Variation in Dental Microwear Textures and Dietary Variation in African Old World Monkeys (Cercopithecidae)

by

Amy Elissa Shapiro

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved April 2015 by the
Graduate Supervisory Committee:

Kaye E. Reed, Chair
Gary T. Schwartz
Peter S. Ungar

ARIZONA STATE UNIVERSITY

May 2015

ABSTRACT

Dietary diversity is an important component of species's ecology that often relates to species's abundance and geographic distribution. Additionally, dietary diversity is involved in many hypotheses regarding the geographic distribution and evolutionary fate of fossil primates. However, in taxa such as primates with relatively generalized morphology and diets, a method for approximating dietary diversity in fossil species is lacking.

One method that has shown promise in approximating dietary diversity is dental microwear analyses. Dental microwear variance has been used to infer dietary variation in fossil species, but a strong link between variation in microwear and variation in diet is lacking. This dissertation presents data testing the hypotheses that species with greater variation in dental microwear textures have greater annual, seasonal, or monthly dietary diversity.

Dental microwear texture scans were collected from Phase II facets of first and second molars from 309 museum specimens of eight species of extant African Old World monkeys (Cercopithecidae; n = 9 to 74) with differing dietary diversity. Dietary diversity was calculated based on food category consumption frequency at study sites of wild populations. Variation in the individual microwear variables complexity (*Asfc*) and scale of maximum complexity (*Smc*) distinguished groups that were consistent with differences in annual dietary diversity, but other variables did not distinguish such groups. The overall variance in microwear variables for each species in this sample was also significantly correlated with the species's annual dietary diversity. However, the overall variance in microwear variables was more strongly correlated with annual frequencies of

fruit and foliage consumption. Although some variation due to seasonal and geographic differences among individuals was present, this variation was small in comparison to the variation among species. Finally, no association was found between short-term monthly dietary variation and variation in microwear textures.

These results suggest that greater variation in microwear textures is correlated with greater annual dietary diversity in Cercopithecidae, but that variation may be more closely related to the frequencies of fruit and foliage in the diet.

ACKNOWLEDGMENTS

I would like to thank my committee, Kaye Reed, Gary Schwartz, and Peter Ungar, for their assistance in completing this dissertation. Thanks in particular go to my committee chair Kaye Reed for her help in all aspects of my research. Peter Ungar also generously provided use of the confocal microscope and microwear software in his lab, without which this research would not have been possible. Anne Stone and Brian Verrelli provided lab access for dental cast creation. Discussions with Jason Kamilar were invaluable for implementation of the methods used here. Laura Stroik provided much guidance in molding, casting, and statistical methods—thanks for being the guinea pig! A special thanks to the students in Peter Ungar's lab at the University of Arkansas for their help with the confocal microscope and laboratory protocols, particularly Sal Caporale, Sarah Livengood, Anna Ragni, Ann Walcutt, and Melissa Zolnierz. Thanks also to Lucas Delezene for his assistance at University of Arkansas. Dave Hughes also provided crucial help with data cleaning.

I would also like to thank the institutions, curators, and collection managers that provided access to specimens. These include Chris Conroy (UC Berkeley Museum of Vertebrate Zoology), Emmanuel Gilissen and Wim Wendelen (Royal Museum of Central Africa), Lawrence Heaney and Bill Stanley (The Field Museum), Georges Lenglet (Royal Belgian Institute of Natural Sciences), and Darren Lunde (National Museum of Natural History). A special thanks is due to Vivek Venkataraman and the Guassa Gelada Research Project for access to rare molds from Guassa geladas. Brenda Benefit also generously provided fossil monkey casts and productive discussion.

Funding for this project was provided by the Arizona State University (ASU) Graduate College (Graduate Education Dissertation Fellowship), ASU Graduate and Professional Students Association (Graduate Research Support Program and Jumpstart Research grants), the ASU School of Human Evolution and Social Change (Graduate Research grant), ASU Chapter of Sigma Xi Grant-in-Aid of Research, and the Elizabeth H. Harmon Research Endowment through the Institute of Human Origins.

Finally, this project would not have been possible without the help and support of many friends and family. Thanks for your continued love and encouragement.

TABLE OF CONTENTS

CHAPTER Page

Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

Outline

This dissertation is set up as a series of three research papers, with an introduction and conclusion to the broader topics discussed. In this introduction, I note the original research questions with which I began the research project by discussing some of the previous biogeographical and ecological research that led me to these questions. I also explain how I could answer these questions using dental microwear texture analysis (DMTA). I was originally interested in macroecological patterns that related primate distribution to ecological variables; could these relationships be detected in the past and might they partially explain the distribution of fossil primates? First, however, I needed a method to reconstruct at least one ecological variable in fossil species. Based on the research discussed in this introduction, I decided that DMTA was one of the best methods to reconstruct dietary breadth, which is the diversity of food categories utilized by an organism. That is, DMTA was the proxy ecological variable that could be used to link hard tissue remains to primate distribution.

Ecological Background

The geographical distribution of species has been linked with the theory of evolution since Darwin used species distributions as evidence of biological change. As he wrote in the first page of *On the Origins of Species*, "the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent [….] seemed to me to throw some light on the origin of species" (Darwin,

1859:1). Fossil species that Darwin found were different than the living species he encountered and offered evidence that species were not static in space and time. Today, we know that species are distributed across the earth in patterns affected by both ecological and historical factors (Lomolino et al., 2006). Ecological factors affect where a species can survive and multiply, while historical factors affect which suitable environments a species can access. Together, these factors affect the size and spatial range of a species (Brown and Maurer, 1989; Brown, 1995; Gaston and Blackburn, 2000). Thus, an understanding of ecological and historical factors is crucial to understanding why fossil species occurred where and when they did.

Ecological factors include abiotic variables, such as soil type, elevation, and the climatic variables of temperature and rainfall, and biotic variables, such as types of vegetation and the presence or absence of competing organisms. The range of suitable environmental variables for a species makes up the species niche. Hutchinson (1957) expanded the work of Grinnell (1917) and Elton (1927) to describe the niche concept in his seminal paper, which is still the model used today. He imagines the species niche represented as an *n*-dimensional hypervolume, with each ecological variable on a separate axis. The tolerance ranges of a species for each variable make up the hypervolume. Those areas that fulfill the species tolerances on all axes can be inhabited by a species; they are within the species niche.

One of the major areas of study for ecologists is determining species' tolerance ranges for a given abiotic or biotic variable (Lomolino et al., 2006; Franklin, 2009). We are still far from knowing which ecological variables control where many species live today. Habitat, which is controlled by a confluence of abiotic variables, is often the only

explicit variable known to influence species distribution. Because habitat encompasses so many aspects of an organism's needs, including substrate use and, often, dietary sources, it is usually considered the main factor that influences a species distribution (e.g. Thorn et al., 2009). Many studies of primate ecology focus on the habitat as a special category distinct from the confluence of factors that affect it. Parsing out which of the abiotic variables that influence habitat are crucial to a primate's distribution is often quite difficult, but it may be important to know which variables that affect environment are more important to a primate's distribution; however, this field has not been an area of major study within primatology.

Although the species niche includes all factors that affect survival and distribution, the niche can be broken down into smaller niches, for example the dietary niche. This niche would include all aspects of the species niche related to diet, such as resource choice, location on the landscape of resource acquisition, and resource processing. However, the dietary niche can be broken down further, such that it includes only the dietary resources. Although this trimming of the dietary niche may lead to overlooking a factor that may be important to the questions asked, it makes the niche easier to quantify, allowing better hypothesis testing.

Patterns in Diversity

Species richness (i.e. the number of species in a sample) has long been recognized to increase with proximity to the equator (Brown and Sax, 2004). Early naturalists, such as Banks, Forster, von Humboldt, Darwin, and Wallace all noticed that there were more species concentrated in the tropics than in temperate areas such as Europe (Brown and

Sax, 2004). Scientists of the Modern Synthesis went further by quantifying this pattern. Dobzhansky (1950) documented increased species richness in trees in the tropics, which was also coupled with decreased abundance. Simpson (1964) similarly characterized North American mammal species richness with a newer methodology using grids. The compilation of quantitative data by the late 1960s led to the understanding that most taxonomic groups were most diverse in the tropics (Brown and Sax, 2004), and paleobiologists showed that this pattern could be seen in the past (Willig et al., 2003) and as far back as the Permian (Stehli et al., 1969). Thus, the focus was shifted to understanding the mechanisms creating this near-universal pattern, called the latitudinal diversity gradient (LDG). Pianka (1966) was the first to critically assess causes of the LDG; he mentions six possibilities, while Rohde (1992), in a wider review, posited 28. A more recent review by Willig et al. (2003) critically reviewed these and included in the six most well-supported the "Rapoport Rescue" hypothesis, which relates the LDG to patterns in range size, thus linking species diversity with species distribution. A closer look at patterns in range size will first be discussed, followed by a closer look at the Rapoport effect, the potential causal mechanism of the Rapoport Rescue hypothesis.

