precipitation is around 1452mm (Aquino *et al*., 2019).

Rio Aguas Clara, Colombia

Lagothrix specimens from the Rio Aguas Claras Area in Huila, Colombia were collected near what is now Cueva de los Guancharos National Park. In their survey of woolly monkey population density within the park, Vargas *et al*., (2014) report that the national park is approximately 2,000 meters above sea level and is covered by secondary Sub-Andean Forest with trees rarely exceeding 30 meters high. Annually there is an average of 2,284 mm of precipitation with 9 out of 12 months comprising the rainy season. The park has a mean annual temperature of 18.8°C (Vargas *et al*., 2014). Woolly monkeys have a generally dense population in this park and rarely go above 2,400 meters (Fonesca *et al*., 2022). Absence of hunting and human interference may explain the high density of the woolly monkeys. They are also the most abundant primate species and have very few primate competitors. Fruit production in the area is similar to lowland production despite it being more mountainous (Vargas *et al*., 2014).

Lagarto, Peru

Lagothrix collected from the Lagarto, Ucayali River, Peru area came from the AMNH, harvested during the Olalla Brother expedition in 1920s. This area is interesting due to a confluence of three rivers which create dispersal barriers for the fauna of the region. The collection site is located at about 233.51meters in elevation (Wiley, 2010). The average temperature ranges from 34.78ºC to 22.87ºC. The area receives an average of 208.93mm of rain each year. This site is slightly warmer and drier than other sites in this dissertation (cf. Vermeer and Tello-Alvarado, 2015).

Urubamba River, Peru

Lagothrix collected from the Urubamba River Mouth area of Peru come from a confluence of Tambo and Urubamba Rivers (10° 42’ S, 73 45’W). Presently this location is the city of Atalaya. Atalaya only became a population center in the 1940s, but these specimens were collected by the Olalla Brothers in 1927 when the area consisted of dense forest as well as some rolling hills, according to their field reports summarized in Wiley (2010). The mean annual temperature of the area is 30° C. The area is very humid and receives approximately 258 mm of rain each year (Wiley, 2010).

4.3.5 Cercopithecus mitis and Cercopithecus ascanius sympatric sites

<u>*Akenge, Kisangani, and Ituri, DRC*</u>

The sites of Akenge, Kisangani, and Ituri are in the northeastern corner of the present-day Democratic Republic of the Congo (DRC). These three sites are situated in dense tropical humid forests characterized by rugged terrain and foothills. The region around the three sites has a tropical climate with stable precipitation with a dry season in June and July (Korchia, 2020). The region has an annual precipitation of 1600 mm and mean monthly temperature of 23–26°C (Batumike *et al*., 2022).

Specimens collected around Kisangani come from the area near present day Lomami National Park, DRC. The area surrounding the park is a mix of dense forest, swamp, savannah, and lowland tropical forest (Batumike *et al*., 2022). The area within and surrounding the park is noted for its high levels of floristic and faunal diversity and is home to eleven species of primates (Korchia, 2020).

The Ituri forest is considered to have the highest biodiversity in the DRC (Oates *et al*.,1987). Within the Ituri forest is the Okapi Wildlife reserve which covers an area of 1,372,625 ha (13,726 sq km) between 1°00'N and 2°29'N, and 28°00'E and 29°04'E. The area within the park ranges in altitude from 700 and 1000 meters. The forest is a mix of tropical evergreen rainforest, swamp forest, and secondary forest (Hart, 1985). Thirteen species of primate are found within the wildlife reserve (Stephenson and Newby, 1997).

Akenge is situated in *terre firme* forest (Xu *et al*., 2017). While the site of Akenge lies in between Kisangani and Ituri, at 0°31'N and 25°12'E, Akenge is treated as a site separate from Kisangani as the Aruwimi River serves as a barrier between the two sites and presents a dispersal barrier (Turner *et al*., 1985).

4.3.6 Cercopithecus ascanius allopatric sites

Kananga and Kunungu, DRC

The allopatric sites of Kananga and Kunugu are located in the swamp forests of the western Democratic Republic of the Congo (Xu *et al*., 2017). These sites sit on the border between equatorial forest and forest-savannah mosaic habitats (East, 1990).

Specimens from Kunungu, DRC were collected near the present day Tumba Lediima Natural Reserve, near the border of the Republic of the Congo and the Congo River. The reserve covers an area of 741,000 ha and is classified as tropical/subtropical moist broadleaf forest (Twagirashyaka, and Inogwabini, 2009). While the area around Kunungu is classified as having moderate biodiversity, *C. ascanius* shares this region with the bonobo and large terrestrial species such the forest elephant (Inogwabini *et al*., 2011).

Kananga, DRC, is located in the southwestern region of the DRC at 05° 53’S, 022° 28’E. The area has an elevation of 655 meters and receives around 1500 mm of rainfall each year with a dry season from May to June (Chapin and Lang., 1924). The region is considered mosaic savannah forest, but patches of vegetation are present (European Commission, Joint Research Centre).

4.3.7 Cercopithecus mitis allopatric sites

Tana River, Kenya

Allopatric *C. mitis* specimens came from Tana River in Kenya. This region is more arid than the DRC samples, but there are very few regions where *C. mitis* is found allopatrically from *C. ascanius*. The Tana River stretches from central Kenya to the Indian ocean. While the area it passes through are mostly open grassland, specimens were collected from forested regions in the central part of Kenya (East 1988). The areas around the river are classified as riverine evergreen gallery forest (de Jong and Butynski, 2009).

4.3.8 Hylobates and Symphalangus sympatric sites

Pelembang, Sumatra

Hylobates agilis and *Symphalangus syndactylus* specimens were collected from around Pelembang, Sumatera, in the 1930s by the J.J. Menden expedition. Pelembang and the surrounding area are of low elevation, with the highest area being 20 meters. In their survey of the region, Whitten and Damanik (2012) report that the vegetation and climate are categorized as tropical rainforest with hot and humid weather year-round with plentiful rainfall. Mean annual temperatures are around 27°C. The region receives around

2,623 mm of rainfall throughout the year and is affected by an annual monsoon season (Whitten and Damanik, 2012).

Inthanon Doi, Thailand

Doi Inthanon National Park in located in northern Thailand. The park is 482km^2 and is part of the Himalayan Mountain range. Elevations range between 800 and 2,565 meters (Hvenegaard and Dearden, 1998). The park is characterized by high humidity and cold temperatures. The park is a mix of evergreen cloud forests and bogs at higher elevations and dry evergreen and mixed deciduous forests at lower elevations. Temperatures average between 1°C and 23°C. Rainfall averages 228-1164 mm annually depending on the altitude (Hvenegaard and Dearden, 1998; Khamyong, 2003).

4.3.9 Hylobates allopatric sites

Dan Sai, Thailand

Dan Sai, Thailand, is located in the western portion of the Loei Province. The Pho Luang Wildlife sanctuary lies within the district borders. The area receives between 1229-2000mm of precipitation annually, with a rainy season from April to October. The region has a temperature range from 4-28°C. In areas where the forest is preserved it is a mix of forest types ranging from dry deciduous dipterocarp, dry evergreen, montane evergreen, and coniferous forest depending on the elevation (Wanchai *et al*., 2012).

No allopatric specimens of *Symphalangus* were available to use as a comparative sample.

4.4 METHODS

4.4.1 Dental Impressions

Coltene President Jet Medium body polyvinylsiloxane dental molding material was used for all dental impressions (Ungar and M'Kirera, 2003). Using dental impressions to capture tooth shape obviates the need to remove specimens from their institutions for scanning and has been shown to capture shape and texture data at resolutions better than 1 micron (Ungar and Williamson, 2000). Prior to the application of the molding material, all specimens were checked for dirt, dust, and debris. Diluted rubbing alcohol was used to clean specimens if dust or dirt was present. Specimens were not used if debris was extreme. Prior to molding, specimens were assessed for dental wear through visual inspection by TSC and a research assistant. Only specimens with very little wear (wear stage 1, or dentin pits less than 1 mm (Buikstra and Ubeleker, 1994) were used. Additionally, molars also had to be intact and if the enamel was chipped or cracked the specimen was not used.

The dental impression molding technique used in this project follows protocols used in the University of Minnesota Dental School (VanHeel and Cererra *pers comm*). A precision tip was attached to the extrusion tube to ensure that the spaces in between teeth were adequately captured by the dental impression. First, impression material was applied to the most posterior tooth by flooding the occlusal basin. In order to prevent air bubbles, material was applied in one continuous application to the occlusal basin, moving forward to the premolars. Next, impression material was applied to the cusps and remaining crown of each tooth. Special care was taken to apply the material in between the interstitial tooth spaces. Before the material had completely set, a final application of material was applied to the crowns again. This second application gently pushed the original material into and crevices and crenulations on the occlusal surface.

Dental impression material was allowed to cure for 5-10 minutes, before gentle manual removal. After removal, molds were checked for large air bubbles, holes, and thin spaces in the impression material. Impressions were redone if large defects were present on the occlusal surface. To ensure correct specimen identification, all molds were placed in small plastic bags with the specimen accession number and species according to its catalog card.

While most impressions were sampled from the right side if all teeth were present and in good condition, for some specimens the left teeth provided better dental topography and impressions were taken from the left side. While this resulted in a mixed left and right sample, all left teeth were mirrored in GeoMagic. Additionally, no species was exclusively represented by either left or right sides in any analysis so as to avoid including non-independent data points. While mixing sexes and sides may introduce some measure of error into the analyses (mainly due to sexual dimorphism causing intra-specific molar size differences), there is a dearth of investigation into potential effects of such methods. (Berthaume and Schorer, 2017).

4.4.2 XRCT scanning

To 3D capture tooth shape, entire molds were scanned with an a X5000 high resolution micro-CT system with a twin head 225 kV x-ray source and a Dexela area detector (3073 x 3889 pixels). Because, dental impression material is impervious to ink of any kind, all molds had to be placed in individually labeled bags and taped to a scanning mount. Each bundle contained 20-45 molds and care was taken to not tape the bags together too tightly for risk of deforming the tooth molds. All bundles were scanned at a resolution between 37-38 micrometers and scan slices were exported as a *.tiff* stack.

4.4.3 Avizo methods

Avizo (Version 2020.1) was used to convert *.tiff* stacks into surface files. First, *.tiff* stacks were imported as completely read volumes with voxel size set to the scanning resolution. Next, the Filter Sandbox Tool was applied to each volume with the Guassian Filter. In order to separate air from the molds, the Interactive Thresholding tool was used with thresholding set to the autogenerated histogram. Slight modifications were made if the preview indicated it was necessary. Then, the Generate Surface tool was employed with unconstrained smoothing turned off and a surface file was saved as an ASCII *.stl* file.

4.4.4 Geomagic Methods

Tooth bundles were imported into Geomagic Design X. First, individual molds had to be identified, named, and exported as a separate file. Once identified, each the dental impression material was cut away from the tooth impression using the Polygonal Selection tool with "Visible Only" selected. To ensure the dental impression side that was pressed against the teeth was facing outward for later analysis, polyfaces were then flipped using the Fix Normal tool.

Next, each individual tooth was copied from the tooth row and pasted as an individual mesh. While best efforts were made to capture interstitial spaces during the application of impression material, holes were present on the mesial and distal edges of some teeth. The Fill Holes tool was used with the Bridge feature set to "interpolate curvature" to fill in the missing section of the tooth. This was primarily for aesthetic purposes given that cropping protocols (see below) ensured that these fabricated areas were not used in analysis.

Teeth were first cropped to the tooth crown based on where the crown dipped to the root. To ensure there were no dangling polyfaces or floating polyfaces outside the tooth, the Fill Holes, Liquify tool was used on the cropped edge. Any extra or missed ployfaces were removed using the Healing Wizard. Finally, whole teeth were exported as *.ply* files.

Teeth were cropped to the lowest point on the occlusal basin following protocols in (Prufrock *et al.,* 2016) and (Berthaume *et al.,* 2019). All teeth were aligned with the Z-axis perpendicular to the occlusal surface and the tooth's mesial and distal edged perpendicular with the X-axis. To guarantee an even cropping method, teeth were oriented so that the bottom edge was parallel with the Front Plane.

After each tooth was aligned, a plane was inserted using the Extreme Geometry option and choosing "lowest point" and teeth were cropped by using the Split tool. The Smooth tool was applied to each tooth set at Level 2. Finally, teeth were down-sampled to approximately 10,000 polyfaces. This level is shown to be best for reducing noise but still allowing capture of informative dental traits (Berthaume *et al.,* 2019). Prior to importing into MolaR, teeth were exported as binary ASCII *.ply* files and checked for consistency in orientation and scale.

4.4.5 MolaR

MolaR statistical software package for R (Pampush *et al.,* 2016) was used to generate dental topographic. Teeth were imported into MolaR using the batch process. Results for DNE, RFI, and OPCR were generated in MolaR data and then exported to a .csv file for use in the Displacement Statistic analysis (see Figure 4.4 for examples of DNE, RFI, and OPCR in *C. mitis* and *C. ascanius* M_2.

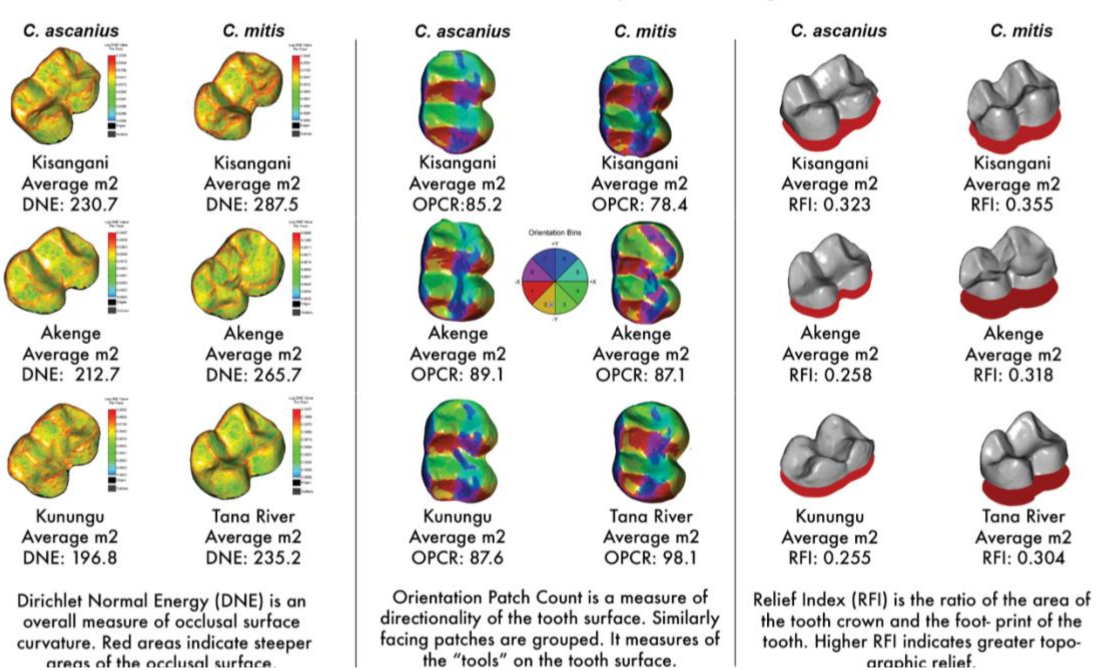

Figure 4.4 Examples of DNE (left), OPCR (middle) and RFI (right) on M_2 for *C. mitis* and *C. ascanius.*

4.4.6 *Displacement Statistic*

The magnitude of character displacement between populations was quantified using the Displacement Statistic (Schroer and Wood, 2015). For each dyad, this equation was performed on 12 tooth and variable combinations, on the lower molar row (see Table 4.1 for sample sizes). The Displacement Statistic is the difference D_S-D_A (Collyer and Adams, 2007), where D_S is the divergence of competing sympatric taxa and D_A represents the divergence of non-competing allopatric taxa (Schluter and McPhail, 1992, Schroer and Wood, 2015; Berthaume and Schroer, 2017). Competition is implied when D_S-D_A>0. Significance of this value is determined through population resampling. For this project, a general linear model (GLM) of the displacement statistic was employed following the work of Collyer and Adams (2007) and adapted in Schroer and Wood (2015) and Berthaume and Schroer (2017). The GLM uses the form $Y=BX+U$, where Y represents the morphological matrix of each dental topographic variable, X is the matrix of general ecological conditions (in this case, dummy variables encoding sympatry or allopatry, and the interaction of these with taxon), and U represents residual error and is assumed to be 0. The equation solves for B by multiplying each side by the inverse of X and the result is a matrix of partial regression coefficients that explain the interaction of ecology and morphology for the sample. This matrix is applied to the least squares mean of the four ecological groups resulting in a phenotypic change vector for each group. D_S represents the difference between values from the two sympatric populations and D_A represents the difference in value between the two allopatric populations. By subtracting D_A from D_S, we get the character displacement statistic.

Significance of the displacement statistic is determined using a probability distribution from randomizations. First, the interaction variable is removed from the X matrix so that specimens are only represented by their taxonomic and ecological coding. Once again, the B matrix is solved and residuals are randomly assigned to individuals. The four phenotypic change vectors are created and assigned a 1 if they are greater than or equal to the observed displacement statistic or 0 if they are less than the observed displacement statistic. This is performed 999 times to obtain a probability distribution of the displacement statistic, with significance assumed if the displacement statistic is less than 5% of the permuted values.

The displacement statistic was calculated for each primate dyad sympatric/allopatric site combination in in R (Version 4.2.1) using code from Schroer and Wood (2015). While molaR values were obtained for all teeth, this study limits the displacement statistic calculation to lower molars only. The reason for this is twofold: 1. Only lower molar DTA values were calculated for *C. ascanius* and *C. mitis* due to COVID-related constraints and 2. Lower molars are shown to more accurately reflect dietary behaviors than upper molars (Berthaume and Schroer 2017).

For each dyad, the three molaR variables (DNE, RFI, OPCR) were used in separate displacement statistic calculations, this is due to the difference in scale that each DTA value represents (e.g OPCR is calculated from 0-360 while RFI is written as a decimal).

Table 4.1: Counts for lower molars analyzed.

	M_1	M_2	M_3
	Ateles		
Alto Yavari	6	5	6
Below San Ignacio	1	1	1
Curaray River Mouth	8	9	7
El Yagual	1	1	1
La Macarena	9	9	7
Mount Duida	5	5	5
Pampa Grande	11	14	11
	Lagothrix		
Alto Yavari	5	4	5
Curaray River Mouth	4	4	3
La Macarena	4	5	4
Lagarto	2	2	2
Pampa Grande	2	3	2
Pozuzo	8	8	6
Rio Aguas Claras	2	2	2
San Agustin	3	3	2
Urubamba	3	3	3
	C. ascanius		
Akenge	6	7	12
Kananga	10	9	0
Kisangani	26	26	22
Kunungu	28	32	27
	C. mitis		
Akenge	10	8	3
Kisangani	18	18	12
Tana	4	4	2
	H. agilis		
Riau	2	2	2
Palembang	4	5	2
	H. lar		
Dan Sai	4	5	2
Inthanon Doi	3	14	5
Aru Bay	3	4	3
	Symphalangus		
Pelembang	3	7	5
Tarussan Bay	2	3	1

4.5 ISOTOPE METHODS

4.5.1 Sample Collection and Preparation

Isotope samples were taken from pelts of wild-caught primates housed at the following institutions: American Museum of Natural History (New York City, N.Y), Field Museum of Natural History (Chicago, I.L), Royal Museum for Central Africa (Turvuren, Belgium), Harvard Museum of Comparative Zoology (Cambridge, M.A). Approximately 20-50 hairs were plucked from the midline of each pelt. The number of hairs varied for each species as some species had coarser hair (*e.g*., guenons) while others had extremely fine and dense hair (*e.g*., woolly monkeys). Sampling left no discernable marks on the specimen. Professional-grade tweezers were used to extract hair samples ensuring that the bulb of each hair was captured. Tweezers were cleaned with a Clorox wipe in between specimens to ensure no cross contamination occurred. Hair was placed in plastic vials labeled with the specimen accession number.

Hair samples were cleaned and prepped in three different labs due to funding and permit constraints. All samples collected in museums in the United States were cleaned at the University of Minnesota Stable Isotope Laboratory following protocols from Crowley (2016). Hair was cleaned prior to analysis to remove dirt, chemical, and lipid material from the samples. First, hair was rinsed using De-Ionized (DI) water. Next, hair vials were filled with DI water and placed in a sonicator for 30 minutes to loosen any foreign material attached to the fur. Water was then poured off the hair. Next, hair was soaked in a chloroform methanol solution for 30 minutes. After soaking, hair was rinsed again in DI water. Waste-water was poured off the hair and vials were refilled with DI water and left to soak for 24 hours to ensure all chemicals were removed. Water was poured off and specimen vials were placed in the drier at 40 degrees C for 5-7 days. The extended drying time ensured no moisture was left in the tubes that could have caused mold or mildew.

All samples collected at the RMCA were prepped at the University of Ghent Isotope Lab. Cleaning procedures were similar with the only difference being a dicholormethane methanol solution was used instead of cholorform/methanol.

Samples from the United States were sent to the University of Florida Isotope Lab and the University of Ghent. A total of 251 hair samples were analyzed for $d^{13}C$, $\delta^{15}N$ and $\delta^{18}O$. $\delta^{18}O$ was measured using a Thermo Electron DeltaV Plus isotope ratio mass spectrometer coupled with a ConFlo IV interface linked to a TCEA (high temperature conversion elemental analyzer). $\delta^{13}C$ and $\delta^{15}N$ were measured using a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer coupled with a ConFlo II interface linked to a Carlo Erba NA 1500 CNHS Elemental Analyzer. Samples were loaded into tin capsules and placed in a 50-position automated Zero Blank sample carousel on a Carlo Erba NA1500 CNS elemental analyzer. After combustion in a quartz column at 1000C in an oxygen-rich atmosphere, the sample gas was transported in a He carrier stream and passed through a hot reduction column (650C) consisting of elemental copper to remove oxygen. The effluent stream then passed through a chemical (magnesium perchlorate) trap to remove water followed by a 0.7 meter GC column at 125 C to separate N_2 from CO_2. The sample gas next passed into a ConFlo II interface and into the inlet of a Thermo Electron Delta V Advantage isotope ratio mass spectrometer running in continuous flow mode where the sample gas was measured relative to laboratory reference N_2 and CO_2 gases. All carbon isotopic results are expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB) (Carter, 2001). All nitrogen isotopic results are expressed in standard delta notation relative to atmospheric nitrogen (AIR) (Crowley, 2012). All oxygen isotopic results are expressed in standard delta notation relative to Standard Mean Ocean Water (SMOW) (Crowley, 2012).

4.5.2 Isotope Analytical Methods

Two-way ANOVAs were used to determine whether stable isotope ratios of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ of each primate pair were significantly different from each other, significantly different at sites where they co-occur, and if they differed within each site. Tukey's HSD with 95% confidence intervals were run to determine which sites had species pairs that differed significantly. All statistical tests were conducted in R (Version 4.2.1).

One note is that the Ituri and Epulu samples came from an overlapping area. However, Epulu samples were collected from a much wider range of locations whereas the Ituri samples were collected from a more localized area. Because of the difference in scale, the two locations are treated as separate..

4.6 RESULTS

4.6.1 Displacement Statistic Results: Ateles-Lagothrix

A total of 240 Displacement Statistic analyses were run for *Ateles* and *Lagothrix*. All possible allopatric and sympatric combinations were run, resulting in 20 site combinations. Overall, 129 of the 240 analyses had larger sympatric vector lengths meaning that there was a greater difference between the sympatric species than when the two allopatric species were compared, none of the analyses were significant at the 0.05 threshold. Across sites, DNE showed the greatest difference in sympatric vector length with 68% of all DNE calculations indicating greater differences in the sympatric sample. RFI had the next highest number of larger sympatric vectors, with 47% of all RFI calculations having greater differences in the sympatric individuals. OPCR had slightly fewer, with 45% being larger across all sites.

Examining tooth position also revealed some patterns in differences between allopatric and sympatric sites. First molars showed the most differences between sympatric *Ateles* and *Lagothrix* with 68% of all variables measured on lower molars having a greater difference between the sympatric species. Third molars (53%) and the combination of m1-m3 (51%) showed similar larger vector lengths across sites. Lower second molars had the fewest largest vector lengths with only 46% of all variables measured returning larger sympatric values.

There were 60 analyses per sympatric site. Analyses were broken up so that each sympatric site was compared to the individual allopatric sites.

The sympatric site specimens of La Macarena were compared to allopatric *Ateles* from Mt. Duida and allopatric *Lagothrix* from Lagarto, Pozuzo, Rio Aguas Claras, San Agustin, and Urubamba. Overall, 40% of all tooth/variable combinations returned larger differences between *Ateles* and *Lagothrix* at La Macarena than at their allopatric site. No single tooth/variable combination was larger across all five allopatric *Lagothrix* sites. At four of the five site combinations m1 DNE values and m1 RFI values had larger sympatric values. Within sites, Rio Aguas Claras had the most sympatric values with 66% of tooth/variable combinations being larger. This was followed by Pozuzo at 52%. San Agustin, Urubamba, and Lagarto each only had three of the 12 combinations return larger sympatric values. Results for each site combination are presented in Appendix A.

The sympatric site of Pampa Grande was compared to the allopatric *Ateles* from Mt. Duida and allopatic *Lagothrix* from Lagarto, Urubamba, Pozuzo, San Agustin, and Rio Aguas Claras. Overall, 58% of all tooth/variable combinations returned larger differences between *Ateles* and *Lagothrix* at Pampa Grande than at their allopatric site. Only M_1 OPCR was larger across all five allopatric *Lagothrix* sites. Within sites, Pozuzo had the most largest sympatric values with 75% of tooth/variable combinations being larger. This was followed by Lagarto and Urubamba which both at 58%. Both San Agustin and Rio Aguas Claras each only had 5 of the 12 combinations return a larger sympatric value.

The sympatric site of Alto Yavari was compared to the allopatric *Ateles* from Mt. Duida and allopatric *Lagothrix* from Lagarto, Urubamba, Pozuzo, San Agustin, and Rio Aguas Claras. Across sites, 73% of all variable combinations had at least one larger sympatric value. Six variables were larger across all five sites: M_1 DNE; M_1 RFI; M_2 DNE; M_3 DNE; M_3 OPCR; M_1, M_2, M_3 DNE. Within sites, Rio Aguas Claras had the highest number of larger sympatric values with 91%. This was followed by Lagarto with 75% of all tooth/variable combinations having larger sympatric vector values. San Agustin had 66% of all tooth/variable combinations having larger sympatric vector values while Pozuzo and Urubamba had 58%.

The sympatric site of Curaray River Mouth was compared to the allopatric *Ateles* from Mt. Duida and allopatric *Lagothrix* from Lagarto, Urubamba, Pozuzo, San Agustin, and Rio Aguas Claras. Across sites, 43% of all variable combinations had at least 1 larger sympatric value. Only M_1 RFI was larger across all five sites. Within sites, San Agustin and Rio Aguas Claras and Urubamba had the highest number of larger sympatric values, both with 50%. Lagarto and Urubamba both had 41% of all tooth/variable combinations with a larger sympatric vector value. Pozuzo had the lowest with only 33%. Results for each site combination are presented in tables in Appendix A.

4.6.2 Displacement Statistic Cercopithecus

C. mitis and *C. ascanius* came from sympatric sites of Kisangani and Akenge, DRC. Allopatric *C. ascanius* came from Kunungu, DRC and Kanaga, DRC and allopatric *C. mitis* from Tana River, Kenya. Of the 48 character displacement analyses, 23 returned larger sympatric vector values, indicating that there was a greater difference in the shape between the two sympatric species compared to the allopatric comparison. While none reached statistical significance, 12 of the analyses had p-values < 0.5 suggesting that the pattern is not random for those variables. Results for each site combination are presented in Appendix A.

The variables in the combination Akenge (sympatic)-Kanaga (allopatric)-Tana River (allopatric) had only two higher sympatric vector lengths: M_3 DNE; M_1, M_2, M_3 DNE. Almost all variables in the combination Akenge (sympatric)-Kunungu (allopatric)-Tana River (allopatric) had larger sympatric vector lengths, except for M_1, M_2, M_3 OPCR. For the combination Kisangani (sympatric) -Kunungu (allopatric)-Tana River (allopatric), five out of the twelve variable/tooth combinations had higher sympatric vector lengths: M_1 RFI; M_2 DNE; M_3 DNE; M_1, M_2, M_3 DNE; M_1, M_2, M_3 RFI (Figure XX). The combination Kisangani-Kananga-Tana River hadsimilar results to Kisangani-Kunugu-Tana River with the addtion of larger sympatric vector lengths for m1 DNE, RFI, OPCR and m3 OPCR.

4.6.3 Displacement Statistic Hylobatids

A total of 24 analyses were run for Hylobatid data. Because the displacement statistic requires that each species has an allopatric and sympatric representative to create a matrix, it was only run on *Hylobates* data because no sympatric siamang samples could be located or accessed for this project. Additionally, no two *Hylobates* species overlap, so they are by default allopatric from each other. Overall, 12 of the 24 analyses returned larger sympatric vector values than the sympatric comparison, but none of the analyses were significant at the 0.05 threshold. Of the larger sympatric values, 75% had p-vlaues < 0.5. Across sites, DNE and RFI both showed the greatest difference in sympatric vector length with 62% each indicating greater differences in the sympatric sample. OPCR showed the fewest larger differences with only 25% being larger across all sites.

When only Dan Sai, Thailand, was considered for allopatric *Hylobates lar*, 50% of variables returned larger sympatric values. No single variable or tooth was consistently larger within this sample.

When considering the allopatric *Hylobates lar* from Dan Sai, Thailand, only 6 of the 12 analyses showed larger sympatric vector values. DNE values were larger across all three tooth positions, however the combination of M_1-M_3 had no larger values. Results for each site combination are presented in tables in Appendix X.

4.6.4 Isotope Results

First, summary statistics were calculated for each sampled site. They are presented in Appendix B. No clear pattern emerged for any primate pair across any isotope measured. Due to complications related to the COVID-19 Pandemic, $\delta^{18}O$ values were not able to be collected for the sites of Kisangani, Epulu, or Kananga.

A two-way ANOVA was run on each isotope value where species, location, and species and location were the grouping variables. Tukey's HSD post-hoc tests were used when Location and Species: Location was significant at $p<0.05$ to investigate which sites had significantly different values and if the taxa present at the sites were significantly different. Results are presented for all isotope values by species dyad:

4.6.4.1 Ateles/ Lagothrix

The two-way ANOVA revealed that *Ateles* and *Lagothrix* were not significantly different in their $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$ values.

All *Ateles/Lagothrix* sites were significantly different across all isotope values: $\delta^{13}C$ (F=10.546, p=0.0004) (Table 4.2) ; $\delta^{15}N$ (F=40.368, p=1.063e-08) (Table 4.4); $\delta^{18}O$ (F=5.9053, p=0.0076) (Table 4.6). To identify which sites significantly differed, a Tukey's HSD was used (Pairwise comparisons are presented in Tables 4.3, 4.5, 4.7). Significant differences were in the following site combinations: for $\delta^{13}C$: Pampa Grande-Alto Yavari ($p<0.0000000$) and Pampa Grande-Curaray River Mouth ($p<0.00000001$);

for δ^{15}N, Curaray River Mouth: Alto Yavari (p<0.00001) and Pampa Grande: Alto Yavari (p<0.00000); for δ^{18}O: Pampa Grande-Alto Yavari (p= 0.0015) and Pampa Grande-Curaray River Mouth (p=0.0058).

Looking within each site, *Ateles* and *Lagothrix* showed significant differences only in their δ^{13}C (F=12.244, p=0.0001); δ^{15}N (F=3.7255, p=0.0377). Tukey's HSD post-hoc comparisons showed that *Ateles* and *Lagothrix* were significantly different only at Curaray River Mouth (δ^{13}C: p=0.0001; δ^{15}N: p= 0.0002).

Table 4.2: ANOVA results for *Ateles* and *Lagothrix* δ^{13}C. Species, location, and within site differences are presented. Bold signifies significance at the p< 0.05 level.

***Ateles/Lagothrix* δ^{13}C**	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	2836.96	1	73661.772	**< 2.2e-16**
Species	0.09	1	2.443	0.1301
Location	0.81	2	10.546	**0.000**
Species:Location	0.94	2	12.244	**0.0001**
Residuals	1.00 26			

Table 4.3: Pairwise comparisons for *Ateles* and *Lagothrix* δ^{13}C Location and Species by Location. Bold signifies significance at the p< 0.05 level.

δ^{13}C Tukey's post hoc tests				
Location	diff	lwr	upr	p adj
Curaray River Mouth-Alto Yavari	0.1539965	-0.04791225	0.3559052	0.1601
Pampa Grande-Alto Yavari	0.7651153	0.53379980	0.9964308	**0.0000**
Pampa Grande-Curaray River Mouth	0.6111188	0.39498844	0.8272492	**0.0001**
Species:Location				
***Lagothrix* :*Ateles*-Alto Yavari**	-0.194	-0.5753477	0.18734775	0.6286
***Lagothrix*:*Ateles* -Curaray River Mouth**	-0.7311326	-1.0878508	-0.3744145	**0.0001**
***Lagothrix* : *Ateles* -Pampa Grande**	0.1387694	-0.2875904	0.5651291	0.9137

Table 4.4: ANOVA results for *Ateles* and *Lagothrix* $\delta^{15}N$. Species, location, and within site differences are presented. Bold signifies significance at the $p< 0.05$ level.

***Ateles Lagothrix*: $\delta^{15}N$**	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	73.421	1	334.4260	**2.298e-16**
Species	0.146	1	0.6669	0.4215
Location	17.725	2	40.3684	**1.063e-08**
Species:Location	1.636	2	3.7255	**0.0377**
Residuals	5.708 26			

Table 4.5: Pairwise comparisons for *Ateles* and *Lagothrix* $\delta^{15}N$ Location and Species by Location. Bold signifies significance at the $p< 0.05$ level.

$\delta^{15}N$ Tukey's post hoc tests				
Location	diff	lwr	upr	p adj
Curaray River Mouth-Alto Yavari*	2.03992449	1.5578547	2.5219943	**0.0001**
Pampa Grande-Alto Yavari	1.96089517	1.4086149	2.5131755	**0.0000**
Pampa Grande-Curaray River Mouth	-0.07902933	-0.5950542	0.4369955	0.9235
Species:Location	diff	lwr	upr	p adj
***Lagothrix*: *Ateles*-Alto Yavari**	0.2420000	-0.6684917	1.1524917	0.9617
***Lagothrix*:*Ateles* :Curaray River Mouth**	-0.3925857	-1.2442726	0.4591013	**0.0002**
***Lagothrix*:*Ateles* belzebuth-Pampa Grande**	0.7722097	-0.2457509	1.7901703	0.2180

Table 4.6: ANOVA results for *Ateles* and *Lagothrix* $\delta^{18}O$. Species, location, and within site differences are presented. Bold signifies significance at the $p< 0.05$ level.

***Ateles Lagothrix* $\delta^{18}O$**	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	595.14	1	627.1239	**< 2.2e-16**
Species	1.16	1	1.2253	0.2784
Location	11.21	2	5.9053	**0.0076**

Table 4.7: Pairwise comparisons for *Ateles* and *Lagothrix* $\delta^{18}O$ Location. Bold signifies significance at the $p< 0.05$ level.

$\delta^{18}O$ Tukey's post hoc tests				
Location	diff	lwr	upr	p adj
Curaray River Mouth-Alto Yavari	0.3407	-0.6615	1.343	0.6791
Pampa Grande-Alto Yavari*	1.8140000	0.6657	2.962	**0.0015**
Pampa Grande-Curaray River Mouth	1.4732389	0.4003	2.5461	0.00581

Cercopithecus

The two-way ANOVA revealed that *C. ascanius* and *C. mitis* were significantly different in only in their δ^{13}C values (F= 15.1847, p = 0.0003) (Tables 4.8; 4.10, 4.12). Isotope values differed significantly by location for δ^{13}C (F= 9.2042, p = 7.0003e-05) and δ^{15}N (F= 3.1688, p = 0.0331). The Tukey's post hoc test (Table 4.9) showed significant differences in their δ^{13}C values between Kisangani: Akenge (p=0.0006), Kisangani: Epulu (p=0.0302); and Kisangani: Ituri (p=0.0003). The Tukey's post-hoc test (Table 4.11) showed significant differences in their δ^{15}N values between Kisangani: Akenge (p=0.0406), Kisangani: Epulu (p=0.0144).

Looking within each site, *C. ascanius* and *C. mitis* showed significant differences only in their δ^{13}C (F=9.2042, p=7.003e-05). Tukey's HSD post-hoc comparisons showed that *C. ascanius* and *C. mitis* were significantly different only at Akenge (δ^{13}C: p=0.007).

Values for δ^{18}O indicated no significant differences in any category (Table 4.12).

Table 4.8: ANOVA results for *C. mitis* and *C. ascanius* δ^{13}C. Species, location, and within site differences are presented. Bold signifies significance at the p< 0.05 level.

δ^{13}C *C. mitis* and *C. ascanius*	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	3970.8	1	22624.6391	**<2.2e-16**
Species	2.7	1	15.1847	**0.0003**
Location	4.8	3	9.2042	**7.003e-05**
Species:Location	3.4	3	6.4319	**0.0009**
Residuals	8.1 46			

Table 4.9: Pairwise comparisons for *C. mitis* and *C. ascanius* δ^{13}C Location and Species by Location. Bold signifies significance at the $p< 0.05$ level.

δ^{13}C Tukey's post hoc tests	**diff**	**lwr**	**upr**	**p adj**
Location				
Epulu-Akenge	-0.22229167	-0.7659610	0.32137769	0.6992
Ituri-Akenge	0.08360577	-0.4479805	0.61519208	0.9751
Kisangani-Akenge	-0.83562500	-1.3672113	-0.30403869	**0.0006**
Ituri-Epulu	0.30589744	-0.2640229	0.87581778	0.4891
Kisangani-Epulu	-0.61333333	-1.1832537	-0.04341299	**0.0303**
Kisangani-Ituri	-0.91923077	-1.4776364	-0.36082515	**0.0003**
Species:Location				
mitis:_ascanius_-Akenge	0.822698	0.1525069	1.4928899	**0.0070**
mitis:_ascanius_-Epulu	-0.460000	-1.2278008	0.3078008	0.5567
mitis:_ascanius_-Kisangani	0.721190	-0.0186809	1.4610618	0.0608
Mitis:_ascanius_-Ituri	0.648750	-0.1093925	1.4068925	0.1436

Table 4.10: ANOVA results for *C. mitis* and *C. ascanius* δ^{15}N. Species, location, and within site differences are presented. Bold signifies significance at the $p< 0.05$ level.