Patterns in Range Size

Range size has been shown to change at different scales in predictable ways in large groups of species. At smaller scales, species range sizes tend to be bimodal, with many species having either very small or very large range size, while fewer species have range sizes in the middle; at larger scales, such as at large regional, continental, and global scales, this pattern disappears, and a unimodal distribution with a strong right

skew emerges: many species have small range sizes, with decreasing numbers having large range sizes (Brown, 1995; Gaston and Blackburn, 2000; Lomolino et al., 2006). This pattern of range size distribution is seen among a wide array of extant orders and classes, such as birds, mammals, and invertebrates (Brown, 1984, 1995; Gaston and Blackburn, 2000), but is also seen in paleontological assemblages of invertebrates (Jablonski, 1986, 1987; Gaston and Blackburn, 2000; Jablonski and Roy, 2003), with range size estimated from sites where species are found. The ubiquity of this pattern may indicate a strong natural law: most species have the smallest of range sizes, while few have very large range sizes. If rarity is indicated by a small range size, then determining why this pattern occurs can help to determine why most species are rare (Gaston, 1994; Gaston and Blackburn, 2000; Harcourt, 2000). Gaston and Blackburn (2000) discuss seven possible mechanisms to explain this pattern. Three of these mechanisms (random sampling, narrow vagrant range sizes, and sample range position) only explain the relationship between smaller scale patterns and larger scale ones, and do not explain the question of patterns at the largest scale. The other four, metapopulation dynamics, niche breadth, niche position, and dynamics of speciation, extinction, and time, will each be discussed briefly below.

Metapopulation dynamics have been indicated in the determination of species range size (Brown, 1995; Gaston and Blackburn, 2000). A metapopulation is a group of spatially distinct populations of a species that interact in some way; the dynamics of this interaction can act to create abrupt edges of ranges such as are seen with discontinuities in environmental variables that determine a species niche (Lennon et al., 1997). A number of models have been explored to model metapopulation dynamics based on the

proportion of sites occupied by a species within a range, as well as the probabilities of immigration and extinction (Levins, 1969, 1970; Hanski, 1982; Tokeshi, 1992). However, these models make a number of unrealistic assumptions, such as the occurrence of discrete, identical, and infinite habitat patches and equal mobility between any two patches. Although Hanski (1994, 1997) addresses some of these problems, this still leaves the issue of use in paleontological settings, which is difficult if not impossible. Thus, although metapopulation dynamics may be able to explain some aspect of extent of occurrence in modern populations, its use in explaining past distributions is problematic.

Two explanations discussed by Gaston and Blackburn (2000) use the niche concept to explain the patterns of range size, based on 1) niche breadth and 2) the position of the niche. The first explanation is based on the correlation of niche breadth with range size. Niche breadth is a term that quantifies the size of the species niche; species with larger breadths have larger niches, meaning they have broader ranges of variables on their niche axes. Species with large niche breadths are often called generalists, while species with small niche breadths are called specialists. These terms are also used when characterizing a single axis of the niche, for example diet; species that exploit a large range of resources are termed dietary generalists, while species that exploit a small range of resources are termed dietary specialists. Although these terms are widely used, there does not appear to be a specific convention about what constitutes the boundaries of these categories, and as there is a continuum of breadths, it can be difficult or arbitrary to categorize species into these groups.

The niche breadth hypothesis, also called the resource breadth hypothesis (Gregory and Gaston, 2000), proposes that those species with larger niche breadths are

able to be more widespread, i.e. have larger species range sizes. This hypothesis has been most strongly supported by Brown and colleagues (Brown, 1984, 1995; Brown et al., 1995; Lomolino et al., 2006). However, Gaston and colleagues (Gaston and Blackburn, 2000; Gregory and Gaston, 2000) point to failures in these studies to control for differences in sample size between rare and widespread species and for spatial and environmental autocorrelation among sites. They indicate the necessity of basing estimations of niche breadth and range size on the same number of observations in restricted and widespread species. They also point out that niches are *n*-dimensional (following Hutchinson, 1957), and perhaps impossible to quantify practically; furthermore, any study trying to use niche breadth may fail to measure a relevant niche variable that influences range size. Although Gaston and Blackwell (2000) ultimately do not believe that niche breadth is a driving force behind range size, they do agree that testing major axes of the niche (i.e. major variables) is the best way to test this hypothesis. Thus, it is possible to refine the niche breadth hypothesis to specific, major aspects of the niche; this technique has been attempted for primates by a number of researchers (e.g. Cowlishaw and Hacker, 1997; Eeley and Foley, 1999; Eeley and Lawes, 1999; Harcourt et al. 2002), as discussed below. A recent meta-analysis of ecological studies looking for a relationship between niche breadth and geographical range size found a strong positive correlation between these two factors across broad taxonomic groups, indicating that this relationship is a general ecological pattern (Slatyer et al., 2013). However, the causes behind this pattern, and why some species deviate from it, are still uncertain (Slatyer et al., 2013)

The second explanation, based on the position of the niche, is better accepted by Gaston and Blackwell (2000). Gregory and Gaston (2000) refer to this hypothesis as the resource availability hypothesis: those species that utilize widespread resources will themselves be widespread, while those that utilize restricted resources will have a restricted species range (Hanski et al., 1993). For example, if there are two species, one of which occupies forests and one of which occupies grasslands, and there is more area of forest present, the species that occupies forests will have a larger range size. This hypothesis differs from the niche breadth hypothesis in that specialist species can be widespread if their resources are also widespread. However, the two hypotheses are not mutually exclusive (Gregory and Gaston, 2000). Although some research has supported this hypothesis (Gregory and Gaston, 2000; Heino, 2005; Lappalainen and Soininen, 2006), other research has refuted it (Passy, 2012); more studies that analyze both niche position and niche breadth are called for (Slayter et al., 2013).

The last explanation laid out by Gaston and Blackwell (2000) suggests that the patterns of species range size are the result of speciation, extinction, and temporal dynamics of range through a species' lifetime. Although a number of models exist of the long-term temporal dynamics of species range size, it remains to be demonstrated if there are any general patterns across these (Gaston and Blackburn 1997, 2000; Gaston 1998). Furthermore, it is not clear how this hypothesis would explain the observed pattern of many small and few large species ranges. However, it seems quite intuitive that these processes shape a species' range size and distribution, since they are what *change* this distribution.

The Rapoport Effect

A further relationship that has been widely studied and links ideas about the LDG and range size patterns is the relationship between latitude and latitudinal range size. Rapoport (1982) noticed that mammal species that lived closer to the equator had species ranges with smaller latitudinal extents (latitudinal range sizes) than did species living farther from the equator; the latitudinal extent of species ranges decreased as latitude decreased. Stevens (1989) championed this relationship and called it Rapoport's Rule, although many researchers call it Rapoport's Effect, or the Rapoport effect, after Blackburn and Gaston (1996), since the relationship appears to be variable (Cowlishaw and Hacker, 1997; Harcourt, 2000; Hernandez Fernandez and Vrba, 2005a; Lomolino et al., 2006). Stevens (1989) was also the first researcher to explicitly propose that this pattern might be caused by climatic variability, such that areas with greater climatic variability have species with larger latitudinal extents. Climatic variability is predicted to select for wider niches, as resource availability will vary more in time and space in areas with higher climatic variability; species with broader niches will be able to survive in areas with high climatic variability by exploiting whichever resources are available, which would not be possible for species with narrow niches (Slove and Janz, 2010). Having broader niches in turn allows species to cross more barriers to dispersal, allowing them to have larger geographic ranges. This pattern requires a certain confounding of variables, since latitudinal extent and absolute range size are both increasing in this case. In addition, many taxa exhibit both the LDG and the Rapoport effect, while taxa that do not exhibit the LDG are generally exceptions to the Rapoport effect (Willig et al., 2003); these facts suggest a link between the Rapoport effect and the LDG, and have suggested

to researchers that the LDG may be caused by the Rapoport effect ("Rapoport Rescue" hypothesis). However, the LDG is a much stronger pattern that the Rapoport effect, and researchers have shown that species that do not exhibit the Rapoport effect still exhibit the LDG (Cowlishaw and Hacker, 1997). Thus, it is more likely that the Rapoport effect is caused by the LDG, such that in areas with higher species richness, species have smaller latitudinal extents (Willig et al., 2003).

Niche Gradients

A further pattern related to the species niche has been suggested by MacArthur (1972) and relates to the above patterns. He suggests that species that live closer to the equator have smaller niches, while those farther from the equator have broader niches. This pattern may relate to patterns in range size as well as the Rapoport effect and the LDG. MacArthur proposed that this pattern was seen in vertebrates and was caused by climatic variation such that more variable areas selected for larger niches while stability allowed for more restricted niches. Vazquez and Stevens (2004) reviewed the evidence for this pattern through a meta-analysis; they concluded that there was evidence for such a global pattern in some taxa, but that due to sample effects the null hypothesis of no pattern across taxa could not be rejected. They also found that while temperature variability gradients did occur in the expected direction across the globe, rainfall variability was not as expected, with more global variability seen closer to the equator. This finding suggested that the mechanism for the pattern as determined by MacArthur (1972) was not responsible for the pattern if it did exist. Vazquez and Stevens (2004) instead suggest that the LDG may be responsible for gradients in niche size through

affects of interspecific interactions causing niche partitioning. This suggestion has implications for the niche gradient in the past; as there is strong support for the LDG in many taxa in the past (e.g. Stehli et al., 1969; Willig et al., 2003), there is a possibility that niche gradients also existed if they are caused by the LDG.

Testing for Patterns in Primates

Latitude, Geographic Range Size, and the Primate Niche

Although the relationships between latitude, species' range size, and niche parameters have been explored in many different organisms, few studies have examined these relationships in mammals (Vazquez and Stevens, 2004), and fewer still in primates.

Cowlishaw and Hacker (1997) examined the Rapoport effect by regressing the latitudinal range extent of African primate species on their latitudinal midpoint. They found that there was no relationship between these two variables overall, but there was a strong relationship in primates whose midpoint fell south of the equator. Following Stevens' (1989) suggestion that latitudinal range is indicative of a species' ability to withstand seasonality, Cowlishaw and Hacker (1997) further examined this rule by using independent contrasts with stepwise multiple regression analyses with six climatic predictor variables that might determine latitudinal range. The only two variables that exhibited a significant relationship with latitudinal range were proportion of rainfall in the wettest month and, for species with midpoints above the equator, altitude. These results suggested to the researchers that latitudinal range in African primates is determined by adaptation to climatic variability, as approximated by rainfall seasonality; those primates that can tolerate climatic variability range farther from the equator.

However, other predictor variables that also approximate climatic variability, namely daily and annual temperature ranges, were not significantly related to latitudinal range. This pattern may indicate that it is seasonality of rainfall, and not climatic variability overall, that may influence latitudinal range.

Since many reports of the Rapoport effect focused on high-latitude, temperate species, Harcourt (2000) explored the Rapoport effect for an equatorial, tropical order, Primates. He used the latitudinal midpoint and latitudinal extent of non-human primate genera across Africa, Madagascar, Asia, and Central and South America in least squares regression and Spearman rank correlation analyses. In addition, he also tested for an association between both latitudinal midpoint and latitudinal extent and two measures of climatic variability: temperature variability, measured as the mean maximum minus mean minimum monthly temperature, and precipitation variability, measured as mean maximum divided by mean minimum monthly precipitation (both for grid cells of 30 arc minutes). A final test was for an association between latitudinal extent and four measures of adaptability: dietary breadth, habitat breadth, body mass, and number of species per genus. Harcourt (2000) found no association between latitudinal midpoint and extent globally, but he did find an association when Madagascar was excluded from the analyses; within Africa, there was no association between these two measures, but when outlier genera were excluded, there was a very strong association. Furthermore, there was a strong association between these measures and both measures of climatic variability within Africa. Finally, Harcourt found an association between three measures of adaptability (dietary breadth, habitat breadth, and number of species per genus) and latitudinal extent, both in primates globally and in Africa alone, and even in groups where

no Rapoport effect was found. There was no association between body mass and latitudinal extent, which has been supported with other analyses by Hernandez Fernandez and Vrba (2005c) on large African mammals.

Hernandez Fernandez and Vrba (2005a) tested whether a variant of habitat breadth varied with latitudinal midpoint for African mammals in the orders Carnivora, Artiodactyla, and Primates. They used the number of biomes in which the species occurs, termed the Biomic Specialization Index (BSI; Hernandez Fernandez, 2001), as a measure of habitat breadth, and found the average BSI per degree of latitude. There was no correlation between BSI and latitudinal midpoint for all mammals (although there was for the Northern hemisphere alone), nor for Primates; however, Primates followed the same trend as the overall mammal trend in average BSI per latitude, with lower averages towards the equator and higher averages towards the poles. However, the Barbary macaque (*Macaca sylvanus*) was an outlier that greatly affected the pattern in Primates, and was removed because it represented a very different biogeographic group, according to the researchers, since macaques are concentrated in Asia and may have originated there (Hernandez Fernandez and Vrba, 2005b; but see Bohm and Mayhew, 2005 for a different opinion). In addition, the researchers used stepwise least squares regression to evaluate which climatic variables best predicted average BSI per latitude band, with a total of 11 possible variables. For Primates overall, the best predictor was average annual precipitation, in contrast to the findings of Cowlishaw and Hacker (1997) that precipitation variability was the best predictor of latitudinal extent. For the southern hemisphere, the strongest predictor was area in each band, which indicates that continental shape may affect biomic specialization in southern African primates.

Other researchers have focused on primate species range size, instead of on latitudinal measures, in relation to ecological variables and the species niche. Eeley and Foley (1999) investigated the relationship between species richness and species range size but also examined whether these measures correlated with dietary and habitat breadth in African catarrhine primates using correlation coefficients. They found a positive correlation with range size, dietary breadth, and habitat breadth, as well as a negative correlation with all of these and species richness. Thus, they found that more specialized species (in both habitat and diet) are found closer to the equator, in smaller ranges, and associated with higher numbers of species. This result still stood after controlling for both spatial autocorrelation and phylogenetic constraints.

Harcourt et al. (2002) found similar results in primate genera across all continents; range sizes of genera were significantly correlated with measures of specialization given as dietary breadth, habitat breadth, maximum latitude, and number of species per genus. Those genera that had small species ranges also had lower dietary and habitat breadths, lower maximum latitude, and fewer species per genus. Other factors examined for correlation were resource requirements (as measured by body size, local density, annual home range, and group size) and population recovery rate (measured by interbirth interval and maximum intrinsic population increase). None of these variables were found to be significantly correlated with generic range size, in contrast to other studies, especially those that found a correlation between local density (i.e. abundance) and range size (Brown, 1984; Gaston, 1994; Brown, 1995; Eeley and Lawes, 1999). Harcourt et al. (2002) also found that range size of genera was not correlated with body mass, as was also found by Harcourt (2000) and when examining latitudinal extent. Other

studies found that taxa with small body masses could have large or small range sizes, but few to no taxa with large body masses could have small range sizes (Gaston, 1994; Hernandez Fernandez and Vrba, 2005c).

In contrast to the studies at the continental and global scale, Lehman (2004) used surveys of the primate community of Guyana and found a correlation between habitat generalists and large geographic range size, but no correlation between dietary specialization or body size and geographic range size. Lehman explains this finding by demonstrating that habitat generalists in Guyana tend to be dietary specialists, and need larger ranges to fulfill their dietary needs since they can exploit fewer resources in each habitat, while dietary generalists can meet requirements in a smaller habitat breadth by exploiting a larger number of dietary categories. These habitats that tend to be inhabited by the dietary generalists are also those habitats with the larger area. This relationship between increased habitat breadth, decreased dietary breadth, and range size merits further analysis, especially as it may support the resource availability hypothesis. However, that study highlights the differences in looking at smaller regions instead of larger or continental scales.

Overall, these studies indicate that there is some support for the Rapoport effect in primates, both globally and within Africa, but that climatic variability and measures of adaptability appear to be stronger forces affecting latitudinal extent and geographic range size. Furthermore, although the Rapoport effect may be a reflection of climatic variability co-varying with latitude, the relationships may not exactly mirror each other; in African primates, climatic variability, rather than latitudinal midpoint, is more strongly related to latitudinal range (Cowlishaw and Hacker, 1997; Eeley and Foley, 1999; Harcourt, 2000).

These studies also show some support for the resource breadth hypothesis (Eeley and Foley, 1999; Harcourt, 2000; Harcourt et al., 2002), although whether dietary or habitat breadth is the driving factor is not clear (e.g. Harcourt, 2002; Lehman, 2004). Although these studies have examined the strength of Rapoport's effect, and some aspects of the resource breadth hypothesis, in primates, there have been no studies that explicitly examine the resource availability hypothesis to explain primate species range size. However, there is support for this hypothesis from a few primate studies (e.g. Nunes, 1995). These results call for explicit testing of these hypotheses within primates. Furthermore, these hypotheses hold promise for increasing our understanding of primate ranges in the fossil record.

Seasonality

Another aspect that affects habitat use and diet in primates is seasonality. Most, if not all, primates are affected by changes to their habitat due to seasonal environmental changes; these changes, in varying degrees of intensity, have been reported in all types of habitats where primates range (Hemingway and Bynum, 2005). One of the aspects that is most affected by seasonality is primate diets; during certain seasons, primates often face food scarcity. Hemingway and Bynum (2005) identified five types of responses to food scarcity caused by seasonal effects in primates when they analyzed 234 studies covering 119 primate species and 105 sites across the globe. These were changes in home range size, changes in time spent foraging, physiological responses, shifts in habitats used, and shifts in diet. Although there were differences among regional communities in types of responses, over 70% of all responses were shifts in diet, involving either an increased or

decreased dietary breadth. Thus, a related aspect of dietary breadth is dietary variability, i.e. how different the diet is through time. Hemingway and Bynum (2005) found that there was a significant relationship between overall dietary variability and dietary breadth; dietary variability decreases as dietary breadth (here the number of food species consumed) increases. Thus, primates that regularly incorporate more species into their diets have less variability in those diets across seasons, while primates that incorporate fewer species have greater variability in diet across seasons. However, the coefficient of determination was quite small ($r^2 = 0.08$, $p < 0.05$, $n = 77$), indicating that dietary breadth explains only a small amount of the variation in dietary variability.

Hemingway and Bynum (2005) also compared dietary CVs (coefficients of variation) of different types of diets. They used least squares regression analyses to look for relationships between overall diet, fruit use, and new leaf use (across all primates and within different continents) and latitude and length of the dry season (measures attempting to quantify seasonality). They found that the CV of overall diet was significantly related to latitude in African primates, but not in primates in other areas; that CV of fruit use was related to latitude in African and Neotropical primates, but to length of the dry season in Asian primates; and that CV of new leaf use was related to length of the dry season in primates from Africa and Madagascar. Thus, within Africa, primates with greater variation in overall monthly diet and in monthly fruit use live in higher latitudes, while primates with greater variation in new leaf use live in areas with longer dry seasons.