C. mitis and _C. ascanius_ δ^{15}N	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	510.35	1	465.6713	**< 2e-16**
Species	0.04	1	0.0326	0.85754
Location	10.42	3	3.1688	**0.0331**
Species:Location	1.79	3	0.5439	0.65473
Residuals	50.41	46		

Table 4.11: Pairwise comparisons for *C. mitis* and *C. ascanius* δ^{15}N δ^{15}N Location. Bold signifies significance at the $p< 0.05$ level.

δ^{15}N	**diff**	**lwr**	**upr**	**p adj**
Epulu-Akenge	0.2658333	-0.799256	1.33092268	0.9103
Ituri-Akenge	-0.7826923	-1.824110	0.25872543	0.2027
Kisangani-Akenge	-1.0542308	-2.095649	-0.01281303	**0.0462**
Ituri-Epulu	-1.0485256	-2.165043	0.06799137	0.0728
Kisangani-Epulu	-1.3200641	-2.436581	-0.20354709	**0.01449**
Kisangani-Ituri	-0.2715385	-1.365497	0.82242032	0.9116

Table 4.12 ANOVA results for *C. mitis* and *C. ascanius* δ^{18}O. Species, location, and within site differences are presented. Bold signifies significance at the $p< 0.05$ level.

C. mitis and _C. ascanius_ δ^{18}O	**Sum Sq**	**Df**	**F value**	**Pr(>F)**
(Intercept)	1135.83	1	804.0125	< 2e-16
Species	0.04	1	0.0311	0.86209
Location	4.44	1	3.1398	0.09333
Species:Location	0.13	1	0.0896	0.7681
Residuals	25.43	18		

Hylobates/ Symphalangus

Stable isotope ratios were also not significantly different between *Hylobates agilis* and *Symphalangus syndactylus* samples (Table 4.13). Because *Hylobates* and *Symphalangus* samples came from the same site, no between site ANOVA was run for the species pair.

Table 4.13: *Hylobates* and *Symphalangus* ANOVA results for $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$.

Hylobates, Symphalangus	**Sum Sq**	**DF**	**F Value**	**Pr(>F)**
$\delta^{13}C$	0.02	1	0.1898	0.6734
$\delta^{15}N$	0.098	1	0.2327	0.641
$\delta^{18}O$	4.90	1	4.0967	0.07364

4.7 DISCUSSION

Character displacement seems to be an important concept when considering the behavioral ecology of closely related organisms as well as potential selection pressures on past populations. Nevertheless, it is a difficult phenomenon to detect and has been subject to intense debate (as reviewed in Losos 2000 and Dayan and Simberloff 2005). Schluter and McPhail (1992) outlined that certain characteristics of the communities in question must be in place and all alternative explanations for resource partitioning to be explored before competition can be considered. They put forth six such criteria that must be met in order to identify character displacement:

(1) The pattern could not occur by chance.

(2) Phenotypic differences should have a genetic basis.

(3) Enhanced differences should result from actual evolutionary shifts.

(4) Morphological differences should reflect differences in resource use.

(5) Sites of sympatry and allopatry should not differ greatly in food, climate, or other environmental features affecting the phenotype.

(6) There must be independent evidence for competition.

Meeting all six criteria is rarely feasible (Roughgarten 1983; Losos 2000; Dayan and Simberloff 2005). The six criteria do provide a cohesive framework to discuss the results of this study.

Criterion 1: "The pattern could not occur by chance."

In order to quantitively measure character displacement, the displacement statistic was employed. While no p-values reached the level of significance, many were under the 0.5 threshold for randomness (Shrorer and Wood 2015). The p-values in this study were likely affected by small sample sizes in one allopatric or sympatric group, as such resampling was based on very small groups for some allopatric taxa. Small sample sizes were unavoidable as this project sought to use very rigorous constraints in geographic location when choosing specimens. Indeed, p-values did get smaller as more specimens were added for certain species, but as the sample size expanded so too did the range of variation within the sample.

Criterion 2: "Phenotypic differences should have a genetic basis" and Criterion 3: "Enhanced differences should result from actual evolutionary shifts."

Tooth shape is correlated with chewing efficiency, and therefore teeth have to maintain a shape that allows them effectively process foods for maximum nutrient and caloric gain. Because of the importance of preprocessing foods for caloric extraction prior to swallowing, it is likely that important aspects of occlusal morphology have genetic underpinnings and that both anatomy and genetic architecture were influenced by natural selection (Ungar *et al*., 2017). Additionally, teeth must be able to withstand potentially challenging mechanical properties of selected foods in order to resist breakdown and maintain longevity. For example, if an animal ingests hard foods that require high pressure to propagate cracks on the food surface, the tooth must have a structure that is more resistant to cracking than the food being eaten. Therefore, the relationship between food property, tooth longevity, and caloric requirements allow for an evolutionary pathway where tooth shape, and thereby dental topography, can have a genetic basis (Berthaume et al 2020).

Criterion 4: "Morphological differences should reflect differences in resource use."

The differences identified in each species pair do reflect potential differences in resource use, especially when related to tooth complexity and tooth height. Tooth complexity is often associated with more complex or mechanically challenging resources and especially in molars as bland as frugivore molars, increased complexity points to differences in mechanically challenging foods at sites where competition is increased.

Criterion 5: "Sites of sympatry and allopatry should not differ greatly in food, climate, or other environmental features affecting the phenotype."

This project carefully chose specimens based on comparability of allopatric and sympatric sites. While this was often difficult to establish given present day ranges of the examined primates, locations studied in this project are thought to be comparable.

Criterion 6: “There must be independent evidence for competition.”

As established in Chapter 2, interspecific primate relationships are complex. Nevertheless, there is ample evidence for competition over food resources, especially fruit resources, between closely related primate pairs (Cords, 1987; Gathua, 1999; Chapman and Chapman, 2000; Fedigan and Jack, 2012; Cristobal-Azkarate *et al.*, 2015; Dias and Rangel-Negrín 2015; Strushaker, 2017). Furthermore, there is evidence of partitioning behavior based on multiple behavioral studies showing primates altering their behavior and supplementing food resources when facing competitor pressure (Cords, 1990; Bryer *et al*., 2013; Strushaker, 2017).

Hence, although it is impossible to fully validate the six criteria suggested by Schluter and McPhail (1992) using currently available data, it is likely that the primate species studied in this project can be considered for character displacement. Patterns within each species pair are discussed below.

4.7.1 Ateles and Lagothrix

Ateles and *Lagothrix* share a complex relationship in areas where they overlap (Link et al. 2012). Because they are both relatively large bodied and feed preferentially on fruits, some degree of habitat partitioning is expected. Additionally, both primates are very sensitive to habitat disturbance, indicating some degree of dietary rigidity (Defler and Defler 1996; Link et al. 2012). While no single variable, tooth, or tooth position consistently displayed larger sympatric vector lengths across all sites, when examining the results of the displacement statistic analysis, a few interesting pattens emerge.

First, DNE showed the largest amount of sympatric vector lengths across sites and teeth. Larger vector lengths indicate a greater difference between the two species being examined. DNE is a measure of tooth curvature/sharpness. Teeth that have higher curvature often have sharper cusps which may indicate an adaptation for processing fibrous foods (Berthaume *et al.* 2020). Both *Lagothrix* and *Ateles* are known for their molars with few surface features and display wide crushing basins and low cusps (Rosenberger *et al.* 2008). This is likely because they minimally process smaller, ripe fruits, instead opting to swallow them mostly intact. While this method is important for seed dispersal and forest regeneration, it also allows both *Ateles* and *Lagothrix* to consume fruits quickly as they move through the canopy (Link and DiFiore 2006). Therefore, an increase in tooth curvature/sharpness may indicate adaptations for processing more mechanically challenging foods if ripe fruits are unavailable.

When looking at variation between sympatric sites, some sites show high percentages of larger sympatric vector lengths, while others show very little. One comparison of note is the differences seen in Curaray River Mouth and Alto Yavari. Alto Yavari and Curaray are very near each other. However, the Amazon River separates the two locations. Both are high in floristic and faunal diversity, especially primates. Additionally, they are both climatically similar. It is puzzling why there would be such high levels of larger sympatric vector lengths between *Ateles* and *Lagothrix* at Alto Yavari (73%) while Curaray had the second fewest larger sympatric values (43%) of any sympatric site no matter the allopatric comparison. This may be indicative of higher fruit productivity at Curaray and is worthy of future study.

When examining the isotope values of specimens from Alto Yavari and Curaray, they are only significantly different in $\delta^{15}N$, which is not unexpected. Looking within each site, *Ateles* and *Lagothrix* are significantly different in $\delta^{15}N$, $\delta^{13}C$, but not in $\delta^{18}O$ at Curaray River Mouth. *Ateles* and *Lagothrix* are not significantly different in $\delta^{15}N$, $\delta^{13}C$, or $\delta^{18}O$ at Alto Yavari. Curaray *Ateles* and *Lagothrix* may feed on similar resources in different parts of the canopy, or different areas of productivity, whereas at Alto Yavari, *Ateles* and *Lagothrix* feed in similar locations but on resources with slightly different mechanical properties (*i.e.,* unripe fruit vs ripe fruit). Studies focused on parsing out these differences may help us better understand how these primates differentially utilized their landscape.

Alternatively, feeding differences may be too simplistic an explanation for the diversity of dental morphology presented here as some of the *Ateles/Lagothrix* results are puzzling. For example, *Ateles* and *Lagothrix* collected from Curarary River Mouth and those collected from Alto Yavari might be expected to yield similar results given their close proximity and therefore similar climates and environments. This was not the case. Individuals from Alto Yavari had larger sympatric vector length differences for a higher number of tooth positions and variable combinations than did individuals from Curaray River Mouth. This shows that, if character displacement is driving these differences, it may not be present at all sites. There could be other factors present at Curaray (i.e greater fruit productivity, less seasonal flooding, or local allopatry) that are causing individuals to look less different than their allopatric counterparts.

The Amazon is notorious for its mix of high biodiversity in some areas and low biodiversity in others. Multiple hypotheses have been put forth over the decades including the Pleistocene Refugia Hypothesis, Andean uplift, riverine barriers, marine transgressions, climatic-driven vegetation shifts, range expansion, habitat gradients, and even domestication (Rocha and Kaefer 2019). Platyrrhine ranges are demonstrated to be influenced and constrained by river boundaries Therefore, allopatry of *Ateles* and *Lagothrix* may not be solely a function of competition or competitive exclusion, but may also have been influenced by climatic or geographic shifts that inhibit gene flow between populations.

4.7.2 C. ascanius and C. mitis

The Displacement Statistic results for C. *ascanius* and *C. mitis* did not show a clear pattern between tooth morphology and site. Some site combinations like Akenge-Kunugu-Tana River had more larger sympatric vector lengths than sites like Akenge-Kananga-Tana River. This difference in morphology may be a function of environmental differences between different allopatric locations. Kananga is a more open habitat and there might be fewer fruit resources or more intense competition with other primate species around the area, which could contribute to similarities in molar shape between Kananga *C. ascanius* and Kisangani *C. ascanius*. Within sites, DNE values for m2 and m3 seem to have the largest differences in sympatric vector lengths, possibly indicative of a difference in sharpness at sites where *C. ascanius* and *C. mitis* are sympatric. When examining the isotope results, there is a difference between *C. ascanius* and *C. mitis* in terms of their δ^{13}C values but not in δ^{15}N or δ^{18}O. When the results of the Tukey's HSD for the two factor ANOVA are analyzed, *C. ascanius* and *C. mitis* are significantly different in their $\delta^{13}C$ values at the site of Akenge. This might indicate a reliance on different food types or feeding at different levels in the canopy. Indeed, *C. ascanius* does have a more depleted signature for $\delta^{13}C$, potentially indicating a focus on resources depleted in $\delta^{13}C$ or foraging lower in the canopy.

4.7.3 Hylobatids

Across all sites RFI showed the largest amount of larger sympatric vector lengths when *Hylobates* specimens were compared to individuals that competed with siamangs. RFI is a measure of topographical relief and cusp height compared to cusp size: higher RFI scores indicate taller cusps. The combination of higher DNE and RFI scores among *Hylobates* when they are sympatric with siamangs could indicate a dietary shift towards less preferred resources such as leaves or less ripe fruit, when ripe fruit is scarce.

Within the dietary isotopes for the sympatric Pelembang *Hylobates agilis* and *Symphalangus syndactylus*, ANOVAs indicated no significant difference in $\delta^{15}N$, δ13C, or $\delta^{18}O$ values. If gibbons and siamangs do partition their diet, it is likely seasonal and dependent on fruit/fig scarcity. Dental traits might indicate this as an adaptation to consuming fallback foods would be important for mastication.

The results of this study open interesting future lines of research for comparing primates at a finer scale or examining different teeth. While this project only examined molars, frugivorous primates often rely on anterior teeth to process fruit hulls and husks (Lambert, 1997). At sites where character displacement was not identified, it might not be that competition overall was less (*e.g.*, Curaray compared to Alto Yavari), but instead that the primates are utilizing a different chewing strategy to process their foods further forward in the mouth and/or swallowing fruits more intact.

4.8 CONCLUSION

Because character displacement can be difficult to identify and its manifestation relies on a strict set of criteria to appear, the examination of multiple sympatric sites when possible aided in creating a broader picture of the potential interactions between primate dyads. Across all three species pairs, the Displacement Statistic was able to identify some differences between allopatric and sympatric samples. Additionally, patterns emerged in dietary isotope differences between species pairs. While the results of this study are mixed, there is a signal pointing to greater differences in primate tooth shape at sites where potentially competing species overlap compared to sites where they do not overlap. Competition is a potential driver of these differences. The results presented here open promising lines of future research into understanding how competition shapes primate behavior and what evidence it leaves on hard tissues.

5. Assessing dietary behavior through dental shape in extinct primates

In the previous chapter, an analysis of both dental shape and dietary isotope in extant primate pairs was examined to test the central hypothesis that primates respond to competition over food resources by feeding on underutilized resources, resulting in character displacement. The results are suggestive that character displacement may be an explanation for greater differences in tooth shape at certain sympatric primate sites but not at others. Additionally, while dietary isotopes were helpful in exploring variation within each species, they only revealed significant differences between a few primate sites.

The results support that primate species alter their feeding behavior as a result of increased competition (Chapter 1), also show expected changes in DTA values that support the ability to potentially process more tough for fibrous foods.

While preferred foods (foods that are more frequently sought out and eaten) likely have the greatest effect on tooth morphology (Kay, 1975), it is unknown the extent to which secondary food mechanical properties have on tooth shape (Ungar *et al*., 2017). Within some species however, tooth shape does seem to correspond with secondary food mechanical properties. For example, Kinzey (1978) compared the teeth of two species of *Callicebus*: *C. moloch* and *C. torquatus*. While both are frugivores, *C. moloch* has longer shearing crests and is observed to fall back on leaves and insects during periods of fruit scarcity. Therefore, if a food is critical for survival, it might influence dental feature even if it is only eaten rarely (Kinzey, 1978). Ungar *et al*. (2017)examined the degree to which fallback foods potentially influence molar morphology using DTA in primarily frugivorous extant platyrrhines. The results of their study indicate that both primary and secondary food choices select for occlusal form. They conclude that the mechanical properties of foods consumed is reflected in tooth functional morphology rather than the frequency in which those foods are consumed (Ungar *et al.*, 2017).

Building off the idea that secondary food items may cause selection for subtle differences in occlusal morphology. The third paper in this project seeks to examine the dental morphology of Early and Middle Miocene eastern African non-cercopithecoid catarrhines. Using DTA, they are compared to a diverse set of extant frugivores. Because most studies over the last two decades have categorized Early Miocene eastern African non-cercopithecoid's as general frugivores, using a frugivore comparison may illuminate subtle differences in feeding strategies. This project predicts that Early and Middle Miocene eastern African non-cercopithecoids that were previously posited to have a folivorous component to their diet will have DTA values that align them with frugivores with a higher leaf intake as part of their fallback dietary strategy.

6. Early Miocene Eastern African Catarrhine Diet

6.1 INTRODUCTION

Early and Middle Miocene eastern African sites preserve a diversity of primate taxa. The catarrhine fossils display diverse body sizes and tooth morphologies while apparently inhabiting small spatial and temporal ranges (Harrison, 2010; Shearer *et al.,* 2015). The teeth of these fossil primates have been extensively described and dietary and paleobiological inferences from their shapes inferred (Kay, 1977; Harrison, 1982; Harrison, 1983; Kay and Unger, 1997; Unger *et al.,* 2004; Grossman, 2008; Deane, 2009; Harrison, 2010; Fleagle, 2013; Shearer *et al.,* 2015; Berthaume and Schroer, 2017; Locke, 2021). While the differences in tooth shape, form, and size are posited to represent different feeding strategies, such as those employed by extant primates in similarly dense communities, recent quantifications of tooth shape and surface texture indicate fewer dietary differences than expected, in some cases finding no difference between taxa (Kay, 1977; Kay and Ungar, 1997; Ungar *et al.,* 2004; Deane, 2009; Shearer *et al.,* 2015). In other words, while eastern African Miocene catarrhine teeth *look* very different, quantitative analyses of tooth shape do not predict similarly varying diets.

Methods of dietary reconstruction have advanced in recent years, but challenges remain. Problems that specifically contribute to a potential underestimation of fossil dietary diversity include a dearth of extant analogs, phylogenetic inertia and small, poorly distributed sample sizes.

Studying dental shape is paramount for reconstructing any extinct animal's diet (Evans, 2013). Dietary reconstruction provides insights into an animal's food preferences, which are specifically influenced by, or influence, metabolic behavior, movement patterns, competition, and habitat preference (Krause, 1986; Stroik, 2014). Establishing measures to illustrate how primate tooth morphology responds to different environments and feeding behaviors can aid in conservation efforts when applied to extant species (Eronen *et al.*, 2010). Within the realm of extinct primates, changes in dietary ecology can aid not only in understanding why such a diversity of primates decreased dramatically after the Miocene, but potentially can identify reasons for extinctions of later hominin ancestors (McGraw *et al.,* 2014).

It is well-established that there is a close relationship between tooth morphology and diet (e.g., Boyer, 2008; Bunn *et al.,* 2011). Because feeding is an integral part of an animal's survival, dental traits are under strong selective pressure to effectively process available foods (Ungar and Kay, 1995; Ungar, 1996; Ungar, 2002; Boyer, 2008; Bunn *et al.,* 2011; Evans, 2013; Venkataraman *et al.,* 2014). These selective pressures include the physical properties of food, which dictate the probability that mastication will fragment food particles into pieces that are more easily processed by the digestive system (Lucas, 2004; Berthaume, 2016). Cheek teeth (i.e., premolars and molars), especially, are used to prepare food for swallowing, so their shape is constrained by the properties of the food, the motions of the jaw during the chewing cycle, and the life span of the organism (Boyer, 2008). The functional demands placed on cheek teeth correspond to variations in their morphology and this correlation is especially strong in primate molar shape (Ungar and M'Kirera, 2003; Boyer *et al.,* 2010; Bunn *et al.,* 2011).

Paleoanthropologists use these dental changes to reconstruct the diet, paleo-environment, ethology, and ancestor-descendent relationships of hominoids over multiple time scales (Ungar and Kay, 1995; Ungar and Scott, 2009; Shearer *et al.,* 2015). These models are often based on extant primate tooth morphology, as teeth are specially adapted toward the fracture properties of the foods they consume (Winchester *et al.*, 2014; Berthaume, 2016). Teeth that process tough or fibrous resources containing high amounts of structural carbohydrates (i.e., leaves, bark, or buds) need well-developed molars to help enhance food breakdown prior to swallowing (Kay, 1977). Foods that have lower levels of structural carbohydrates (i.e., fruits) need less preparation prior to swallowing as they have higher levels of soluble carbohydrates and are therefore more easily digested (Kay, 1977).

The analysis of extant species with known diets allows for comparisons to be made and applied to extinct primates. Because tooth shape varies between primate species, these shapes can help parse out the occupation of distinct environmental niches to reduce food competition (Cuozzo *et al.,* 2012; Godfrey *et al.,* 2012; Ledogar *et al.,* 2013; Winchester *et al.,* 2014). However, our understanding of food mechanical properties and their relationship to dental shape is imperfect. While dental shape trends do persist in extant species with observable diets, a mismatch can occur in certain species where the tooth shape does not reflect observed behavior or dental microwear (the most famous example being the teeth of the Pleistocene fossil genus *Paranthropus*) (Sponheimer *et al.,* 2013). Thus, it is important to keep in mind that dietary mismatches occur when examining ecological partitioning and inferring dietary behaviors within the fossil record (Berthaume, 2016).

6.1.1 Early and Middle Miocene Eastern African Catarrhine Dental Traits

This project examines nine genera of Miocene catarrhines from fossil localities in present day Kenya. Primates included in this study span a timeline from 20-15.5 Ma. Traits pertinent to dietary behavior are presented below as well as summarized in Table 6.1.

Dendropithecus (20-17 mya) is represented by *D. macinnesi* and was originally described by Le Gros Clark and Leakey (1950) as a distinct species of *Limnopithecus*. *Dendropithecus* was created (Andrews and Simons, 1977) to account for structural differences in the post-crania that distinguished the fossils from members of *Limnopithecus.* The holotype BMNH 16650 is a nearly complete mandible from Rusinga Island, Kenya, which is where the majority of *Dendropithecus* specimens have been found (Le Gros Clark and Leakey, 1950). Subsequent discoveries also suggest it was at Songhor, Karungu, and Koru (Harrison, 2010). *Dendropithecus* is similar in tooth and limb size to hylobatids with an estimated body size of 5-9kg (Andrews and Simons, 1977; Shearer *et al.,* 2015). Specimens attributed to *Dendropithecus* show a high degree of sexual dimorphism (Fleagle and Kay, 1985). Lower molars are quite broad and exhibit widely spaced, conical cusps. *D. macinnesi* molars have numerous well-developed crests connecting molar cusps (Harrison, 2010; Fleagle, 2013). Due to *D. macinnesi* molar shape and topography, some researchers have placed it into a folivore/frugivore niche (e.g., Harrison, 1993; Fleagle, 2013), while others (Shearer *et al.,* 2015) have assigned it to a more generalized frugivore dietary strategy.

Equatorius africanus (24-16 Ma) is a large-bodied taxon found primarily on

Maboko Island and in the Tugen Hills (Ward and Duren, 2002). These specimens were previously attributed to *Kenyapithecus africanus* which united *K. africanus* and *K. wickeri* as cogeneric taxa (Ward et al 1999). Upon the discovery of fossil material in the Tugen Hills in the 1990s, the Tugen Hills specimens appeared more similar to the Maboko Island fossils but less similar to the specimens included in *K. wickeri* (Ward and Duren 2002). These differences led Ward et al (1999) to erect *Equatorius africanus* to include the thickly enameled hominoids from the Tugen Hills and Maboko Island. Fossil localities date from 15.5-14 Ma (Ward and Duren, 2002). Body size estimates place it between 20 and 40 kg, around the size of extant *Papio* or *Mandrillus* (Harrison, 2010). Dentally, *Equatorius* displays cheek teeth with reduced lingual cingula, thick molar enamel and low relief cusps (Kelley *et al.,* 2002).

Kalepithecus songhorensis (20-19 Ma) is a small-bodied catarrhine found at Early Miocene sites (Harrison, 1988). Once it was referred to *Micropithecus* on the basis of due to similarity in incisor and molar shape (Harrison, 1982), but it was later posited that these similarities were a result of convergence and the fossil material was placed into its own genus: *Kalepithecus* (Harrison 1988). The molars of *K. songhorensis* are broad with a well-developed lingual cingulum, low rounded cusps and poorly developed crests (Harrison, 2010). Deane (2009) examined the incisor curvature of *Kalepithecus* and concluded that it was a seasonal frugivore.

Limnopithecus (20-19 Ma) represents a genus of small-bodied catarrhines likely restricted to the Early Miocene (Harrison, 2010). Fossils appear at the Kenyan Tinderet (MacInnes 1943; Harrison, 1988) and Kisingiri (Le Gros Clarke and Leakey, 1950) sites as well as Napak, Uganda (Walker, 1968; Fleagle and Simons, 1978). Harrison (2010) describes the genus *Limnopithecu*s as having upper molars with high conical cusps and well-developed lingual cingula. The lower molars are rectangular with high sharp cuspids, mesial and distal foveae are broad, the talonid basin is deep and the buccal cingulum weakly developed (Harrison, 2010). These traits appear to be similar to frugivores (Harrison, 1981; Harrison, 1988; Cote *et al.,* 2016). Kay and Ungar (1997), however, found that shearing crest length suggested a folivorous niche.

Limnopithecus legetet (20-19 Ma) was first described from a mandible found at Koru (Hopwood, 1933). Early descriptions emphasized their similarities with *Pliopithecus* and gibbons (see Cote *et al.,* 2016). Some *Limnopithecus* fossil material has been attributed to *Lomorupithecus* (Pickford, 2010) but this is not substantiated by more recent analysis (Cote *et al*., 2016). *L. legetet* is defined by broad, rectangular lower molars with high sharp cusps and occlusal crests (Harrison, 2010). A decade later researchers erected *Limnopithecus evansi* (20-19 Ma) to describe distinct material from excavations at Songhor (MacInnes, 1943). *L. evansi* was differentiated from *L. legetet* based on slightly longer yet narrower molars with differently arranged cusps (Cote *et al.,* 2016). Specimens attributed to *L. evansi* have lower, more rounded lower molar cusps, small distal fovea (Harrison, 1988). Further collecting has revealed that specimens assigned to *L. evansi* are restricted to Songhor and the Mteitei Valley and *L. legetet* at Koru, Legetet, Chamtwara, Rusinga, and Williams Flat (Cote *et al.,* 2016).

Harrison (1988) suggested that the differences in dentition and locality of *Limnopithecus* taxa were the result of adaptation to different ecological conditions. The faunal and geologic evidence from both Tinderet and Kisingiri localities, however, suggest similar tropical rainforests (Harrison, 1988). Evidence from gastropods found at the different sites however, might indicate somewhat drier conditions at Songhor, due to rain shadowing effects (Pickford, 1983; Harrison, 1989). This slight change in environment may have led to subtle dietary differences between these congeneric species (Harrison, 1988).

Micropithecus clarki (20-19 Ma) is the smallest Early Miocene eastern African primate (3-4kg) and has been found at Koru and Napak (Fleagle, 2013). Fossil material from Middle Miocene localities on Maboko Island, Kenya have led some researchers to propose a second species, *M. leakeyorum* (16-15 Ma) (Harrison, 1989). Benefit (1991) however proposed that the Maboko Island material was more similar to *Simiolus*. Because this remains unresolved, this paper categorizes the Maboko Island specimens as *M. leakeyorum*.

Harrison (2010) characterized the genus *Micropithecus* by distinctive dental proportions compared to other Early Miocene taxa: large incisors and small cheek teeth. The molars are ovoid with low round crests and the upper molars display reduced cingula. Both Harrison (2010) and Shearer *et al.,* (2015) note that the broad and bunodont molars, which are smaller than anterior dentition, point to reconstruction of the genus as a frugivore. Harrison (1989) points out that larger M3 and sharper cusps and crest seen in the dentition of *M. leakeyorum* compared to material attributed to *M. clarki* represents a shift to rely on more fibrous material during the Middle Miocene (Harrison, 1989).

Nyanzapithecus (17.5-15 Ma) fossil material is attributed to three different species: *N. vancourveringi* from Rusinga; *N. harrisoni* from the Samburu Hills; and *N. pickfordi* from the Middle Miocene on Maboko Island (Harrison, 2010), this project however only examines *N. vancourveringi* and *N. pickfordi*. The genus is characterized by lower molars that are very long and narrow with rounded cusps and poorly developed buccal cingulum (Harrison, 2010). While sharing similarities with *R. gordoni* tooth morphology it is also considered to be a more folivorous primate (Fleagle, 2013).

Proconsul represents a genus of medium- and large-bodied catarrhine species: *Proconsul africanus, Proconsul meswae,* and *Proconsul major*. Species are differentiated based on estimated body size as well as dental details (Harrison, 2010). McNulty *et al.* (2015) describe *Proconsul* molars as having wide rhomboid-shaped molars with extensive cingulum development, conical cusps, and sharp occlusal crests. *Proconsul major* has shorter shearing-crest lengths than any extant primate, potentially indicating a frugivorous dietary strategy (Kay and Ungar, 1997). Additionally, microwear studies found low rates of scratches and a higher proportion of pits, indicating soft fruit eating behavior (Ungar, 1998). *Proconsul* mandibular shape seems consistent with a soft fruit dietary strategy as its morphology suggests high vertical chewing forces and limited torsional forces (Bilsborough and Rae, 2014).

Proconsul africanus (20-19 Ma) is found in the Tinderet region of Kenya (Harrison, 2010). Fossil material attributed to *P. africanus* has been categorized as a frugivore due to its intermediate incidence of microwear pitting, consistent with extant soft fruit eating primates (Ungar *et al.,* 2004). Harrison (1993) noted it having some traits associated with folivory but does not give a method underlying his conclusions besides craniodental comparisons.

Fossil material assigned to *Proconsul major* (20-19 Ma) comes from the Kenyan sites of Songhor, Koru, Legetet, Chamtwara (Le Gros Clark & Leakey, 1950; Martin, 1981) and the Ugandan sites of Napak and Moroto (Senut *et al.,* 2000). Body size estimates based on post-cranial remains indicate that *P. major* had a body weight of 60-90kg (Harrison, 2010). The dental remains of *P. major* are around 20% larger than other *Proconsul* or *Ekembo* species (see Harrison, 2010). *P. major* is largely considered to have been a frugivore based on its poorly developed shearing crests (Kay, 1977; Kay and Ungar, 1997) and microwear pit frequencies comparable with modern soft fruit eaters (Ungar *et al.,* 2004). Harrison (1993) noted traits to the dentition of *P. major* that indicated folivory though this is based on broad comparisons of cranial dental anatomy and no specific traits were listed.

Recently, McNulty *et al.* (2015) reassigned *Proconsul heseloni* and *Proconsul nyanzae* to the genus *Ekembo* due to extensive dental differences. They describe *Ekembo* species (20-18 Ma) as showing more bunodont molar cusps which occupy more occlusal surface area than cusps in molars attributed to *Proconsul*. Additionally, they note that *Ekembo* displays molar crests that are inflated and meld into cusps and molar cingula that are reduced compared to *Proconsul* (McNulty *et al.,* 2015). Both species of *Ekembo* have dental traits consistent with frugivory based on shearing crest length (Kay, 1977; Kay and Ungar, 1997) as well as based on dental pitting levels consistent with soft fruit eating (Ungar, 1994; Grossman, 2008; Shearer *et al.,* 2015).

Rangwapithecus (20-19 mya) is a medium- to large-bodied catarrhine and fossils are attributed to one species, *Rangwapithecus gordoni* (Harrison, 2010). Its body size is estimated to be similar to that of *Proconsul africanus* and *Ekembo hesloni* (Hill *et al.,* 2013). The molars of *R. gordoni* have low cusps but large shearing crests with secondary enamel wrinkling. Lower molars increase in size anteriorly to posteriorly and have a well-developed buccal cingulum (Harrison, 2010). The large shearing crests suggest a diet that had a folivorous component (Kay and Ungar, 1997; Hill *et al.,* 2013). Microwear studies seem to corroborate this dietary strategy though the folivory of *Rangwapithecus* is deemed to be less extensive than modern taxa (*i.e. Alouatta*, *Gorilla*, *Trachypithecus*) (Ungar *et al.,* 2004; Shearer *et al.,* 2015).

Simiolus (17.5-13.7 mya) is another smaller-bodied Early Miocene primate (Harrison, 2010). It is comprised of *S. enjiesi* (17.5-16.8 Ma) from Kalodirr, Locherangan, and Moruorot, Kenya (Leakey & Leakey, 1987; Anyonge *et al.,* 1991; Rose *et al.,* 1992) and *S. andrewsi* (13.7 Ma) from Fort Ternan, Kenya (Harrison, 2010). The teeth of *Similous* are mosaics of characteristics found in other genera, and most closely resembles a mixture of features from *Dendropithecus* and *Rangwapithecus* (Harrison, 2010). The molars are long and have high sharp crests (Harrison, 2010; Fleagle, 2013). Based on microwear analysis it has been reconstructed as a frugivore (Grossman, 2008).

Despite the diversity of body sizes and tooth shapes, many dietary studies conclude that these diverse primates, at least from African sites, were fruit generalists (Kay, 1977; Kay and Ungar, 1995; Grossman 2008; Shearer *et al.,* 2015; Locke, 2021). Because many of these primates probably existed within the same geographic and temporal space, frugivory would present issues of feeding competition especially during times of fruit scarcity.

Table 6.1: Early and Middle Miocene eastern African catarrhine body mass, age range and locality information

Species	Body mass	Age Range	Locality
Dendropithecidae			
Dendropithecus macinnesi	6-8 kg[1]	20-17 Ma[2,3]	Rusinga Island, Kenya[10]; Karungu, Kenya[11]; Mfangano Island, Kenya[11]; Songhor, Kenya[12]; Koru, Kenya[12]
Simiolus enjessi	4-6 kg[1]	17.5-16.8 Ma[4]	Kalodirr, Kenya[12]; Locherangan, Kenya[13]; Moruorot, Kenya[14]
Simiolus andrewsi	4-6 kg[1]	13.7 Ma[5]	Fort Ternan, Kenya[1]
Micropithecus clarki	2.9-4.3 kg[1]	20-19 Ma[3]	Koru, Kenya[11]; Napak, Uganda[15]
Micropithecus leakeyorum	2.9-4.3 kg[1]	16-15 Ma[6]	Maboko Island, Kenya[16]
Proconsulidae			
Proconsul major	60-90 kg[1]	20-19 Ma[3]	Songhor, Kenya[9]; Koru, Kenya[17] Mteitei Valley, Kenya[17]; Napak, Uganda[30]
Proconsul africanus	10-20 kg[1]	20-19 Ma[3]	Songhor Kenya[32]; Koru, Kenya[19]; Napak, Uganda[31]
Ekembo heseloni	10-20 kg[1]	20-18.5 Ma[2]	Rusinga Island, Kenya[20]; Mfangano Island, Kenya[21]
Ekembo nyanzae	28-40 kg[1]	20-18 Ma[2]	Rusinga Island, Kenya[20]; Mfangano Island, Kenya[21]
Nyanzapithecinae			
Nyanzapithecus pickfordi	8-11 kg[1]	16–15 Ma[6,7]	Maboko Island, Kenya[22]
Nyanzapithecus vancouveringorum	8-11 kg[1]	17.5–17 Ma[2]	Rusinga Island, Kenya[23]; Mfangano Island, Kenya[23]
Rangwapithecus gordoni	10-12 kg[1]	20-19 Ma[3]	Songhor, Kenya[23] ; Koru, Kenya[24]; Lower Kapurtay, Kenya[24]
Incertae sedis			
Limnopithecus evansi	5 kg[1]	20-19 Ma[3]	Songhor, Kenya[25]; Mteitei Valley, Kenya[11]
Limnopithecus legetet	5kg[1]	20-19 Ma[3]	Koru, Kenya[19]; Williams Flat, Kenya[11]; Rusinga Island, Kenya[9]; Napak, Uganda[15]; Bukwa, Uganda[26]
Kalepithecus songhorensis	5kg[1]	20-19 Ma7	Songhor, Kenya[11]; Koru, Kenya[27]; Mteitei Valley, Kenya[27]

Equatorius africanus	20-40kg[1]	16-14 Ma[6]	Maboko Island, Kenya[28]; Kipsaramon, Kenya[29]

Citations

1. Harrison, 2010
2. Peppe *et al.,* 2011
3. Bishop *et al.,* 1969
4. Boschetto *et al.,* 1992
5. Pickford *et al*., 2006
6. Feibel & Brown, 1991
7. Pickford & Andrews, 1981
8. Behrensmeyer *et al.,* 2002
9. Le Gros Clark & Leakey, 1950
10. Andrews, 1978
11. Harrison, 1988
12. Leakey & Leakey, 1987
13. Anyonge *et al.,* 1991
14. Rose *et al.,* 1992
15. Fleagle & Simons, 1978
16. Harrison, 1989
17. Martin, 1981
18. Senut *et al.,* 2000
19. Hopwood 1933
20. Pickford *et al.,* 2009
21. Ruff *et al.,* 1989
22. Harrison, 1986
23. Andrews 1974
24. Cote *et al.,* 2014
25. MacInnes, 1943
26. Walker 1968
27. Harrison, 1962
28. Benefit, 2003
29. Ward *et al.,*1999
30. MacLatchy & Rossie, 2005
31. Pickford *et al*., 2021
32. McNulty *et al.,* 2015

6.1.2 Dietary Quantification in Early Miocene Eastern African Catarrhines

Early dietary estimates of Early and Middle Miocene of eastern African non-cercopithecoid catarrhines were based on qualitative descriptions of dental shape (Kay, 1977). One of the first to attempt to quantify and correlate tooth shape to diet category was Richard Kay (1977) with the development of the shearing quotient. Shearing quotient (SQ) is the "calculated residual from a regression of the summed length of mesiodistal crests over the length of the occlusal table" (Kay and Ungar, 2004). Shearing quotient, however, is sensitive to differences in molar size so shearing ratio (SR) which is similarly calculated is used to compare more distantly related taxa (Strait, 1993; Boyer *et al.,* 2015; Locke, 2021). Shearing ratio is used when body size (via reported body mass in extant taxa or approximations of body mass via tooth size and tooth length) is accounted for in the equations (Strait, 1993; Boyer *et al.,* 2015). The application of SQ has been successfully used to parse out folivores and insectivores from frugivores (Bunn *et al.,* 2011). Because folivores have a higher level of structural carbohydrates in the leaves, bark, and stems chewed, sharper crests are needed to break down the food prior to swallowing. Frugivores, on the other hand, have a diet with fewer structural carbohydrates and higher in soluble carbohydrates, which require less processing (Kay, 1977). Higher SQs and SRs are correlated with longer shearing crests and are generally associated with folivorous and insectivorous primates (Kay, 1977; Strait, 1993). Frugivorous primates have lower, flatter crests and correspondingly lower, negative SQ and SR values (Kay, 1977; Strait, 1993). Within the frugivorous primates, hard object feeders can be differentiated by even lower SQ and SRs. These patterns seem to hold across all major primate groups (Bunn *et al.,* 2011). These two methods provided important context when inferring diet in fossil primates due to the well-established relationship between crest length and diet category.