In contrast to the study of Hemingway and Bynum (2005), Chapman and Chapman (1990) found no relationship between seasonality (measured as the CV of

rainfall) and dietary variability, as compared with correlation coefficients; however, their measure of dietary variability was calculated as the sum of between-month variance in use of each of five major food categories weighted by the percent of the total diet each category comprised. It's not clear how this measure compares to that of Hemingway and Bynum (2005), nor how looking at major categories in the diet compares to looking at number of species utilized. Standardizing the methodology of studying dietary variability is a major aspect that needs to be addressed, as studies cannot be compared quantitatively until this occurs.

One of the major issues in paleoanthropology in the last decade, which relates to seasonality, has been the relative importance of "fallback foods" in the diet and evolution of primates, particularly of hominins (see Lambert, 2009, and other articles from Special Issue on Fallback Foods (2009), Am J Phys Anth 140(4)). The definition of fallback foods is quite generalized (Hemingway and Bynum, 2005; Lambert, 2009, and references therein), but indicates a dietary resource that is less preferred and critical to species survival during times of food scarcity (Altmann, 1998; Lambert, 2007). Thus, utilization of fallback foods is one example of a dietary shift during food scarcity. However, the relationship between fallback foods and dietary breadth is not clear. Since Hemingway and Bynum (2005) found that primates that incorporated more species into their diets (one measure of dietary breadth) had less dietary variability, we might expect that species with greater dietary breadth would be less likely to rely on fallback foods during times of scarcity. More seasonal environments may encourage greater dietary variability, but they may also encourage greater dietary breadth (Hemingway and Bynum, 2005).

Primate Dietary Niche Space

Reconstructing the diet of fossil primates is one of the main objectives for many paleoanthropologists, as diet relates to so many aspects of adaptation, distribution, and evolution. Researchers rely on data preserved in the fossil record, such as morphology, and their relationships to diet in extant primates to infer dietary ecology. In extant primates, diet can be determined by analyzing the contents of stomachs (of shot primates) or of feces, or by directly observing primate foraging and ingestion (Harding, 1981). Analyzing stomach or feces contents does not necessarily identify all items in a primate's diet, however, nor are amounts of each item or proportions of total diet available through this type of analysis. However, these methods can be a reliable way to capture at least a portion of a primate's diet through direct examination, as well as through isotopic analyses. By far, though, the main method of determining diet in extant primates is through observational studies. However, depending on the main goal of the research, the characterization of diets may differ. Diet may be characterized by the number of food categories or species eaten; quantities, proportions, or amounts of food items eaten; or biochemical or nutritional analyses of items eaten (Rowe, 1996; Campbell et al., 2011). Although no studies have used all of these methods, some primates have been studied long enough where many of these methods have been used (Rowe, 1996; Campbell et al., 2011). In the absence of these broad characterizations of diet in a single study, compilations of diet from multiple sources (e.g. Rowe, 1996; Campbell et al., 2011; Butynski et al., 2013) are normally used by researchers not directly observing diets themselves (e.g. Chapman et al., 1999; Eeley and Foley, 1999; Harcourt et al., 2002).

Because diet is not directly observable in the past, methods of dietary reconstruction for fossil primates must rely on measures that correlate with specific diets, determined through the above methods, in extant primates. These can be broadly grouped into those methods that rely on adaptations found in morphology and those that rely on traces left by the diet in or on fossil remains (Ungar, 1998). The first group relies on the link between morphology and adaptation, while the second group does not.

Adaptive Methods

One way to estimate diet of fossil primates is to determine what foods the primates are adapted to eat. The evolutionary pressures to better exploit the resources a primate ingests lead to dentition that is adapted to a primate's diet. Methods that rely on this relationship tend to use either explanations relating to the allometry or morphology of the dentition (Ungar, 1998).

Dental allometry has been hypothesized to relate to primate diet for at least half a century (Robinson, 1954; Ungar, 1998). Larger molars were associated with an herbivorous diet requiring grinding or shearing (Robinson, 1954); larger incisors were associated with diets requiring more preparation, such as of fruits with outer shells, while smaller incisors were associated with folivory (Fleagle, 2013). Although some of these trends were seen to hold true among closely related groups (Ungar and Grine, 1991), other evidence showed these relationships to break down between higher taxonomic levels, or even among closely related groups (Kay, 1977; Strait, 1993; Anapol and Lee, 1994; Ungar, 1996). Since these relationships are not reliable for all groups studied, they

cannot be considered a natural law in the adaptative sense, and should not be used in the reconstruction of diet of fossil taxa, at least in the absence of other data (Cartmill, 2002).

In contrast to dental allometry, studies using dental morphology have had greater success in explaining adaptations to diet and using these to reconstruct diets of fossil primates. Since the function of dentition is to "fracture and fragment solid foods" (Lucas and Teaford, 1994:1), it is assumed that the morphology of the dentition is adapted to the mechanics of processing those foods that are most often eaten or are most important to the fitness of the organism. Although primates have generally been considered to have less specialized dentitions than other mammals, there are clear indications that the primate dentition is adapted to primate diets (Lucas and Teaford, 1994). Anthropoid primates have broad, spatulate incisors that have been related to increased incisal biting for processing of food, especially fruit, compared to strepshirines (e.g. Kay and Hiiemae, 1974; Kay and Hylander, 1978). However, incisor morphology has not been greatly studied at higher levels of taxa. Most studies of dental morphology in relation to diet have concentrated on the shape of the molars (Ungar, 1998). Specific morphologies have been related to the mechanics of shearing, crushing, and grinding, three distinct mechanical processes used to break down food before ingestion (Kay and Hiiemae, 1974; Kay, 1984; Ungar, 2002; but see also Lucas and Teaford, 1994). Kay and Hiiemae (1974) showed an association between morphology and these dental functions. Shearing occurs during occlusion by the leading edges of crown crests on postcanine teeth, and to minimize the area of simultaneous occlusion these edges are usually concave. Crushing occurs between planar surfaces of teeth, such as wear planes, cusp tips, and fossae between cusps and ridges. Grinding involves both shearing and crushing, and in primates occurs between

planar surfaces that move across each other. Increased use of foods that require one or another of these functions for fracture puts adaptive pressure on increasing the amount of functional space on the tooth that acts in these functions. Kay (1975) measured lower second molar features related to these functions, and found that expectations of increased shearing features were met in both folivores and insectivores (> 45% of the diet comprising leaves or insects, respectively) across primates. Frugivores had shorter shearing crests. Benefit (1987) expanded on these ideas by regressing measures of shearing and cusp flare against the percent fruit and foliage in extant cercopithecid yearly diets; she found a significant correlation between these measures and diet, and thus her regression is often used to estimate diet in fossil cercopithecids (e.g. Ungar et al., 2008b). However, the prediction intervals of estimates are large, limiting the potential use of this method for yielding yearly dietary proportions in fossil primates. Furthermore, studies of dental morphology have focused on unworn or minimally worn teeth, since these preserve the original morphology of the tooth; this requirement limits the fossils that can be used for analysis with these methods.

More recently, methods utilizing three-dimensional digital imaging to measure slope, shape, and relief of dentition have shown promise for distinguishing diet among closely related mammals, including primates (Reed, 1997; Jernvall and Selanne, 1999; Ungar and M'kirera 2003; Dennis et al., 2004; Boyer, 2008; Ungar and Bunn, 2008). Ungar and M'kirera (2003) found differences between *Pan troglodytes* and *Gorilla gorilla* in cusp slope, and related these to dietary differences between the two species. They also found that these methods were robust and thus applicable to worn teeth; even at later wear stages, cusp slopes of the two species were significantly different from each

other. Boyer (2008) applied these methods to strepsirrhine primates and was able to distinguish broad dietary categories of frugivory, folivory, insectivory, and omnivory within this group. Thus, methods using three-dimensional dental scans have recently improved our ability to distinguish dietary categories based on dental morphology, and are also applicable to worn teeth.

Although dental morphology can inform us about the broad dietary categories of primates, it requires the assumption that morphology directly indicates actual dietary behavior, rather than behavior to which the morphology is adapted; it also is constrained by phylogenetics, so that methods are often only applicable among closely related species. Thus, these methods are not ideal for any but the broadest dietary characterizations in the fossil record.

Non-adaptive Methods

Methods that rely on traces that indicate what an animal actually ate complement reconstructions based on dental morphology and may be more informative about the actual dietary niche of a species. Two primary methods exist for determining what an animal actually ate in the past: examining the wear caused by diet on an animal's teeth (dental microwear), and examining the chemical elements an animal displays in its tissues (stable isotope analyses). Although stable isotope analyses capture the variation in particular isotopes in the diet when an animal was forming its tissues, the results of these analyses do not distinguish between broader food categories (such as meat, leaves, or fruit) that comprise the diet. Since many studies of wild primate diets record only these broader food categories, it is more likely to differentiate the diversity of the dietary niche

using a method that distinguishes broader food categories. For these reasons, dental microwear analyses are more appropriate to examine variation and diversity in primate diets.

Dental Microwear

Dental microwear analyses are, collectively, the techniques used to study microscopic wear on teeth. This wear can be due to both attrition (tooth on tooth wear) and abrasion (food on tooth wear); studies have traditionally linked specific diets to microwear features (specific wear patterns) and directionality of wear (Gordon, 1982; Teaford and Walker, 1984; Teaford, 1988; Ungar, 1998). These features are termed pits and scratches, and can vary in size and shape (e.g., Teaford and Walker, 1984; Grine, 1986). Because this type of wear is very shallow, it can be effaced by further wear; in experimental primate feeding studies, Teaford and Oyen (1989) demonstrated that microwear could be erased in as little as 24 hours, with the average persistence of microwear being a week. Thus, microwear captures diet over a very short period of time, on the scale of weeks at most.