In Kay's first study (1977), he applied SQ to Miocene hominoids from Rusinga Island and Songhor. He compared them to a range of folivorous and frugivorous hominoids and platyrrhines. His results grouped all fossil specimens with frugivorous hylobatids on the PCA excepting *D. macinnesi*, which was closer to gorilla. Kay's (1977) analysis concluded that Miocene hominoids were primarily frugivorous, and more similar to each other in diet than apes of today are.

Kay and Ungar (1997) expanded this dataset to include comparisons of European Miocene hominoids as well as additional specimens from Songhor, Koru, and Mfangano, Kenya. The results again showed that Early Miocene eastern African catarrhines had lower SR values, more in line with frugivores (Kay and Ungar, 1997). They found that

SR values were exceedingly low when compared to any primate from their extant sample. But, while the samples had low SR values, those values spanned the same absolute ranges as those of extant hominoids. Based on this, Kay and Ungar (1997) posited that the range of dietary behaviors was similar to that found in extant taxa, but with less shearing crest development and were thus less well adapted for cutting up food. For example, they found that *Rangwapithecus* had the highest value at 0.27 and argued that this could still represent a primate with a folivorous component to its diet, yet without the specialized molars seen in extant folivores. They hypothesized that this “downshift” in values might be due to a Red Queen effect, as these catarrhines did not have to compete with cercopithecoids, so were able to have more generalized molar forms (Kay and Ungar, 1997).

While these measures advanced efforts to quantify differences in diet, ultimately SQ and SR are limited to unworn teeth as they rely on anatomical landmarks to obtain crest measurements (Ungar and Williamson, 2000, Bunn *et al.,* 2011). While teeth are adapted to wear in ways which maintain functionality, even minimal tooth wear can obscure anatomical landmarks like crests leading to difficulties in captureing a dietary signal (Bunn *et al.,* 2008). Because there are so few unworn teeth in the fossil record, it is difficult to get a sample size that allows statistical testing (Ungar and M’Kirera 2003).

While the relationship between overall tooth morphology and diet is strong across clades, dental shape has the potential to reflect lineage-scale adaptations rather than current feeding patterns. To expand the time scale of dietary analysis to include the most recent foods eaten, microwear analysis is often employed (Scott *et al.,* 2006) Microwear is important for establishing interactions with food during an animal's life; it can anchor morphological traits to the diet that was eaten by an animal within the last few weeks of life (Davis and Pineda Munoz, 2016). Notwithstanding differential diet preferences in the weeks leading to death, there are sufficient microwear studies on taxa ranging from bovids to rodents to primates that give fairly accurate representations of foods consumed habitually during life (Shearer *et al.,* 2015). While more research is needed into how long certain food type signals last on teeth, if depositional environment plays a factor in obliterating microwear, or if certain aspects of the environment (e.g., canopy height, volcanic ash) mask actual dietary signals, microwear can provide potentially misleading information on temporal and spatial differences in diet (Ungar *et al.,* 2012).

Microwear has been used for over 50 years, originally using high-resolution photographs. Scanning Electron Microscope (SEM) techniques were employed to gain better depth-of-field as shadows would sometimes obscure scratches (Scott *et al.,* 2006; Evans, 2013; Arman *et al.,* 2016). With this technique, researchers would count and measure pits and scratches on a high-resolution image of a section of the tooth surface (Scott *et al.,* 2006). Ungar *et al.,* (2004) used the SEM approach and compared microwear patterns to the Miocene catarrhine SQ ratios established in Kay and Ungar (1997). While sample sizes limited statistical comparisons, most Miocene taxa examined showed pit percentages close to soft frugivores. They found *Micropithecus* and *Rangwapithecus*, however, had more incidences of scratching, again suggesting a folivorous component to the diet. This study corroborated dental shape reflecting actual diet within the Early Miocene eastern African catarrhines (Ungar *et al.,* 2004)

While SEM approaches to quantifying microwear texture provided better resolution, studies remained few and sample sizes remained small due to the time-consuming nature of counting pits and scratches (Ungar *et al.,* 2003). While semi-automated techniques were introduced to speed up the process and reduce inter-observer variability, these techniques were still plagued with issues of subjectivity and the methodology continued to produce limited studies (Scott *et al.,* 2006). To reduce costs associated with SEM scanning, low magnification light microscopy has been advocated. Arman *et al.* (2016) found this method, however, poses problems as few research groups have been unable to replicate each other's studies using this technique as differences between newer and older confocal profilers have called the comparability between studies into question. Additionally, differentiating between antemortem wear and postmortem wear is difficult with this technique (Scott *et al.,* 2006; Scott *et al.,* 2012; Ramdarshan *et al.,* 2011).

Three-dimensional profilometry using automated software began to be employed in 2004 (e.g., Ungar 2004). This approach used software to generate a three-dimensional point-cloud of wear facet 9 on the M_2 and created a three-dimensional depth profile. From this point-cloud, surface complexity, anisotropy, heterogeneity, and textural fill volume are measured. When applied to a large sample of extant primates representing nearly every primate clade, three dimensional profilometry found agreement with observed dietary behaviors in the extant primate sample (Scott *et al.,* 2006).

Scott *et al.,* (2012) found that in extant groups, hard object feeders show higher frequencies of microscopic pitting, larger pits, and more complex texture. They confirmed that more folivorous or tough diets are associated with striations and anisotropic microwear texture. The ultimate cause of these patterns are small abrasives in or on food such as phytoliths or grit, which causes differences in patterns from the food's mechanical properties and methods of occlusion (Scott *et al.,* 2012).

Shearer *et al.,* (2015) expanded Ungar *et al.*'s (2004) study using 3D profilometry. The results of that study were surprising in that, while there were apparent differences between taxa, none were significant, suggesting that all taxa sampled consumed foods of similar mechanical properties, most likely soft fruit. This is not to say they were eating the same fruit species, however, and confounding factors such as high grit level, low sample sizes, and incorrect species attribution may be masking differences in dietary signals (Shearer *et al.,* 2015). The studies by Ungar *et al.,* (2004) and Shearer *et al.,* (2015) provided an anchor for morphological examinations of fossil catarrhine teeth. Previous studies examining Early and Middle Miocene eastern African catarrhine diet are summarized in Table 6.2.

6.1.3 Dental Topographic Analysis

Many of these early methods relied on landmarks of the tooth surface. Since dietary wear can obliterate landmarks, to facilitate larger sample sizes and the inclusion of worn teeth, a suite of quantification methods termed Dental Topographic Analysis (DTA) was developed (Zuccotti *et al.* 1998). Dental Topographic Analysis represents a method for finding subtle dietary differences by quantifying the tooth surface. DTA takes into account the entirety of the molar occlusal surface and quantifies differences in tooth shape across specimens (Evans, 2013). Changes and/or differences in molar shape affect molar occlusion and therefore how effectively food items are processed by the organism's teeth (Berthaume *et al.,* 2020).

DTA has been applied across a wide array of research questions (Winchester *et al.,* 2014; Pampush *et al.,* 2016; Berthaume and Schroer, 2017), but typically analyses follow a similar protocol: digitization of a tooth surface, digital processing, and, finally, shape quantification (Berthaume *et al.,* 2020). The variables computed most often in DTA studies are Direchlet Normal Energy (DNE), Relief Index (RFI), and Orientation Patch Count Rotated (OPCR), and these have been shown to reliably identify dietary category membership as well as correlate to mechanical properties of food items across primates and other mammals (Evans *et al*., 2007; Boyer, 2008; Bunn *et al.,* 2011; Evans, 2013; Winchester *et al.,* 2014).

Dirichlet Normal Energy (DNE) is a quantification of occlusal curvature. The higher the curvature of the occlusal surface, the higher the DNE value (Bunn *et al*., 2011). With respect to diet, teeth with higher DNE scores are more specialized for shearing compared to teeth that have lower DNE values. Normally insectivores are shown to have the highest DNE values followed by folivores. Omnivores and frugivores have the lowest DNE values (Berthaume *et al.,* 2020). It is important to note that curvature values can be artificially inflated by enamel topography such as crenulations, deep enamel folding, or robust cingula. Therefore, taxa whose teeth are characterized by these features may have DNE values similar to folivores despite not following a folivorous dietary strategy (Allen *et al.,* 2015).

Relief Index (RFI) is a quantification of the 3D occlusal surface's cusp height compared to the ratio of the 3D areas footprint (Berthaume *et al*., 2019). Teeth with taller crowns and longer crests have higher RFI values. Folivores and insectivores are expected to have high RFI values while frugivores have lower values (Boyer, 2008).

Orientation Patch Count Rotated (OPCR) is used to quantify the complexity of the tooth surface (Evans, 2007). The surface of the tooth is divided into many distinct patches, each of which is assigned a cardinal direction. The tooth is rotated a set number of times, and the final OPCR value is calculated from the mean if the total number of differently facing patches. More complex teeth have a greater number of surface features or "tools" (e.g., crenulations, beaded cingula, cusps with multiple faces) available for food processing. High OPCR is associated with more cusps or more crenulations on the tooth surface. Animals that process leaves tend to have higher OPCR values (Wilson *et al.,* 2012).

The first study to examine Early Miocene eastern African non-cercopithecoid catarrhines using DTA was Locke (2021), who examined worn and unworn M_2s using DNE, OPCR, and Occlusal Relief (a form of RFI). The results of his DTA analysis were consistent with previous studies using measures of cusp relief and microwear: generalize frugivore behavior across taxa.

Table 6.2: Summary of previous dietary reconstruction studies.

	Kay, 1977	Harrison, 1982	Harrison, 1993	Kay & Ungar, 1997	Ungar *et al.*, 2004	Grossman 2008	Shearer *et al.*, 2015	Locke, 2021
Dendropithecidae								
D. macinnesi	Frug	Fol	Fol (Frug)	Frug	Frug	Frug	Gen	Fru
S. enjessi	N/A	N/A	Frug/Fol	N/A	N/A	Frug/Fol	N/A	N/A
S. andrewsi	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
M. clarki	N/A	Frug	Frug	N/A	Fol/Frug	N/A	Frug	N/A
M. leakeyorum	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Proconsulidae								
P. major	Frug	Frug	Fol/Frug	Frug	Frug	Frug	Frug	Frug
P. africanus	N/A	Frug	Fol/Frug	N/A	Frug	Frug	Frug	NA
E. heseloni	Frug	N/A	N/A	Frug	N/A	Frug	Frug	Frug
E. nyanzae	Frug	Frug	Fol/Frug	Frug	Frug	Frug	Frug	Frug
Nyanzapithecinae								
N. pickfordi	N/A	N/A	N/A	N/A	N/A	Fol/Frug	N/A	N/A
N. vancouveringorum	N/A	N/A	Fol	N/A	N/A	N/A	N/A	N/A
R. gordoni	Frug/Fol	Fol	Fol	Fol	Fol	Frug	Gen	Frug/Fol
Incertae sedis								
L. evansi	N/A	N/A	Frug (Fol)	Frug/Fol	N/A	Frug	Gen	Frug/Fol
L. legetet	Frug	Frug	Frug/Fol	Frug/Fol	N/A	Frug	Gen	Frug/Fol
K. songhorensis	N/A	N/A	Frug	N/A	N/A	N/A	N/A	N/A

Citations:

Kay, 1977	Shearing quotient
Harrison, 1982	Ratio of Incisor size to molar size
Harrison, 1993	Method not stated
Kay and Ungar, 1997	Shearing quotient
Ungar *et al.,* 2004	Microwear with SEM
Grossman 2008	Microwear with low-magnification stereomicroscopy
Shearer *et al.,* 2015	Microwear using Scale-sensitive fractal analysis
Locke, 2021	Dental Topographic Analysis

While the research on Early Miocene eastern African non-cercopithecoid catarrhines has been thorough and well executed, questions remain to be answered as to how all of these primates were able to exist, presumably in sympatry in some cases, as soft fruit generalists. A large frugivorous biomass may have presented challenges in terms of competition, especially during times of fruit scarcity due to seasonality or pressure from other frugivorous creatures. What is needed now is an examination of differences in the tools used to process fruits. Soft object frugivory still indicates many dietary possibilities and to narrow down diet types, different criteria may need to be employed. As explored in Chapter 2 and Chapter 4, extant frugivorous primates employ multiple strategies to mitigate feeding competition (i.e., resource switching; dietary supplementation; narrowing dietary breadth), therefore, Miocene catarrhines might be presumed to follow similar feeding strategies. Subtle changes in dietary behavior through the supplementation of resources with different fracture properties may have led to adaptation in the features of the molar occlusal surface.

6.2 STUDY DESIGN

6.2.1 Aims

In this paper, I expand on the study of Locke (2021), using the following DTA measures to categorize and quantify Early Miocene eastern African non-cercopithecoid dentition: DNE, RFI, and OPCR. This study investigates if secondary dietary behaviors can be identified in the molar shape of eastern African Miocene catarrhines While most studies categorize almost all Early Miocene eastern African catarrhines as soft fruit generalists, researchers have identified some evidence which points to alternate feeding strategies (e.g.folivory in *D. macinnesi* (Harrison, 1993), *R. gordoni* (Harrison, 1982, 1993; Kay and Ungar, 1997; Ungar *et al.,* 2004); Folivory/frugivory in *P. major* (Harrison, 1993) and *M. clarki* (Ungar *et al.,* 2004). As demonstrated in the previous chapters, extant primate frugivores will often supplement fruit resources with a mix of leaves, animal prey, and seeds when fruit is scarce, or competition is high. Furthermore, these alternate dietary behaviors are reflected in dental shape. Therefore, this paper compares Miocene catarrhines to a diverse array of primate frugivores using DTA to reveal alternate dietary strategies in Miocene catarrhines.

6.2.2 Predictions

This paper compares Early and Middle Miocene eastern African non-cercopithecoid molar topography to a diverse set of extant frugivores. Because most studies over the last two decades have categorized Early Miocene eastern African non-cercopithecoid's as general frugivores, using a frugivore comparison may illuminate subtle differences in feeding strategies. This project predicts that Early and Middle Miocene eastern African non-cercopithecoids that were previously posited to have a folivorous component to their diet will have DTA values that align them with frugivores with a higher leaf intake. Such a result might indicate the importance of leaf consumption as part of a fallback dietary strategy.

6.3 METHODS AND MATERIALS

6.3.1 Primate Sample

The fossil catarrhine sample came from the National Museum of Kenya, Nairobi, Kenya. It consists of upper and lower molars from each molar position (n=192). The following species were sampled: *Dendropithecus macinnesi*, *Ekembo heseloni*, aff. *Ekembo*, *Kenyapithecus africanus*, *Limnopithecus legetet*, *Limnopithecus evansi*, *Kalepithecus songhorensis, Micropithecus leakeyorum, Micropithecus clarki*, *Nyanzapithecus pickfordi*, *Nyanzapithecus vancouveringorum*, *Proconsul africanus*, *Proconsul major*, *Rangwapithecus gordoni*, *Simiolus enjiessi*. Taxonomic identifications follow Harrison 2010, except for *Ekembo* specimens. This genus was originally sampled to include members of both species (*E.heseloni*, *E. nyanzae*) but new specimen allocations by McNulty *et al.,* (in revision) suggest that none of the current sample can be reliably placed in *E. nyanzae*. The extant comparative sample (n=1,005) consists of *Cercopithecus ascanius*, *C. mitis, Ateles belzebuth, Lagothrix lagotricha, Alouatta spp., Hylobates lar, H. agilis,* and *Symphalangus syndactylus.* For a complete list of extant and fossil specimens used see APPENDIX C.

6.3.2 Dental Impressions

Dental impressions were taken from 197 Miocene catarrhine teeth. Dental impressions were taken using Coltene President Jet Medium body polyvinylsiloxane dental molding material (Ungar and M'Kirera, 2003). This approach obviates the need to remove specimens from their institutions and has been shown to capture shape and texture data at resolutions better than 1 micron (Ungar and Williamson, 2000). All specimens were checked for dirt, dust, and debris prior to each impression. If debris was extreme, the specimen was not used. Specimens were wiped with diluted rubbing alcohol if there was dirt or dust present.

The dental impression molding technique used in this project follows protocols used in the University of Minnesota Dental School (VanHeel and Cererra personal communication). Impression material was applied by first flooding the occlusal basin of the most posterior tooth and moving forward to the premolars in one continuous application in order to prevent air bubbles. Impression material was then applied to the cusps and remaining crown of the tooth with special care taken to capture the interstitial spaces between teeth. A precision tip was attached to the extrusion tube to ensure that the spaces in between teeth were adequately captured by the dental impression. A final application of material was applied to the crowns again, allowing the original material to be gently pushed into crevices and crenulations on the occlusal surface.

While Coltene Whaledent guarantees impression material set times of two minutes, this project found that slightly longer set times were sometimes needed. Molds were allowed to cure for around 5-10 minutes (temperature and humidity dependent) before gentle manual removal. All molds were placed in small plastic bags with the specimen accession number and species according to its catalog card. Molds were checked for large air bubbles, holes, and thin spaces in the impression material. Impressions were redone if large defects were present on the occlusal surface.

Only specimens with very little wear (wear stage 1, or dentin pits less than 1 mm (Buikstra and Ubeleker, 1994; Wetselaar, 2020) were used. Wear stage was established through visual inspection by TSC and a research assistant. Molars also had to have no chipping or cracks to ensure that the molding process would not further damage the specimen. When possible, impressions were taken from right and left sides, as well as upper and lower first through third molars. Impressions from the right side were preferred when all teeth were present and in good condition. If the left teeth provided better dental topography, these impressions were used instead. This resulted in a mixed left and right sample, and therefore left teeth were mirrored in GeoMagic. No individual was exclusively represented by either left and right sides in any analysis so as to avoid including non-independent data points. While mixing sexes and sides may introduce some measure of error into the analyses, there is a dearth of investigation into potential effects of such methods (Berthaume and Schroer, 2017).

6.3.3 XRCT scanning

Molds were scanned with an a X5000 high resolution micro-CT system with a twin head 225 kV x-ray source and a Dexela area detector (3073 x 3889 pixels). All molds were placed in individually labeled bags and taped to a scanning mount. Care was taken to not tape the bags together too tightly for risk of deforming the tooth molds. XRCT scanning was done in batches of 20-45 mold bundles. All bundles were scanned at a resolution between 37-38 micrometers. Scan slices were exported as a .tiff stack.

6.3.4 Avizo methods

First, *.tiff* stacks were imported into Avizo (Version 2020.1) as completely read volumes, and voxel size was set to the scanning resolution. The Filter Sandbox Tool was applied to each volume with the Guassian Filter. Next, the Interactive Thresholding tool was used to separate air from the molds. Thresholding was set to the autogenerated histogram with slight modification if the preview indicated it was necessary. Then, the Generate Surface tool was employed with unconstrained smoothing turned off. Finally, a surface file was saved as an ASCII .stl file.

6.3.5 Geomagic Methods

Tooth bundles were imported into Geomagic Design X. Individual molds were identified, named, cut, and exported as separate files. Each mold was then cut using the Polygonal Selection tool to highlight the outside of the mold with "Visible Only" selected. The polyfaces of the outer portion of each mold were selected and then deleted, leaving only the dental impression. Polyfaces were then flipped using the Fix Normal tool, to make sure the side that was pressed against the teeth was facing outward for later analysis.

Individual teeth were copied from the tooth row and pasted as individual meshes. Despite best efforts to capture interstitial spaces, some teeth had holes on either side where the mesial and distal edges met. In this case, as long as the gap was not too large, the Fill Holes tool was used with the Bridge feature set to "interpolate curvature". The interpolation of these interstitial spaces was primarily done for aesthetic purposes given that cropping protocols (see below) ensured that these fabricated areas were not used in analysis.

Whole teeth were first edited to include only the tooth crown by using a visual estimation of the cervix of the tooth based on where the crown dipped to the root. Next, the Fill Holes, Liquify tool was used on the cropped edge to ensure there were no dangling polyfaces or floating polyfaces outside the tooth. Finally, the Healing Wizard was used to clean up any extra or missed polyfaces. These whole teeth were exported as .ply files.

Cropping each tooth to a comparable height was done following protocols in (Prufrock *et al.,* 2016) and (Berthaume *et al.,* 2019), where the lowest point on the occlusal basin was used to mark where teeth should be cropped. Prior to cropping, all teeth were aligned with the Z-axis perpendicular to the occlusal surface and the tooth's mesial edge increasing in the x direction. Teeth were oriented so that they were parallel with the Front Plane which is directly perpendicular to the Z-axis in GeoMagic. This ensured an even cropping method.

After alignment, a plane was inserted on each tooth using the Extreme Geometry option and choosing "lowest point". Each mold was then cropped using the Split tool and choosing its individual plane as the cropping point. Next, teeth were smoothed, using the Smooth tool set at Level 2. Finally, teeth were down-sampled to approximately 10,000 polyfaces. This level is shown to be best for reducing noise but still allowing capture of informative dental traits (Berthaume *et al.,* 2019). Teeth were exported as binary ASCII *.ply* files, checked for consistency in orientation and scale, then imported into MolaR. for analysis.

6.3.6 MolaR

Dental Topographic variables were generated using MolaR statistical software package for R (Pampush *et al.,* 2016). Teeth were imported into MolaR using the batch process. Results for DNE, RFI, OPCR, OPC, Slope, 3D area, and 2D area were generated in MolaR data and then exported to a .csv file for statistical analyses.

6.3.7 Testing tooth wear and tooth surface texture effects

While the aim of this paper is not to establish the effects of tooth wear on DTA analysis, it is worth mentioning as tooth wear or extraneous tooth texture may contribute to certain dietary signals. While all fossil teeth used in this project were unworn or very slightly worn (Buikstra and Ubeleker 1994), teeth begin to wear the minute they come in contact with food (Ungar, 2004). Therefore, it was important to establish what effects even slightly worn cusps may have had on the fossil sample's DTA scores. Additionally, since this project broadly compared across fossil taxa, surface texture of the tooth was important to consider as well. Some teeth had surface texture resulting from surface features (crests, beading, crenulations) while others had texture that was the result of taphonomic processes. Establishing how much surface texture influenced DTA scores was important to consider as well.

To quantify these potential confounding factors, a wear stage 0-3 was assigned to each tooth as well as a texture stage 0-4. A score of "0" indicated no visible wear present and no visible texture present. A score of "1" meant light wear (e.g. small dentin pitting on one crest) or light texture (e.g. surface features visible on one part of the tooth). A score of 2 indicated either one larger area of dentin exposure or dentin pitting on more than one cusp. A score of 2 for texture meant two areas of texture visible on the tooth surface. A wear score of 3 meant that all cusps had some dentin exposure. A texture stage of 3 indicated that texture covered 50% of the tooth surface. A texture stage of 4 meant the entire tooth surface had texture of some sort. Wear and texture stage were assigned by visual inspection by TSC and by a research assistant independently and scores were averaged for each tooth.

To explore if wear or texture was contributing to the DTA scores on the lower second molars of fossil sample, ordinary least squares regression was performed for each DTA variable. Additionally, to visual the effects of wear and texture, a principle component analysis of the lower second molar DTA scores was examined with wear and texture score superimposed on the individual specimens

6.3.8 Statistical Tests for Diet

Initial comparisons used average values for each dietary variable at the genus level. Dietary variable averages were calculated for the molar row (upper or lower) and each tooth position.

To better allow for comparisons with extant taxa, only lower molar rows and lower second molars were examined in subsequent analyses. The reasons for this are twofold: first, only lower molar information was collected for *Alouatta* and *Cercopithecus* and second, while using both upper and lower teeth would create a larger sample size, many of the upper and lower teeth came from different fossil individuals and could potentially represent different species, confounding a dietary signal. First, ANOVAs with post-hoc pairwise comparisons were used to identify whether there were significant differences between fossil genera in each DTA variable. Next ANOVAs with post-hoc comparisons were used to identify if there were significant differences between fossil and extant DTA variables. A third set of ANOVAs with post-hoc comparisons were performed at the species level to assess differences among presumably closer related taxa All ANOVAs were calculated using R (Version 4.2.1).

Next, a discriminant function analysis (DFA) was used to plot the fossil sample on a folivore/frugivore continuum based on extant sample. *Ateles, Lagothrix, C. ascanius, C. mitis,* and *Hylobates* were classed as frugivores and *Alouatta* and *Symphalangus* were classified as folivores. Two DFAs were performed: one which included the entire folivore/frugivore extant sample and a second where *C. ascanius* and *C. mitis* were dropped due to their highly derived bilophodont dentition.

While DTA analysis was performed on both upper and lower molars 1-3, only lower second molars were used in the DFA. Again, the reason for this is twofold. First, lower second molars accurately reflect diet and have a high accuracy when used to predict diet (Berthaume and Schroer, 2017). Second, as stated above, this allowed for greater comparability with the folivorous extant primate *Alouatta*. Because most of the extant primates are highly frugivorous, a frugivore-folivore dichotomy was used for the DFA. The folivore/frugivore dichotomy was determined based on secondary diet behavior as established in Chapter 1. Finally, principal component analysis was utilized to summarize and explore the variance between the fossil sample and the sample of extant frugivores. DFAs and the PCA were run in R (Version 4.2.1).

6.4 RESULTS

6.4.1 Wear and Texture Analysis

Regressions were performed to examine the extent to which wear stage and texture stage influenced each DTA variable. Results are presented in Table 6.5 and 6.6.

Wear did not have a significant impact on any DTA variable. Texture on the other hand was highly correlated with DNE and OPCR but not RFI.

Table 6.3: Regression results of DTA score compared to wear stage. Significance notated in bold.

DTA by wear	Df	Estimate	Std. Error	Pr(>|t|)	F	R^2
DNE	35	-4.356	55.497	0.938	0.00616	0.000176
RFI	35	0.0006629	0.0082468	0.936	0.006462	0.0001846
OPCR	35	17.03	16.50	0.309	1.065	0.02954

Table 6.4: Regression results of DTA score compared to wear stage. Significance notated in bold.

DTA by texture	Df	Estimate	Std. Error	Pr(>|t|)	F	R^2
DNE	35	126.37	24.41	**9.39e-06**	26.8	0.4337
RFI	35	0.003583	0.004782	0.459	0.5613	0.01578
OPCR	35	34.742	7.832	**8.70e-05**	19.68	0.3599

A PCA examining the effects of wear stage and a PCA examining the effects of texture stage on the three DTA variables from fossil sample was performed. A bivariate plot of the first two PC scores colored by wear stage is presented in Figure XX. These two axes comprise 98% of the total variance. When wear stage is superimposed onto the lower second molar PC scores, there are no apparent groupings (Figure 6.1).

Next a bivariate plot of the first two PC scores colored by texture stage is presented in Figure XX. “Texture” represented both taphonomic texture as well as texture from dental surface features (i.e. crenulations, beading, etc). The two axes comprise 98% of the total variance. Texture stage, interestingly, is potentially driving variation along PC 1. Texture stage 0 and 1 are almost exclusively on the negative axis of PC 1 while stages 2, 3, and 4 fall progressively along the positive axis (Figure 6.2). The higher scores are almost only represented by *Rangwapithecus* and *Proconsul* molars, however. While this may be picking up a taphonomic signal, this could also be a function of *Rangwapithecus* teeth having more enamel wrinkling and *Proconsul* teeth displaying crenulations.

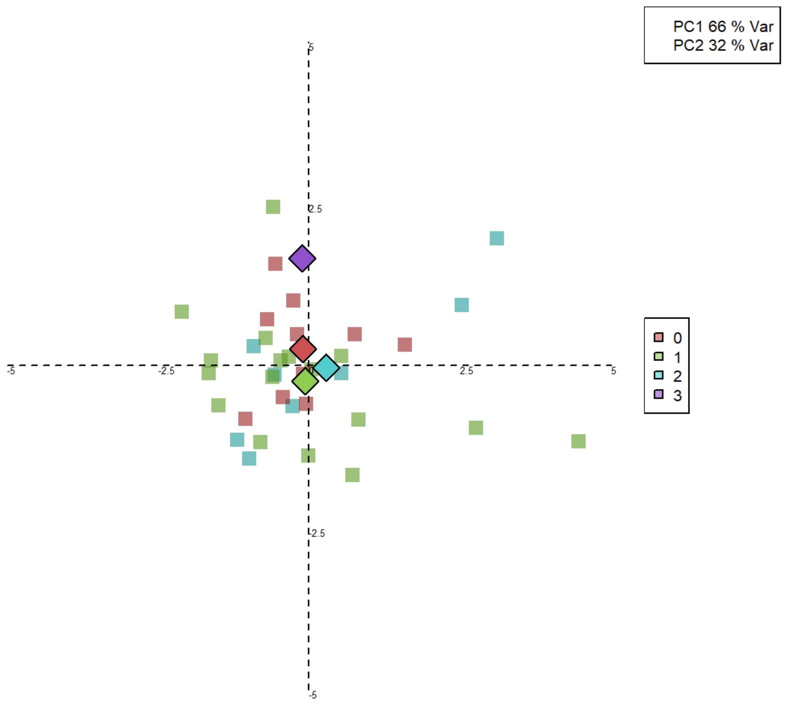

Figure 6.1: Wear stage (0-3) superimposed on lower second molar PCA. Diamonds represent means.

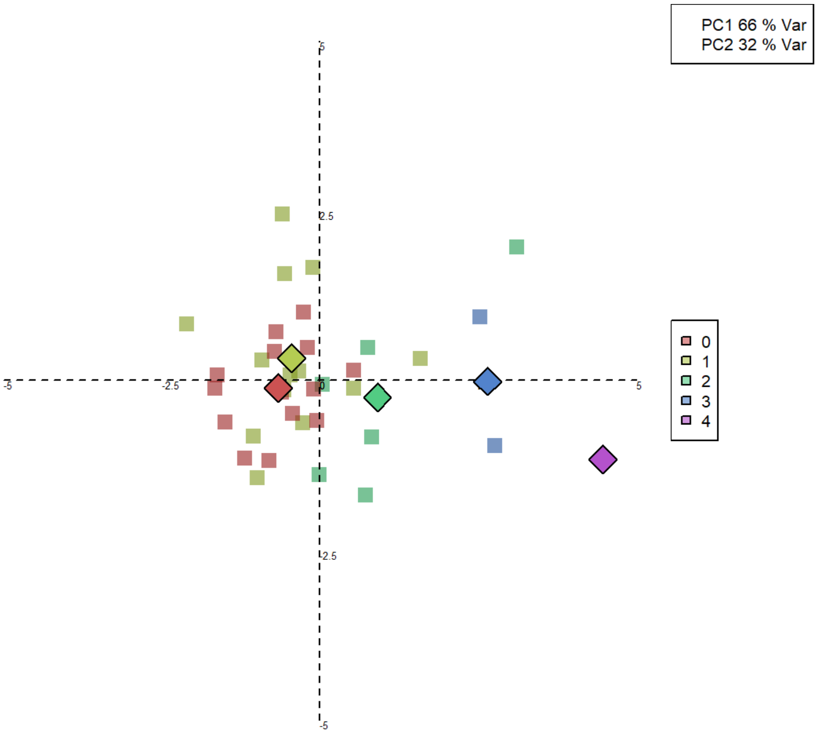

Figure 6.2: Texture stage (0-4) superimposed on PCA of lower second fossil molars. Diamonds represent means.

6.4.2 Dietary Analysis

6.4.2.1 DNE:

DNE averages are presented in Table 6.5 and Figure 6.3. All fossils had higher average DNE values than most extant primates, except for *Alouatta* and *Symphalangus*. *Dendropithecus*, *Kalepithecus*, *Micropithecus*, and *Simiolus* have lower molar row averages near *Alouatta. Dendropithecus* has a lower molar row average similar to *Symphalangus.* Within the fossil sample, *Rangwapithecus*, *Proconsul*, *Ekembo*, and *Nyanzapithecus* all had the largest averages for upper and lower molar rows. *Simiolus*, *Dendropithecus*, *Micropithecus*, and *Kalepithecus* had the lowest average DNE scores across the lower molar row while *Simiolus*, *Micropithecus*, *Equatorius*, *Limnopithecus* had the lowest scores across the upper molar row. *Dendropithecus*, interestingly, had the largest difference in between upper and lower row average DNE scores.

The ANOVA indicated that there were significant differences among fossil genera in their molar row DNE scores (Table 6.8). Tukey's HSD post-hoc tests reveal, however, that these differences are primarily driven by the Nyanzapithecines: *Rangwapithecus* *Nyanzapithecus*, and *Simiolus* (Table 6.9). *Ekembo* did not have significantly larger DNE scores than any other genus. *Proconsul* was only significantly larger in DNE scores than *Dendropithecus*, *Micropithecus*, and *Simiolus.*

When comparing the fossil and extant DNE averages , the ANOVA indicated that there were significant differences (Table 6.10). Tukey's HSD post-hoc tests (Table 6.11) showed *Dendropithecus* and *Kalepithecus* were not significantly different than any of the extant genera. *Ekembo*, *Proconsul,* and *Rangwapithecus* had DNE averages that were significantly different from all extant taxa. *Limnopithecus* was significantly different than all extant taxa except *Alouatta. Equatorius* and *Nyanzapithecus* were significantly different from *Ateles, Cercopithecus, Hylobates,* and *Lagothrix* but not *Alouatta* or *Symphalangus*. *Micropithecus and Simiolus* were only significantly different from *Ateles.*

Examining for DNE differences by fossil species by ANOVA indicated that there were significant differences in the DNE scores at the Species level (Table 6.12). Tukey's HSD post-hoc tests (Table 6.13) showed that there were no significant differences within each genus. *P. major* had significantly larger DNE scores than *D. macinnesi* and *S. enjiessi. R. gordoni* had significantly larger DNE scores than *D. macinnesi*, *E. heseloni*, *L. evansi*, *L. legetet*, *M. clarki, M. leakeyorum*, and *P. major*.

6.4.2.2 RFI

RFI averages are presented in Table 6.6 and Figure 6.4. For RFI, *Alouatta* had a higher lower molar row average than all fossils except *Simiolus* (upper and lower), *Nyanzapithecus* (lower only), and *Kalepithecus* (upper only). For RFI, *Simiolus*, *Nyanzapithecus*, *Equatorius*, and *Ekembo* had the largest values across the molar row. These values are similar to the average RFI values for *Alouatta* and *Cercopithecus*.

The ANOVA indicated that there were significant differences among fossil genera in their molar row RFI scores (Table 6.8). Tukey's HSD post-hoc tests reveal (Table 6.9), however, that these differences are primarily driven by the Nyanzapithecines: *Rangwapithecus* *Nyanzapithecus*, and *Simiolus*. For RFI, *Nyanzapithecus* had significantly larger values than all other genera except *Simiolus.*

RFI averages had fewer significant differences between extant and fossil genera (Table 6.10). *Proconsul* was significantly different from *Alouatta* and Nyanzapithecus was significantly different from *Ateles, Hylobates, and Lagothrix* (the extant primates with the lowest average RFI scores and the most bunodont molars). *Simiolus* was significantly different than *Ateles* and *Lagothrix* (Table 6.11). The species level ANOVA indicated significant diffences, only *Nyanzapithecus pickfordi* had significantly different RFI scores (Table 6.12 and Table 6.14).

6.4.2.3 OPCR

OPCR averages are presented in Table 6.7 and Figure 6.5. For OPCR, all fossils had larger average molar row values than extants the exception being limited to the lower molar row average of *Dendropithecus* being slightly smaller than *Alouatta*. *Rangwapithecus*, *Proconsul*, *Ekembo*, and *Nyanzapithecus* all had the largest averages for upper and lower molar rows.

The ANOVA indicated significant differences among fossil genera OPCR scores (Table 6.8). Tukey's HSD post-hoc tests (Table 6.9) reveal that *Rangwapithecus* had significantly larger complexity scores when compared to every other genus. *Ekembo* and *Proconsul* both had significantly larger OPCR than *Dendropithecus* and *Simiolus.*

When comparing the fossil specimens to the extant sample, OPCR averages for *Ekembo, Limnopithecus*, *Nyanzapithecus*, *Proconsul*, and *Rangwapithecus* were significantly different from all extant primates (Table 6.10 and Table 6.11). *Dendropithecus* was significantly different than *Ateles*. *Equatorius*, *Kalepithecus*, and *Simiolus* were significantly different form *Cercopithecus*. *Micropithecus* was significantly different than *Ateles* and *Cercopithecus*.

Considering these variables in combination, *Dendropithecus*, *Limnopithecus*, *Equatorius*, *Micropithecus*, and *Simiolus* all had DNE average scores less than 500 and OPCR scores less than 225. This indicates slightly less-complex and less sharp teeth. The RFI scores, however, do not follow the expected pattern as often species with sharp teeth also have high cusps. For example, while *Simiolus* had the lowest DNE and OPCR averages it displays the highest RFI average. *Equatorius* and *Micropithecu*s have high RFI scores as well despite their low DNE and OPCR scores.

At the species level while OPCR values were significantly different the pattern is very similar to the differences between species seen in the DNE scores. *Rangwapithecus* was significantly different than all taxa except *Ekembo* spp. *Dendropithecus was significantly* different than both *E. heseloni* and *P. major*.

Table 6.5 Average values in DNE scores across upper and lower molars for fossil catarrhines and extant primates.

DNE	M_1-M_3	M_1	M_2	M_3	M^1-M^3	M^1	M^2	M^3
Dend	286.08	263.84	336.18	188.23	522.98	496.93	557.97	521.56
Ekem	529.38	517.26	424.86	766.67	765.85	686.67	836.49	901.73
Equa	455.58	NA	542.05	412.35	429.11	407.48	450.74	NA
Kale	277.47	352.47	303.72	NA	502.99	502.99	NA	NA
Limn	447.43	401.06	373.38	628.07	445.98	418.64	525.79	380.96
Micr	315.08	330.09	307.98	297.16	409.45	414.07	394.91	417.83
Nyan	488.45	341.99	NA	561.68	526.06	499.21	NA	543.95
Proc	580.34	526.76	569.23	699.13	648.02	1133.95	543.29	562.14
Rang	819.84	592.29	904.67	1048.37	721.4	608.3	690.62	1194.19
Simi	311.08	323.96	323.73	266.23	374.56	281.51	385.15	457.02
Alouatta	358.74	284.06	331.63	591.57	NA	NA	NA	NA
Ateles	194.92	189.19	209.49	183.66	189.27	204.76	196.13	156.96
Cerc	224.35	197.01	243.89	226.55	NA	NA	NA	NA
Hylo	222.06	235.24	221.76	206.73	201.21	211.03	199.77	187.21
Lagothr	223.16	212.64	207.48	230.65	201.14	218.14	201.99	181.17
Symph	289.94	289.42	281.34	304.71	285.98	276.46	291.96	290.27

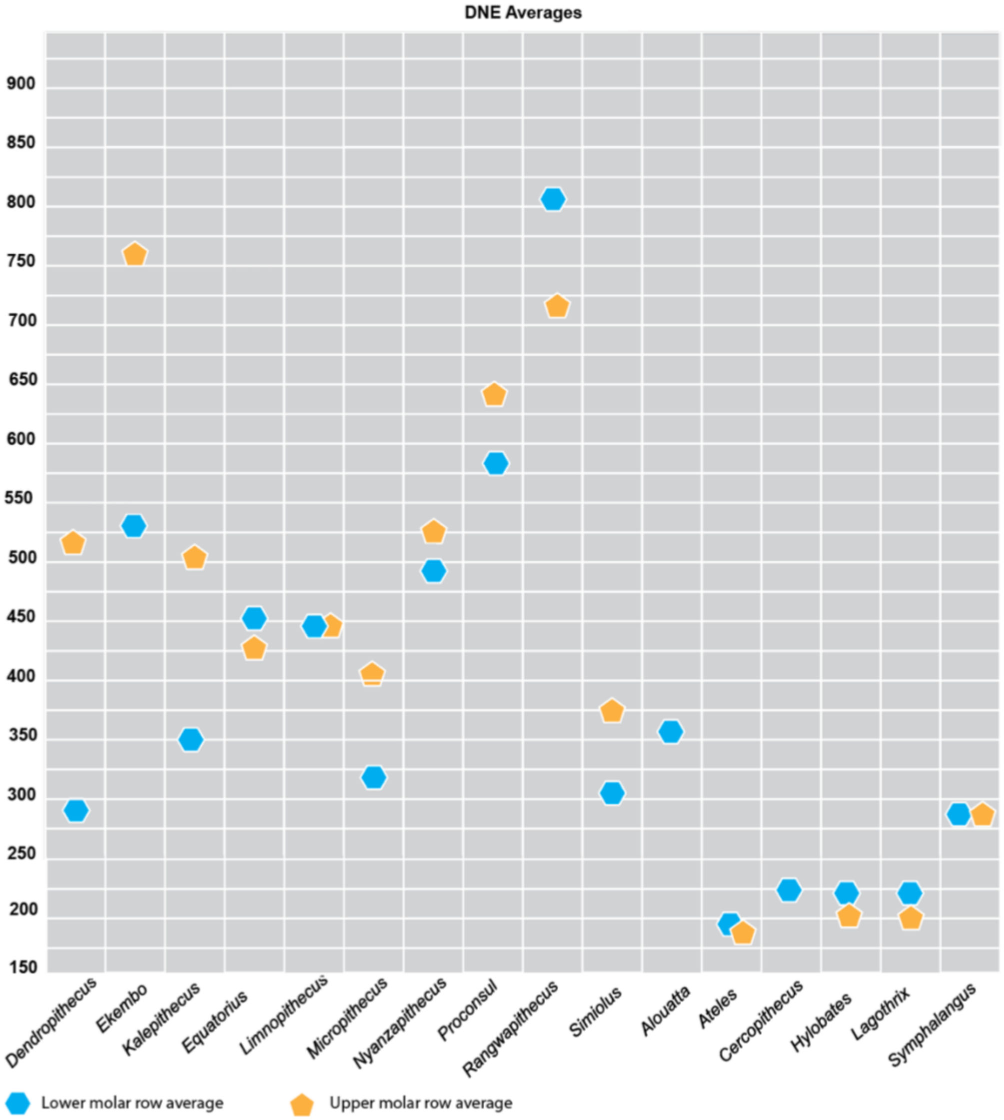

Figure 6.3 Average DNE values by genus for upper molar row average and lower molar row average.

Table 6.6: Average values in RFI scores across upper and lower molars for fossil catarrhines and extant primates.

RFI	M_1-M_3	M_1	M_2	M_3	M^1-M^3	M^1	M^2	M^3
Dend	0.2657	0.2695	0.2751	0.2203	0.2839	0.2824	0.2953	0.2611
Ekem	0.2864	0.2795	0.2582	0.2770	0.2881	0.2972	0.2754	0.2815
Equa	0.3070	NA	0.2661	0.3275	0.2651	0.2577	0.2725	NA
Kale	0.2501	0.2446	0.2584	NA	0.3467	0.3467	NA	NA
Limn	0.2798	0.2836	0.2771	0.2784	0.2723	0.2461	0.3107	0.2675
Micr	0.2829	0.3047	0.2634	0.2661	0.2829	0.2687	0.2907	0.2942
Nyan	0.3788	0.2995	NA	0.4184	0.2983	0.2681	NA	0.2969
Proc	0.2568	0.2743	0.2523	0.2363	0.2729	0.2988	0.2806	0.2484
Rang	0.2827	0.2729	0.3061	0.2531	0.2828	0.2761	0.2916	0.2848
Simi	0.3344	0.352	0.3203	0.3045	0.3352	0.2884	0.3763	0.3408
Alouatta	0.3261	0.3064	0.3231	0.3783	NA	NA	NA	NA
Ateles	0.2415	0.2443	0.2338	0.2477	0.2277	0.2246	0.2336	0.2231
Cerc	0.3035	0.2817	0.3099	0.3211	NA	NA	NA	NA
Hylo	0.2557	0.2701	0.2543	0.2412	0.2453	0.2577	0.2426	0.2289
Lagothr	0.2526	0.2684	0.2525	0.2455	0.2329	0.2355	0.2298	0.2334
Symph	0.2617	0.2635	0.2539	0.2733	0.2676	0.2622	0.2715	0.26843

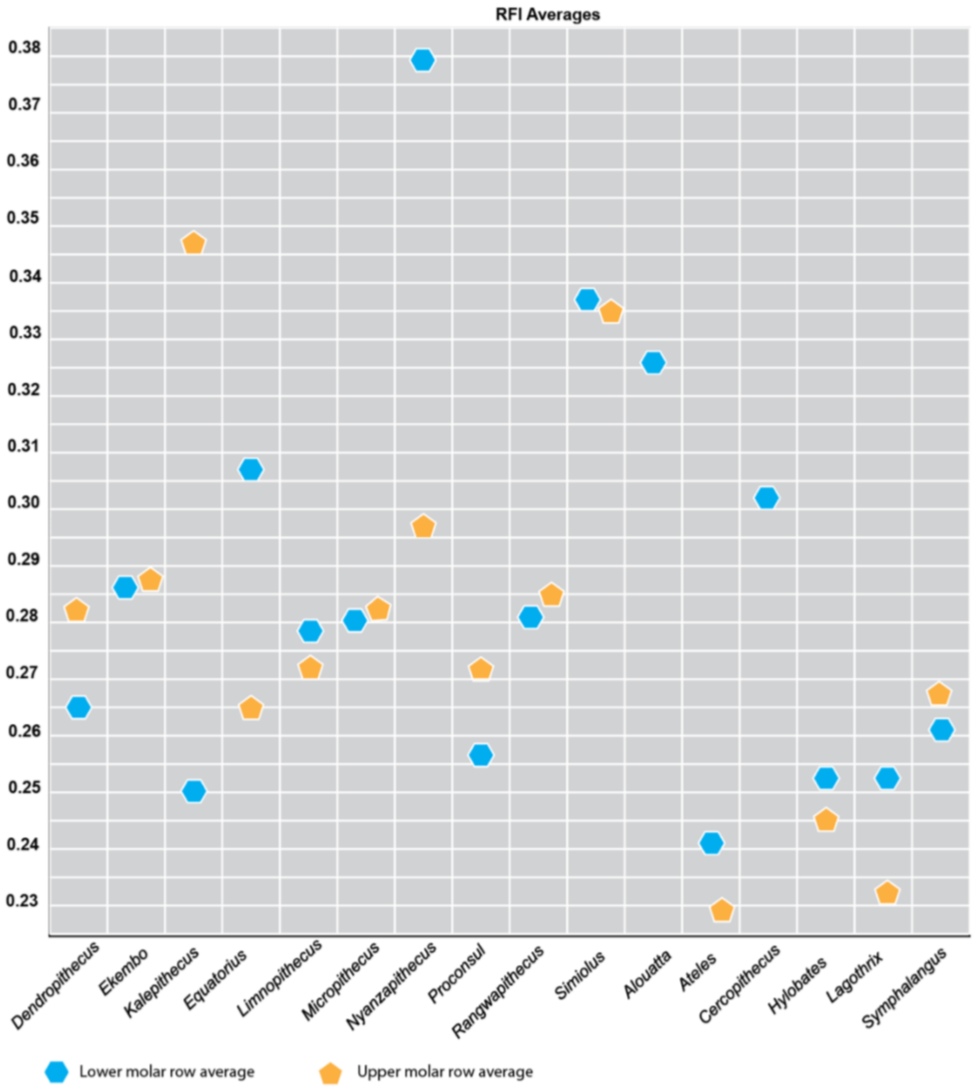

Figure 6.4: Average RFI values by genus for upper molar row average and lower molar row average.

Table 6.7: Average values in OPCR scores across upper and lower molars for fossil catarrhines and extant primates.

OPCR	M_1-M_3	M_1	M_2	M_3	M^1-M^3	M^1	M^2	M^3
Dend	128.05	110.56	143.68	143.62	236.15	238.65	230.41	244.06
Ekem	228.66	231.34	203.79	308.95	303.18	267.80	344.06	345.25
Equa	174.5	NA	197.88	162.81	217.125	191.5	242.75	NA
Kale	178.4	185.58	167.62	NA	225	225	NA	NA
Limn	214.17	180.66	199.95	285.75	237.71	245.75	225.96	239.25
Micr	165.54	158.95	172	170.08	196.86	217.56	171.62	194.5
Nyan	228.83	160	NA	263.25	270.57	299.31	NA	251.41
Proc	242.56	212.16	238.01	306	269.58	395.38	228.79	267.88
Rang	354.41	319.73	350.37	423.12	305.87	286.17	302.32	383.68
Simi	141.48	144.02	151.31	125.37	150.79	148.12	132.25	172
Alouatta	119.46	112.63	107.62	122.12	NA	NA	NA	NA
Ateles	118.96	120.32	125.36	109.81	103.09	105.27	104.76	97.49
Cerc	85.36	92.11	83.31	80.17	NA	NA	NA	NA
Hylo	118.56	118.77	123.55	107.25	104.37	105.34	106.11	99.87
Lagothr	121.48	119.72	120.03	124.51	106.55	113.86	104.31	101.41
Symph	129.91	122.2	136.43	125.46	125.21	123.82	125.81	126.66

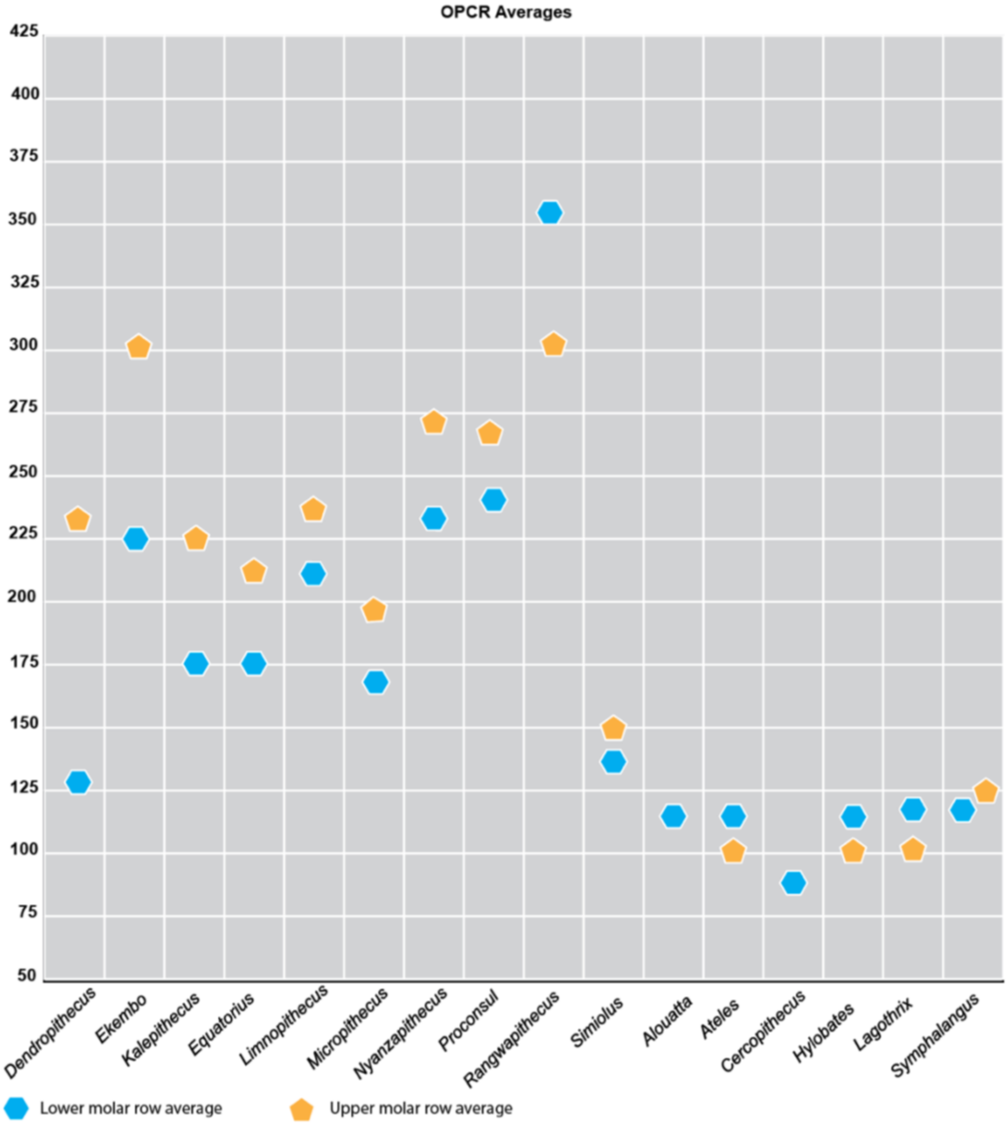

Figure 6.5: Average OPCR values by genus for upper molar row average and lower molar row average.

Table 6.8: ANOVA results comparing each DTA variable by fossil genus, lower molars only. Significant results notated in bold if p< 0.05.

ANOVA DTA ~ Genus, Lower molar only				
	Sum Sq	Df	F value	Pr(>F)
DNE	3224274	9	9.475	**2.941e-10**
RFI	0.07069	9	4.6537	**3.853e-05**
OPCR	509356	9	13.893	**13.647e-14**

Table 6.9: Results of Tukey's HSD post-hoc test for each DTA variable. Significant results notated in bold if p< 0.05.

DNE	**Dend**	**Ekem**	**Equa**	**Kale**	**Limn**	**Micr**	**Nyan**	**Proco**	**Rang**
Ekem	243.29								
Equa	169.49	-73.79							
Kale	36.39	-206.9	-133.11						
Limn	161.34	-81.94	-8.15	124.95					
Micr	34.02	-209.26	-135.4	-2.361	-127.32				
Nyan	202.36	-40.92	32.86	165.97	41.01	168.33			
Proc	**294.25**	50.96	124.75	257.86	132.91	**260.23**	91.89		
Rang	**533.75**	**290.46**	364.25	**497.3**	**372.4**	**499.72**	331.38	**239.49**	
Simi	31.38	-211.91	-138.1	-5.01	-129.96	-2.64	-170.98	**-262.87**	**-502.3**
RFI	**Dend**	**Ekem**	**Equa.**	**Kale**	**Limn**	**Micr**	**Nyan**	**Proc**	**Rang**
Ekem	0.0053								
Equa	0.0412	0.0359							
Kale	-0.016	-0.021	-0.0576						
Limn	0.0141	0.0087	-0.0271	0.0305					
Micr	0.0215	0.0162	-0.0197	0.0379	0.0074				
Nyan	**0.1131**	**0.1077**	0.07181	**0.1294**	**0.0989**	**0.0915**			
Proc	-0.008	-0.0142	-0.0501	0.0074	-0.023	-0.0304	**-0.122**		
Rang	0.0169	0.0116	-0.0242	0.0333	0.0028	-0.0045	**-0.0961**	0.0259	
Simi	0.0606	**0.0552**	0.0193	0.077	0.0464	0.0391	-0.0524	**0.0695**	0.0436
OPCR	**Dend**	**Ekem**	**Equa**	**Kale**	**Limn**	**Micro**	**Nyan**	**Proc**	**Rang**
Ekem	**107.51**								
Equa	46.44	-61.06							
Kale	42.44	-65.06	-4.00						
Limn	86.12	-21.39	39.67	43.67					
Micr	34.83	-72.67	-11.61	-7.61	-51.28				
Nyan	100.78	-6.72	54.33	58.33	14.66	65.94			
Proc	**114.51**	7.00	68.06	72.06	28.39	79.67	13.73		
Rang	**226.35**	**118.83**	**179.9**	**183.9**	**140.23**	**191.51**	**125.56**	**111.8**	
Simi	20.28	**-87.22**	-26.16	-22.16	-65.83	-14.54	-80.49	**-94.2**	**-206.1**

Table 6.10: ANOVA results for DTA variables between extant primates and fossil primates. Significant results notated in bold if p< 0.05.

ANOVA DTA ~ Genus, lower				
	Sum Sq	Df	F value	Pr(>F)
DNE	11903400	15	89.031	**< 2.2e-16**
RFI	0.7107	15	13.2	**< 2.2e-16**
OPCR	2199006	15	100.46	**< 2.2e-16**

Table 6.11: Results of Tukey's HSD post-hoc test for each DTA variable. Significant results notated in bold if p< 0.05.

DNE	***Alouatta***	***Ateles***	***Cercopith***	***Hylobates***	***Lagothrix***	***Symphalangus***
Ateles	**-163.82**	-				
Cercopithecus	**-134.38**	29.43	-			
Hylobates	**-136.08**	27.14	-2.29	-		
Lagothrix	**-135.25**	28.57	-1.18	1.1	-	
Symphalangus	-68.79	**95.02**	65.58	67.88	66.77	-
Dendropithecus	-72.65	91.16	61.73	64.02	62.59	-3.85
Ekembo	**170.63**	**334.45**	**305.02**	**307.71**	**306.21**	**239.43**
Equatorius	96.84	**260.66**	**231.23**	**233.92**	**232.09**	165.64
Kalepithecus	-36.26	127.55	98.12	100.41	99.31	32.53
Limnopithecus	88.69	**252.51**	**223.08**	**225.37**	**224.26**	**157.49**
Micropithecus	-38.62	**125.19**	95.76	98.05	96.94	30.17
Nyanzapithecus	129.71	**293.53**	**264.09**	**266.79**	**265.28**	198.51
Proconsul	**221.6**	**385.42**	**355.99**	**358.68**	**357.17**	**290.4**
Rangwapithecus	**461.09**	**624.92**	**595.48**	**598.18**	**596.67**	**529.89**
Simiolus	-41.27	**122.54**	93.11	95.4	94.3	27.52
RFI	***Alouatta***	***Ateles***	***Cerc***	***Hylobates***	***Lagothrix***	***Symphalangus***
Ateles	**-0.084**					
Cercopithecus	-0.022	**0.062**				
Hylobates	**-0.071**	0.014	**-0.047**			
Lagothrix	**-0.073**	0.011	**-0.051**	-0.003		
Symphalangus	**-0.064**	0.0202	-0.041	0.006		
Dendropithecus	-0.0604	0.024	-0.037	0.01002	0.013	0.003
Kalepithecus	0.047	0.036	-0.025	0.022	0.018	0.009
Ekembo	-0.055	0.029	-0.032	0.015	0.054	0.045
Kenyapithecus	-0.019	0.065	0.003	0.051	0.003	0.012
Limnopithecus	-0.046	0.038	-0.023	0.024	0.027	0.018
Micropithecus	-0.0404	0.044	-0.017	0.03004	0.034	0.025
Nyanzapithecus	0.0526	**0.137**	0.075	**0.123**	**0.126**	0.117
Proconsul	**-0.069**	0.015	-0.046	0.0011	0.004	-0.004
Rangwapithecus	-0.043	0.041	-0.021	0.027	0.03	0.021
Simiolus	0.0126	**0.097**	0.035	0.0831	**0.073**	0.064
OPCR	***Alouatta***	***Ateles***	***Cerc***	***Hylobates***	***Lagothrix***	***Symphalangus***
Ateles	-0.5	-				
Cercopithecus	**-34.09**	**-33.59**	-			
Hylobates	-0.901	1.76	**33.19**	-		
Lagothrix	2.01	2.52	**36.11**	2.92	-	
Symphalangus	10.44	10.94	**44.54**	11.34	8.42	-
Dendropithecus	8.58	**9.08**	42.68	9.48	6.56	-1.86
Ekembo	**116.09**	**116.59**	**150.19**	**116.99**	**114.07**	**105.65**
Equatorius	55.03	55.53	**89.13****	55.93	53.01	44.58
Kalepithecus	51.03	51.53	**85.13****	51.93	49.01	40.58
Limnopithecus	**94.7**	**95.2**	**128.8**	**95.61**	**-92.68**	**84.26**
Micropithecus	43.41	43.91*	**77.51**	44.32	41.39	32.97
Nyanzapithecus	**109.36**	**109.86**	**143.46**	**110.26**	**107.34**	**98.92****

Proconsul	**123.09**	**123.59**	**157.19**	**123.99**	**121.07**	**112.65**
Rangwapithecus	**234.93**	**235.43**	**269.03**	**235.83**	**232.91**	**224.49**
Simiolus	28.871	29.37	**62.96**	29.77	26.85	18.42

Table 6.12: ANOVA results comparing each DTA variable by fossil species, lower molars only. Significant results notated in bold if $p < 0.05$.

Table 6.x				
ANOVA DTA ~ Species, Lower molar only				
	Sum Sq	Df	F value	Pr(>F)
DNE	3469025	14	6.6846	2.971e-09
RFI	0.07762	14	3.2858	0.0002
OPCR	530835	14	9.4955	9.264e-13

Table 6.13 Results of Tukey's HSD post-hoc test for DNE across fossil species Significant results notated in bold if $p < 0.05$.

DNE	D.m	E.h	E.s	Eq.a	K.s	L.e	L.l	M.c	M.l	N.p	P.a	P.m	R.g	S.a
E.h	217.75	-												
E.s	422.09	204.34	-											
Eq.a	169.49	-48.25	-252.59	-										
K.s	65.82	-151.93	-356.27	-103.67	-									
L.e	-44.89	-262.65	-466.99	-214.39	110.71	-								
L.l	190.81	-26.93	-231.27	21.31	-124.99	235.71	-							
M.c	53.02	-164.73	-369.07	-116.47	12.8	97.91	-137.79	-						
M.l	26.35	-191.39	-395.73	-143.14	39.46	71.25	-164.46	-26.66	-					
N.p	202.36	-15.38	-219.72	32.86	136.54	247.26	11.55	149.34	176.01	-				
P.a	116.25	-101.49	-305.84	-53.24	50.43	161.15	-74.56	63.23	89.89	-86.11	-			
P.m	**303.62**	85.87	-118.46	134.12	237.8	348.527	112.81	250.6	277.27	101.26	187.37	-		
R.g	**533.75**	**316**	111.66	364.25	467.93	**578.654**	**342.94**	**480.73**	**507.4**	331.38	417.5	**230.12**	-	
S.a	-5.56	-223.31	-427.65	-175.06	-71.38	39.33	-196.37	-58.58	-31.91	-207.92	-121.81	-309.18	-539.31	-
S.e	-39.37	-257.12	-461.46	-208.87	-105.19	5.52	-230.18	-92.39	-65.72	-241.73	-155.62	**-343**	-573.12	-33.81

D.m: *Dendropithecus macinnesi*
E.h: *Ekembo heseloni*
E.s: *Ekembo spp.*
Eq.a: *Equatorius africanus*
K.s: *Kalepithecus songhorensis*
L.e: *Limnopithecus evansi*
L.l: *Limnopithecus legetet*
M.c: *Micropithecus clarki*

M.l: *Micropithecus leakeyorum*
N.p: *Nyanzapithecus pickfordi*
P.a: *Proconsul africanus*
P.m: *Proconsul major*
R.g: *Rangwapithecus gordoni*
S.a: *Simiolus andrewsi*
S.e: *Simiolus enjessi*

Table 6.14: Results of Tukey's HSD post-hoc test for RFI across fossil species Significant results notated in bold if p< 0.05.

RFI	D.m	E.h	E.s	Eq.a	K.s	L.e	L.l	M.c	M.l	N.p	P.a	P.m	R.g	S.a
E.h	0.0043	-												
XE.s	0.0121	0.0077	-											
Eq.a	0.0412	0.0369	0.0292	-										
K.s	0.0127	0.0083	0.0006	-0.0285	-									
L.e	0.0181	0.0138	0.0061	-0.0231	-0.0054	-								
L.l	0.0135	0.0091	0.0014	-0.0277	-0.0007	-0.0046	-							
M.c	0.0142	0.0098	0.0021	-0.0271	-0.0014	-0.0039	0.0006	-						
M.l	0.0220	0.0176	0.0099	-0.0192	-0.0092	0.0038	0.0084	0.0078	-					
N.p	**0.1131**	**0.1087**	0.101	0.0718	**0.1003**	0.0949	**0.0995**	**0.0988**	0.0911	-				
P.a	-0.0904	-0.0948	-0.1025	-0.1317	-0.1032	-0.1086	-0.1039	-0.1046	-0.1124	**-0.2035**	-			
P.m	-0.0046	-0.009	-0.0167	-0.0459	-0.0173	-0.0228	-0.0181	-0.0188	-0.0266	**-0.1177**	0.0858	-		
R.g	0.0169	0.0126	0.0049	-0.0242	0.0042	-0.0012	0.0034	0.0027	-0.0051	**-0.0961**	0.1074	**0.0216**	-	
S.a	0.0608	0.0564	0.0487	0.0195	0.048	0.0426	0.0472	0.0465	0.0387	-0.0522	0.1512	0.0654	0.0438	-
S.e	0.1343	0.1299	0.1222	0.0931	0.1216	0.1161	0.1208	0.1201	0.1123	0.02127	0.2248	0.1389	0.1173	0.0735

D.m: *Dendropithecus macinnesi*
E.h: *Ekembo heseloni*
E.s: *Ekembo spp.*
Eq.a: *Equatorius africanus*
K.s: *Kalepithecus songhorensis*
L.e: *Limnopithecus evansi*
L.l: *Limnopithecus legetet*
M.c: *Micropithecus clarki*
M.l: *Micropithecus leakeyorum*
N.p: *Nyanzapithecus pickfordi*
P.a: *Proconsul africanus*
P.m: *Proconsul major*
R.g: *Rangwapithecus gordoni*
S.a: *Simiolus andrewsi*
S.e: *Simiolus enjessi*

Table 6.15: Results of Tukey's HSD post-hoc test for OPCR across fossil species Significant results notated in bold if $p < 0.05$.

OPCR	D.m	E.h	E.s	Eq.a	K.s	L.e	L.l	M.c	M.l	N.p	P.a	P.m	R.g	S.a
E.h	**103.75**	-												
E.s	133.82	30.07	-											
Eq.a	46.44	-57.30	-87.37	-										
K.s	47.02	-56.72	-86.79	0.57	-									
L.e	12.01	-91.74	-121.81	-34.44	-35.01	-								
L.l	96.71	-7.04	-37.11	50.25	49.68	84.69	-							
M.c	44.98	-58.76	-88.83	-1.45	-2.037	32.98	-51.71	-						
M.l	30.07	-73.68	-103.75	-16.37	-16.95	18.06	-66.63	-14.91	-					
N.p	100.78	-2.97	-33.04	54.33	-53.75	88.77	4.07	55.79	70.71	-				
P.a	151.82	48.07	18.01	105.38	-104.8	139.82	55.12	106.83	121.75	51.04	-			
P.m	**112.54**	8.79	-21.27	66.1	-65.52	100.54	15.84	67.55	82.47	11.76	-39.28	-		
R.g	**226.35**	**122.59**	92.52	**179.91**	**-179.32**	**214.34**	**129.64**	**181.36**	**196.27**	125.56	74.52	**113.8**	-	
S.a	0.55	-103.20	-133.27	-45.89	46.47	-11.45	-96.15	-44.43	-29.52	-100.23	-151.27	**-111.99**	**-225.8**	-
S.e	-6.30	-110.05	-140.12	-52.75	53.32	-18.31	-103.01	-51.29	-36.37	-107.08	-158.13	-118.85	**-232.65**	-6.85

D.m: *Dendropithecus macinnesi*
E.h: *Ekembo heseloni*
E.s: *Ekembo spp.*
Eq.a: *Equatorius africanus*
K.s: *Kalepithecus songhorensis*
L.e: *Limnopithecus evansi*
L.l: *Limnopithecus legetet*
M.c: *Micropithecus clarki*
M.l: *Micropithecus leakeyorum*
N.p: *Nyanzapithecus pickfordi*
P.a: *Proconsul africanus*
P.m: *Proconsul major*
R.g: *Rangwapithecus gordoni*
S.a: *Simiolus andrewsi*
S.e: *Simiolus enjessi*

6.4.3 Discriminant Function Analysis

Next a DFA with cross-validation of lower second molars was run for all extant genera and fossil catarrhines. Because most of the extant primates are highly frugivorous, a frugivore-folivore dichotomy was used for the DFA (see Methods). Ultimately this project is interested in where each fossil genera falls on the dietary continuum.

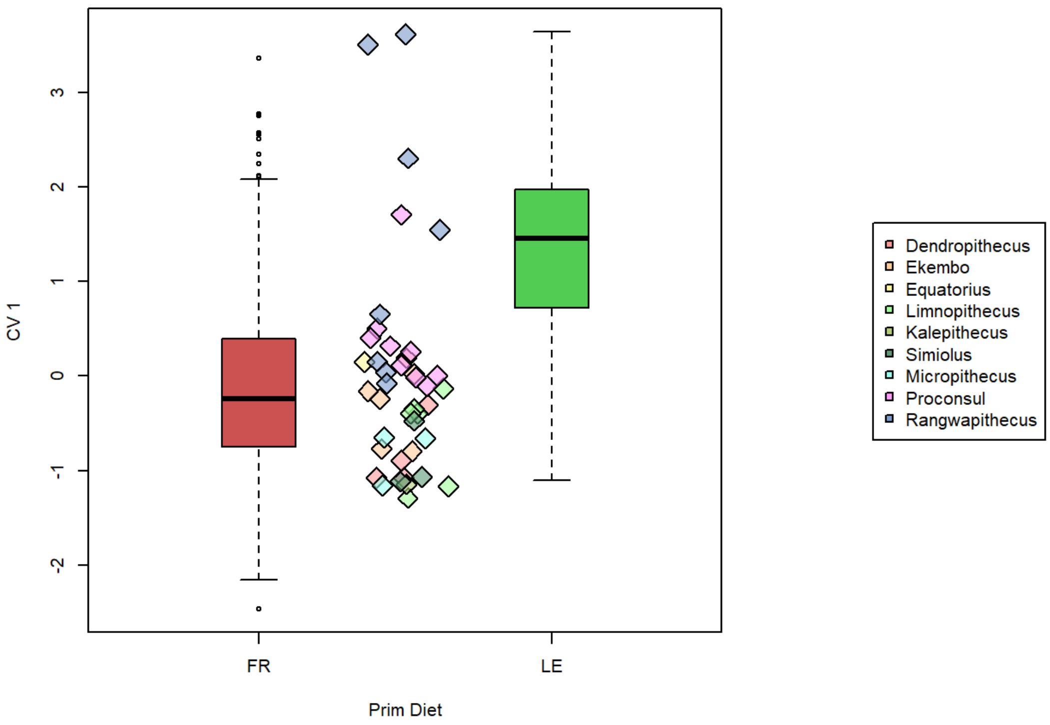

Figure 6.5: DFA results showing how each fossil genus plots in comparison to extant frugivore (red box) and folivores (green box).

Table 6.16: cross-validation for DFA of fossils using extant as diet classifier.

	Frugivore	**Folivore**
Frugivore	268	7
Folivore	18	5
Overall classification accuracy 91.61%		

While this DFA classified the total extant sample with 91% accuracy (results summarized in Table 6.16 and illustrated in Figure 6.6), this is likely because of the uneven distribution of frugivores and folivores. Because there were 275 frugivores and only 23 folivores, the DFA is pulling the values from the latter group toward frugivore (White and Ruttenberg, 2007). While it did classify 97% of frugivores correctly, only 21% of folivores were correctly classified. The five folivores classified belonged to *Alouatta* (4) and *Symphalangus* (1). The following interpretations are made with this in mind: the best combination of variables for discriminating between these groups will likely misclassify some more folivorous teeth into the frugivore category. It is still beneficial, however, to look at trends along this continuum.

While most fossil genera fall heavily within the frugivore end of CV1, *Rangwapithecus* plots within the folivore end of the DFA. One specimen of *Proconsul* (KNM SO 914) is positioned outside of the fossil frugivore group and the remaining *Proconsul* specimens plus the only *Equatorius* specimen all group closely at the high end of that larger fossil clustering. While the other fossil taxa plot towards the lower end of the frugivore clump, they do not appear to be stratifying based on genus indicating there is a high amount of variation not only among all fossil specimens but within each genus.

Again interpretations are cautious do to the heavily uneven sample sizes between folivores and frugivores.

A second DFA was run with a different sampling of extant primates. Because cercopithecoids have a highly derived bilophodont molar morphology unlike hominoids and non-cercopithecoid catarrhines, *Cercopithecus ascanius* and *Cercopithecus mitis* were dropped from this analysis leaving *Symphalangus* as the totality of the folivore sample. Overall, the DFA classified 88% of all samples correctly with 96% accuracy for frugivores and 43% accuracy for folivores. Positions of fossil genera along the resulting CV1 are largely the same as with the first DFA, with *Rangwapithecus*, *Equatorius,* and some *Proconsul* plotting toward the folivore end of the axis(Figure 6.7). This lends some confidence to interpreting broad fossil trends from these analyses despite the poor cross-validation results for folivores. Perhaps the main difference between the two DFAs is that in this second one the *Proconsul* specimens do not cluster as tightly as in the first. Cross validation results are presented in Table 6.17.

Table 6.17: Cross-validation for DFA of fossils using extant as diet classifier, no *Cercopithecus* included in the analysis.

	Frugivore	**Folivore**
Frugivore	123	5
Folivore	13	10
Overall classification accuracy 88.608%		

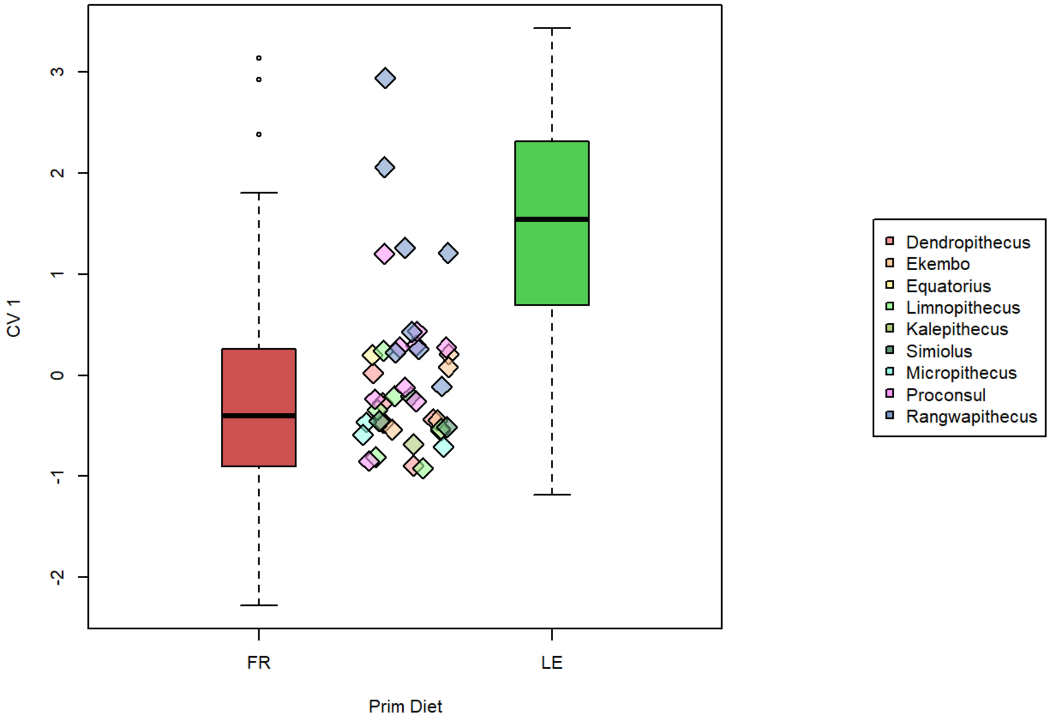

Figure 6.6: DFA results showing how each fossil genus plots in comparison to extant frugivore (red box) and folivores (green box). *Cercopithecus* removed.

6.4.4 Principal Components Analysis

To understand how the shapes of fossil catarrhine teeth align with the extant taxa, a PCA of the lower second molar DTA scores was computed. PCA results are reported in Figure 6.8-6.9. In Figure 6.8 DNE and OPCR (cusp sharpness and cusp complexity) are the primary contributors to variance along PC1 while RFI (cusp height) drives the variation along PC2. As seen in Figure 6.9, most of the extant taxa cluster on the negative side of PC1, except *Alouatta* which slightly spreads out along positive PC1 and positive PC2. While the extant species are predominantly on the negative axis of PC1, the majority of fossils specimens plot along the positive axis of PC1. Interestingly, the extant specimens tend to spread out more along PC2 than the fossils sampled here. The split appears to correlate with cusp height as *Ateles*, *Lagothrix*, *Hylobates*, and *Symphalangus* plot mostly on the negative end of PC2 axis while *C. mitis*, *C. ascanius*, and *Alouatta* plot on PC2 positive. This corresponds to the difference in RFI scores between the extant species.