Good reviews exist elsewhere summarizing the major studies of dental microwear analyses and the evolution of the methods used (e.g. Teaford, 1988; Rose and Ungar, 1998; Teaford, 2007; Scott, 2012). Traditionally, dental microwear analyses have focused on the use of scanning electron microscopy (SEM) to capture microwear through use of micrographs, photos of microwear. From these micrographs, pits and scratches are counted and measured, either by eye or with various semi-automated computer programs (Ungar et al., 1991; Merceron et al., 2005), and the directionality of wear is noted.

Teaford and Walker (1984) created a standard protocol for the use of SEM in primates by using the second molar and magnification of 500x; up until this time, there was no set protocol, so studies could not be quantitatively compared (Ungar et al., 2008b).

Problems with the expense and time of SEM led to the development of the method of low-magnification stereomicroscopy (LMSM; Solounias and Hayek, 1993; Semprebon et al., 2004). This procedure involves counting microwear features at lower magnifications and under white light. Although this method fixed issues of expense and some issues of time, it still suffered from issues of inter-observer error. Because researchers identify and count features by hand, the inter-observer error is still high, as it is in SEM; furthermore, because a picture cannot be taken and reliably used, areas on the tooth are not explicitly identified, making it near impossible to exactly identify the area used to count features for replication by other researchers.

More recently, a new type of microwear analysis, called dental microwear texture analysis (DMTA), combined scanning confocal microscopy with scale-sensitive fractal analyses to measure surface topography at different scales (Ungar et al., 2003; Scott et al., 2005, 2006). Microwear data are captured in three-dimensional space using a white-light scanning confocal microscope. Using topographic analysis software, the data are leveled, defects are removed, and the surfaces are measured using volumes, areas, and vectors, resulting in a quantitative description of the surfaces at multiple scales. This method allows for greater repeatability of measurements since these are identified and directly measured by a computer instead of by an observer, effectively negating inter-observer error. Furthermore, it resolves the issue of characterizing a three dimensional

surface in two dimensions, a problem inherent in SEM and LMSM. It is also faster, easier to use, and less costly than SEM and LMSM (Ungar et al. 2003, Scott et al. 2005, 2006).

Dental microwear texture analysis with scale-sensitive fractal analyses uses five main measurements that relate to the surface topography of teeth at different scales. Area-scale fractal complexity (*Asfc* or complexity) is a measure of the relative area of a surface as it changes with scale. A tiling algorithm calculates the relative area of the surface using tiles of a given size (i.e., at different scales); complexity is the slope of a line fit to the steepest part of a curve of relative area versus the logarithm of scale multiplied by -1000. As scale decreases, more complex surfaces have a greater increase in surface area than less complex surfaces (Figure 1.1). Complexity has been shown to be greater in animals that eat harder and grittier foods (Ungar et al., 2003; Scott et al., 2005, 2012; Scott, 2012).

A further variable related to complexity is the scale of maximum complexity (*Smc*), which corresponds to the scale at which the surface is most complex. Surfaces with larger features have higher *Smc*, which is related to the size of the wear-causing particles (Fig. 1.2).

Heterogeneity of area-scale complexity (*HAsfc* or heterogeneity) is a variable that relates to the variation in complexity across a single scan. Heterogeneity is calculated as the median deviation of complexity divided by the median complexity value when a scan is broken down into smaller areas using an equal number of rows and columns (Scott et al., 2006); the standard scales used are the coarser-scaled 3x3 division (*HAsfc9)* and the finer-scaled 9x9 division (*HAsfc81).* Heterogeneity relates to how varied the surface texture is across a scan; greater heterogeneity corresponds with greater variation in

texture across the scan (Fig. 1.2). Heterogeneity is related to the variation in size of wear causing particles, which could potentially correspond with variation in diet (Scott et al., 2006, 2012).

Exact proportion Length-scale anisotropy of relief (*epLsar* or anisotropy) is a measure of the directionality of surface wear. Anisotropy is calculated using a series of relative length measures taken at different orientations for a given scale of observation; these are then normalized by dividing them by the sum of relative lengths from all orientations, paired with their direction, and treated as a vector. The length of the mean vector for a given scale is the anisotropy value (the standard is to use the finest scale, 1.8 μm); more features in a single direction increase anisotropy while more features in many directions decrease anisotropy (Fig. 1.1). Anisotropy has been shown to be greater in animals that eat more tough foods (Ungar et al., 2003; Scott et al., 2005, 2012; Scott, 2012).

Textural fill volume (*Tfv*) is a measurement of the volume of the relief of the tooth surface using square cuboids of a given size to fill the surface. It relates to both the shape of the surface, i.e. the concavity, convexity, or flatness of the surface, and the texture of the surface, i.e. the scratches or pits on the concave, convex, or flat surface (Fig. 1.2; Scott et al., 2006). Textural fill volume is calculated by taking the volume at a fine scale and subtracting the volume at a coarse scale, which approximates the volume due to the texture of the surface; the standard is to use square cuboids at 2 μm for the fine scale and 10 μm for the coarse scale (Scott et al., 2006).

Implementation of Microwear Analyses

Extant Primates

There have been a number of studies of microwear in extant primates, with variable use as comparisons to fossil taxa. The first major quantitative study of microwear was by Teaford and Walker (1984) who examined occlusal molar microwear in extant primates with known and extreme dietary differences. These researchers also defined a set protocol for particular molar facets and a specific microscope magnification (500X); these protocols allowed the data set to be quantitatively compared with other data sets and standardized the quantitative procedure (Ungar, 1998). These researchers were able to compare frequencies of microwear features and dimensions across primate species at these specifications; they found that frugivores had higher ratios of pits to scratches, and within frugivores, those species that focused on hard objects had the highest relative frequencies of pits. Folivores, on the other hand, had higher ratios of scratches to pits, and had higher directionality to their microwear features. Experimental work with captive vervets by Teaford and Oyen (1989) further demonstrated the link between diet and microwear. These researchers showed that vervets fed soft monkey chow had fewer microwear features than those fed hard monkey chow. Thus, they were able to experimentally show that, within a controlled sample of a single species, harder diets created more microwear features on teeth, while softer diets created fewer. This demonstrated that microwear was controlled by mechanical properties of ingested food.

Over the last two decades, the data from microwear studies has increased our understanding of the range of signals from diet, as well as the intraspecific variation caused by seasonality, different habitats, and differences in diet between individuals.

Teaford (1985) compared occlusal molar microwear by SEM in three species of *Cebus* and found that although there are differences between individuals within each species in the number of features on different molar facets, these differences are less than the differences between species. He also showed that there are differences in molar microwear between closely related species, at least within the genus *Cebus*, even though the species have similar diets. Further work by Teaford and Robinson (1989) showed a seasonal difference in size and frequency of pitting within *Cebus nigrivittatus* at dry tropical woodland sites, but did not show differences among sites of humid and dry forests or seasonal differences at humid forest sites. Teaford and Glander (1991) further demonstrated that ecology could create intraspecific differences in microwear. They found differences in microwear features between *Aloutta palliata* from tropical dry forests and tropical moist forests, while seasonality was controlled for by having both samples from the wet season. Merceron et al. (2010) showed differences in the seasonality of occlusal molar microwear between and within different sexes of roe deer; the different sexes were observed to eat different diets during different seasons, and some of these differences were observable in the microwear texture signatures of sexes by season. In contrast, Nystrom et al. (2004) found little difference in baboon occlusal molar microwear between age and sex groups; they also found little difference in microwear between groups that lived in different habitats (although these habitats were fairly similar, being within a larger study area). However, their findings suggest that exogenous grit is an important factor in the microwear of terrestrial catarrhines, particularly those living in semiarid habitats (Nystrom et al., 2004). In contrast to these findings, Daegling and Grine (1999) found that the dietary components in terrestrial catarrhines was

implicated in their molar microwear. They compared *Papio ursinus* from South Africa to *Theropithecus gelada* (studied by Teaford, 1993) and found significant differences between the two species in microwear features; *P. ursinus* had wider scratches and wider and longer pits than did *T. gelada*. *P. ursinus* also had higher frequencies of pitting. Since both species forage terrestrially, the researchers inferred that the differences in wear were related to differences in diet but especially to differences in the consumption of exogenous grit, specifically to the frequent consumption of underground resources in *P. ursinus*. Scott et al. (2012) more recently published a large study of microwear textures of 21 anthropoid primates. These textures provide a baseline of wear patterns that are linked with specific diets in primates, including 11 African primates, eight cercopithecines and three hominoids. Their data supported the previously-discoverd links between microwear textures and diets, namely greater complexity and higher frequencies of hard object or seed eating and greater anisotropy and higher frequencies of foliage consumption. Additionally, their data show a wide range of values for anthropoid primates, demonstrating the relationship between variation in diet and variation in microwear.