Compared to the extant sample, there is a very large spread in the fossil taxa data. As seen in the DFA, *Rangwapithecus* is the most distinct of the fossil genera. Here, *Rangwapithecus* spreads out along PC1 likely because of its sharp crests which correlates with high DNE scores. *Proconsul and Ekembo* also cluster along positive PC1 though most form a cluster and are less widespread than *Rangwapithecus*. This pattern likely has to do with the larger DNE and OPCR scores recorded for both genera. *Equatorius* plots within the same region as *Ekembo* and *Proconsul.* It is important to note that there was only one lower second molar from *Equatorius* used in the analysis and the high DNE values from this tooth are likely causing it to plot with similarly large *Proconsul* and *Ekembo.* Potentially, overall molar size may be a factor in the overall greater DNE values, as *Proconsul* here includes *P. major* with some of the overall largest teeth in the fossil sample. Molar area was not recorded for this project, but it presents and interesting future direction.

In regard to PC2, most fossil specimens plot on either side of the axis regardless of genus though it is worth noting that all specimens of *Micropithecus* and a majority of *Proconsul* specimens plot on the negative side of PC2, corresponding to low average RFI

M_2 scores (0.2634 and 0.2523, respectively) compared to the fossil group as a whole (average M_2 RFI: 0.2752)   This is similar to their distribution in the DFA.

There is a cluster of fossil individuals near the origin of the PCA comprised of *Dendropithecus*, *Micropithecus*, *Limnopithecus*, and *Simiolus*. This is similar to the cluster on the more negative side of CV 1 in the DFA

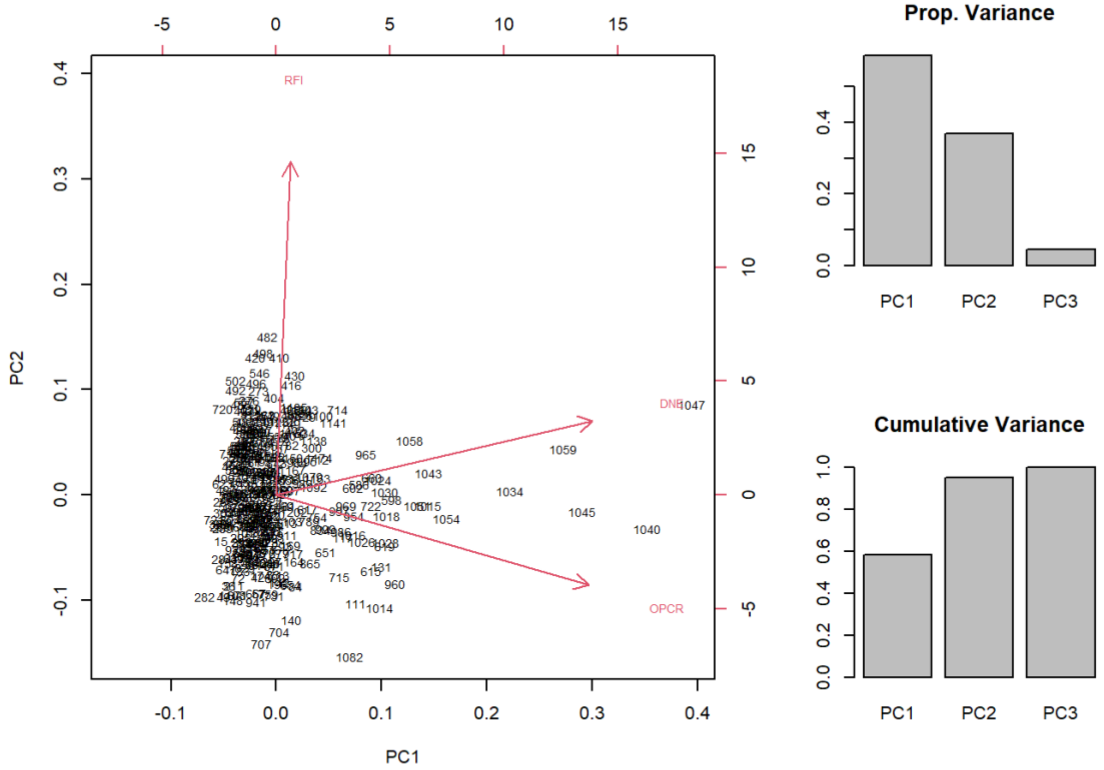

Figure 6.7: PCA of lower second molar scores for both extant and fossil specimens. Left: Biplot of DNE, OPCR, and RFI, arrows show the loadings of each variable of the PCA. Right top: Bar graph showing proportion of variance contributing to each PC axis: PC1 0.58; PC2 0.36; PC3 0.04. Right bottom: Bar graph showing cumulative variance for each PC axis: PC1 0.58; PC2 0.95; PC3 1.0.

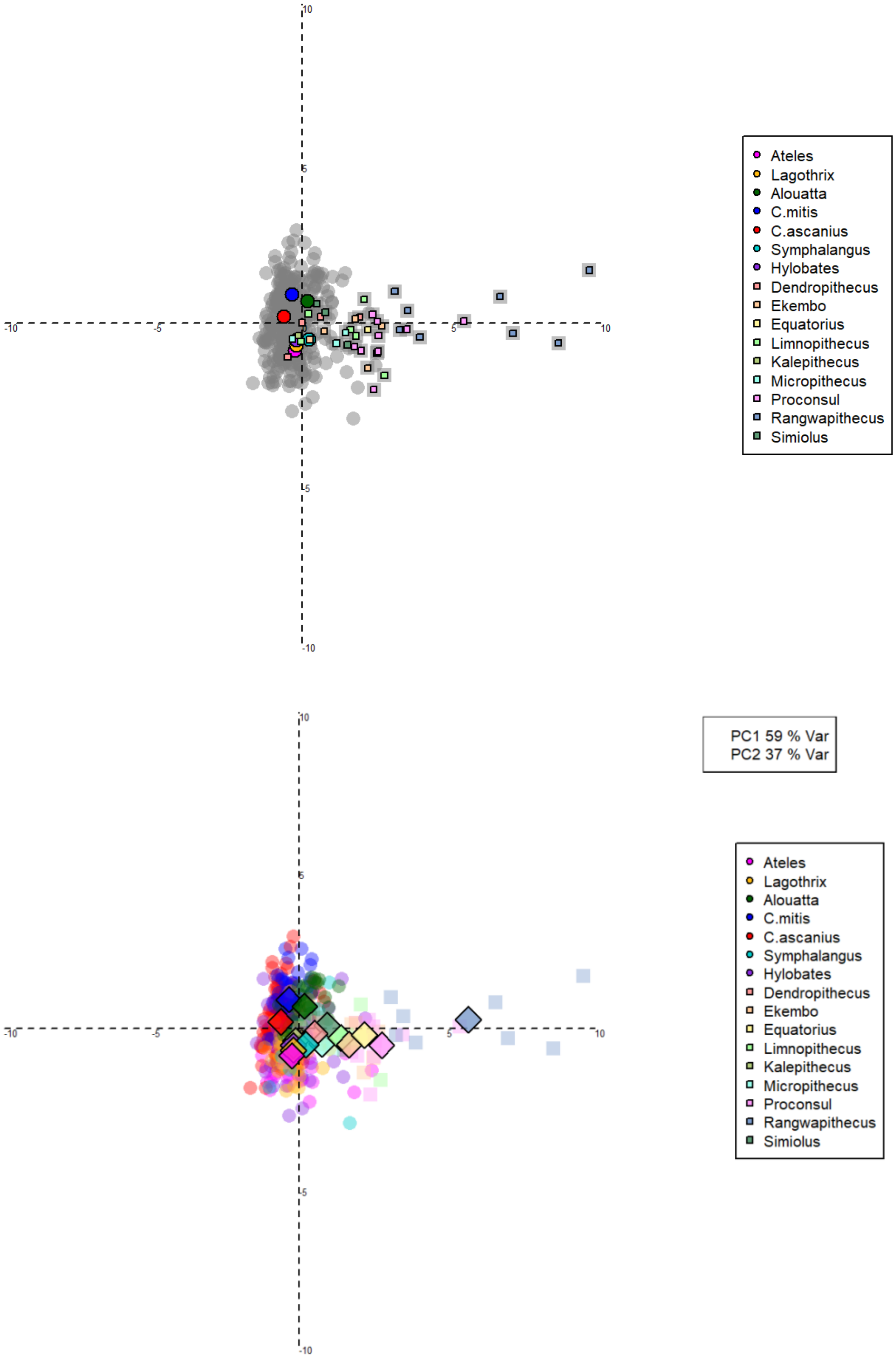

Figure 6.8: PCA plot of lower molar scores for both fossil and extant genera. The top plot shows the all fossil specimens but only the centroids for each extant group. The bottom plot shows all fossil specimens and all extant specimens. Diamonds represent species means.

6.5 DISCUSSION

Miocene catarrhines have been largely classified as frugivores using a variety of methods of diet estimation, though multiple studies have identified potential indications for folivory in some taxa (Kay, 1977; Harrison, 1993; Kay and Ungar, 1997; Grossman, 2008). This study investigated if secondary dietary behaviors can be identified in the molars of eastern African Miocene catarrhines,

Results of the DTA analysis performed here reflect dietary behaviors in the extant frugivore plus *Alouatta* sample. As demonstrated in Chapter 1, the frugivore sample relies on secondary food resources when ripe fruits are scarce, or competition is greater. For example, while both *Ateles* and *Lagothrix* rely primarily on ripe fruit, *Lagothrix* seeks out more insect resources when fruit resources are scarce (Ange-van Heugten, 2014). This behavior is consistent with higher DNE scores across the molar row, which indicate sharper cusps that can be used to process insects with tough shells. Subtle DTA differences are also present in *Hylobates* and *Symphalangus*. While both seek out figs, *Symphalangus* supplements its diet with leaves. This behavior is reflected in the RFI scores of these two genera. Because DTA can track subtle changes in dental shape, one might expect it to indicate help elucidate subtle dietary adaptations in the fossil sample. The results of this study, however, are not so straightforward.

All fossil primates had larger DNE and OPCR scores than most of the extant frugivore. Many scores were in the same range as *Alouatta* DNE and OPCR scores. As care was taken to scan both fossil and extant teeth at similar resolutions and to post-process the 3D models using the same protocols, these overall higher differences in DTA scores are likely due to actual differences in tooth shape or differences in surface texture. Here surface texture was evaluated as either texture on the surface that appeared taphonomic (i.e. bumpy texture, enamel divots and cracks not due to wear) or surface texture from actual tooth features (crenulations, large cingula, beading). Features on the tooth surface will impact DTA scores like OPCR and in this project it appears DNE as well. The regressions show that there was a strong correlation between those two variables and the amount of texture present on the tooth surface.

In addition to larger overall DTA scores in the fossil taxa, many genera displayed wide ranges between upper and lower average molar row values. This may be due to taphonomic mixing in the sample. Very few fossil specimens had matched upper and lower dentition from the same individual. A salient example comes from, *Dendropithecus* which had the lowest lower molar average DNE and OPCR scores but a typical upper tooth row average. The *Dendropithecus* sample may have high variation in DTA scores as recently some specimens included here have been posited to have different taxonomic assignments (see Jansma, 2019). Indeed, many of the new assignments assessed by Jansma (2019) were in the *Dendropithecus* upper molar sample.

6.5.1 Dendropithecus

Dendropithecus has been classified as a frugivore (Kay, 1977; Kay and Ungar, 1997; Ungar *et al.,* 2004; Grossman 2008; Locke, 2021) a folivore (Harrison, 1982; Harrison, 1993) and a generalist (Shearer *et al.,* 2015).

Average DTA values as well as the results from the ANOVAs and PCA show very few significant differences between *D. macinnesi* and any of the extant genera. The only significant difference is between *Dendropithecus* and *Ateles* OPCR scores, which makes sense as *Ateles* has very little molar complexity. The *Dendropithecus* results are similar to the SQ results found by Kay and Ungar (1997) where they found that *Dendropithecus* has some of the least well-developed shearing crests. While the RFI values are not the lowest for *Dendropithecus*, the DNE values are. Because DNE does measure sharpness via curvature, the results here follow Kay and Ungar (1997).

6.5.2 Ekembo/Proconsul

Proconsul major has been classified as a frugivore (Kay, 1977; Harrison, 1982; Kay and Ungar, 1997; Ungar *et al.,* 2004; Grossman 2008; Shearer *et al.,* 2015; Locke, 2021) and as a folivore/frugivore (Harrison, 1993). *P. africanus* has been classified as a frugivore (Harrison, 1982; Ungar *et al.,* 2004; Grossman 2008; Shearer *et al.,* 2015) and as a folivore/frugivore (Harrison, 1993). Both species of *Ekembo* have been classified as frugivores (Kay, 1977; Harrison, 1982; Kay and Ungar, 1997; Ungar *et al.,* 2004; Grossman 2008; Shearer *et al.,* 2015; Locke, 2021), with Harrison (1993) suggesting *E. nyanzae* was a folivore/frugivore.

In this project, both genera have similarly high DNE and OPCR scores, distributing in a similar direction along the PC1 axis. This is likely due to surface texture on the specimens. While some texture may be the results of taphonomic processes, likely DNE and OPCR were also picking up enamel crenulations. Crenulations are thought to appear on teeth for species that need to resist crack propagation due to the consumption of tough or hard foods (Vogel, 2009). This relationship is seen in both *Pongo* and *Chiropotes* molars (Martin *et al.,* 2003; Ledogar *et al.,* 2013). Cingula also are thought to help buttress the tooth when hard foods are consumed but they are not used for crushing or grinding food until wear becomes extreme (Allen *et al.,* 2015). A limitation of DTA analysis is its inability to distinguish between crenulations and cingula and high cusp curvature (Allen *et al.,* 2015). Therefore, higher DNE scores may not indicate overall sharper cusps but instead teeth with more surface features (e.g. crenulations). The fact that the OPCR scores are, on average, high for the same group of genera points to the possibility that the DTA picked up on higher surface complexity as most specimens of *Proconsul* were scored between 2-4 for surface texture. Furthermore, that RFI remained low indicates that *Ekembo* and *Proconsul* have very bunodont molars. The low molar crests combined with the crenulated surface texture may point to affinities with hard or brittle object feeding (Berthaume *et al.,* 2020). While no hard object feeders were analyzed in this project, comparing fossil primates to extant primates with high levels of surface crenulations may illuminate secondary feeding strategies on hard objects. Overall *Proconsul/Ekembo* display teeth with surface features that may point to alternative dietary strategies

6.5.3 Equatorius

Equatorius africanus has thick molar enamel and a reduced cingulum (Benefit and McCrossin 1989). While *E. africanus* has more primitive traits than other possible hominoid ancestors from the Middle Miocene, overall changes to dental shape in this taxon compared to Early Miocene forms were proposed to represent a shift to more tough foods or an omnivorous niche in response to increased competition from cercopithecoids (Harrison, 1989). The sample of *Equatorius* sampled here, however, did not have DTA values that were significantly different from the Early Miocene sample. From these results, we cannot conclude anything other than *Equatorius* was processing generalized fruit resources..

6.5.4 Kalepithecus

Kalepithecus songhorensis has been classified as frugivore (Harrison, 1993). Specimens from *Kalepithecus* fall solidly with *Ateles*, *Lagothrix*, and *Hylobates*. It has low DNE, RFI, and OPCR values, some within range of the extant genera. Likely it represents a strategy for generalized frugivory.

6.5.5 Limnopithecus

Limnopithecus evansi has been classified as a frugivore (Harrison, 1993; Grossman 2008), as a frugivore/folivore (Kay and Ungar, 1997), and as a generalist (Shearer *et al.,* 2015). Similarly, *L. legetet* has been classified as a frugivore (Kay, 1977; Harrison, 1982; Grossman 2008), as a frugivore/folivore (Harrison, 1993; Kay and Ungar, 1997; Locke, 2021) and as a generalist (Shearer *et al.,* 2015). Some researchers have posited an ecological difference between *L. evansi* and *L. legetet* as an explanation for the apparent allopatry between the species. While no DTA values for the lower molar row were significantly different between *L. evansi* and *L. legetet*, when the averages of only lower second molars are examined, there is a slight difference between the two species. This corresponds to observations by Harrison (1993) and others, the *L. legetet* specimens examined here had higher average DNE and OPCR values than *L. evansi*. Interestingly, *L. evansi* had a slightly larger RFI value. Because RFI is a ratio between surface area (the footprint) over the total surface area (height), narrower molars may cause a larger RFI value due to a smaller footprint

6.5.6 Micropithecus

Micropithecus clarki has been classified as a frugivore (Harrison, 1982; Harrison, 1993; Shearer *et al.,* 2015) and as a folivore/frugivore (Ungar *et al.,* 2004). The diet *M. leakeyorum* has not been quantified and this paper is the first to do so. Once again, it should be noted that *M. clarki* and *M. leakeyorum* have been proposed to belong to separate genera (Benefit 1991). When DTA variables were tested at the species level for lower second molars, neither *M. clarki* nor *M. leakeyorum* indicated there no evidence for dietary differences from the tooth anatomy.

Harrison (1989) suggested that Middle Miocene catarrhines were more folivorous than early Miocene catarrhines. This has been posited due to the rise of cercopithecoids and subsequent competition over fruit resources but may be due to expansion of woodland habitats during the middle Miocene. *Micropithecus* may demonstrate an example of a shift from highly specialized frugivory to a diet that is more generalized and accommodating more young leaves or coarser fruits. While this project found no significant differences in lower molar DTA values within any genus, the general trend of

Micropithecus molars indicates a shift from taller crests in the Early Miocene *M. clarki* to lower RFI values in the Middle Miocene *M. leakeyorum*. DNE and OPCR values are also larger in *M. clarki* than in *M. leakeyorum*.

While almost all teeth used in this project were considered unworn or lightly worn, wear stage was assigned within the sample. Because teeth begin to wear the minute they touch food, many species have adaptations that allow teeth to wear in ways that remain beneficial to the animal especially if their diet has a lot of fibrous material (*i.e.* colobines). While the regression did not indicate a signficnat correlation between wear and any DTA variable, the *M. clarki* sample had a much lower wear score than the *M. leakeyorum* sample. Additionally, while the slight differentiation in wear did not produce significant differences between the two species, this is potentially a future avenue of investigation in terms of DTA measures of surface topography.

6.5.7 Nyanzapithecus

N. pickfordi has been classified as a folivore/frugivore (Grossman 2008) and *N. vancouveringorum* as a folivore (Harrison, 1993). Harrison (1986) noted in his description of *N. pickfordi* material from Maboko Island, Kenya, that the molar shape was potentially specialized, similarities between *Nyanzapithecus* and *Rangwapithecus*. Unfortunately, no lower second molar specimens were available to include in the DFA or PCA for this project. When average values are considered, however, *Nyanzapithecus* had typical lower molar row DNE and OPCR values compared to the other fossil species but the RFI values of *Nyanzapithecus* are the highest. *Nyanzapithecus* is distinguished by its long and narrow teeth. The length of the teeth, however, would not cause RFI to be artificially higher. While *Nyanzapithecus* does have low cusps they are often described as "voluminous" and created a "crowded" occlusal surface (Harrison, 1986). The crowded nature of the teeth may be inflating RFI height as teeth were cropped to the lowest area on the tooth.

If the teeth of *Nyanzapithecus* do represent an adaptation for more fibrous items, the comparisons with extant taxa may illuminate similarities. When considering the ANOVAs, the posthoc tests comparing the RFI scores of *Nyanzapithecus* and each extant genera show that the fossil RFI scores are not significantly different from *Alouatta*, *Cercopithecus*, and *Symphalangus* but that they are significantly different from the extant taxa that are more frugivorous. This project concludes that *Nyanzapithecus* had some adaptations for folivory.

6.5.8 Rangwapithecus

Rangwapithecus has high RFI, DNE, and OPCR averages. Due to the long shearing crests and high molars, *Rangwapithecus* is often considered to have some folivorous adaptations (Kay, 1977; Kay and Ungar, 1997 (but see Grossman 2008 and Shearer *et al.,* 2015)). The high crests and elongated molars are likely what is pushing high RFI values. Indeed, this is seen not only in the DTA averages, but *Rangwapithecus* has significantly different DNE and OPCR values from most other fossil taxa. *Rangwapithecus* falls within the folivore range in the DFA. Cote *et al.,* (2014) note the high amount of crenelations and sharp crests on fossils assigned to *Rangwapithecus*. This might be an adaptation for processing tougher and more fibrous materials. This project finds support for a folivorous component to the diet of *Rangwapithecus*.

6.5.9 Simiolus

Simiolus enjessi has been classified as a frugivore/folivore (Harrison, 1993; Grossman 2008). No dietary classification has been performed on *S. andrewsi* and this paper is the first to present this data. As a genus, *Simiolus* had the lowest DNE and OPCR values but some of the highest RFI values. This follows previous studies (Harrison, 1983 and Grossman 2008) pointing to potentially folivorous adaptations. There were no significant differences between *S. enjessi* and *S. andrewsi*, but *S. enjessi* had slightly higher curved and more complex teeth than *S. andrewsi* despite having slightly lower RFI values. High DNE can however indicate sharper teeth. Likely these high RFI or high sharpness indicates some adaptation for the ability to process tougher or more fibrous resources.

Molar shape in Early Miocene eastern African catarrhines has been proposed to be an example of the Red Queen Effect (Kay and Ungar, 1997). Coined by Van Valen (1973), the Red Queen Effect is invoked to describe the relationship between constant competition between and the need for continuous evolution between competitors. The trait or traits under selective pressure will adapt to maintain the same level of adaptedness as seen in competitor taxa (Van Valen 1973; Whitlock 1996; Kay and Ungar, 1997).

In their study of Early Miocene catarrhine shearing crest length, Kay and Ungar proposed the Red Queen Effect as an explanation for the apparent downshift in the fossil taxa shearing crest lengths compared to the extant taxa. Despite the Early Miocene eastern African catarrhines displaying shorter molars, the range of dietary behaviors represented by Kay and Ungar's (1997), was similar to the range seen in frugivorous extant apes. In his study of incisor curvature, Deane (2009), found corroborating results for a downshift in incisor shape.

Two potential explanations have been proposed. The first is that, since the Early Miocene, plants have evolved to better resist being eaten by primates and in return primates have had to evolve higher shearing crests to contend with the tougher properties of plant materials. In this scenario, Early Miocene catarrhines are not eating different foods than modern taxa, just that the foods they were eating required less processing power. The second potential explanation is competition with cercopithecoids. Cercopithecoids have a highly derived masticatory traits: cheek pouches as well as tall crested bilophodont molars. These have been proposed to confer a competitive advantage in cercopithecoids compared to hominoids. With the rise of cercopithecoids between the Early and Middle Miocene, Early Miocene catarrhines may have had to start evolving higher shearing crests to better compete for food resources.

The results of this project are in line with Kay and Ungar's (1997) conclusions that Miocene catarrhines display a different type of tooth adaptation compared to modern taxa. In this sample, DNE and OPCR scores were quite large in the fossil sample. This is a function of non-taphonomic texture on the tooth surface. Many of the fossil species examined here have complex and highly detailed molars. While shearing crests may be low in fossil taxa, potentially teeth were adapting to plants with different mechanical properties than seen today

6.6 CONCLUSION

This study compared the teeth of non-cercopithecoid catarrhines from the Early and Middle Miocene of eastern Kenya to a diverse set of extant frugivorous primates in to parse out subtle dietary differences in the fossil sample. While the fossil sample did not overlap well with the extant sample, a few patterns can be observed.

Non-cercopithecoid catarrhines from the Early and Middle Miocene of eastern Kenya have incredibly diverse tooth morphology. Overall, the fossil taxa have teeth that display quite different shapes than extant analogues. The ranges of DTA values and averages by tooth type and position confirm this. Most fossil taxa fall within the range of a platyrrhine or hominoid type frugivore rather than being similar to a cercopithecoid. This may be due to the primitive molar shape of the fossils sampled here. Species that exhibit crenulations or large occlusal accouterments (*i.e.* cingula, inflated cusps) had high DNE and OPCR scores. It is interesting that the teeth of *Proconsul*, *Ekembo*, and *Rangwapithecus* did have enough enamel wrinkling to inflate DNE scores causing their sharpness to be on par with highly crested species like *Alouatta*. While the functional importance of crenulations is not fully understood (Berthaume *et al.,* 2021), they may represent an adaptation to tough or hard objects in future research.

While the extant sample represented a range of frugivorous behaviors, most of the Miocene taxa were significantly different across DTA values than the extant primates and this is illustrated in the PCA as the fossil sample occupies a different portion of the PCA space. The Miocene taxa were probably following a soft-fruit strategy, the overall shape differences, however, potentially indicates that the fossil taxa had a different set of tooth tools to effectively process food items. This project does not conclude that Early and

Middle Miocene eastern African catarrhine taxa had teeth that were simple. The opposite is in fact indicated through the investigation of surface texture on DTA scores. This opens interesting future lines of evidence regarding the dietary benefits of occlusal features like crenulations, cingula, and enamel beading and their significance in primate evolution.

7. Summary

The role that diet plays in shaping primate adaptations has long been recognized as a powerful selective force in changing and maintaining primate traits (Simpson, 1933). While dietary ecology permeates multiple areas of the primate Bauplan, dental shape is perhaps the most salient (Butler, 1983). Because the oral cavity is the starting point for digestion and nutrient extraction, it is logical that it and its contents would be adapted to best process food resources (Lucas, 2004). Specifically, teeth which are used to shear, crush, grind, and process most resources prior to swallowing (Lucas 2004). Indeed, teeth are more than just passive platforms on which food is crushed, they adapted to the mechanical properties of the foods consumed (Ungar *et al*., 2017). While teeth must minimally be able to efficiently process the resources most eaten by an animal, studies have further demonstrated that fallback or secondary dietary items can influence selection for certain tooth shapes and features (Kinzey, 1978; Lambert *et al*., 2004; Ungar *et al*., 2017).

Many primates prefer ripe fruit resources and will consume them when available. Fruit, however, is more limited than a resource like leaves, and fruit patches can be easily defended or depleted by more dominant primates or primates which live in larger groups. Adapting behavior to consume less preferred resources when competition is high is a way to ensure nutritional needs are met. The relationship between tooth shape and food mechanical properties has been likened to an evolutionary “death match.” As teeth evolve to process food items more effectively, the food items also evolve to resist being eaten (Ungar et. al. 2017). It has been posited that teeth have evolved to process fallback resources more effectively over preferred resources, as fallback resources are often consumed during periods of scarcity and are necessary for survival. Often fallback foods are considered to be more mechanically challenging than primary food resources (Ungar, 2008). Therefore, while secondary resources may only be consumed intermittently, their importance towards animal survival may cause a greater impact on dental shape adaptations (Ungar *et al*., 2017).

Ultimately when competition causes a feature to change and become more different from the features present in a competitor, the trait or taxon is said to have undergone character displacement (Brown and Wilson, 1956). While character displacement can be difficult to discern from other random forces shaping adaptions, it exists as a hypothetical framework with which to examine changes in primate dietary behavior and dental shape (Losos, 2000).

Therefore, this project attempted to answer the following question: How do primates change their diets when faced with competition and does this dietary change affect their dental morphology and dietary isotopes. It was examined both within extant and fossil taxa.

The first project surveyed published studies of feeding behavior from three families of primarily frugivorous primates. Because behaviors that are a result of character displacement can be subtle and easily missed, this first project aimed to quantify subtle differences in food intake from non-fruit resources. The results of Chapter 2 are cautiously interpreted as indicating certain primate taxa (*Lagothrix* and *Ateles*) do modify their behavior to feed on less preferred resources when facing competition from other primate taxa. The results of *C. mitis* and *C. ascanius* and *Hylobates* and

Symphalangus are less straightforward. However, these results may have been confounded by the number of studies available (only one study could be found where *C. ascanius* was allopatric from *C. mitis*) and the way in which foods were assigned to dietary categories by researchers (e.g., some studies included figs as “fruits” while other studies placed figs in the category “other”). Additionally, while this chapter used rainfall as a proxy for fruit productivity, rainfall is only a small component of site climate. Future directions using this line of inquiry would add in more climatic variables (e.g., mean annual temperature, elevation) as well as more information on the community structure. While the seven primate genera were chosen due to their close phylogenetic relationship, many of the sites sampled have other primate species present which may present more competition. Additionally looking at site community structure would be an important future direction: primates compete not only with other primates but with birds and other mammals.

Chapter 4 sought to address whether competition, and therefore assumed reliance on less preferred resource, manifested in dental differences. Two methods were used: dental topographic analysis to capture an adaptive signal and stable isotope analysis to capture an in-life signal. Stable isotope analysis was also employed to not only investigate differences in at each site. Certain species and site combinations appear to have contradictory results. For example, *Ateles* and *Lagothrix* collected from Curaray River Mouth and those collected from Alto Yavari might be expected to yield similar results given their proximity and therefore similar climates and environments. This was not the case. Individuals from Alto Yavari showed a greater difference in DTA values than did individuals from Curaray River Mouth. This shows that, if character displacement is driving these differences, it may not be present at all sites. There could be other factors present at Curaray (e.g., greater fruit productivity, less seasonal flooding, or local allopatry) that are causing individuals to look less different than their allopatric counterparts. Stable isotope analysis revealed that the only difference between Curarray and Alto Yavari was in the $\delta^{15}N$ values, which is not unexpected.

This opens interesting future lines of research for comparing primates at a finer scale or examining different teeth. In this project, only molars were examined. Yet, frugivorous primates often rely on anterior teeth to process fruit hulls and husks; it might not be that competition is less at Curaray than at Alto Yavari, but instead that the primates at the former site process their foods further forward in the mouth and/or swallow fruits more intact than at Alto Yavari. In contrast, Alto Yavari specimens may be supplementing their diets with tougher foods, such as insects and leaves, during periods of higher competition.

While vertical displacement was unable to be established due to a difficulty in ground truthing the isotopic values, the isotopes do indicate interesting dietary shifts within each site. For example, *C. ascanius* and *C. mitis* vary significantly in their $\delta^{13}C$ ratios, but not, however, in their $\delta^{18}O$ ratios. This might indicate a slight reliance on food from different parts of the canopy or different food parts (i.e., fruits vs leaves).

Additionally, the historic method of primate specimen collection may be confounding the isotope results. Many of these primates were harvested *en masse* during research expeditions. Collectors were likely shooting primates that were easy to sight and retrieve. These primates likely were lower in the canopy. If primates were harvested from similar canopy layers, vertical stratification would be difficult to detect.

Chapter 6 attempted to parse out subtle dietary behaviors in a diverse set of fossil primates. Previous studies had been unable to categorize many Miocene fossil taxa other than generalized frugivore while others observed some dental traits that corresponded to non-fruit item consumption. The results of this study were surprising in that upper and lower teeth within the same genus showed vastly different average DTA scores across variables and tooth positions. This might be due to very few upper and lower teeth coming from the same individual and additionally some genera span millions of years. When compared to the DTA values of the extant set, most fossil catarrhines fell within the range of a platyrrhine or hominoid type frugivore rather than being similar to a cercopithecoid. This is likely due to the primitive molar form of the fossils sampled here. Interestingly, species that exhibit crenulations or large occlusal accouterments (*i.e.,* cingula, inflated cusps) had high DNE and OPCR scores. This is likely a limitation of molaR and recent updates to the program may solve some of the false inflation issues in these two measures. It is interesting that the teeth of *Proconsul*, *Ekembo*, and *Rangwapithecus* did have enough enamel wrinkling to inflate DNE scores causing their sharpness to be on par with highly crested species like *Alouatta*. While the functional importance of crenulations is not fully understood (Berthaume *et al.,* 2021), they may represent be an adaptation to tough or hard objects in future research.

In sum, this project attempted to examine how primates change their behavior due to differing levels of competition and if those behavioral changes manifest in dental adaptation to secondary food resources and chemical adaptations to different resources or resources at different canopy levels. This project indicates there is some support for secondary resource use at sites with higher levels of competition and that this is reflected in dental adaptations for processing tough or fibrous resources. However, this was not observed within every species pair, or at every site, or within each fossil genera. While there is some support for character displacement and secondary resource use, more research is needed across a greater variety of dietary categories.

Bibliography

Abramsky, Z., Rosenweig, M., & Subach, A. (1998). Do gerbils care more about competition or predation? *Oikos*, 83(1): 75–84.

Adams, D. C., & Rohlf, F. J. (2000). Ecological character displacement in Plethodon: biomechanical differences found from a geometric morphometric study. *Proceedings of the National Academy of Sciences*, 97(8): 4106-4111.

Agostini, I., Holzmann, I., & Di Bitetti, M.S. (2010) Ranging patterns of two syntopic howler monkey species (*Alouatta guariba* and *A. caraya*) in Northeastern Argentina. *International Journal of Primatology* 31: 363-381.

Alatalo, R.V., Gustafsson, L., & Lundberg, A. (1986). Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of nonexperimental data. *The American Naturalist* 127(6): 819-834.

Allen, J.A., Carriker, M.A., & Elliot, D.G. (1910). Mammals from the Caura District of Venezuela: With Description of a New Species of Chrotopterus. *Order of the Trustees, American Museum of Natural History*.

Allen, K.L., Cooke, S.B., Gonzales, L.A., Kay, R.F. (2015). Dietary inference from upper and lower molar morphology in platyrrhine primates. *PLoS One* 10(3):e0118732.

Allgas, N., Shanee, S., Shanee, N., & Collongues de Palomino, H. (2018) Rapid Survey of the Primate Density and Biomass at Katakari, Pacaya Samiria National Reserve, Peru. *Primate Conservation* 32: 57-66.

Almeida-Silva, B., Guedes, P.G., Boubli, J.P., Strier, K.B. (2005). Deslocamento terrestre eo comportamento de beber em um grupo de Barbados (*Alouatta guariba clamitans*) Cabrera, en Minas Gerais, Brasil. *Neotropical Primates* 13(1): 1-3.

Alves, I. and Guix, J.C. (1992). Feeding habits of *Alouatta caraya* in a semi-natural area (SE Brazil). *Mammalia* 56: 469-492.

Ange-van Heugten, K.D. (2014). "Recent advances in woolly monkey nutrition." In Thomas R. Defler and Pablo R. Stevenson (Eds.) *The Woolly Monkey: Behavior Ecology, Systematics, and Captive Research* (Pp 83-92). Springer.

Andrews, P. (1974). New species of Dryopithecus from Kenya. *Nature* 249: 188-190.

Andrews, P. (1978). A revision of the Miocene Hominoidea of East Africa. *Bulletin of the British Museum (Natural History) (Geology Series)* 30: 85-224.

Andrews, P. and Simons, E. (1977) A new African Miocene gibbon-like genus, *Dendropithecus* (Hominoidea, Priamtes) with distinctive postcranial adaptations: Its significance to origin of Hylobatidae. *Folia Primatologica*, 28: 161-169.

Anhuf, D., & Winkler, H. (1999). Geographical and ecological settings of the Surumoni-crane-project (Upper Orinoco, Estado Amazonas, Venezuela). *Anzeiger Mathematisch-naturwissenschaftliche Klasse Abt. I*, 135: 3-23.

Anthony, M. R., & Kay, R. F. (1993). Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. *American Journal of Science*, 293(A), 356.

Anyonge, W., 1991. Fauna from a new Lower Miocene locality west of Lake Turkana, Kenya. *Journal of Vertebrate Paleontology* 11: 378-90.

Aquino, R., López, L., Falcón, R., Dìaz, S., & Gálvez, H. (2019). First inventory of primates in the montane forests of the Pasco and Ucayali Regions, Peruvian Amazon. *Primate Conservation*, 33: 1-11.

Arditit S.I. (1992) "Variaciones estacionales en la actividad y dieta de *Aotus azarae* y *Alouatta caraya* en Formosa, Argentina.*" Boletín Primatológico Latinoamericano*, 3:11–30.

Arman, S.D., Ungar, P.S., Brown, C.A., DeSantis, L.R., Schmidt, C., & Prideaux, G.J. (2016). Minimizing inter-microscope variability in dental microwear texture analysis. *Surface Topography: Metrology and Properties*, 4(2): 024007.

Asensio-Herrero, N., Cristóbal-Azkarate J., Dias, P.A.D., Veà J.J., Rodríguez-Luna E. (2007) "Foraging habits of Alouatta *palliata mexicana* in three forest fragments." *Folia Primatologica* 78:141–153.

Ayliffe, L. K., and Chivas, A. R. (1990) "Oxygen Isotope Composition of the Bone Phosphate of Australian Kangaroos : Potential as a Palaeoenvironmental Recorder." *Geochimica et Cosmochimica Acta* 54: 2603–2609.

Barbour, M. G. (2007). Stable oxygen isotope composition of plant tissue: a review. *Functional Plant Biology*, 34: 83–94.

Batumike, R., Imani, G., Bisimwa, B., Mambo, H., Kalume, J., Kavuba, F., & Cuni-Sanchez, A. (2022). Lomami Buffer Zone (DRC): Forest composition, structure, and the sustainability of its use by local communities. *Biotropica*, 54(2): 289-300.

Beaudrot, L., Struebig, M.J., Meijaard, E., *et al.* (2013) “Interspecific interactions between primates, birds, bats, and squirrels may affect community composition on Borneo.” *American Journal of Primatology*, 75: 170-185.

Beeson, M., Tame, S., Keeming, E., & Lea, S. E. G. (1996). Food habits of guenons (Cercopithecus spp.) in Afro-montane forest. *African Journal of Ecology*, 34(2): 202-210.

Begun, D. R., Henke, W., & Tattersall, I. (2015). *Handbook of paleoanthropology*.

Behrensmeyer, A. K., Deino, A. L., Hill, A., Kingston, J. D., Saunders, J. J., 2002. Geology and geochronology of the middle Miocene Kipsaramon site complex, Muruyur Beds, Tugen Hills, Kenya. *Journal of Human Evolution*, 42: 11-38.

Benefit, B.R. (1991) The taxonomic status of Maboko small apes. *American Journal of Physical Anthropology*, 85(Supp 12): 50–51

Benefit, B. R. (2003). A comparison of Kenyapithecus and Simiolus from middle Miocene deposits at Fort Ternan and Maboko Island. *American Journal of Physical Anthropology* (pp. 64-64).

Benefit, B.R. & McCrossin, M. (1989). New primate fossils from the Middle Miocene of Maboko Island, Kenya. *Journal of Human Evolution*, 18: 493–497.

Berthaume, M.A. (2016) Food Mechanical Properties and Dietary Ecology. *American Journal of Physical Anthropology*, 159: S79–104.

Berthaume, M. A., & Schroer, K. (2017). Extant ape dental topography and its implications for reconstructing the emergence of early Homo. *Journal of Human Evolution*, 112: 15-29.

Berthaume, M. A., Winchester, J., & Kupczik, K. (2019). Effects of cropping, smoothing, triangle count, and mesh resolution on 6 dental topographic metrics. *PLoS One*, 14(5): e0216229.

Berthaume, M.A., Lazzari, V., Guy, F. (2020) The landscape of tooth shape: Over 20 years of dental topography in primates. *Evolutionary Anthropology*, 29: 245–262.

Bicca-Marques, J.C. (1992) Drinking behavior in the black howler monkey (*Alouatta caraya*). *Folia Primatologica,* 58: 107-111.

Bicca-Marques, J.C., Calegaro-Marques, C. (1994) Exotic plant species can serve as staple food sources for wild howler populations. *Folia Primatologica*, 63: 209–211.

Bicca-Marques, J.C., Muhle, C.B., Prates, H.M., Garcia de Oliveira, S., Calegaro-Marques C. (2009) Habitat impoverishment and egg predation by *Alouatta caraya. International Journal of Primatology,* 30: 743-748.

Bilsborough, A., Rae, T.C. (2014). Hominoid Cranial Diversity and Adaptation. In: Henke, W., Tattersall, I. (eds) *Handbook of Paleoanthropology*. Springer, Berlin, Heidelberg

Bishop, W. W., Miller, J. A., & Fitch, F. J., 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science*, 267: 669-699

Bol'shakov, V.N., Vasil. A. G., Yu, V., et al. (2015) "Coupled Biotopic Variation in Populations of Sympatric Rodent Species in the Southern Urals." *Russian Journal of Ecology*, 46 (4): 339–344.

Boschetto, H.B., Brown, F.H., McDougall, I., (1992). Stratigraphy of the Lothidok Range, northern Kenya, and K/Ar ages of its Miocene primates. *Journal of Human Evolution*, 22: 47-71.

Bouliere, F. (1985) "Primate communities: Their structure and role in tropical ecosystems." *International Journal of Primatology*, 6(1): 1-26.

Bovicino, C.R. (1989) "Ecologia e comportamento de *Alouatta belzebul* (Primates: Cebidae) na Mata Atlantica." *Revista Nordestina De Biologia*, 6(2):149-179.

Boyer, D.M. (2008) "Relief Index of Second Mandibular Molars Is a Correlate of Diet among Prosimian Primates and Other Euarchontan Mammals." *Journal of Human Evolution*, 55: 1118–1137.

Boyer, D. M., Evans, A.R., Jernvall, J. (2010) "Evidence of dietary differentiation among late Paleocene-Early Eocene Plesiadapids." *American Journal of Physical Anthropology*, 142: 194-210.

Boyer, D. M., Winchester, J., & Kay, R. F. (2015). The effect of differences in methodology among some recent applications of shearing quotients. *American Journal of Physical Anthropology*, 156(1): 166–178.

Bravo, S.P. and Zunio, G.E. (1999) "Germination of seeds from three species dispersed by black howler monkeys (*Alouatta caraya).*" *Folia Primatologica,* 71: 342-345.

Bravo, S.P. and Sallenave, A. (2003) "Foraging behavior and activity patterns of *Alouatta caraya* in the Northeastern Argentinean Flooded Forest." *International Journal of Primatology*, 24: 825–846.

Brown, W.L. and Wilson E.O. (1956) “Character Displacement.” *Systematic Zoology,* 5(2): 49-64.

Bryer, M.A.H., Chapman, C.A., and Rothman, J.M. (2013) “Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*).” *Behaviour*, 150: 277-293.

Bunn, J. M., Boyer, D. M., Lipman, Y., St. Clair, E.M., Jernvall, J., and Daubechies, I., (2011) “Comparing Dirichlet Normal Surface Energy of Tooth Crowns , a New Technique of Molar Shape Quantification for Dietary Inference , With Previous Methods in Isolation and in Combination.” *American Journal of Physical Anthropology*, 145: 247–61.

Buikstra, J. E., & Ubelaker, D. H. (1994). *Standards for data collection from human skeletal remains*. Arkansas Archaeological Survey Research Series No. 44. Fayetteville: Arkansas Archaeological Survey.

Butler, P. M. (1983). Evolution and mammalian dental morphology. *Journal de Biologie Buccale*, 11(4): 285-302.

Butynski, T.M. (1990) “Comparative ecology of blue monkeys (*Cercopithecus mitis)* in high and low density subpopulations.” *Ecological Monographs*, 60(1):1-26.

Butynski, T.M. (2015) “The guenons: An overview of diversity and taxonomy.” In Mary E. Glenn and Marina Cords (Eds) *The Guenons: Diversity and Adaptation in African Monkeys.*

Butynski, T. M., & De Jong, Y. A. (2020). Taxonomy and biogeography of the gentle monkey Cercopithecus mitis Wolf, 1822 (Primates: Cercopithecidae) in Kenya and Tanzania, and designation of a new subspecies endemic to Tanzania. *Primate Conservation*, 34: 71-127

Buzzard, P.J. (2006) “Ecological partitioning of *Cercopithecus campbelli, C. petaurista, and C. diana* in the Taï Forest.” *International Journal of Primatology*, 27(2): 529-558.

Bryer, M. A., Chapman, C. A., & Rothman, J. M. (2013). Diet and polyspecific associations affect spatial patterns among redtail monkeys (Cercopithecus ascanius). *Behaviour*, 150(3-4), 277-293.

Bryer, M.A.H., Chapman, C.A., Raubenheimer, D. Lambert, J.E., Rothman, J.M. (2015) “Macronutrient and energy contributions of insects to the diet of a frugivorous monkey (*Cercopithecus ascanius*).” *International Journal of Primatology*, 36: 839-854.

Camargo, C.C., Porfírio, S., Rylands, A.B., Langguth, A. (2008) "Variação sazonal e longitudinal nos padrões de comportamento em uma população de *Alouatta belzebul* (Primates: Atelidae) do Nordeste brasileiro." In: Ferrari SF, Rimoli J (eds) *A primatologia no Brasil* 9. Sociedade Brasileira de Primatologia, Biología Geral e Experimental—UFS, Aracaju, Brazil.

Campbell, C.J. (2000) *The reproductive biology of black-handed spider monkeys (Ateles geoffroyi): integrating behaviour and endocrinology*. PhD Thesis. Berkley: University of California.

Carter, M. L. (2001) *Sensitivity of stable isotopes (^{13}C, ^{15}N, and ^{18}O) in bone to dietary specialization and niche separation among sympatric primates in Kibale National Park, Uganda.* Doctoral Dissertation, University of Chicago.

Carter, M.L. and Bradbury M. W. (2016) "Oxygen Isotope Ratios in Primate Bone Carbonate Reflect Amount of Leaves and Vertical Stratification in the Diet." *American Journal of Primatology* 78: 1086–97.

Castellanos, H. G. (1998). Floristic composition and structure, tree diversity, and the relationship between floristic distribution and soil factors in El Caura Forest Reserve, southern Venezuela. *Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring*, 507-533.

Castellanos, H.G., Chanin P. (1996) "Seasonal differences in food choice and patch preference of long-haired spider monkeys (*Ateles belzebuth*)." In: Norconk MA, Rosenberger LA, Garber PA, editors. *Adaptive radiations of neotropical primates*. pp 451–466.

Cavalcante, T., Strier, K., & Bicca-Marques, J. (2021). Degree of Frugivory Predicts Rates of Food-Related Agonism and Intragroup Proximity in Wild Gray Woolly Monkeys (*Lagothrix lagotricha cana*). *International Journal of Primatology*, 42(4), 533-547.

Celeira de Lima, M.M., Sampaio, I., dos Santos Vieira, R., Schneider, H. (2007) "Spider monkey, Muriqui and woolly monkey relationships revisited." *Primates*, 48:55-63.

Cerling, T. E., Hart, J. A., & Hart, T. B. (2004). Stable isotope ecology in the Ituri Forest. *Oecologia*, 138(1), 5-12.

Chapin, J. P., & Lang, H. (1924). Size-variation in Pyrenestes, a genus of weaver-finches. *Bulletin of the AMNH*; v. 49, article 4.

Chapman, C. A. (1987a) "Flexibility in Diets of Three Species of Costa Rican Primates." *Folia Primatologica* 49:90-105.

Chapman, C.A. (1987b). Spider monkey social-organization-determinants of group living. *International Journal of Primatology* 8(5): 476-476).

Chapman, C.A and Chapman L.J. (1991) "The foraging itinerary of spider monkeys: When to eat leaves?" *Folia Primatologica* 56:162-166.

Chapman, C. A., and Chapman, L. J. (1996) "Mixed-Species Primate Groups in the Kibale Forest: Ecological Constraints on Association." *International Journal of Primatology* 17 (1): 31–50.

Chapman, C.A and Chapman L.J. (2000) "Interdemic variation in mixed species association patterns: common diurnal primates of Kibale National Park, Uganda." *Behavioral Ecology and Socialbiology* 47(3):129-139.

Chase, J. M., & Leibold, M. A. (2003) *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.

Chaves, O.M., Stoner, K.E., and Arroyo-Rodriguez (2012) Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. *Biotropica*, 44(1): 105-113.

Chiarello A.G. (1993) "Activity pattern of the brown howler monkey *Alouatta fusca*, Geoffroy 1812, in a forest fragment of southeastern Brazil." *Primates*, 34:289–293

Chiarello, A.G. (1994) "Diet of the brown howler monkey *Alouatta fusca*in a semi-deciduous forest fragment of southeastern Brazil." *Primates*, 35(1): 25-34.

Chiarello, A. G. (1995). Density and habitat use of primates at an Atlantic forest reserve of southeastern Brazil. *Revista Brasileira de Biologia*, 55(1), 105-110.

Cifuentes, E.F., Ramırez M.A., León J, Galvis N, Vargas S, Stevenson P.R. (2013) "Dieta de los churucos colombianos (*Lagothrix lagothricha lugens*) en relación con la productividad de frutos en el Parque Nacional Natural Cuevade Los Guacharos." In: Defler T.R., Stevenson P.R., Bueno M.L., Guzman-Caro D.C. (eds) *Primates Colombianos en Peligro de Extinción*. Asociación Primatologica Colombiana, Bogota, pp 294–312.

Codron, D., Lee-Thorp, J. A., Sponheimer, M., de Ruiter, D., & Codron, J. (2008). What insights can baboon feeding ecology provide for early hominin niche differentiation? *International Journal of Primatology*, 29, 757-772.

Collins, A. (2008) “The taxonomic status of spider monkeys in the 21st century.” Pp. 50–78 in C. J. Campbell, ed. *Spider monkeys: the biology, behavior and ecology of the genus Ateles.* Cambridge Univ. Press, Cambridge.

Collyer, M. L., & Adams, D. C. (2007). Analysis of two-state multivariate phenotypic change in ecological studies. *Ecology*, 88(3), 683-692.

Colorado Zuluaga, G. J. (2015). How ecological communities are structured: a review on ecological assembly rules. *Revista EIA*, (24), 27-53.

Cords, M. (1986) “Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis.” Journal of Animal Ecology*, 55(3): 811-827.

Cords, M. (1987) *Mixed Species Association of Cercopithecus monkeys in the Kakamega Forest, Kenya*. University of California Publication in Zoology.

Cords, M. (1990) “Mixed-species association of East African guenons: General patterns or specific examples?” *American Journal of Primatology*, 21: 101-114.

Cote, S., Nasser M., and Nengo I. (2014) “Additional Mandibles of *Rangwapithecus gordoni*, an Early Miocene Catarrhine from the Tinderet Localities of Western Kenya.” *American Journal of Physical Anthropology*, 153 (3): 341–52.

Cote, S., McNulty, K.P., Stevens, N.J., Nengo, I.O. (2016) “A detailed assessment of maxillary morphology of *Limnopithecus evansi* with implications for taxonomy of the genus.” *Journal of Human Evolution*, 94: 83-91.

Cristobal-Azkarate, J., Urbani, B., Asensio, N. (2015) “Interactions of howler monkeys with other vertebrates: A review.” In Martin M. Kowalewski, Paul A. Garber, Liliana Cortes-Ortiz, Bernardo Urbani, and Dionisios Youlatos (Eds). *Howler Monkeys: Behavior, Ecology, and Conservation.* Springer.

Crowley, B. E. (2012). Stable isotope techniques and applications for primatologists. *International Journal of Primatology*, 33, 673-701.

Crowley, B. E. (2014) “Oxygen Isotope Values in Bone Carbonate and Collagen Are Consistently Offset for New World Monkeys.” *Biology Letters*, 10 (11).

Crowley, B. E., Godfrey, L. R., Thomas, P., Koch, P. L., Dominy, N. J., and Zermen, P. (2012) “Extinction and Ecological Retreat in a Community of Primates.” *Proceedings of the Royal Society*, 279: 3597–3605.

Cuozzo, F.P., Ungar, P.S., Sauther, M. (2012) “Primate Dental Ecology: How teeth respond to the environment.” *American Journal of Physical Anthropology,* 148(2):159-162.

Dammhahn, M., & Kappeler, P. M. (2014). Stable isotope analyses reveal dense trophic species packing and clear niche differentiation in a Malagasy primate community. *American Journal of Physical Anthropology*, 153(2), 249-259.

Darwin, C. (1864). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* (A new edition / revised and augmented by the author.. ed.). New York: D. Appleton and Company.

Davis, M., & Pineda Munoz, S. (2016). The temporal scale of diet and dietary proxies. *Ecology and Evolution*, 6(6), 1883–1897.

Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: the next generation. *Ecology Letters,* 8(8), 875-894.

Dayan, T., Tchernov, E., Yom-Tov, Y., & Simberloff, D. (1989). Ecological character displacement in Saharo-Arabian Vulpes: outfoxing Bergmann's rule. *Oikos,* 263-272.

De Almeida Rocha, J.M., Pinto, M.P., Boubil, J.P, and Grelle, C.E.V. (2015) “The role of competition in structuring primate communities under different productivity regimes in the Amazon.” *PLOS One:* 1-15.

De Jong, Y.A. & Butynski, T.M. 2009. *Primate Biogeography, Diversity, Taxonomy and Conservation of the Coastal Forests of Kenya.* Report to the Critical Ecosystem Partnership Fund. Eastern Africa Primate Diversity and Conservation Program, Nanyuki, Kenya.

De León, L. F., Podos, J., Gardezi, T., Herrel, A., & Hendry, A. P. (2014). Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists. *Journal of Evolutionary Biology*, 27(6), 1093-1104.

De Souza, L.L., Ferrari, S.F., da Costa, M.L. et al. (2002) “Geophagy as a Correlate of Folivory in Red-Handed Howler Monkeys (*Alouatta belzebul*) from Eastern Brazilian Amazonia.” *Journal of Chemical Ecology*, 28: 1613–1621.

Deane, A. S. (2009) “Early Miocene Catarrhine Dietary Behaviour : The Influence of the Red Queen Effect on Incisor Shape and Curvature.” *Journal of Human Evolution*, 56 (3): 275–85.

Detwiler, K.M (2002) “Hybridization between Red-tailed Monkeys (*Cercopithecus ascanius*) and Blue Monkeys (*C. mitis*) in East African Forests.” In Mary E.

Glenn and Marina Cords (Eds). *The Guenons: Diversity and Adaptation in African Monkeys* (Pp 79-98).

Dew, J. L. (2001) *Synecology and Seed Dispersal in Woolly Monkeys (Lagothrix Lagotricha Poeppigii) and Spider Monkeys (Ateles Belzebuth Belzebuth) in Parque Nacional Yasuni, Ecuador*, University of California, Davis, California.

Dew, J.L. (2005) "Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poepogii* and *Ateles belzebuth belzebuth*." *International Journal of Primatology*,26(5): 1107-1135.

Defler, T.R. and Defler, S.B. (1996) "Diet of a group of *Lagothrix lagothricha lagothricha* in Southeastern Colombia." *International Journal of Primatology*, 17(2): 161-190.

Diamond J.M. (1975) "Assembly of species communities". In: Cody M.L., Diamond J.M. (Eds). *Ecology and evolution of communities*. Cambridge, MA: Harvard University Press. p 342– 444.

DiFiore, A. (2004) "Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest." *International Journal of Primatology*, 25(4): 767-801.

DiFiore T. and Link, A. (2008) "Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity." *Journal of Tropical Ecology,* 22(3): 235-246.

DiFiore, A. and Rodman, P.S. (2001) "Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigiii)* in a neotropical *terra firma* forest." *International Journal of Primatology*, 22, 449–480.

DiFiore, A., Link, A., and Dew, J.L. (2008) "Diets of wild spider monkeys". *In* Christina J. Campbell (Ed). *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles* Cambridge University Press, Pp 81- 137.

East, R. (1988). *Antelopes: global survey and regional action plans. Part 1: East and Northeast Africa*. IUCN.

East, R. (1990). *Antelopes: global survey and regional action plans. Part 3: West and Central Africa*. IUCN.

Elders, A.A. (2009) "Hylobatid diets revisited: The importance of body mass, fruit availability and interspecific competition." In S. Lappan and D.J Whittaker (Eds). *The Gibbons Developments in Primatology: Process and Prospects* (Pp 133-159).

Elders, A.A. (2013) *Competition among three primate species at Way Canguk, Sumatra, Indonesia.* Ph.D Dissertation. Stony Brook University.

Else, J., Eley, R., Suleman, M., & Lequin, R. (1985). Reproductive biology of Sykes and blue monkeys (*Cercopithecus mitis*). *American Journal of Primatology*, 9(3), 189-196.

Eronen, J. T., Polly, P. D., Fred, M., Damuth, J., Frank, D. C., Mosbrugger, V., ... & Fortelius, M. (2010). Ecometrics: the traits that bind the past and present together. *Integrative Zoology*, 5(2), 88-101.

European Commission, Joint Research Centre (2022). The Digital Observatory for Protected Areas (DOPA), October 2022, Ispra, Italy

Evans, A. R., Wilson, G. P., Fortelius, M., & Jernvall, J. (2007). High-level similarity of dentitions in carnivorans and rodents. *Nature*, 445(7123), 78-81.

Evans, Alistair R. (2013). “Shape Descriptors as Ecometrics in Dental Ecology.” *Hystrix* 24 (1): 1–8.

Fairgrieve, C. 1995. *The Comparative Ecology of Blue Monkey (Cercopithecus mitis stuhlmanni) in Logged and Unlogged Forest, Budongo Forest Reserve, Uganda: The Effect of Logging on Habitat and Population Density*, Ph.D. Thesis, University of Edinburgh, Edinburgh, Scotland

Fairgrieve, C., & Muhumuza, G. (2003). Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni Matschie*) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *African Journal of Ecology*, 41(2), 141–149.

Fedigan L.M., Jack K.M. (2012) Tracking neotropical monkeys in Santa Rosa: Lessons from a regenerating Costa Rican Dry Forest. In: Kappeler P., Watts D. (eds) *Long-Term Field Studies of Primates*. Springer, Berlin, Heidelberg.

Feibel, C. S., Brown, F. H., 1991. Age of the primate-bearing deposits on Maboko Island, Kenya. *Journal of Human Evolution*, 21, 221-5.

Felton, A.M., Felton, A., Wood, J.T., Lindenmayer. D.B. (2008) Diet and Feeding Ecology of Ateles chamek in a Bolivian Semihumid Forest: The Importance of Ficus as a Staple Food Resource. *International Journal of Primatology* 29: 379-403.

Fernandez, V.A., Pave, R., Peker, S. M., Perez-Rueda, M.A. (2017) “Interspecific interactions between wild black and gold howler monkeys (*Alouatta caraya*) and other mammals in northeastern Argentina.” *Acta Ethologica* 20(1):17-26.

Fleagle, J.G. (2013) *Primate Adaptation and Evolution.* Academic Press, San Diego.

Fleagle, J.G.and Kay, R.F. (1985) "The paleobiology of catarrhines" In: Delson, E. (Ed), *Ancestors: The Hard Evidence.* Alan R. Liss, New York. Pp 23-36.

Fleagle, J.G., Simons, E.L., 1978. Micropithecus clarki, a small ape from the Miocene of Uganda. *American Journal of Physical Anthropology* 49, 427-40.

Flores-Escobar, E., Sanpera, C., Jover, L., Cortés-Ortiz, L., Rangel-Negrín, A., Canales-Espinosa, D., & Dias, P. A. D. (2020). Isotopic niche partitioning in two sympatric howler monkey species. *American Journal of Physical Anthropology*, 172(3), 438-446.

Fonseca, M.L., Ramírez-Pinzón, M.A., McNeil, K.N. et al. (2022). Dietary preferences and feeding strategies of Colombian highland woolly monkeys. *Scientific Reports* 12, 14364.

Fourie, N.H. et al (2008). Biogeochemical and Craniometric Investigation of Dietary Ecology, Niche Separation, and Taxonomy of Plio-Pleistocene Cercopithecoids From the Makapansgat Limeworks. *American Journal of Physical Anthropology* 135(2): 121-135.

Frogge, H., Jones, R. A., Angedakin, S., Busobozi, R., Kabagambe, P., Angwela, F. O., ... & Brown, M. (2022). Constraints on population growth of blue monkeys (Cercopithecus mitis) in Kibale National Park, Uganda. *Behaviour*, 1-27.

Ganzhorn, J. U. (1989) "Niche separation of seven lemur species in the eastern rainforest of Madagascar." *Oecologia*, 79, 279–286.

Ganzhorn, J. U. (1997). Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. *Journal of Zoology*, 241(3), 533-542.

Ganzhorn J.U. (1999) "Body mass, competition and the structure of primate communities." In: Fleagle J.G., Janson C.H., and Reed K.E., (Eds). *Primate communities*. Cambridge, UK: Cambridge University Press. p 141-157.

Gathua, M. (1999) "Social Interactions between two sympatric forest guenons, *Cercopithecus ascanius* and *Cercopithecus mitis*, in Kenya." *Folia Primatologica* 71:353-355.

Gathua, M. (2000). Intraspecific *Variation in Foraging Patterns of Redtail Monkeys (Cercopithecus ascanius) in the Kakamega Forest, Kenya*. Ph.D. Thesis, Columbia University, New York.

Gautier-Hion, A. (1980). Seasonal Variations of Diet Related to Species and Sex in a Community of Cercopithecus Monkeys. *Journal of Animal Ecology*, 49(1), 237–269.

Gautier-Hion, A., Quris, R., & Gautier, J.-P. (1983) "Monospecific vs. polyspecific life: a comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys." *Behavioral Ecology and Sociobiology* 12: 325–335.

Gause G.F. (1934) *The Struggle for Existence*. Williams and Wilkins Company, Baltimore.

Godfrey, L. R., Winchester, J. M., King, S. J., Boyer, D. M., & Jernvall, J. (2012). Dental topography indicates ecological contraction of lemur communities. *American Journal of Physical Anthropology*, 148(2), 215-227.

Gonzalez, M., Clavijo, L., Betancur, J., Stevenson, P.R. (2016) "Fruits eaten by woolly monkeys (*Lagothrix lagotricha*) at local and regional scales." *Primates* 57:241-251.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London*. Series B. Biological Sciences, 205(1161), 581-598.

Gittens, S.P, and Raemakers, J.J (1980) Siamang, Lar, and Agile Gibbons. In David J. Chivers (Ed) *Malayan Forest Primates* pp 63-106.

Glander KE (1981) "Feeding patterns in mantled howling monkeys." In: Kamil AC, Sargent T.D. (eds) *Foraging behavior: ecological, ethological and psychological approaches*. Garland, New York.

Grossman A. *Ecological and morphological diversity in catarrhine primates from the Miocene of Africa*. State University of New York at Stony Brook; 2008.

Guillotin, M., Dubost, G., & Sabatier, D. (1994) "Food choice and food competition among the three major primate species of French Guiana". *Journal of Zoology*, 233(4): 551–579.

Harrison, T. (1981) "New finds of small fossil apes from the Miocene locality at Koruin Kenya." *Journal of Human Evolution*. 10, 129-137.

Harrison, T., 1982. *Small-bodied apes from the Miocene of East Africa*. Ph.D. thesis, University of London.

Harrison, T., 1986a. New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Oreopithecidae. *American Journal of Physical Anthropology* 71, 265-84.

Harrison, T. (1988) "A taxonomic revision of the small catarrhine primates from the Early Miocene of East Africa." *Folia Primatologica* 50: 59-108.

Harrison, T. (1989) A new species of *Micropithecus* from the middle Miocene of Kenya. *Journal of Human Evolution* 18: 537-557.

Harrison, T. (1993) Cladistic Concepts and the Species Problem in Hominoid Evolution. In *Species, Species Concepts and Primate Evolution* (Advances in Primatology, pp. 345-371). Boston, MA: Springer US.

Harrison, T. (2002) "Late Oligocene to middle Miocene catarrhines from Afro-Arabia." In: Hartwig, W.C. (Ed.), *The Primate Fossil Record.* Cambridge University Press, Cambridge, Pp. 311-333.

Harrison, T. (2010) "Dendropithecoidea, Proconsuloidea, and Hominoidea." In: Werdelin, L. Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley: University of California Press, Pp 429-469.

Hart, T.B. 1985. *The ecology of a single-species-domi-nant forest and of a mixed forest in Zaire, Africa*. PhD thesis, Michigan State University, East Lansing, USA.

Hernandez-Camacho J. and Cooper, R.W. (1976) "The nonhuman primates of Colombia." Richard W. Thorington, and Paul G, Battelle (eds) in *Neotropical Primates : Field Studies and Conservation : Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates:* pp 35-69.

Herrera, C. M. (1978). Niche-shift in the genus Parus in southern Spain. *Ibis*, 120(2), 236-240.

Hertler, C., & Volmer, R. (2008). Assessing prey competition in fossil carnivore communities—a scenario for prey competition and its evolutionary consequences for tigers in Pleistocene Java. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257(1-2), 67-80.

Hickey, M. B. C., Acharya, L., & Pennington, S. (1996). Resource partitioning by two species of vespertilionid bats (Lasiurus cinereus and Lasiurus borealis) feeding around street lights. *Journal of Mammalogy*, 77(2), 325-334.

Hill, A., Nengo, I. O., Rossie, J.B. (2013) "A *Rangwapithecus gordoni* mandible from the early Miocene site of Songhor, Kenya." *Journal of Human Evolution*. 65: 490-500.

Hogstad, O. (1978). Differentiation of foraging niche among tits, Parus spp., in Norway during winter. *Ibis*, 120(2), 139-146.

Hopwood, A.T., (1933). Miocene primates from British East Africa. *The Annals and Magazine of Natural History* 11, 96-8.

Houle, A., Vickery, W. L. and Chapman, C.A. (2006) “Testing mechanisms of coexistence among two species of frugivorous primates.” *Journal of Animal Ecology*, 75: 1034-1044.

Houle, A., W. L. Vickery, and C.A. Chapman (2007) “Within-tree variation in fruit primary productivity among 18 tree species in Kibale National Park, Uganda.” *International Journal of primatology*, 28: 1197-1217.

Houle, A., C.A. Chapman, and W.L. Vickery (2010) “Intratree vertical variation of fruit density and the nature of contest competition in frugivores.” *Behavioral Ecology & Sociobiology*, 64: 429-441.

Huber, O. (2001). Conservation and environmental concerns in the Venezuelan Amazon. *Biodiversity & Conservation*, 10(10), 1627-1643.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, 93, 145–159.

Hvenegaard, G., & Dearden, P. (1998). Linking ecotourism and biodiversity conservation: a case study of doi inthanon national park, thailand. *Singapore Journal of Tropical Geography*, 19(2), 193-211.

Inogwabini, BI. (2020). *Assessing the Needs in Lands in the Lake Tumba Landscape. In: Reconciling Human Needs and Conserving Biodiversity: Large Landscapes as a New Conservation Paradigm. Environmental History*, vol 12. Springer, Cham.

Isbell, L. A. and Young, T.P. (2002) “Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity.” *Behaviour* 139:177-202.

Iwanaga, S., Ferrari, S. F. (2002) “Geographic Distribution of Red Howlers (*Alouatta*).” *International Journal* 23 (6): 1245–56.

Janson, C. (1985) “Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*).” *Behavioral Ecology and Sociobiology*, 18(2): 125–138.

Jansma, R. J. (2019). *Anatomy, Systematics, and Evolution of Catarrhines from the Late Oligocene and Early Miocene of Eastern Africa.* Ph.D Thesis. University of Minnesota.

Jernvall, J. T. (1995). Mammalian molar cusp patterns: developmental mechanisms of diversity. *Acta Zool. Fenn* 198:(1-61).

Kamilar, J. M. (2009). Interspecific variation in primate countershading: effects of activity pattern, body mass, and phylogeny. *International Journal of Primatology*, 30(6), 877-891.

Kamilar, J.M. and Ledogar, J.A. (2011) "Species co-occurrence patterns and dietary resource competition in primates." *American Journal of Physical Anthropology* 144: 131-139.

Kaplin, B. A., & Moermond, T. C. (1998) "Variation in seed handling by two species of forest monkeys in Rwanda." *American Journal of Primatology*, 45(1), 83–101.

Kay, R. F. (1975). The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology*, 43(2), 195-215.

Kay, R F. (1977) "The Evolution of Molar Occlusion in the Cercopithecidae and Early Catarrhines." *American Journal of Physical Anthropology* 46 (2): 327–52.

Kay, R. F. (1977) "Diets of Early Miocene African Hominoids." *Nature* 268 (18): 628–30.

Kay, R. F. and W. Hylander. 1978. The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia); pp. 173-191 in G. Montgomery (ed.), The Ecology of Arboreal Folivores. Smithsonian Institution Press, Washington, D.C.

Ungar, P. S., & Kay, R. F. (1995). The dietary adaptations of European Miocene catarrhines. *Proceedings of the National Academy of Sciences,* 92(12), 5479-5481.

Kay, R.F., Ungar, P.S. (1997) "Dental evidence for diet in some Miocene catarrhines with comments on the effects of phylogeny on the interpretations of adaptation." In: Begun, D.R., Ward, C., Rose, M. (Eds.), *Function, Phylogeny and Fossils: Miocene Hominoids and Great Ape and Human Origins*. Plenum Press, New York, Pp. 131-151.

Ungar, P.S., Teaford, M., & Kay, R.F. (2004). Molar microwear and shearing crest development in Miocene catarrhines. *Anthropologie* (1962-), 42(1), 21-35.

Keller, J., Cicak, T., McNulty, K., and Fox, D. (2017) “Resolving Rodent Ecology Using 3D Dental Shape Descriptors.” American Mammology Society Annual Meeting: Moscow, Idaho.

Kelley, J., Ward, S., Brown, B., Hill, A., Duren, D.L., 2002. Dental remains of Equatorius africanus from Kipsaramon, Tugen Hills, Baringo District, Kenya. *Journal of Human Evolution* 42, 39-62.

Khamyong, S., Lykke, A., Seramethakun, D., & Barfod, A. (2003). Species composition and vegetation structure of an upper montane forest at the summit of Mt. Doi Inthanon, Thailand. *Nordic Journal of Botany, 23*(1), 83-97.

Kinzey, W. (1978). Feeding behaviour and molar features in two species of titi monkey. *Recent Advances in Primatology*, 373-385.

Klein, L., & Klein, D. (1973). Observations on two types of neotropical primate intertaxa associations. *American Journal of Physical Anthropology*, 38(2), 649-653.

Klein, L. L. and Klein, D. B. (1976) “Neotropical primates: Aspects of habitat usage, population density, and regional distribution in La Macarena, Colombia” Richard W. Thorington, and Paul G, Battelle (eds) in *Neotropical Primates : Field Studies and Conservation : Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates:* pp 70-78.

Klein, L. L. and Klein, D. B. (1977) “Feeding behaviour of the Colombian spider monkey.” In Clutton-Brock, T. H. (Eds.). *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes* (Pp. 153-181).

Korchia, C. S. F. (2020). *Behavioral Ecology of Cercopithecus lomamiensis in the Lomami National Park and Buffer Zone, Democratic Republic of the Congo* (Doctoral dissertation, Florida Atlantic University).

Krause, D.W. (1986) “Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America.” Contributions to Geology Univeristy of Wyoming Special Paper 3: 95-117.

Krigbaum, J., Berger, M. H., Daegling, D. J., and McGraw, W. S. (2013) “Stable Isotope Canopy Effects for Sympatric Monkeys at Taï Forest, Côte d’Ivoire.” *Biology Letters* 9 (4): 6–10.

Lambert, J. E. (2001). Red-tailed guenons (Cercopithecus ascanius) and Strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology*, 22(2), 189.

Lambert, J.E. (2002) "Resource switching and species coexistence in guenons: a community analysis of dietary flexibility." In: Glenn ME, and Cords M, editors. *The guenons: diversity and adaptation in African monkeys*. New York: Kluwer Academic/Plenum Publishers. p 309-323.

Lawes, M.J., Henzi, S.P., Perrin, M.R. (1990) "Diet and feeding behavior of Samango monkeys (*Cercopithecus mitis labiatus*) in Ngoye Forest, South Africa." *Folia Primatologica* 54: 57-69.

Lawes, M.J. (1991) "Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in Cape Vidal dune forest, South Africa." *Journal of Zoology* 224: 149-173.

Leakey, R.E., Leakey, M.G., 1987. A new Miocene small-bodied ape from Kenya. *Journal of Human Evolution* 16, 369-87.

Lee-Thorp, J. A., Sealy, J. C., & Van Der Merwe, N. J. (1989). Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*, 16(6), 585-599.

Ledogar, J.A., Winchester, J.M., St. Clair, E.M., Boyer, DM., (2013) "Diet and dental topography in pitheciine seed predators." *American Journal of Physical Anthropology* 150(1):107-121.

Link, A., & Di Fiore, A. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *Journal of Tropical Ecology*, 22(3), 235-246.

Link, A., Galvis, N., Marquez, M., Guerrero, J., Solano, C., and Stevenson, P.R. (2012) "Diet of the critically endangered Brown Spider Monkey (*Ateles hybridus*) in an Inter-Andean lowland rainforest in Colombia." *American Journal of Primatology* 74: 1097-1105.

Lister, B. C. (1976). The nature of niche expansion in West Indian Anolis lizards I: ecological consequences of reduced competition. *Evolution*, 659-676.

Locke, E. (2021). Molar Shape, Function, and Tooth Wear in the Evolution of Cercopithecoid Bilophodonty. Ph. D Dissertation. Arizona State University.

Longinelli, Antonio. 1984. "Oxygen Isotopes in Mammal Bone Phosphate : A New Tool for Paleohydrological and Paleoclimatological Research ?" *Geochimica et Cosmochimica Acta* 48: 385–90.

Losos, J. B. (2000). Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences*, 97(11), 5693-5695.

Lowry, B. E., Wittig, R. M., Pittermann, J., & Oelze, V. M. (2021). Stratigraphy of stable isotope ratios and leaf structure within an African rainforest canopy with implications for primate isotope ecology. *Scientific reports*, 11(1), 1-11.

Lucas, Peter W. 2004. *Dental Functional Anatomy: How Teeth Work*. Cambridge: Cambridge University Press.

Ludwig, G., Aguiar, L.M., Svoboda, W.K. et al. (2008) "Comparison of the diet of *Alouatta caraya* (Primates:Atelidae) between a riparian island and mainland on the Upper Parana River, southern Brazil." *Revista Brasileira de Zoologica* 25(3): 419-426.

Macho, G. A., and Lee-Thorp, J.A. (2014) "Niche Partitioning in Sympatric Gorilla and Pan from Cameroon: Implications for Life History Strategies and for Reconstructing the Evolution of Hominin Life History." *PLoS ONE* 9 (7).

MacInnes, D.G., 1943. Notes on the East African Miocene primates. Journal of the East Africa and Uganda Natural History Society 17, 141-81.

MacKinnon, J. (1977). A comparative ecology of Asian apes. *Primates,* 18, 747-772.

MacKinnon, J. R., & MacKinnon, K. S. (1980) "Niche differentiation in a primate community." In D. J. Chivers (Ed.), *Malayan forest primates* (pp. 167–190).

Mantilla-Meluk, H. (2013). Subspecific variation: an alternative biogeographic hypothesis explaining variation in coat color and cranial morphology in Lagothrix lugens (Primates: Atelidae). *Primate Conservation*, 26(1), 33-48.

Mariotti, A. (1983). Atmospheric nitrogen is a reliable standard for natural 15N abundance measurements. *Nature* 303:685-687.

Marsh, L.K. (2003) "Because Conservation Counts: Primates and fragmentation." In Lauren K. Marsh and Colin A. Chapman (Eds). *Primates in Fragments* (Pp 3-11).

Marshall, A.J. and Wrangham, R.W. (2007) "Evolutionary consequences of fallback foods." *International Journal of Primatology* 28:1219-1235.

Marshall RC, Orwin DFG, Gillespie JM. 1991. Structure and biochemistry of mammalian hard keratin. *Electron Microscopy Reviews* 4:47–83.

Martínez-Esquivel LM (2010) "Comparación de hábitos alimentarios y su relación con las infecciones parasíticas en los monos congo (*Alouatta palliata*), de Chomes y Palo Verde, Costa Rica." BSc thesis, Universidad de Costa Rica, San José

Martin, L., 1981. New specimens of *Proconsul* from Koru, Kenya. *Journal of Human Evolution* 10, 139-150.

Martin LB, Olejniczak AJ, Maas MC (2003) Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. *Journal of Human* Evolution 45: 351–367.

Martin, C. H., & Genner, M. J. (2009). High niche overlap between two successfully coexisting pairs of Lake Malawi cichlid fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(4), 579-588.

Martins, M.M. (2008) “Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparison of fruit type, color, and seed size.” *Primates* 49:1-8.

Matsuda, I., & Izawa, K. (2008). Predation of wild spider monkeys at La Macarena, Colombia. *Primates; Journal of Primatology*, 49(1), 65–68.

McGraw, W.S., Vick, A.E., Daegling, D.J. (2014) “Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptations.” *American Journal of Physical Anthropology* 154:413-423.

McNulty, K.P. (2010) “Apes and Tricksters : The Evolution and Diversification of Humans ’ Closest Relatives.” *Evolution Education Outreach*, 322–32.

McNulty, K. P., Begun, D. R., Kelley, J., Manthi, F. K., and Mbua, E. N. (2015) “A Systematic Revision of *Proconsul* with the Description of a New Genus of Early Miocene Hominoid.” *Journal of Human Evolution* 84. Elsevier Ltd: 42–61.