Fossil Primates

The ultimate goal of dental microwear analyses is to reconstruct the diet when diet is unknown, particularly for fossil animals. Primates, particularly hominins, have been one of the primary groups to be studied. Wear on fossil dentition is compared to that on extant dentition of primates of known diets. The earliest studies of fossil primates focused on hominins, and this focus has been carried through today, mostly by Grine, Teaford, Ungar, and their colleagues (Grine, 1986, 1987; Scott et al., 2005; Grine et al.,

2006a,b, 2012; Ungar et al., 2008a, 2010). Grine (1986, 1987) analyzed occlusal molar microwear of *Paranthropus robustus* and *Australopithecus africanus* by SEM and found that *P. robustus* showed higher densities of features, higher frequencies of pitting, and more heterogeneity in wear patterns than did *A. africanus*. Comparing frequencies of pitting, Grine concluded that *P. robustus* ate a high proportion of hard objects, while *A. africanus* ate more fruit or leaves; he was not able to directly compare lengths of scratches to an extant sample because of differences in methodology. Ungar and Grine (1991), using SEM, also found more striations on *A. africanus* incisors, indicating utilization of more abrasive foods. Ryan and Johanson (1989) also analyzed incisor microwear in *A. afarensis*, and argued that a mix of fine scratches and pits, a pattern in between that of *Gorilla* and *Papio*, indicated the use of incisors in preparing gritty plant foods. Grine et al. (2006a,b) also analyzed occlusal molar microwear by SEM in *A. afarensis* and *A. anamensis* and found that they had lower proportions of pitting than extant hard object feeders, and most closely resembled gorillas and chimpanzees in their microwear features and densities.

New utilization of microwear texture analysis has allowed further quantification of microwear in hominins; Scott et al. (2005) showed that *A. africanus* had higher anisotropy and lower complexity in occlusal molar microwear than did *P. robustus*, which directly corresponds to findings of Grine (1986, 1987). Interestingly, Ungar et al. (2008a, 2010) found that *P. robustus* differed greatly from *P. boisei* in its occlusal dental microwear textures; *P. boisei* had higher levels of anisotropy and lower levels of surface complexity, indicating that *P. boisei* did not consume hard objects as microwear suggests *P. robustus* did. Furthermore, *A. afarensis* and *A. anamensis* had textures more similar to

P. boisei than to *P. robustus*, and did not show textures expected for increasing use of hard object feeding (Ungar et al., 2010)

Although hominins have experienced a long history of dental microwear analysis, the associated fossil cercopithecids found at African sites have received less attention. In one of the first analyses, Teaford (1993) used SEM on occlusal molar surfaces of East African specimens of fossil *Theropithecus*. He found more pitting and higher frequencies of wear in *T. brumpti* than in *T. oswaldi* and *T. gelada*, which he interpreted as indicating a diet containing more fruit or grit for *T. brumpti*. He also found similar frequencies and sizes of pits and scratches in *T. oswaldi* and *T. gelada*, suggesting that diets in the two species were similar. Ungar and Teaford (1996) used SEM to analyze microwear incidence on occlusal and non-occlusal surfaces of cercopithecid incisors from the Turkana Basin, Laetoli, and Olduvai Gorge. They found that non-occlusal microwear showed all fossil cercopithecines to fall within the extant cercopithecine range, while some colobines fell within this range; these results might indicate the incorporation of grit into the diet through utilization of foods from the ground, as indicated by high percentage of incidence in *Cercopithecoides williamsi*, long regarded as a terrestrial colobine (Birchette, 1981). Non-occlusal incisor microwear may thus be a good predictor of substrate use (although *Rhinocolobus*, thought to be an arboreal colobine, has high percentages as well). The occlusal microwear indicates that fossil colobines were more similar to extant colobines than fossil cercopithecines were to extant cercopithecines; fossil cercopithecines had less pitting on their teeth, perhaps indicating less hard object feeding. However, low sample sizes of fossil taxa hamper the applicability of this method to these fossil taxa. In contrast, Teaford et al. (2008) used SEM to analyze occlusal molar

microwear of the same sample. Their results proved similar to those of Ungar and Teaford (1996) in that they showed low frequencies of pitting. El-Zaatari et al. (2005) analyzed occlusal molar microwear of South African cercopithecids from Makapansgat, Sterkfontein, Kromdraai, and Swartkrans. They found that the fossil group had less pitting than modern baboons (*Papio ursinus*) and hard object feeders (*Lophocebus albigena*), and smaller scratch breadths than these analogs, suggesting a diet of softer foods in general. Overall, the microwear evidence suggested more similarity between diets in the fossil species than seen today in the extant sample, even between different habitats reconstructed for the sites.

Conclusion

Dental microwear texture analyses have the potential to help reconstruct dietary breadth in fossil primates, since they involve variables that relate to different aspects of the material properties and mastication of foods. Although researchers have inferred greater variation in the food categories of primate diets based on greater variance in microwear (e.g. Scott et al., 2005; Ungar et al., 2008a, 2010), there is not yet strong evidence that links variation in microwear textures to variation in diet. This fact should create some wariness in inferring greater dietary variation given greater microwear texture variance since anthropoids have been shown to have great variation in their textures overall (Scott et al., 2012). To test the relationship between microwear texture variation and dietary variation in primates, a study involving specimens with known provenience and a range of diets, both specialized and broad, is required. This

dissertation examines this relationship and tests whether dietary breadth can be inferred from dental microwear texture variation in primates.

In Chapter 2, "Variation in dental microwear textures as a proxy for interspecific differences in annual dietary diversity in African Old World Monkeys (Cercopithecidae)," I examine the link between annual dietary variation and variation in six dental microwear texture variables within a diverse group of eight species of extant African Cercopithecidae. I test the hypothesis that dental microwear textures vary more in species with greater dietary diversity by employing three different methods: 1) variance in individual microwear variables, 2) mean heterogeneity, and 3) overall summed weighted variance using principal components analysis.

In Chapter 3, "Intraspecific differences in dental microwear textures among African Old World Monkeys (Cercopithecidae) and their relationship to seasonal and geographic variation," I test for intraspecific differences in dental microwear variance among seasons and geographic areas in five species of Cercopithecidae. These tests help identify whether results from Chapter 2 can be explained by sampling a species from different numbers of habitats or localities, from a larger geographic area, or from different seasons.

In Chapter 4, "The relationship between monthly dietary variation and variation in dental microwear in African Old World Monkeys (Cercopithecidae)," I examine whether monthly variation in food category consumption relates to variation in dental microwear textures in six species of Cercopithecidae. I test for differences in microwear variation among species that have similar annual dietary diversities but vary their diets monthly. The goal is to identify if species that have a more even annual use of dietary categories

differ from species that vary their dietary category use monthly, which would have implications for identifying fallback food use in fossil species.

References

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press, 608pp.

Anapol F, Lee S. 1994. Morphological adaptation to diet in platyrrhine primates. Am J Phys Anthropol 94:239-261.

Benefit, BR. 1987. The Molar Morphology, Natural History, and Phylogenetic Position of the Middle Miocene Monkey *Victoriapithecus*, and Their Implications for Understanding the Evolution of the Old World Monkeys. PhD Dissertation, New York University.

Birchette M. 1981 Postcranial remains of *Cercopithecoides*. Am J Phys Anthropol 54:201

Blackburn TM, Gaston KJ. 1996. A sideways look at patterns in species richness, or why there are so few species outside the tropics. Biodivers Lett 3:44-53.
Bohm M, Mayhew PJ. 2005. Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata: Cercopithecidae). Biol J Linn Soc 85:235-246.

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Brown JH. 1984. On the relationship between abundance and distribution of species. Am Naturalist 124:255-279.

Brown JH. 1995. Macroecology. Chicago: University of Chicago Press, 284 pp.

Brown JH, Maurer BA. 1989. Macroecology: the division of food and space among species on continents. Science 243:1145-1160.

Brown JH, Sax DF. 2004. Geographic gradients in diversity. In: Lomolino MV, Sax DF, Brown JH, eds. Foundations of Biogeography: Classic Works with Commentaries. The University of Chicago Press, Chicago, 1328 pp.

Brown JH, Mehlman DW, Stevens GC. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

Butynski TM, Kingdon J, Kalina J, eds. 2013. Mammals of Africa: Volume 2, Primates. London: Bloomsbury, 560 pp.

Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. 2011. Primates in Perspective. Oxford: Oxford University Press, 864 pp.

Cartmill M. 2002. Paleoanthropology — science or mythological charter? Anthropol Res 58:183-201.

Chapman CA, Chapman LJ. 1990. Dietary variability in primate populations. Primates 31:121-128.

Chapman CA, Gautier-Hion A, Oates JF, Onderdonk DA. 1999. African primate communities: determinants of structure and threats to survival. In: Fleagle JG, Janson CH, Reed KE, eds. Primate Communities. Cambridge: Cambridge University Press, pp 1-37.

Cowlishaw G, Hacker JE. 1997. Distribution, diversity, and latitude in African primates. Am Nat 150:505-512.

Daegling DJ, Grine FE. 1999. Occlusal microwear in *Papio ursinus*: The effects of terrestrial foraging on dental enamel. Primates 40:559-572.

Darwin C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray, 502 pp.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125:152-161.

Dobzhansky T. 1950. Evolution in the tropics. Reprinted in: Lomolino MV, Sax DF, Brown JH, eds. Foundations of Biogeography: Classic Works with Commentaries. Chicago: The University of Chicago Press, 1328 pp.

Eeley HAC, Foley RA. 1999. Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodivers Conserv 8:1033-1056.

Eeley HAC, Lawes MJ. 1999. Large scale patterns of species richness and species range size in anthropoid primates. In: Fleagle JG, Janson CH, Reed KE, eds. Primate Communities. Cambridge: Cambridge University Press, pp. 191-219.

El-Zaatari S, Grine FE, Teaford MF, Smith HF. 2005. Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. J Hum Evol 49:1–26.

Elton C. 1927. Animal Ecology. London: Sidgwick and Jackson, 207 pp.

Fleagle JG. 2013. Primate Adaptation and Evolution: 3rd Edition. San Diego: Academic Press, 464 pp.

Franklin J. 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge: Cambridge University Press, 338 pp.

Gaston KJ. 1994. Rarity. Population and Community Biology Series 13. London; New York: Chapman and Hall, 205 pp.

Gaston KJ. 1998. Species-range size distributions: products of speciation, extinction and transformation. Phil Trans R Soc B 353:219-230.

Gaston KJ, Blackburn TM. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. J Animal Ecol 66:579-601.

Gaston KJ, Blackburn TM. 2000. Pattern and process in macroecology. Oxford: Blackwell Science, 377 pp.

Gordon K. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am J Phys Anthropol 59:195-215.

Gregory RD, Gaston KJ. 2000. Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. Oikos 88:515-526.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. J Hum Evol 15:783-822.

Grine FE. 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. Scanning Microscopy 1:647-656.
Grine FE, Ungar PS, Teaford MF. 2006. Was the Early Pliocene hominin '*Australopithecus*' *anamensis* a hard object feeder? S Afr J Sci 102:301

Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297-319.

Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am J Phys Anthropol 148:285-317.

Grinnell J. 1917. The niche-relationships of the California Thrasher. Auk 34:427–433.

Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210-221.

Hanski I. 1994. A practical model of metapopulation dynamics. J Animal Ecol 63: 151-162.

Hanski I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. In: Hanski I, Gilpin ME, eds. Metapopulation Biology: Ecology, Genetics, and Evolution. San Diego: Academic Press, pp 69-91.

Hanski I, Kouki J, Halkka A. 1993. Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs RE, Schluter D, eds. Species Diversity in Ecological Communities. Chicago: University of Chicago Press, pp. 108-116.

Harcourt AH. 2000. Latitude and latitudinal extent: a global analysis of Rapoport effect in a tropical mammalian taxon: Primates. J Biogeog 27:1169-1182.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization, and extinction in primates. J Biogeogr 29:445-456.

Harding RS. 1981. An order of omnivores: nonhuman primate diets in the wild. In: Harding RS, Teleki G, eds. Omnivorous primates: gathering and hunting in human evolution. New York: Columbia University Press, pp. 191-214.

Heino J. 2005. Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. Freshwater Biol 50: 1578-1587.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 57-103.

Hernández Fernández, M. 2001. Discriminant bioclimatic capacity of terrestrial mammal faunas. Global Ecol Biogeogr 10:113-128.

Hernández Fernández M, Vrba ES. 2005a. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. J Biogeogr 32:903-918.

Hernández Fernández M, Vrba ES. 2005b. Body size, biomic specialization and range size of African large mammals. J Biogeogr 32:1243-1256.

Hernández Fernández M, Vrba ES. 2005c. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. Evol Ecol 19:199-219.

Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427.

Jablonski D. 1986. Background and mass extinctions: The alternation of macroevolutionary regimes. Science 231:129-133.

Jablonski D. 1987. Heritability at the species level: Analysis of geographic ranges of Cretaceous mollusks. Science 238:360-363.

Jablonski D, Roy K. 2003. Geographical range and speciation in fossil and living mollusks. Proc R Soc Lond B 270:401-406.

Jernvall J, Selänne L. 1999. Laser confocal microscopy and geographic information systems in the study of dental morphology. Palaeontol Electron 2:18.

Kay RF. 1975. Allometry and early hominids. Science 189:61-64.

Kay, R.F. 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.

Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, eds. Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys and apes. New York: Columbia University Press, pp. 21-53.

Kay RF, Hiiemae KM. 1974. Jaw movement and tooth use in recent and fossil primates. Am J Phys Anthropol 40:227-256.

Kay RF, Hylander WL. 1978. The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In: Montgomery GG, ed. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution, pp. 173–191.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee and Cercopithecoid model for interpreting the evolution of the hominin diet. In: Ungar PS, ed. Evolution of the human diet: the known, the unknown, and the unknowable. Oxford: Oxford University Press, pp. 324-343.

Lambert JE. 2009. Primate fallback strategies as adaptive phenotypic plasticity: scale, process, and pattern. Am J Phys Anthropol 140:759-766.

Lappalainen J, Soininen J. 2006. Latitudinal gradients in niche breadth and position - regional patterns in freshwater fish. Naturwissenschaften 93:246-250.

Lehman SM. 2004. Biogeography of the primates of Guyana: effects of habitat use and diet on geographic distribution. Int J Primatol 25:1225-1242.

Lennon JJ, Turner JRG, Connell D. 1997. A metapopulation model of species boundaries. Oikos 78:486-502.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15: 237-240.

Levins R. 1970. Extinction. In: Gesternhaber M, ed. Some mathematical problems in ecology. Providence, RI: American Mathematical Society, pp. 77-107.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd edition. Sunderland: Sinauer Associates, pp. 845.

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, eds. Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge: Cambridge University Press, pp. 173-203.

MacArthur RH. 1972. Geographical Ecology: Patterns in the distribution of species. New York: Harper and Row, 269 pp.

Merceron G, Blondel C, De Bonis L, Koufos GD, Viriot L. 2005. A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). Palaios 20:551-561.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542.
Nunes A. 1995. Foraging and ranging patterns in white-bellied spider monkeys. Folia Primatol 65:85–99.

Nystrom P, Phillips-Conroy JE, Jolly CJ. 2004. Dental microwear in anubis and hybrid baboons (*Papio hamadryas*, s.l.) living in the Awash National Park, Ethiopia. Am J Phys Anthropol 125:279-291.

Passy SI. 2012. A hierarchical theory of macroecology. Ecol Lett 15:923-934.

Pianka ER. 1966. Latitudinal gradients in species diversity: a review of concepts. Am Nat 100: 33-46.

Rapoport EH. 1982. Areography: Geographical Strategies of Species. Oxford: Pergamon Press, 286 pp.

Reed DNO. 1997. Contour mapping as a new method for interpreting diet from tooth morphology. Am J Phys Anthropol (S24):194.

Robinson, JT. 1954. The genera and species of the Australopithecinae. Am J Phys Anthropol 12:181-200.

Rohde K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514-527.

Rose JC, Ungar PS. 1998. Gross dental wear and dental microwear in historical perspective. In: Alt KW, Rosing FW, Teschler-Nicola M, eds. Dental Anthropology: Fundamentals, Limits, and Prospects. Vienna: Springer, pp. 349-386.

Rowe N. 1996. The pictorial guide to the living primates. Charlestown, RI: Pogonias Press.

Ryan AS, Johanson DC. 1989. Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and nonhuman primates. J Hum Evol 18:235-268.

Scott JR. 2012. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution. PhD Dissertation, University of Arkansas.

Scott RS, Ungar PS, Bergstromb TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436: 693-695

Scott RS, Ungar PS, Bergstromb TS, Brown CA, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51: 339-349

Semprebon GM, Godfrey LR, Solounias N, Sutherland MR, Jungers WL. 2004. Can low-magnification stereomicroscopy reveal diet? J Hum Evol 47:115-144.

Simpson GG. 1964. Species density of North American recent mammals. Syst Zool 13:57-73.

Slatyer RA, Hirst M, Sexton JP. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol Lett 16:1104-1114.

Slove J, Janz N. 2010. Phylogenetic analysis of the latitude-niche breadth hypothesis in the butterfly subfamily Nymphalinae. Ecol Entomol 35:768-774.

Solounias N, Hayek LC. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. J Zool 229: 421-445.

Stehli FG, Douglas RG, Newell ND. 1969. Generation and maintenance of gradients in taxonomic diversity. Science 164:947-949.

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240-256.

Strait SG. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. J Mammal 74:391-402.

Teaford MF. 1985. Molar microwear and diet in the genus *Cebus*. Am J Phys Anthropol 66:363-370.

Teaford MF. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microscopy 2:1167-1175.

Teaford MF. 1993. Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In: Jablonski NG, ed. *Theropithecus:* the Life and Death of a Primate Genus. Cambridge: Cambridge University, pp. 331-349.

Teaford MF. 2007. What do we know and not know about dental microwear and diet? In: Ungar PS, ed. Evolution of the human diet: the known, the unknown, and the unknowable. Oxford: Oxford University Press, pp. 106-131.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. Am J Phys Anthropol 80:447-460.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401.

Teaford MF, Walker AC. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am J Phys Anthropol 64:191-200.

Teaford MF, Ungar PS, Kay RF. 2008. Molar shape and molar microwear in the Koobi Fora monkeys: ecomorphological implications. In: Jablonski NG, Leakey MG, eds. Koobi Fora Research Project. Volume 6. The Fossil Monkeys. San Francisco: Occasional Paper of the California Academy of Sciences, pp. 337-358.

Thorn JS, Nijman V, Smith D, Nekaris KAI. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). Divers Distrib 15:289–298.

Tokeshi M. 1999. Species Coexistence. Cambridge: Cambridge University Press, 454 pp.

Ungar PS. 1996. Relationship of incisor size to diet and anterior tooth use in sympatric Sumatran anthropoids. Am J Primatol 38:145-156.

Ungar PS. 1998. Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evol Anth 6:205-217.

Ungar PS. 2002. Reconstructing the diets of fossil primates. In: Plavcan JM, Kay RF, Jungers W, van Schaik CP, eds. Reconstructing behavior in the primate fossil record. New York : Kluwer Academic/Plenum, pp. 261-296.

Ungar PS. 2014. Some musing on the history of dental microwear research and the role of texture analysis. Podium Presentation. Inferring Diet and Dental Function from Dental Microwear Textures: Society of Vertebrate Paleontology 74th Annual Meetings Workshop.