Mendes, S.L. (1989) “Estudo ecologico de *Alouatta fusca* (Primates:Cebidae) na Estacao biologica de Caratinga, MG.” *Revista Nordestina de Biologia* 6(2): 71-104.

Mendes SL (1989) Estudo ecológico de Alouatta fusca (Primates: Cebidae) na Estação de Caratinga, MG. Rev Nord Biol 6:71–104.

Mendes-Pontes AR (1997) Habitat partitioning among primates in Maraca Island, Roraima, northern Brazilian Amazonia. *International Journal of Primatology* 18:131–157

Milton K (1980) *The foraging strategy of howler monkey: a study in primate economics. Columbia* University Press, New York.

Milton K. (1981) “Food choice and digestive strategies of two sympatric primate species.” *American Naturalist* 117:476–495.

Mittermeier, R.A. and van Roosleman, M.G.M. (1981) “Preliminary Observations on Habitat Utilization and Diet in Eight Surinam Monkeys.” *Folia Primatologica* 36: 1-39.

M’Kirera, Francis, and Peter S. Ungar. 2003. “Occlusal Relief Changes with Molar Wear in *Pan Troglodytes Troglodytes* and *Gorilla Gorilla Gorilla*.” *American Journal of Primatology* 60 (2): 31–41.

Morris, D.W., Fox, B.J., Luo, J. and Monamy, V. (2000) “Habitat-dependent competition and the coexistence of Australian heathland rodents.” *Oikos* 91: 294-306

Morse, D. H. (1974) “Niche Breadth as a Function of Social Dominance.” *The American Naturalist*, 108(964), 818–830.

Muhle C.B. (2008) “Estratégias adaptativas de um grupo de bugios-pretos, *Alouatta caraya* (Humboldt, 1812), em um bosque dominado por eucaliptos.” MSc thesis, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS.

Neha, S. A., Khatun, U. H., & Ul Hasan, M. A. (2021). Resource partitioning and niche overlap between hoolock gibbon (Hoolock hoolock) and other frugivorous vertebrates in a tropical semi-evergreen forest. *Primates*, 62, 331-342.

Neville, M., Castro, N., and Marmol, A. (1976) “Censusing primate populations in the reserved area of the Pacaya and Samiria Rivers, Department Loreto, Peru.” *Primates* 17(2): 151-181.

Nunes, A. (1998) “Diet and Feeding Ecology of *Ateles belzebuth belzebuth* at Maracá Ecological Station, Roraima, Brazil.” *Folia Primatologica* 69: 61-76.

Oates, J.F., Gartlan, J.S. and Struhsaker, T.T. 1987. A framework for African rainforest primate conservation. In *Primate Conservation in the Tropical Rainforest* (eds C. W. Marsh and R. A. Mittermeier), pp. 321-327. Alan R. Liss, Inc., New York, USA.

O’Brien, T. G., & Kinnaird, M. F. (2011). Demography of agile gibbons (Hylobates agilis) in a lowland tropical rain forest of southern Sumatra, Indonesia: Problems in paradise. *International Journal of Primatology*, 32, 1203–1217.

Oelze, V. M., Fuller, B. T., Richards, M. P., Fruth, B., Surbeck, M., Hublin, J. J., & Hohmann, G. (2011). Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. *Proceedings of the National Academy of Sciences*, 108(24), 9792-9797.

Oelze, V. M., Head, J. S., Robbins, M. M., Richards, M., and Boesch, C. (2014) “Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis." *Journal of Human Evolution* 66: 95–106.

Oelze, V. M. (2016). Reconstructing temporal variation in great ape and other primate diets: A methodological framework for isotope analyses in hair. American Journal of Primatology, 78(10), 1004-1016.

Oka, K., Hirasaki, E., Hirokawa, Y., Nakano, Y., and Kumakura, H. (2010) "Brief Communication : Three-Dimensional motion analysis of hindlimb during brachiation in a White-Handed Gibbon (*Hylobates Lar*)." *American Journal of Physical Anthropology* 142: 650–54.

Palombit, R.A. (1995) Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus)* and lar gibbons (*Hylobates lar). Folia Primatologica* 68: 321-337.

Pampush, J. D., Winchester, J. M., Morse, P. E., Vining, A. Q., Boyer, D. M., & Kay, R. F. (2016). Introducing molaR: a new R package for quantitative topographic analysis of teeth (and other topographic surfaces). *Journal of Mammalian Evolution*, 23, 397-412.

Pave, R., Peker, S.M. Rano, M. and Ramirez, C. (2009) "Nectar feeding on am exotic tree (*Grevillea robusta*) by *Alouatta caraya* and its possible role in flower pollination." *Neotropical Primates* 16(2): 61-64.

Peppe, D. J., Deino, A. L., McNulty, K. P., Lehmann, T., Harcourt-Smith, W. E., Dunsworth, H. M., Fox, D. L., 2011. New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). *American Journal of Physical Anthropology*, 144 (S52), 237.

Peres, C.A. (1993) Primate responses to phenological changes in an Amazonian *terra firme* Forest. *Biotropica* 26 (1): 98-112.

Peres, C.A. (1994) "Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in Central Amazonia: Comparisons with other Atelines". *International Journal of Primatology* 15, 333–372.

Pfennig, D.W., Pfennig, K.S. (2010) "Character displacement and the origins of diversity." *American Society of Naturalists* 176 (S1): S26–44.

Pickford, M. (1983). Sequence and Environments of the Lower and Middle Miocene Hominoids of Western Kenya. In: Ciochon, R.L., Corruccini, R.S. (eds) *New Interpretations of Ape and Human Ancestry*. Advances in Primatology. Springer, Boston, MA.

Pickford, M. and Andrews, P. (1981). The Tinderet Miocene sequence in Kenya. *Journal of Human Evolution*, 10, 11-33.

Pickford, M., Sawada, Y., Tayama, R., Matsuda, Y. K., Itaya, T., Hyodo, H., Senut, B. (2006). Refinement of the age of the Middle Miocene Fort Ternan Beds, Western Kenya, and its implications for Old World biochronology. *Comptes Rendus Geoscience* 338, 545-55.

Pickford, M., Senut, B., Gommery, D., Musiime, E. (2009). Distinctiveness of *Ugandapithecus* from *Proconsul*. *Estudios Geológicos* 65, 183-241.

Pickford, M., Musalizi, S., Senut, B., Gommery, D., & Musiime, E. (2010). Small apes from the early Miocene of Napak, Uganda. *Geo-Pal Uganda*, (3), 1-110.

Pinto, A. C. B., Azevedo–Ramos, C. and de Carvalho Jr., O. (2003) "Activity patterns and diet of the howler monkey *Alouatta belzebul* in areas of logged and unlogged forest in Eastern Amazonia." *Animal Biodiversity and Conservation* 26(2): 39–49.

Pinto, A.C.B. and Setz, E.Z.F. (2004) "Diet of *Alouatta belzebul discolor* in an Amazonian Rain Forest of Northern Mato Grosso State, Brazil." *International Journal of Primatology* 25(6): 1197-1211.

Pontes, A.R.M. (1997)" Habitat partitioning among primates in Maraca Island, Roraima, Northern Brazilian Amazonia." *International Journal of Primatology* 18(2): 131-157.

Prates H.M. (2007) "Ecologia e comportamento de um grupo de bugios pretos (*Alouatta caraya)* habitante de um pomar em Alegrete, RS, Brasil." MSc thesis, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil.

Prates, H.M. and Bicca-Marques, J.C. (2008) Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an Orchard Forest. *International Journal of Primatology* 29: 703-715.

Prufrock, K. A., Boyer, D. M., & Silcox, M. T. (2016). The first major primate extinction: an evaluation of paleoecological dynamics of North American stem primates using a homology free measure of tooth shape. *American Journal of Physical Anthropology*, 159(4), 683-697.

Puertas, P., & Bodmer, R. E. (1993). Conservation of a high diversity primate assemblage. *Biodiversity & Conservation*, 2(6), 586-593.

Putnam, R.J. and Wratten, S.D. (1984) *Principles of Ecology*. Chapman and Hall, 386 pp.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Racz, G. & Demeter, A. (1998). Character displacement in mandible shape and size in two species of water shrews (Neomys, Mammalia: Insectivora. Acta Zool. Acad. Sci. H., 44, 165–175.

Raemaekers, J. J. (1977). Gibbons and Trees: Comparative Ecology of the Siamang and Lar Gibbons, PhD Dissertation, Cambridge University, Cambridge.

Raemaekers, J. (1978). Changes through the day in the food choice of wild gibbons. *Folia Primatologica,* 30(3), 194-205.

Raemaekers, J.J. (1979) "Ecology of sympatric gibbons." *Folia Primatologica* 31: 227-245.

Raemaekers JJ (1984) Large versus small gibbons: relative roles of bioenergetics and competitionin their ecological segregation in sympatry. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N (eds) *The lesser apes: evolutionary and behavioural biology*. Edinburgh University Press, Edinburgh, pp 209–218

Raemakers, J.J. and Chivers, D.J. (1980) "Socio-ecology of Malayan forest primates." In D. J. Chivers (Ed.), *Malayan forest primates* (pp. 279- 302).

Ramdarshan, A., Alloing-Séguier, T., Merceron, G., and Marivaux, L. (2011) "The Primate Community of Cachoeira (Brazilian Amazonia): A Model to Decipher Ecological Partitioning among Extinct Species." *PLoS ONE* 6 (11).

Reichard, U.H. and Preuschoft, H. (2016) "Why is the siamang larger than other Hylobatids?" In U.H. Reichard (Ed). *Evolution of Gibbons and Siamang, Developments in Primatology: Progress and Prospects* (Pp: 169-183).

Reitsema, L. J. (2012). Introducing fecal stable isotope analysis in primate weaning studies. *American Journal of Primatology*, 74(10), 926-939.

Rímoli A.O., Valdivino E.M., Rímoli J., Ferrari S.F. (2008) "Behavior patterns of a group of black howler monkeys *Alouatta caraya* (Humboldt, 1812) in a forest fragment in Terenos, Mato Grosso do Sul: a seasonal analysis." In: Rímoli J, Ferrari SF (eds) *A primatologia no Brasil 9. Sociedade Brasileira de Primatologia, Biología Geral e Experimental*—UFS, Aracaju, Brazil.

Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (Alouatta pigra): the role of lipids. *American Journal of Primatology*, 79(4), 1-15.

Robinson, B.W. & Wilson, D.S. (1994). Character release and displacement in fishes – a neglected literature. *American Naturalist*, 144, 596–627

Rocha, D.G., Kaefer, I.L (2019) What has become of the refugia hypothesis to explain biological diversity in Amazonia? *Ecology and Evolution* 9: 4302– 4309.

Rodríguez-Luna E., Domínguez-Domínguez L.E., Morales-Mávil J., Martínez-Morales M.M. (2003) "Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island." In: Marsh L.K. (ed) *Primates in fragments: ecology and conservation.* Kluwer Academic, New York.

Rose, M. R., & Lauder, G. V. (Eds.). (1996). Adaptation. Academic Press.

Rosenberger, A.L., Halenar, L. and Cooke, S.B. (2011), The Making of Platyrrhine Semifolivores: Models for the Evolution of Folivory in Primates. *Anatomical Record* 294: 2112-2130

Rosenberger, A. L., Halenar, L., Cooke, S. B., & Hartwig, W. C. (2008). Morphology and evolution of the spider monkey, genus Ateles. Spider monkeys: Behaviour, ecology and evolution of the genus *Atele*s, 19-49.

Rosenberger, A. L., & Kinzey, W. G. (1976). Functional patterns of molar occlusion in platyrrhine primates. *American Journal of Physical Anthropology*, 45(2), 281-297.

Roughgarden, J. (1983). Competition and theory in community ecology. *American Naturalist*, 122, 583–601.

Rudran, R. (1977). *Socio ecology of the blue monkeys (Cercopithecus mitis stuhlmanni) of the Kibale Forest, Uganda.* Smithsonian Institution Press.

Ruette, S., Larroque, J., Albaret, M., and Vandel, J.M. (2015) "Quantifying the age- and sex-dependent morphological variation in two syntopic mustelids : *Martes martes* and *Martes foina*." *Mammalian Biology* 80 (5): 414–423.

Ruff, C., Walker, A., & Teaford, M. (1989). Body mass, sexual dimorphism and femoral proportions of Proconsul from Rusinga and Mfangano Islands, Kenya. *Journal of Human Evolution*, 18(6), 515-536.

Rumiz D.I., Zunino G.E., Obregozo M.L., Ruiz J.C. (1986) "*Alouatta caraya*: habitat and resource utilization in northern Argentina". In: Taub D.M., King A.W. (Eds)

Current perspectives in primate social dynamics. Van Nostrand Reinhold Company, New York

Russo, S. E., Campbell, C.J., Dew, J.L., Stevenson, P.R. and Suarez, S.A. (2005) "A multi-forest comparison of dietary preferences and seed dispersal by *Ateles spp*." *International Journal of Primatology* 26(5):1,017-1,037.

Sandberg, P. A., Loudon, J.E., and Sponheimer, M. (2012) "Stable isotope analysis in primatology : A critical review." *American Journal of Primatology* 74: 969–89.

Santillán, Alfredo & Tegnér, Fredrik & Hammer, Matthias & Mazzolli, Marcelo. (2015). Expedition report: Amazonian plethora: biodiversity monitoring of jaguars, pumas, primates and other flagship species of the Peruvian Amazon.

Schlichte, H. J. (1978). A preliminary report on the habitat utilization of a group of howler monkeys (Alouatta villosa pigra) in the National Park of Tikal, Guatemala. *The Ecology of Arboreal Folivores*, 551-561.

Schluter, D. & McPhail, J.D. (1992). Ecological character displacement and speciation in sticklebacks. *American Naturalist*, 140, 85–108.

McPhail, J.D., and Schluter D. (1992) "Ecological Character Displacement and Speciation in Sticklebacks." *The American Naturalist* 140 (1): 85–108.

Schreier, B.M., Harcourt, A. H., Coppeto, S. A., and Somi, M. F. (2009.) "Interspecific competition and niche separation in primates : A global analysis." *Biotropica* 41 (3): 283–91.

Schroer, K., & Wood, B. (2015). The role of character displacement in the molarization of hominin mandibular premolars. *Evolution*, 69(6), 1630-1642.

Scott, R.S., Ungar,P.S., Bergstrom, T.S. et al (2006). "Dental microwear texture analysis: technical implications." *Journal of Human Evolution* 51(4): 339-349.

Scott, R.S, Teaford, MF., Ungar, PS. (2012) "Dental microwear and anthropoid diets." *American Journal of Physical Anthropology* 147(4):551-579.

Scott, J. E., Campbell, R. M., Baj, L. M., Burns, M. C., Price, M. S., Sykes, J. D., & Vinyard, C. J. (2018). Dietary signals in the premolar dentition of primates. *Journal of Human Evolution*, 121, 221-234.

Senut, B., Pickford, M., Gommery, D., & Kunimatsu, Y., 2000. Un nouveau genre d'hominoïde du Miocène inférieur d'Afrique orientale: Ugandapithecus major (Le Gros Clark & Leakey, 1950). Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science 331, 227-33.

Serio-Silva J.C. (1995) Patrón diario de actividades y hábitos alimenticios de *Alouatta palliata* en semilibertad. In: Rodríguez-Luna E, Cortés-Ortiz L, Contreras JM (eds) *Estudios primatológicos en México*, vol II. Universidad Veracruzana, Xalapa.

Serio-Silva J.C., Rico-Gray V., Hernández-Salazar L.T., Espinosa-Gomez R. (2002) "The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico." *Journal of Tropical Ecology* 18:913–928.

Shearer, B. M,, Ungar, P.S., McNulty, K. P., Harcourt-Smith, W. E. H., Dunsworth, H. M., and Teaford, M. F. (2015) "Dental microwear profilometry of African non-cercopithecoid catarrhines of the Early Miocene." *Journal of Human Evolution* 78: 33–43.

Sheppard, D. J. (2000). Ecology of the Budongo Forest redtail: Patterns of habitat use and population density in primary and regenerating forest sites. University of Calgary.

Schoeninger, M. J., Iwaniec, U.T. (1997) "Stable isotope ratios indicate diet and habitat use in New World Monkeys." *American Journal of Physical Anthropology* 83: 69–83.

Schoeninger, M. J., Iwaniec, U. T., & Nash, L. T. (1998). Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Oecologia*, 222-230.

Shoobridge, D. (2002) Tambopata National Reserve and Bahuaja-Sonene National Park. http://www. Parkwatch.org

Silva E.C. (1981) "A preliminary survey of brown howler monkeys (*Alouatta fusca*) at the Cantareira Reserve (São Paulo, Brazil)." *Review of Brasil Biology* 41:897–909.

Simmen B (1992) Competitive utilization of Bagassa fruits by sympatric howler and spider monkeys. *Folia Primatologica* 58:155–160

Simpson, G. G. (1933). The" plagiaulacoid" type of mammalian dentition a study of convergence. *Journal of Mammalogy*, 14(2), 97-107.

Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. Journal of Human evolution, 32(6), 523-559.

Snodderly DM, Ellis KM, Lieberman SR, Link A, Fernandez-Duque E, Di Fiore A (2019) Initiation of feeding by four sympatric Neotropical primates (Ateles belzebuth, Lagothrix lagotricha poeppigii, Plecturocebus (Callicebus) discolor, and Pithecia aequatorialis) in Amazonian Ecuador: Relationships to photic and ecological factors. PLoS ONE 14(1): e0210494.

Sponheimer, M., Codron D., Passey, B. H., De Ruiter, D.J., Cerling, T. E., and Lee-thorp, J. A. (2009) "using carbon isotopes to track dietary change in modern , historical , and ancient primates." *American Journal of Physical Anthropology* 140: 661–70.

Sponheimer, M., Alemseged, Z., Cerling, T. E., Grine, F. E., Kimbel, W. H., Leakey, M. G., ... & Wynn, J. G. (2013). Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences*, 110(26), 10513-10518.

Sponheimer, M., and Lee-Thorp, J. (1999) "oxygen isotopes in enamel carbonate and their ecological significance." *Journal of Archaeological Science* 26: 723–28.

Stephenson, P. J., & Newby, J. E. (1997). Conservation of the Okapi Wildlife Reserve, Zaire. *Oryx*, 31(1), 49-58.

Stevenson, P.R (1999) "Feeding rates and daily path range of the Colombian woolly monkeys as evidence for between- and within-group competition." *Folia Primatologica* 71: 399-408.

Stevenson, P.R. (2001) "The relationship between fruit production and primate abundance in Neotropical communities." *Biological Journal of the Linnean Society* 72: 161-178.

Stevenson, P.R. (2006) "Activity and ranging patterns of Colombian woolly monkeys in north-western Amazonia." *Primates* 47: 239-247.

Stevenson, P.R. ,Quiñones, M. J., & Ahumada, J. A. (1994) "Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia." *American Journal of Primatology* 32: 123-140.

Stevenson, P. R., Quiñones, M. J., & Ahumada, J. A. (2000) Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica*, 32, 533–544.

Strait, S. (1993). Differences in occlusal morphology and molar size in frugivores and faunivores. *Journal of Human Evolution*, 25(6), 471-484.

Stroik, L. K. (2014) "Dietary competition in an extant mammalian guild : Application of a quantitative method to evaluate reconstructed niche overlap in paleocommunities." *International Journal of Plant Sciences* 35: 1222–52.

Struhsaker, T. T. (1978). Food habits of five monkeys species in the Kibale Forest, Uganda. *Behaviour.*

Struhsaker, T. T. (1980). Comparison of the behaviour and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. *African Journal of Ecology*, 18(1), 33-51.

Strushaker, T.T (2017) Dietary variability in redtail monkeys (*Cercopithecus ascanius schmidti*) of Kibale National Park, Uganda: The role of time, space, and hybridization. *International Journal of Primatology*.

Suarez, S.A. (2006) Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. *International Journal of Primatology* 27(2):411-436.

Sulzman, E. W. (2007). Stable isotope chemistry and measurement: a primer. *Stable isotopes in ecology and environmental science*, 2, 1-21.

Symington, M.M. (1987) Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*) *Behaviour* 105: 117-134.

Tashiro Y. (2006) "Frequent insectivory by two guenons (*Cercopithecus lhoesti and Cercopithecus mitis*) in the Kalinzu Forest, Uganda." *Primates.* 47(2):170-3.

Tate, G. H. H., & Hitchcock, C. B. (1930). The Cerro Duida region of Venezuela. *Geographical Review,* 20(1), 31-52.

Temerin, L. A., & Cant, J. G. (1983). The evolutionary divergence of Old World monkeys and apes. *The American Naturalist*, 122(3), 335-351.

Terborgh, J. (1983). *Five New World Primates*. (Monographs in behavior and ecology). Princeton: Princeton University Press.

Terborgh, J. (1990). Mixed flocks and polyspecific associations: Costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology*, 21(2), 87-100.

Turner, T., Maiers, J., & Mott, C. (1985) Comparative distance measures in two species of Cercopithecus monkeys-*Cercopithecus aethiops* and *Cercopithecus mitis*. *American Journal of Physical Anthropology* 66(2): 238-238.

Twagirashyaka, F. and Inogwabini, B.I. (2009). Lake TéLé-Lake Tumba Landscape. In: De Wasseige, C., Devers, D., De Marcken, P., Eba'a, R. A., Nasi, R. and Mayaux, P. (eds). The Forests of the Congo Basin - State of the Forest 2008. Publications Office of the European Union : 305–316.

Tweheyo, M. and Obua,J. (2001) Feeding habits of chimpanzees (*Pan troglodytes*), red-tail monkeys (*Cercopithecus ascanius schmidti*) and blue monkeys

(*Cercopithecus mitis stuhlmanii*) on figs in Budongo Forest Reserve, Uganda. *African Journal of Ecology.*

Tyler, C.L. and Leighton, L.R. (2011) Detecting competition in the fossil record: Support for character displacement among Ordovician brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307: 205–217.

Ulrich, W. (2004). Species co-occurrences and neutral models: reassessing JM Diamond's assembly rules. *Oikos*, 107(3), 603-609.

Ungar, P. (1994). Incisor microwear of Sumatran anthropoid primates. *American Journal of Physical Anthropology*, 94(3), 339-363.

Ungar, P.S. (1996) "Dental Microwear of European Miocene Catarrhines : Evidence for Diets and." *Journal of Human Evolution* 31: 335–66.

Ungar, P. (2002). Reconstructing the diets of fossil primates. Plavcan, J., Kay, R. F., Jungers, W., & van Schaik, C. P. (Eds.). (2001). *Reconstructing behavior in the primate fossil record.* Springer Science & Business Media*.,* 261-296.

Ungar, P. S. (2004). Dental evidence for the diets of fossil primates from Rudabánya, northeastern Hungary with comments on extant primate analogs and "noncompetitive" sympatry. *Raccolta Di Monografie Paleontologiche*, 90, 97-111.

Ungar, P.S., and Kay, R.F. (1995) "The dietary adaptations of European Miocene catarrhines." *Proceedings of the National Academy of Sciences* 92: 5479–81.

Ungar, P. S., & M'Kirera, F. (2003). A solution to the worn tooth conundrum in primate functional anatomy. *Proceedings of the National Academy of Sciences*, 100(7), 3874-3877.

Ungar, P. S., & Williamson, M. (2000). Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. *Palaeontologia electronica*, 3(1), 1-18.

Ungar P.S., Teaford, M.F., Kay, R.F. (2004) Molar microwear and shearing crest development in Miocene catarrhines. *Anthropologie* 42(1):21–35

Ungar P. S., Scott, R. S. (2009) "Dental evidence for diets of early homo." In *The First Humans: Origins of the Genus Homo*, edited by Fleagle J. G Grine F. E., Leakey R. E., 121–134. New York: Springer-Verlag.

Ungar, P., Brown, C., Bergstrom, T., & Walker, A. (2003). Quantification of Dental Microwear by Tandem Scanning Confocal Microscopy and Scale-Sensitive Fractal Analyses. *Scanning*, 25(4), 185-193.

Ungar, P. S., Scott, J. R., Mcnulty, K. P., Harcourt-Smith, W. E., Lehmann, T., & Dunsworth, H. M. (2012, January). Environments of early Miocene Rusinga Island and Songhor: Evidence from the dental microwear of tragulids. In *American Journal of Physical* Anthropology (Vol. 147, pp. 289-290).

Ungar, P., Healy, C., Karme, A., Teaford, M., & Fortelius, M. (2018). Dental topography and diets of platyrrhine primates. *Historical Biology*, 30(1-2), 64-75.

Van der Merwe, N. J., & Medina, E. (1991). The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *Journal of archaeological science*, 18(3), 249-259.

van Roosmalan, M.G.M. (1988) "Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam."

Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory*, 1: 1-30.

Vargas, S. A., León, J., Ramírez, M., Galvis, N., Cifuentes, E., & Stevenson, P. R. (2014). Population density and ecological traits of highland woolly monkeys at Cueva de los Guácharos National Park, Colombia. In *High altitude primates* (pp. 85-102). Springer, New York, NY.

Venkataraman, V., Glowacka, H., Fritz, J., Clauss, M., Seyoum, C., Nguyen, N., & Fashing, P. (2014). Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). *American Journal of Physical Anthropology*, 155(1), 17-32.

Vermeer, J. and Tello-Alvarado, J.C. (2015) "The Distribution and Taxonomy of Titi Monkeys (Callicebus) in Central and Southern Peru, with the Description of a New Species," *Primate Conservation* 29: 9-29.

Vogel, E. R., Haag, L., Mitra-Setia, T., Van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology*, 140(4), 716-726.

Volmer, R., Hertler, C., and Van Der Geer, A. (2016) "Niche overlap and competition potential among tigers (*Panthera Tigris*), sabertoothed cats (*Homotherium Ultimum, Hemimachairodus Zwierzyckii*) and Merriam's dog (*Megacyon Merriami*) in the Pleistocene of Java." *Palaeogeography, Palaeoclimatology, Palaeoecology* 441: 901–11.

Walker, A., Rose, M.D., 1968. Fossil hominoid vertebra from the Miocene of Uganda. *Nature* 217, 980-1.

Wallace, R.B. (2005) “Seasonal variations in diet and foraging behavior of *Ateles chamek* in a Southern Amazonian Tropical Forest.” *International Journal of Primatology* 26(5):1053-1075.

Wallace, R.B. (2008) “The influence of feeding patch size and relative fruit density on the foraging behavior of the black spider monkey *Ateles chamek”. Biotropica* 40(4): 501-506.

Wanchai, P., Stanford, C. B., Thirakhupt, K., & Thanhikorn, S. (2012). Home range of the impressed tortoise, *Manouria impressa* (Günther, 1882) at Phu Luang Wildlife Sanctuary, Loei Province, Thailand. *Tropical Natural History*, 12(2), 165-174.

Ward, S.C., Duren, D.L., 2002. Middle and late Miocene African hominoids. In: Hartwig, W. (Editor) *Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 385-98.

Ward, S., Brown, B., Hill, A., Kelley, J., Downs, W., 1999. *Equatorius*: a new hominoid genus from the middle Miocene of Kenya. *Science* 285, 1382-6.

Wetselaar P., Wetselaar-Glas M.J.M., Katzer L.D., Ahlers M.O. (2020) Diagnosing tooth wear, a new taxonomy based on the revised version of the Tooth Wear Evaluation System (TWES 2.0). *Journal Oral Rehabilitation* 47(6):703-712

White, J. W., & Ruttenberg, B. I. (2007). Discriminant function analysis in marine ecology: some oversights and their solutions. *Marine Ecology Progress Series*, 329, 301-305.

Whitlock, M. C. (1996). The Red Queen Beats the Jack-Of-All-Trades: The Limitations on the Evolution of Phenotypic Plasticity and Niche Breadth. *The American Naturalist*, 148, S65–S77

Whitten, T., Damanik, S. J. (2012). Ecology of Sumatra. Hong Kong: Tuttle Publishing.

Wiens, J. (1989). The ecology of bird communities (Cambridge studies in ecology). Cambridge [England] ; New York: Cambridge University Press.

Wiley, R. H. (2010). Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. Bulletin of the American Museum of Natural History, 2010(343), 1-68.

Wilson, G. P., Evans, A. R., Corfe, I. J., Smits, P. D., Fortelius, M., & Jernvall, J. (2012). Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. *Nature*, 483(7390), 457-460.

Winchester, J.M., Boyer, D. M., St. Clair, E. M., Gosselin-Ildari, A.D., Cooke, S.B. and Ledogar, J. A (2014) "Dental topography of platyrrhines and prosimians: convergence and contrasts." *American Journal of Physical Anthropology* 153 (1): 29–44.

Xu, L., Saatchi, S.S., Shapiro, A. et al.(2017) Spatial Distribution of Carbon Stored in Forests of the Democratic Republic of Congo. *Scientific Reports* 7, 15030.

Yom-Tov, Y. (1991). Character displacement in the psammophile Gerbillidae of Israel. *Oikos*, 60, 173–17

Zuccotti, L. F., Williamson, M. D., Limp, W. F., & Ungar, P. S. (1998). Modeling primate occlusal topography using geographic information systems technology. *American Journal of Physical Anthropology*, 107(1), 137-142.

Zunino, G.E. (1986) *Algunos aspectos de la ecología y etología del mono aullador negro (Alouatta caraya) en hábitat fragmentados*. PhD dissertation, Universidad de Buenos Aires, Buenos Aires.

Appendix A

Sympatric Location: Curaray River Mouth, Peru **Ateles Allopatric Location: Mt. Duida, Venezuela** **Lagothrix Allopatric Location: Pozuzo, Peru**					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	21.53	26.73	-5.20	0.51
M1	RFI	0.06	0.02	0.04	0.47
M1	OPCR	7.36	13.98	-6.62	0.59
M2	DNE	4.16	36.19	-32.03	0.68
M2	RFI	0.017	0.020	-0.002	0.53
M2	OPCR	4.46	22.44	-17.98	0.69
M3	DNE	59.30	77.97	-18.68	0.48
M3	RFI	0.04	0.01	0.02	0.38
M3	OPCR	23.94	19.35	4.58	0.48
M1,M2,M3	DNE	3.45	29.57	-26.12	0.70
M1,M2,M3	RFI	0.05	0.03	0.02	0.48
M1,M2,M3	OPCR	4.28	13.80	-9.52	0.68
Sympatric Location: Curaray River Mouth, Peru **Ateles Allopatric Location: Mt. Duida, Venezuela** **Lagothrix Allopatric Location: Rio Aguas Claras**					

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	18.82	16.23	2.60	0.47
M1	RFI	0.07	0.01	0.07	0.25
M1	OPCR	4.03	20.63	-16.60	0.61
M2	DNE	15.01	1.03	13.98	0.16
M2	RFI	0.03	0.05	-0.02	0.48
M2	OPCR	7.30	121.13	-113.82	0.63
M3	DNE	34.89	18.22	16.67	0.44
M3	RFI	0.04	0.08	-0.04	0.56
M3	OPCR	6.38	0.98	5.39	0.41
M1,M2,M3	DNE	0.59	12.03	-11.44	0.62
M1,M2,M3	RFI	0.06	0.00	0.06	0.26
M1,M2,M3	OPCR	1.96	6.39	-4.43	0.52

Sympatric Location: Curaray River Mouth, Peru
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: San Augustin

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	12.56	3.91	8.65	0.33
M1	RFI	0.07	0.02	0.05	0.26
M1	OPCR	1.28	23.21	-21.93	0.71
M2	DNE	9.58	0.00	9.58	0.34
M2	RFI	0.03	0.04	-0.01	0.52
M2	OPCR	18.57	26.42	-7.85	0.49
M3	DNE	1.56	96.69	-95.13	0.72
M3	RFI	0.07	0.04	0.03	0.34
M3	OPCR	13.44	4.00	9.44	0.39
M1,M2,M3	DNE	6.67	15.66	-8.99	0.59
M1,M2,M3	RFI	0.06	0.02	0.04	0.42
M1,M2,M3	OPCR	10.14	24.16	-14.02	0.58

Sympatric Location: Curaray River Mouth, Peru
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Urubamba

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	19.35	12.57	6.78	0.42
M1	RFI	0.08	0.04	0.04	0.45
M1	OPCR	5.00	35.44	-30.43	0.63
M2	DNE	6.19	18.04	-11.85	0.59
M2	RFI	0.03	0.03	0.00	0.49

M2	OPCR	7.60	72.42	-64.82	0.66
M3	DNE	19.95	19.18	0.77	0.40
M3	RFI	0.09	0.01	0.08	0.27
M3	OPCR	20.85	85.96	-65.11	0.52
M1,M2,M3	DNE	16.22	12.78	3.44	0.44
M1,M2,M3	RFI	0.02	0.05	-0.03	0.56
M1,M2,M3	OPCR	1.73	52.73	-51.00	0.70
Sympatric Location: Curaray River Mouth, Peru **Ateles Allopatric Location: Mt. Duida, Venezuela** **Lagothrix Allopatric Location: Lagarto**					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	21.89	36.32	-14.42	0.53
M1	RFI	0.07	0.01	0.06	0.24
M1	OPCR	5.15	28.12	-22.97	0.63
M2	DNE	0.83	19.77	-18.94	0.47
M2	RFI	0.06	0.01	0.04	0.28
M2	OPCR	7.09	81.36	-74.27	0.64
M3	DNE	63.40	11.93	51.47	0.37
M3	RFI	0.04	0.03	0.01	0.33
M3	OPCR	42.75	48.48	-5.73	0.48
M1,M2,M3	DNE	9.90	13.30	-3.40	0.46
M1,M2,M3	RFI	0.06	0.03	0.02	0.48
M1,M2,M3	OPCR	1.77	53.38	-51.62	0.68
Sympatric Location: Alto Yavari **Ateles Allopatric Location: Mt. Duida, Venezuela** **Lagothrix Allopatric Location: Pozuzo, Peru**					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	143.97	20.35	123.62	0.46
M1	RFI	0.08	0.04	0.04	0.50
M1	OPCR	3.13	4.98	-1.85	0.66
M2	DNE	27.87	16.36	11.51	0.47
M2	RFI	0.01	0.04	-0.04	0.73
M2	OPCR	47.50	23.30	24.19	0.43
M3	DNE	106.73	24.20	82.53	0.47
M3	RFI	0.00	0.01	-0.01	0.63
M3	OPCR	37.31	12.85	24.46	0.40
M1,M2,M3	DNE	67.88	20.23	47.65	0.49
M1,M2,M3	RFI	0.022	0.026	-0.005	0.53

M1,M2,M3	OPCR	33.48	5.76	27.72	0.40

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Rio Aguas Claras

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	97.23	8.68	88.55	0.28
M1	RFI	0.08	0.01	0.07	0.29
M1	OPCR	16.04	13.84	2.20	0.45
M2	DNE	27.09	4.87	22.21	0.28
M2	RFI	0.01	0.02	-0.01	0.58
M2	OPCR	27.02	0.30	26.72	0.25
M3	DNE	77.60	36.47	41.12	0.46
M3	RFI	0.01	0.00	0.01	0.38
M3	OPCR	39.92	13.93	25.99	0.35
M1,M2,M3	DNE	67.31	7.64	59.67	0.32
M1,M2,M3	RFI	0.02	0.00	0.02	0.24
M1,M2,M3	OPCR	27.66	9.16	18.50	0.35

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: San Augustin

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	97.23	2.89	94.35	0.22
M1	RFI	0.07	0.01	0.06	0.33
M1	OPCR	16.04	5.46	10.58	0.33
M2	DNE	27.09	17.07	10.02	0.40
M2	RFI	0.01	0.03	-0.02	0.64
M2	OPCR	26.48	34.12	-7.64	0.58
M3	DNE	77.60	68.11	9.48	0.51
M3	RFI	0.01	0.03	-0.02	0.60
M3	OPCR	39.92	12.37	27.55	0.31
M1,M2,M3	DNE	74.24	18.39	55.86	0.44
M1,M2,M3	RFI	0.03	0.01	0.01	0.40
M1,M2,M3	OPCR	27.78	19.37	8.41	0.48

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Urubamba

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	107.32	12.44	94.88	0.33

M1	RFI	0.08	0.05	0.03	0.47
M1	OPCR	6.74	28.65	-21.91	0.65
M2	DNE	10.12	0.75	9.37	0.37
M2	RFI	0.01	0.04	-0.03	0.69
M2	OPCR	25.75	42.87	-17.12	0.57
M3	DNE	77.60	6.11	71.49	0.25
M3	RFI	0.01	0.07	-0.06	0.63
M3	OPCR	50.04	35.58	14.46	0.49
M1,M2,M3	DNE	75.26	0.28	74.98	0.27
M1,M2,M3	RFI	0.03	0.03	0.00	0.49
M1,M2,M3	OPCR	25.69	35.20	-9.51	0.49

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Lagarto

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	97.23	17.83	79.41	0.33
M1	RFI	0.08	0.03	0.05	0.39
M1	OPCR	16.04	4.53	11.51	0.35
M2	DNE	27.09	23.61	3.48	0.46
M2	RFI	0.03	0.02	0.00	0.47
M2	OPCR	27.02	46.01	-19.00	0.56
M3	DNE	77.60	19.59	58.01	0.34
M3	RFI	0.01	0.04	-0.03	0.63
M3	OPCR	39.92	22.31	17.61	0.39
M1,M2,M3	DNE	67.31	20.34	46.96	0.41
M1,M2,M3	RFI	0.02	0.03	-0.01	0.57
M1,M2,M3	OPCR	27.66	24.28	3.37	0.48

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Pozuzo, Peru

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	58.49	26.73	31.77	0.48
M1	RFI	0.06	0.04	0.01	0.48
M1	OPCR	82.57	11.44	71.13	0.45
M2	DNE	13.96	18.02	-4.06	0.50
M2	RFI	0.02	0.00	0.02	0.28
M2	OPCR	24.68	37.52	-12.84	0.60
M3	DNE	44.44	6.75	37.68	0.27

M3	RFI	0.03	0.01	0.03	0.42
M3	OPCR	15.39	3.98	11.41	0.36
M1,M2,M3	DNE	30.28	39.05	-8.77	0.48
M1,M2,M3	RFI	0.02	0.01	0.00	0.46
M1,M2,M3	OPCR	18.98	4.46	14.52	0.32

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Rio Aguas Claras

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	39.7	77.2	-37.5	0.5
M1	RFI	0.02	0.01	0.01	0.5
M1	OPCR	42.7	7.1	35.6	0.3
M2	DNE	42.0	26.1	15.9	0.4
M2	RFI	0.05	0.00	0.04	0.2
M2	OPCR	64.5	81.3	-16.9	0.5
M3	DNE	67.4	64.1	3.3	0.5
M3	RFI	0.1	0.1	0.0	0.5
M3	OPCR	0.0	0.0	0.0	0.5
M1,M2,M3	DNE	49.8	35.6	14.2	0.5
M1,M2,M3	RFI	0.00	0.02	-0.02	0.7
M1,M2,M3	OPCR	19.3	34.7	-15.4	0.4

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: San Augustin

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	40.04	75.22	-35.18	0.55
M1	RFI	0.00	0.05	-0.05	0.67
M1	OPCR	67.37	17.48	49.89	0.38
M2	DNE	50.36	31.74	18.62	0.44
M2	RFI	0.02	0.01	0.01	0.40
M2	OPCR	22.11	155.54	-133.43	0.52
M3	DNE	58.10	95.49	-37.39	0.57
M3	RFI	0.01	0.09	-0.08	0.64
M3	OPCR	64.81	16.63	48.18	0.35
M1,M2,M3	DNE	21.62	17.93	3.69	0.45
M1,M2,M3	RFI	0.02	0.03	-0.01	0.57
M1,M2,M3	OPCR	28.61	12.42	16.18	0.35

Sympatric Location: La Macarena
Ateles Allopatric Location: Mt. Duida, Venezuela

Lagothrix Allopatric Location: Urubamba

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	47.49	44.00	3.49	0.48
M1	RFI	0.04	0.03	0.02	0.38
M1	OPCR	85.90	54.50	31.40	0.51
M2	DNE	36.69	19.54	17.15	0.43
M2	RFI	0.01	0.01	0.00	0.38
M2	OPCR	11.77	57.17	-45.40	0.71
M3	DNE	37.60	21.91	15.69	0.43
M3	RFI	0.00	0.08	-0.08	0.72
M3	OPCR	64.25	20.66	43.58	0.44
M1,M2,M3	DNE	55.83	12.23	43.60	0.41
M1,M2,M3	RFI	0.02	0.04	-0.02	0.59
M1,M2,M3	OPCR	38.06	84.04	-45.99	0.51

Sympatric Location: La Macarena
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Lagarto

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	21.99	16.31	5.68	0.42
M1	RFI	0.01	0.01	-0.01	0.46
M1	OPCR	70.56	15.81	54.76	0.43
M2	DNE	59.78	0.40	59.38	0.23
M2	RFI	0.05	0.06	-0.01	0.49
M2	OPCR	34.65	11.19	23.46	0.29
M3	DNE	56.96	8.79	48.17	0.24
M3	RFI	0.05	0.05	0.00	0.45
M3	OPCR	26.63	34.87	-8.25	0.58
M1,M2,M3	DNE	55.85	16.18	39.67	0.25
M1,M2,M3	RFI	0.01	0.05	-0.04	0.60
M1,M2,M3	OPCR	43.09	42.77	0.32	0.48

Sympatric Location: La Macarena
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Pozuzo, Peru

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	30.23	25.12	5.11	0.50
M1	RFI	0.02	0.04	-0.02	0.54
M1	OPCR	21.11	0.42	20.69	0.27
M2	DNE	28.49	16.24	12.25	0.42

M2	RFI	0.02	0.03	0.00	0.49
M2	OPCR	2.78	26.59	-23.82	0.73
M3	DNE	35.15	48.52	-13.38	0.51
M3	RFI	0.02	0.02	0.00	0.43
M3	OPCR	11.05	0.96	10.10	0.32
M1,M2,M3	DNE	30.76	28.63	2.14	0.49
M1,M2,M3	RFI	0.03	0.02	0.01	0.52
M1,M2,M3	OPCR	2.58	10.46	-7.88	0.69

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Rio Aguas Claras

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	48.47	17.14	31.33	0.39
M1	RFI	0.04	0.00	0.04	0.20
M1	OPCR	34.30	16.11	18.19	0.38
M2	DNE	44.00	12.52	31.48	0.34
M2	RFI	0.01	0.05	-0.04	0.55
M2	OPCR	6.83	1.25	5.58	0.30
M3	DNE	34.79	64.32	-29.53	0.49
M3	RFI	0.04	0.05	-0.01	0.51
M3	OPCR	16.30	4.56	11.75	0.30
M1,M2,M3	DNE	21.34	4.98	16.35	0.30
M1,M2,M3	RFI	0.04	0.01	0.03	0.30
M1,M2,M3	OPCR	2.99	15.31	-12.32	0.59

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: San Augustin

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	20.75	37.74	-16.99	0.54
M1	RFI	0.04	0.04	0.00	0.46
M1	OPCR	34.90	46.73	-11.82	0.48
M2	DNE	42.31	33.14	9.17	0.51
M2	RFI	0.00	0.06	-0.06	0.68
M2	OPCR	2.97	63.67	-60.70	0.67
M3	DNE	32.13	49.86	-17.73	0.55
M3	RFI	0.02	0.15	-0.13	0.57
M3	OPCR	11.35	34.75	-23.40	0.64
M1,M2,M3	DNE	40.92	17.21	23.71	0.46

M1,M2,M3	RFI	0.02	0.04	-0.02	0.50
M1,M2,M3	OPCR	11.96	28.51	-16.55	0.55

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Urubamba

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	18.89	6.04	12.84	0.27
M1	RFI	0.004	0.000	0.004	0.46
M1	OPCR	5.32	8.32	-2.99	0.53
M2	DNE	22.72	33.51	-10.79	0.52
M2	RFI	0.03	0.10	-0.07	0.49
M2	OPCR	5.68	10.14	-4.47	0.43
M3	DNE	14.75	17.46	-2.71	0.50
M3	RFI	0.02	0.04	-0.02	0.58
M3	OPCR	17.50	61.75	-44.25	0.53
M1,M2,M3	DNE	28.88	6.50	22.38	0.36
M1,M2,M3	RFI	0.02	0.03	-0.01	0.46
M1,M2,M3	OPCR	12.32	43.21	-30.89	0.59

Sympatric Location: Alto Yavari
Ateles Allopatric Location: Mt. Duida, Venezuela
Lagothrix Allopatric Location: Lagarto

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	47.18	36.32	10.86	0.47
M1	RFI	0.05	0.01	0.04	0.31
M1	OPCR	34.63	12.69	21.94	0.37
M2	DNE	31.32	50.93	-19.60	0.53
M2	RFI	0.01	0.06	-0.06	0.63
M2	OPCR	8.27	46.65	-38.37	0.62
M3	DNE	32.13	40.47	-8.34	0.51
M3	RFI	0.01	0.05	-0.04	0.60
M3	OPCR	2.76	54.02	-51.26	0.68
M1,M2,M3	DNE	32.25	33.46	-1.21	0.51
M1,M2,M3	RFI	0.02	0.03	-0.01	0.50
M1,M2,M3	OPCR	13.05	24.33	-11.28	0.51

Sympatric location:Akenge
C. ascanius allopatric location: Kananga

C. mitis allopatric location: Tana River					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
m1	DNE	57.63	65.57	-7.94	0.51
m1	RFI	0.01	0.02	-0.01	0.59
m1	OPCR	2.63	30.00	-27.37	0.71
m2	DNE	35.19	35.63	-0.43	0.50
m2	RFI	0.04	0.05	-0.01	0.51
m2	OPCR	7.19	19.52	-12.33	0.58
m3	DNE	52.38	9.07	43.30	0.29
m3	RFI	0.01	0.03	-0.02	0.63
m3	OPCR	2.79	16.21	-13.42	0.66
m1, m2, m3	DNE	43.42	35.01	8.41	0.50
m1, m2, m3	RFI	0.02	0.03	-0.01	0.53
m1, m2, m3	OPCR	2.52	18.33	-15.81	0.67
Sympatric location:Akenge **C. ascanius allopatric location: Kunungu** **C. mitis allopatric location: Tana River**					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
m1	DNE	80.16	57.28	22.88	0.5
m1	RFI	0.07	0.02	0.05	0.43
m1	OPCR	19.80	4.35	15.45	0.68
m2	DNE	32.53	30.37	2.16	0.54
m2	RFI	0.10	0.04	0.06	0.5
m2	OPCR	9.52	2.79	6.73	0.44
m3	DNE	60.58	59.61	0.97	0.49
m3	RFI	0.07	0.05	0.02	0.51
m3	OPCR	56.66	16.77	39.89	0.49
m1, m2, m3	DNE	49.60	46.70	2.91	0.49
m1, m2, m3	RFI	0.05	0.04	0.01	0.49

m1, m2, m3	OPCR	11.50	15.53	-4.03	0.56
Sympatric location:Kisangani **C. ascanius allopatric location: Kunungu** **C. mitis allopatric location: Tana River**					
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
m1	DNE	57.79	60.87	-3.08	0.51
m1	RFI	0.05	0.04	0.01	0.48
m1	OPCR	10.17	12.13	-1.96	0.54
m2	DNE	73.70	50.58	23.12	0.50
m2	RFI	0.03	0.05	-0.02	0.50
m2	OPCR	1.13	13.56	-12.43	0.69
m3	DNE	91.92	51.05	40.87	0.55
m3	RFI	0.00	0.02	-0.02	0.69
m3	OPCR	14.05	14.49	-0.44	0.59
m1, m2, m3	DNE	67.41	48.74	18.67	0.49
m1, m2, m3	RFI	0.03	0.03	0.01	0.50
m1, m2, m3	OPCR	4.70	15.68	-10.98	0.55
		kisangani kananga			
		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
m1	DNE	54.79	62.06	-7.27	0.50
m1	RFI	0.05	0.01	0.04	0.24
m1	OPCR	10.21	49.24	-39.03	0.53
m2	DNE	68.73	41.57	27.16	0.53
m2	RFI	0.03	0.06	-0.02	0.51
m2	OPCR	5.45	21.41	-15.96	0.54
m3	DNE	93.77	31.01	62.76	0.54
m3	RFI	0.01	0.02	-0.01	0.54
m3	OPCR	18.15	0.50	17.65	0.26
m1, m2, m3	DNE	66.08	39.61	26.47	0.50

m1, m2, m3	RFI	0.02	0.01	0.00	0.43
m1, m2, m3	OPCR	5.09	19.73	-14.64	0.53

Hylobates Sympatric Location: Pelembang, Sumatra
Hylobates allopatric location: Inthanon Doi, Thailand

		Sympatric Vector Length	**Allopatric Vector Length**	**Difference**	**P-Value**
M1	DNE	67.05	2.64	64.42	0.27
M1	RFI	0.11	0.17	-0.06	0.47
M1	OPCR	47.55	50.73	-3.18	0.52
M2	DNE	98.43	34.70	63.73	0.49
M2	RFI	0.07	0.06	0.01	0.48
M2	OPCR	30.13	39.97	-9.85	0.50
M3	DNE	136.69	46.67	90.03	0.52
M3	RFI	0.12	0.03	0.09	0.47
M3	OPCR	22.50	20.12	2.38	0.51
M1,M2, M3	DNE	12.03	63.84	-51.81	0.64
M1,M2, M3	RFI	0.10	0.11	0.00	0.50
M1,M2, M3	OPCR	25.86	35.49	-9.63	0.49

Hylobates Sympatric Location: Pelembang, Sumatra
Hylobates Allopatric location: Dan Sai, Thailand

		Sympatric Vector Length	Allopatric Vector Length	Difference	P-Value
M1	DNE	7.69	2.86	4.83	0.43
M1	RFI	0.11	0.18	-0.07	0.51
M1	OPCR	36.65	33.38	3.28	0.49
M2	DNE	0.63	39.15	-38.52	0.62
M2	RFI	0.10	0.01	0.08	0.37
M2	OPCR	35.94	39.68	-3.74	0.43
M3	DNE	117.39	55.96	61.43	0.49

M3	RFI	0.17	0.07	0.09	0.51
M3	OPCR	7.62	17.82	-10.19	0.51
M1,M2, M3	DNE	8.15	6.92	1.23	0.44
M1,M2, M3	RFI	0.10	0.11	0.00	0.52
M1,M2, M3	OPCR	29.78	43.16	-13.38	0.50

Appendix B

Cercopithecus ascanius							
δ^{15}N	Site	Sym/Allo	N	Min.	Max.	Mean	Std. dev.
	Kanaga	Allo	8	4.950	7.890	6.758	0.970
	Kunungu	Allo	7	6.682	10.805	9.533	1.312
	Kisangani	Sym	7	7.199	8.323	7.576	0.408
	Akenge	Sym	7	7.650	9.240	8.539	0.687
	Epulu	Sym	6	8.47	9.980	9.297	0.488
	Ituri	Sym	5	7.170	9.41	8.000	1.118
δ^{13}C							
	Kanaga	Allo	8	-23.540	-19.210	-22.470	1.371
	Kunungu	Allo	7	-24.719	-22.990	-23.994	0.531
	Kisangani	Sym	7	-25.090	-24.021	-24.522	0.368
	Akenge	Sym	7	-24.280	-23.230	-23.817	0.396
	Epulu	Sym	6	-23.680	-22.860	-23.347	0.307
	Ituri	Sym	5	-24.410	-23.260	-23.670	0.449
δ^{18}O							
	Kanaga	Allo	8	12.14	15.79	14.1	1.270
	Akenge	Sym	5	14.31	16.47	15.072	0.926
	Ituri	Sym	5	11.78	14.4	13.74	1.10
Cercopithecus mitis							
δ^{15}N	Site	Sym/Allo	N	Min.	Max.	Mean	Std. dev.
	Tana	Allo	5	3.670	5.820	4.766	1.063
	Kisangani	Sym	6	6.342	8.150	7.260	0.860
	Akenge	Sym	4	8.770	9.650	9.225	0.363
	Epulu	Sym	6	7.919	9.080	8.204	0.440
	Ituri	Sym	9	4.150	9.870	7.516	2.068
δ^{13}C							
	Tana	Allo	5	-22.790	-21.310	-21.728	0.608
	Kisangani	Sym	6	-24.130	-23.384	-23.802	0.283
	Akenge	Sym	4	-23.200	-22.310	-22.838	0.393
	Epulu	Sym	6	-24.378	-23.371	-23.805	0.430
	Ituri	Syn	8	-24.040	-22.000	-23.021	0.637
δ^{18}O			N	Min.	Max.	Mean	Std. dev.
	Tana	Allo	5	14.39	16.22	15.767	0.770
	Akenge	Sym	4	13.75	17.82	15.212	1.793

	Ituri	Sym	8	12.84	16.22	14.193	1.0353

Ateles							
δ^{15}N		Sym/Allo	N	Min.	Max.	Mean	Std. dev
	Santarem	Allo	5	8.241	9.253	8.786	0.401
	Mt Duida	Allo	6	4.683	7.143	6.024	0.841
	El Yagual	Allo	4	5.032	5.543	5.284	0.211
	Curaray	Sym	10	4.903	6.976	6.133	0.588
	Pampa Grande	Sym	4	5.023	5.867	5.528	0.371
	Alto Yavari	Sym	5	3.317	4.216	3.831	0.325
δ^{13}C							
	Santarem	Allo	5	-23.119	-22.854	-22.995	0.122
	Mt Duida	Allo	6	-23.363	-22.893	-23.093	0.171
	El Yagual	Allo	4	-22.746	-22.577	-22.658	0.089
	Curaray	Sym	10	-23.856	-22.918	-23.496	0.254
	Pampa Grande	Sym	4	-23.375	-23.019	-23.220	0.153
	Alto Yavari	Sym	5	-24.017	-23.718	-23.819	0.125
δ^{18}O							
	Santarem	Allo	5	12.950	14.100	13.550	0.411
	Mt Duida	Allo	6	12.620	15.680	13.777	1.135
	El Yagual	Allo	4	11.750	13.400	12.618	0.890
	Curaray	Sym	10	9.490	12.370	11.401	0.957
	Pampa Grande	Sym	4	12.120	14.080	13.053	0.884
	Alto Yavari	Sym	5	9.890	12.390	10.910	1.106

Lagothrix							
δ^{15}N		Sym/Allo	N	Min.	Max.	Mean	Std. dev
	Rio Mecanya	Allo	5	5.630	6.586	6.196	0.376
	Urubamba	Allo	3	5.462	6.888	6.115	0.721
	La Macerena	Sym	4	5.719	6.953	6.362	0.647
	Curaray	Sym	4	5.039	6.445	5.741	0.583
	Pampa Grande	Sym	4	6.174	6.502	6.302	0.147
	Alto Yavari	Sym	5	3.531	4.675	4.073	0.411
δ^{13}C							
	Rio Mec	Allo	5	-24.153	-23.880	-23.999	0.134
	Rio Mecanya	Allo	3	-24.197	-23.585	-23.932	0.314

	Urubamba	Sym	4	-22.907	-22.723	-22.833	0.080
	La Macerena	Sym	4	-24.505	-23.985	-24.225	0.240
	Curaray	Sym	4	-23.224	-22.987	-23.083	0.112
	Pampa Grande	Sym	5	-24.194	-23.808	-24.015	0.142
δ^{18}O							
	Rio Mecanya	Allo	5	13.340	14.750	13.988	0.556
	Urubamba	Allo	4	12.720	13.300	13.078	0.250
	La Macerena	Sym	5	10.550	13.910	11.592	1.324
	Curaray	Sym	4	12.300	14.190	13.048	0.899
	Pampa Grande	Sym	4	11.080	14.750	13.988	0.556
	Alto Yavari	Sym	3	11.260	13.300	13.078	0.250

Hylobates							
δ^{15}N		Sym/Allo	N	Min.	Max.	Mean	Std. dev
	Pelembang	Sym	5	3.323	3.891	3.607	0.238
	Mt Angka	Allo	33	1.577	5.785	3.229	0.929
δ^{13}C							
	Pelembang	Sym	5	-23.899	-23.264	-23.545	0.257
	Mt Angka	Allo	33	-22.735	-21.770	-22.341	0.256
δ^{18}O							
	Pelembang	Sym	5	10.210	13.670	12.034	1.338
	Mt Angka	Allo	33	12.340	16.240	14.071	1.086
Symphalangus							
δ^{15}N		Sym/Allo	N	Min.	Max.	Mean	Std. dev
	Pelembang	Sym	6	2.485	4.716	3.797	0.845
δ^{13}C							
	Pelembang	Sym	6	-24.219	-23.280	-23.622	0.319
δ^{18}O							
	Pelembang	Sym	6	9.560	11.850	10.693	0.850

Appendix C

Catalog Number	Genus	Location	Position	Tooth	DNE	RFI	OPCR
KNM CA 1806	Dendropithecus maccinesi	Chamtwara	upper	m2	350.46	0.2040	172.25
KNM CA 1827	Micropithecus	Chamtwara	upper	m3	416.39	0.2705	170.75
KNM CA 1864	Dendropithecus	Chamtwara	upper	m1	396.09	0.1746	198.38
KNM CA 2121	Dendropithecus maccinesi	Chamtwara	upper	m1	459.69	0.3457	156.88
KNM CA 384	Dendropithecus maccinesi	Chamtwara	lower	m2	278.14	0.2840	116.5
KNM CA 430	Dendropithecus maccinesi	Chamtwara	upper	m3	486.50	0.2818	195
KNM RU 1669	Dendropithecus maccinesi	Rusinga	upper	m1	499.35	0.2952	264.75
KNM RU 1669	Dendropithecus maccinesi	Rusinga	upper	m2	483.33	0.3171	198.25
KNM RU 1788	Dendropithecus maccinesi	Rusinga	upper	m1	396.22	0.3585	160.12
KNM RU 1796	Dendropithecus maccinesi	Rusinga	upper	m1	735.29	0.3532	289.62
KNM RU 1849	Dendropithecus maccinesi	Rusinga	upper	m1	634.18	0.2751	464.62
KNM RU 1849	Dendropithecus maccinesi	Rusinga	upper	m2	536.15	0.2208	243
KNM RU 1849	Dendropithecus maccinesi	Rusinga	upper	m3	573.65	0.2382	325.12
KNM RU 1850	Dendropithecus maccinesi	Rusinga	lower	m1	214.61	0.2475	93.62
KNM RU 1850	Dendropithecus maccinesi	Rusinga	lower	m2	188.23	0.2194	115.5
KNM RU 1851	Dendropithecus maccinesi	Rusinga	lower	m3	188.23	0.2204	100.5
KNM RU 1852	Dendropithecus maccinesi	Rusinga	upper	m1	431.00	0.2551	218
KNM RU 1853	Dendropithecus maccinesi	Rusinga	upper	m2	567.34	0.3128	216.62
KNM RU 1854	Dendropithecus maccinesi	Rusinga	upper	m1	322.84	0.2024	156.88
KNM RU 1855	Dendropithecus maccinesi	Rusinga	upper	m2	416.51	0.2465	165.75
KNM RU 1856	Dendropithecus maccinesi	Rusinga	upper	m3	488.10	0.2247	213.38
KNM RU 1866	Dendropithecus maccinesi	Rusinga	upper	m2	696.54	0.3803	252.25
KNM RU 1893	Dendropithecus maccinesi	Rusinga	lower	m2	479.54	0.2990	199.12
KNM RU 1992	Dendropithecus maccinesi	Rusinga	lower	m1	313.08	0.2916	127.5
KNM RU 2029	Dendropithecus maccinesi	Rusinga	upper	m2	612.11	0.3339	210.5

KNM RU 2046	Dendropithecus maccinesi	Rusinga	lower	m2	340.79	0.2983	143.62
KNM RU 14229	Dendropithecus maccinesi	Rusinga	upper	m2	812.20	0.3524	370.12
KNM RU 2028	Dendropithecus maccinesi	Rusinga	upper	m2	547.11	0.2904	245
KNM SO 457	Dendropithecus maccinesi	Songhor	upper	m3	538.02	0.2996	242.75
KNM RU 14243	Ekembo hesloni	Rusinga	upper	m2	951.36	0.2538	357.62
KNM RU 1677	Ekembo aff	Rusinga	upper	m2	865.17	0.2999	445.88
KNM RU 1677	Ekembo aff	Rusinga	upper	m3	794.84	0.2676	339.88
KNM RU 1677	Ekembo aff	Rusinga	upper	m1	476.79	0.2674	235.25
KNM RU 1678	Ekembo hesloni	Rusinga	lower	m1	612.09	0.2695	301.62
KNM RU 1678	Ekembo hesloni	Rusinga	lower	m2	568.26	0.2792	227.5
KNM RU 1696	Ekembo hesloni	Rusinga	upper	m1	663.78	0.3030	259.5
KNM RU 1710	Ekembo spp	Rusinga	upper	m2	859.43	0.2562	285
KNM RU 1721	Ekembo hesloni	Rusinga	upper	m1	1105.00	0.2942	440.62
KNM RU 1734	Ekembo spp	Rusinga	lower	m2	482.80	0.2907	184.75
KNM RU 1764	Ekembo spp	Rusinga	lower	m3	933.56	0.2649	339
KNM RU 1789	Ekembo hesloni	Rusinga	lower	m1	570.05	0.2557	263.88
KNM RU 2000	Ekembo hesloni	Rusinga	lower	m1	373.63	0.2475	201.88
KNM RU 2032	Ekembo hesloni	Rusinga	lower	m1	713.28	0.3115	231.75
KNM MW 161	Ekembo spp	Mfwangano	upper	m1	663.58	0.2827	249.5
KNM RU 1741	Ekembo spp	Rusinga	upper	m1	622.24	0.2922	207.88
KNM RU 1742	Ekembo hesloni	Rusinga	upper	m1	703.05	0.3096	243.12
KNM RU 1936	Ekembo hesloni	Rusinga	lower	m1	531.66	0.3024	204.5
KNM RU 1954	Ekembo spp	Rusinga	upper	m2	670.01	0.2918	287.75
KNM RU 2036	Ekembo hesloni	Rusinga	upper	m1	572.29	0.3315	238.75
KNM RU 2087	Ekembo hesloni	Rusinga	lower	m2	301.89	0.2496	130.62
KNM RU 2087	Ekembo hesloni	Rusinga	lower	m1	549.92	0.3231	275.88
KNM RU2087	Ekembo hesloni	Rusinga	lower	m2	430.37	0.2096	248.38
KNM RU2087	Ekembo hesloni	Rusinga	lower	m3	724.18	0.2673	345.62
KNM RU2087	Ekembo hesloni	Rusinga	lower	m2	327.82	0.2730	160.25
KNM RU2087	Ekembo hesloni	Rusinga	lower	m1	270.26	0.2472	139.88
KNM RU2087	Ekembo hesloni	Rusinga	lower	m2	438.07	0.2472	271.25
KNM RU2087	Ekembo hesloni	Rusinga	lower	m3	642.29	0.2990	242.25
KNM RU 1780	Ekembo spp	Rusinga	upper	m3	1008.63	0.2956	350.62
KNM MB 14260	Equatorius africanus	Maboko	lower	m2	542.06	0.2660	197.88

KNM MB 14261	Equatorius africanus	Maboko	upper	m1	407.49	0.2577	191.5
KNM MB 14266	Equatorius africanus	Maboko	upper	m2	450.74	0.2725	242.75
KNM MB 14262	Equatorius africanus	Maboko	lower	m3	428.19	0.3275	172.5
KNM RU 14236	Equatorius africanus	Rusinga	lower	m3	396.51	0.3275	153.12
KNM CA 1297	Limnopithecus legetet	Chamtwara	upper	m1	459.77	0.2645	213.5
KNM CA 1803	Limnopithecus legetet	Chamtwara	lower	m2	417.50	0.2704	216.5
KNM CA 1822	Limnopithecus legetet	Chamtwara	lower	m1	487.86	0.2997	179
KNM CA 1830	Limnopithecus legetet	Chamtwara	upper	m2	735.07	0.3095	312.88
KNM CA 1901	Limnopithecus legetet	Chamtwara	lower	m1	320.88	0.2998	113.25
KNM CA 2125	Limnopithecus legetet	Chamtwara	lower	m3	543.25	0.2355	303.25
KNM CA 2151	Limnopithecus legetet	Chamtwara	lower	m1	349.40	0.3114	150.62
KNM CA 348	Limnopithecus legetet	Chamtwara	lower	m2	397.76	0.2150	311.88
KNM CA 350	Limnopithecus legetet	Chamtwara	lower	m1	321.17	0.2203	152.38
KNM CA 639	Limnopithecus legetet	Chamtwara	lower	m3	656.26	0.3068	291.38
KNM CA 579	Limnopithecus legetet	Chamtwara	lower	m1	604.45	0.3060	326.25
KNM KO 7	Limnopithecus legetet	Koru	lower	m3	751.97	0.3048	308.75
KNM KNM LG 1454	Limnopithecus legetet	Legetet	lower	m2	515.37	0.3323	195.5
KNM LG 36	Limnopithecus legetet	Legetet	upper	m1	543.86	0.2688	278.38
KNM LG 911	Limnopithecus legetet	Legetet	upper	m1	392.93	0.2381	261.75
KNM SO 425	Limnopithecus evansi	Songhor	lower	m1	322.64	0.2648	162.5
KNM SO444	Limnopithecus	Songhor	lower	m2	427.32	0.2766	195.75
KNM SO444	Limnopithecus	Songhor	lower	m3	560.79	0.2666	239.62
KNM SO424	Limnopithecus	Songhor	lower	m2	263.93	0.3110	140
KNM SO443	Limnopithecus	Songhor	upper	m1	278.01	0.2129	229.38
KNM SO459	Limnopithecus	Songhor	upper	m3	373.34	0.2417	217.5
KNM SO913	Limnopithecus	Songhor	lower	m2	218.45	0.2569	140.12
KNM SO935	Limnopithecus	Songhor	upper	m2	421.72	0.3130	168.25
KNM SO936	Limnopithecus	Songhor	upper	m2	420.59	0.3097	196.75
KNM SO940	Limnopithecus	Songhor	upper	m3	388.58	0.2934	261

KNM CA1888	Kalepithecus songhorensis	Chamtwara	lower	m1	423.93	0.2629	212.25
KNM CA 388	Kalepithecus songhorensis	Chamtwara	lower	m1	383.10	0.1745	216.38
KNM CA 2256	Kalepithecus songhorensis	Chamtwara	upper	m1	503.00	0.3467	225
KNM SO378	Kalepithecus songhorensis	Songhor	lower	m1	250.39	0.2966	128.12
KNM SO378	Kalepithecus songhorensis	Songhor	lower	m2	232.50	0.2634	125.25
WK 16958_ll_m1.ply	Simiolus enjiessi	Kalodirr	lower	m1	379.46	0.3145	169.88
WK 16960_ll_m2.ply	Simiolus enjiessi	Kalodirr	lower	m2	334.59	0.3234	133.75
WK 18116_lr_m1.ply	Simiolus enjiessi	Kalodirr	lower	m1	436.36	0.3392	205
WK 18116_lr_m2.ply	Simiolus enjiessi	Kalodirr	lower	m2	374.94	0.2535	210
KNM MB11648	Micropithecus leakeyorum	Maboko	upper	m3	445.26	0.3279	211.5
KNM MB11654	Micropithecus leakeyorum	Maboko	upper	m2	418.57	0.2693	157.25
KNM MB11795	Micropithecus leakeyorum	Maboko	lower	m3	351.35	0.2519	194.62
KNM MB14258	Micropithecus leakeyorum	Maboko	lower	m3	275.39	0.3068	123.5
KNM MB9766	Micropithecus leakeyorum	Maboko	upper	m2	401.72	0.3181	146
KNM MB11652	Micropithecus leakeyorum	Maboko	lower	m1	310.58	0.3047	156.25
KNM CA 2228	Micropithecus clarki	Chamtwara	upper	m1	367.94	0.2257	210
KNM CA 380	Micropithecus clarki	Chamtwara	lower	m1	318.49	0.3203	172.38
KNM CA 380	Micropithecus clarki	Chamtwara	lower	m2	218.65	0.2549	115.12
KNM CA 380	Micropithecus clarki	Chamtwara	lower	m1	263.86	0.2816	113.62
KNM CA 380	Micropithecus clarki	Chamtwara	lower	m2	369.56	0.2793	206.38
KNM CA 380	Micropithecus clarki	Chamtwara		m3	264.75	0.2397	192.12
KNM CA 386	Micropithecus clarki	Chamtwara	lower	m1	365.95	0.3197	149.38
KNM CA 606	Micropithecus clarki	Chamtwara	lower	m2	335.75	0.2563	194.5
KNM CA 612	Micropithecus clarki	Chamtwara	upper	m1	404.06	0.2822	245.75

KNM CA 620	Micropithecus clarki	Chamtwara	lower	m1	391.59	0.2975	203.12
KNM CA 625	Micropithecus clarki	Chamtwara	upper	m1	442.24	0.3152	184.12
KNM CA 643	Micropithecus clarki	Chamtwara	upper	m1	442.05	0.2519	230.38
KNM LG 1474	Micropithecus clarki	Legetet	upper	m3	391.86	0.2841	201.25
KNM LG 54	Micropithecus clarki	Legetet	upper	m2	364.43	0.2849	211.62
KNM MW48	Nyanzapithecus vancouveringorum	Mfwangano	upper	m3	413.35	0.3669	221.62
KNM MB11645	Nyanzapithecus pickfordi	Maboko	upper	m3	454.40	0.2360	240.75
KNM MB11784	Nyanzapithecus pickfordi	Maboko	upper	m3	764.12	0.2879	291.88
KNM MB11786	Nyanzapithecus pickfordi	Maboko	upper	m1	565.86	0.2338	307.38
KNM MB125	Nyanzapithecus pickfordi	Maboko	upper	m1	432.58	0.3025	291.25
KNM MB14269	Nyanzapithecus pickfordi	Maboko	lower	m1	342.00	0.2995	160
KNM MB9743	Nyanzapithecus pickfordi	Maboko	lower	m3	626.94	0.4503	341.38
KNM MB1161	Nyanzapithecus pickfordi	Maboko	lower	m3	496.44	0.3867	185.12
KNM SO1112	Proconsul africanus	Songhor	lower	m2	402.34	0.1753	279.88
KNM CA 1298	Proconsul major	Chamtwara	lower	m2	639.00	0.2774	271
KNM CA 1771	Proconsul major	Chamtwara	lower	m2	444.31	0.2402	201.75
KNM CA 1773	Proconsul major	Chamtwara	lower	m1	408.31	0.2447	193.25
KNM CA 2229	Proconsul major	Chamtwara	lower	m2	583.81	0.2530	212.12
KNM CA 393	Proconsul major	Chamtwara	lower	m3	460.39	0.1797	249.5
KNM CA 394	Proconsul major	Chamtwara	lower	m1	320.66	0.2596	147
KNM CA 1872	Proconsul major	Chamtwara	upper	m2	482.02	0.2840	214.5
KNM CA 397	Proconsul major	Chamtwara	upper	m3	499.61	0.2088	247.88
KNM LG 1389	Proconsul major	Legetet	lower	m3	691.36	0.2675	319.75
KNM LG 1460	Proconsul major	Legetet	lower	m2	552.85	0.2990	205.5
KNM LG 452	Proconsul major	Legetet	lower	m1	374.69	0.2747	193.88
KNM LG 452	Proconsul major	Legetet	lower	m2	456.83	0.2346	216
KNM LG 452	Proconsul major	Legetet	lower	m1	439.54	0.2194	203.88
KNM LG 452	Proconsul major	Legetet	lower	m2	519.53	0.2336	239.38
KNM LG 452	Proconsul major	Legetet	lower	m3	602.46	0.2349	280.88
KNM LG 47	Proconsul major	Legetet	lower	m2	599.01	0.2786	200.62
KNM LG 1815	Proconsul major	Legetet	upper	m3	624.67	0.2880	287.88

KNM CA 392	Proconsul major	Chamtwara	upper	m2	476.24	0.2408	238.38
KNM SO541	Proconsul major	Songhor	lower	m1	684.22	0.3042	261.5
KNM SO914	Proconsul major	Songhor	lower	m2	925.45	0.2791	315.88
KNM SO915	Proconsul major	Songhor	lower	m1	628.43	0.2951	218.38
KNM SO917	Proconsul major	Songhor	lower	m1	831.47	0.3224	267.25
KNM SO920	Proconsul major	Songhor	lower	m3	1042.33	0.2634	373.88
KNM SO485	Proconsul major	Songhor	upper	m2	671.62	0.3172	233.5
KNM SO542	Proconsul major	Songhor	upper	m1	1133.96	0.2988	395.38
KT 31234	Rangwapithecus gordoni	Songhor	lower	m2	1303.92	0.2285	435
KT 31234	Rangwapithecus gordoni	Songhor	lower	m3	1358.30	0.2459	448.88
KNM SO1958	Rangwapithecus gordoni	Songhor	lower	m1	487.49	0.2902	248
KNM SO1958	Rangwapithecus gordoni	Songhor	lower	m2	617.14	0.3221	280.5
KNM SO374	Rangwapithecus gordoni	Songhor	lower	m1	633.46	0.2596	321.25
KNM SO374	Rangwapithecus gordoni	Songhor	lower	m2	1047.62	0.2676	409.5
KNM SO401	Rangwapithecus gordoni	Songhor	upper	m1	894.60	0.2390	383.5
KNM SO420	Rangwapithecus gordoni	Songhor	lower	m2	1475.22	0.3694	445.62
KNM SO434	Rangwapithecus gordoni	Songhor	lower	m1	746.29	0.3636	319.25
KNM SO450	Rangwapithecus gordoni	Songhor	lower	m3	762.16	0.2684	316.88
KNM SO463	Rangwapithecus gordoni	Songhor	lower	m1	440.10	0.3110	243.5
KNM SO463	Rangwapithecus gordoni	Songhor	lower	m2	546.56	0.2908	289
KNM SO463	Rangwapithecus gordoni	Songhor	lower	m3	713.08	0.2398	349.75
KNM SO464	Rangwapithecus gordoni	Songhor	lower	m3	1359.97	0.2584	577
KNM SO486	Rangwapithecus gordoni	Songhor	lower	m2	659.09	0.2676	301.38
KNM SO522	Rangwapithecus gordoni	Songhor	lower	m1	444.63	0.1956	329.75
KNM SO905	Rangwapithecus gordoni	Songhor	lower	m1	559.78	0.2784	322.5
KNM SO905	Rangwapithecus gordoni	Songhor	lower	m1	834.36	0.2120	453.88
KNM SO906	Rangwapithecus gordoni	Songhor	lower	m2	607.65	0.3541	245.12
KNM SO908	Rangwapithecus gordoni	Songhor	lower	m2	980.23	0.3486	396.88

KNM SO931	Rangwapithecus gordoni	Songhor	upper	m1	679.23	0.2843	326.75
KNM SO932	Rangwapithecus gordoni	Songhor	upper	m1	738.72	0.2750	382.25
KNM SO938	Rangwapithecus gordoni	Songhor	upper	m2	515.15	0.3030	273
KNM SO938	Rangwapithecus gordoni	Songhor	upper	m2	633.87	0.2763	281.5
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m1	596.63	0.2550	253
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m2	770.10	0.2765	262.25
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m3	1058.89	0.2480	325.25
KNM SO944	Rangwapithecus gordoni	Songhor	upper	m1	386.48	0.2944	224.62
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m1	534.44	0.2660	246.38
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m2	787.92	0.2733	315
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m3	1329.50	0.3217	442.12
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m1	428.03	0.3187	186.75
KNM SO700	Rangwapithecus gordoni	Songhor	upper	m2	746.09	0.3294	379.88
KNM WK 16955	Simiolus enjiessi	Kalodirr	lower	m1	246.72	0.4001	121.75
KNM WK 16960	Simiolus enjiessi	Kalodirr	upper	m1	281.52	0.2885	148.12
KNM WK 16960	Simiolus enjiessi	Kalodirr	upper	m2	385.15	0.3764	132.25
KNM WK 16960	Simiolus enjiessi	Kalodirr	upper	m3	457.02	0.3409	172
KNM FT 17	Simiolus andrewsi	Fort Ternan	lower	m1	317.82	0.2933	112.88
KNM FT 20	Simiolus andrewsi	Fort Ternan	lower	m1	239.49	0.4131	110.5
KNM FT 20	Simiolus andrewsi	Fort Ternan	lower	m2	312.87	0.3173	168.88
KNM FT 20	Simiolus andrewsi	Fort Ternan	lower	m3	250.21	0.3455	104.75
KNM FT 23	Simiolus andrewsi	Fort Ternan	lower	m3	282.26	0.2636	146