Ungar PS, Bunn JM. 2009. Dental topography and diets of four old world monkey species. Am J Primatol 71:466-477.

Ungar PS, Grine FE. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. J Hum Evol 20:313-340.

Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. Proc Natl Acad Sci USA, 100: 3874–3877.

Ungar PS, Teaford MF. 1996. A preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. Am J Phys Anthropol 100:101-113.

Ungar PS, Simons J-C, Cooper JW. 1991. A semiautomated image analysis procedure for the quantification of dental microwear. Scanning 13:31-36.

Ungar, PS, Brown, CA, Bergstrom, TS, Walker, A. 2003.Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning 25:185-193.

Ungar PS, Grine FE, Teaford MF. 2008a. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3(4):e2044.

Ungar PS, Scott RS, Scott JR, Teaford MF. 2008b. Dental microwear analysis: historical perspectives and new approaches. In: Irish JD, Nelson GC, eds. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press, pp 389-425.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis.* Phil Trans R Soc B 365: 3345-3354.

Vazquez D, Stevens RD. 2004. The latitudinal gradient in niche breadth: concepts and evidence. Am Naturalist 164:E1-E19.

Willig MR, Kaufmann DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu Rev Ecol Syst 34:273-309.

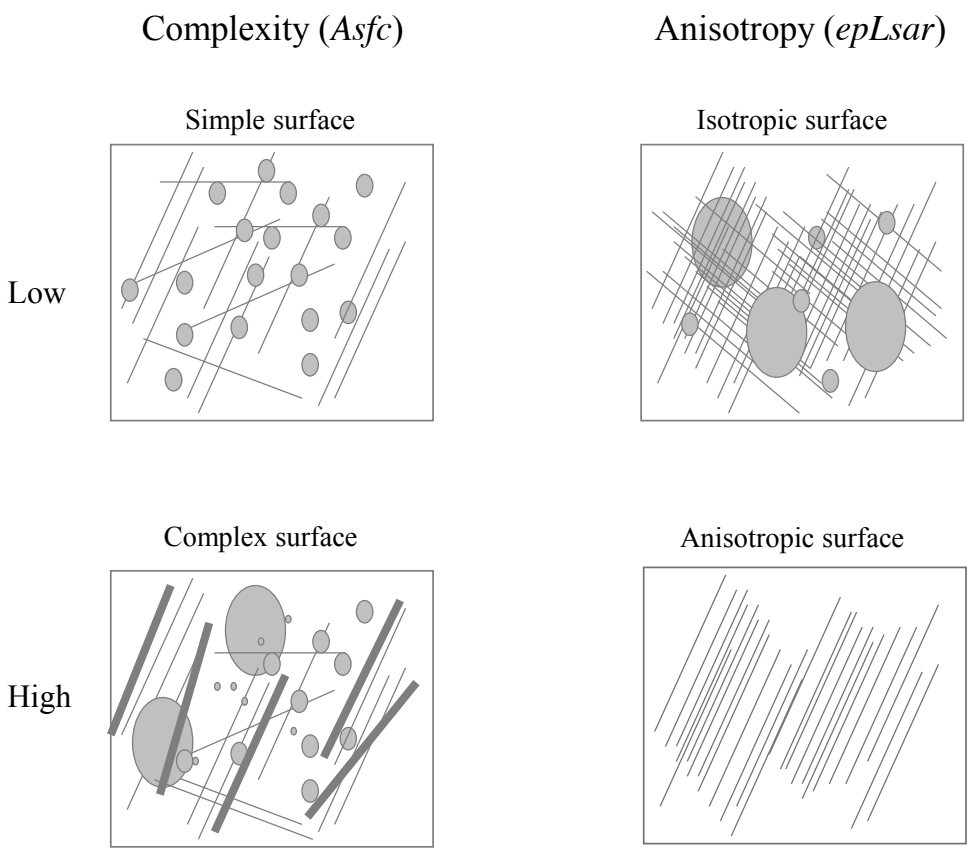

Figure 1.1. Examples of Complexity and Anistropy. Hypothetical microwear texture images showing low and high complexity (*Asfc*) and anisotropy (*epLsar*) (From Ungar, 2014).

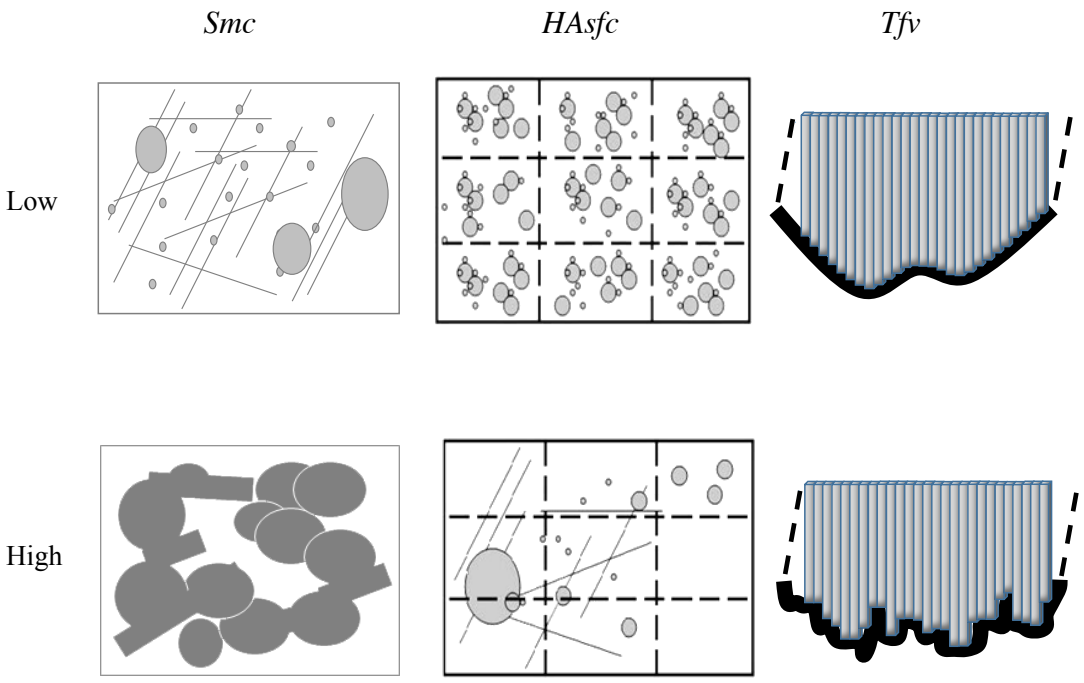

Figure 1.2. Examples of Scale of Maximum Complexity (*Smc*), Heterogeneity (*HAsfc*), and Textural Fill Volume (*Tfv*). Hypothetical microwear texture images showing low and high values of *Smc*, *HAsfc*, and *Tfv* (from Ungar, 2014).

CHAPTER 2

VARIATION IN DENTAL MICROWEAR TEXTURES AS A PROXY FOR INTERSPECIFIC DIFFERENCES IN ANNUAL DIETARY DIVERSITY IN AFRICAN OLD WORLD MONKEYS (CERCOPITHECIDAE)

Introduction

Dietary diversity, a measure of the number and evenness of food categories incorporated into the diet, is important to species ecology and evolution. Among closely related species, those with less diverse diets tend to have smaller distributions, to inhabit a smaller range of habitats, and to be less abundant (Gaston and Blackburn, 2000; Harcourt et al., 2002; Lomolino et al., 2006; IUCN, 2010). Lower dietary diversity has been implicated in the decline and extinction of numerous species, while greater diversity has been implicated in species's survival in relation to competitors (African mammals: Potts, 1998; African wild dogs: Mbizah et al., 2012; bats: Boyles and Storm, 2007; bovids: Bowman et al., 2010; North American cougars: DeSantis and Haupt, 2014; North American vertebrates: Swihart et al., 2003; primates: Harcourt et al., 2002). This is not to say that dietary specialization, and a necessarily lower dietary diversity, is an evolutionary dead end; indeed, dietary specialization can allow for the exploitation of empty dietary niches, as seen in numerous species radiations (Schluter, 2000). However, among closely related species, those with more diverse diets are more likely to be flexible in their dietary choices, to inhabit a broader range of habitats, and to be less vulnerable to environmental change (e.g. Harcourt et al., 2002).

That dietary diversity is related to these aspects of species ecology and evolution makes it important to ascertain in fossil species, as inferring dietary diversity in fossil

species would benefit reconstructions of niche space and species evolution. However, quantifying dietary diversity in fossil species is difficult since methods of dietary reconstruction most often rely on the main category or categories of foods eaten by species rather than the overall composition of the diet (e.g. Kay, 1975, 1984; Rosenberger and Kinzey, 1976; Strait, 1993). This fact is particularly problematic for studies of fossil primates, as paleoanthropologists have long used arguments related to dietary diversity to explain differences in morphology, distribution, and evolutionary fate of fossil species, particularly hominins. Robinson's dietary hypothesis (1954, 1956) proposed that the major difference between the fossil hominin species *Australopithecus africanus* and *Paranthropus robustus* was their dietary diversity. He suggested that while *Paranthropus* had a specialized vegetarian diet, *Australopithecus* had expanded its diet to include larger amounts of meat, making it a more generalized omnivore. Robinson hypothesized that dietary expansion (i.e. a more diverse diet) had allowed the survival of the *Australopithecus* lineage, ultimately leading to *Homo*, while dietary specialization (i.e. a less diverse diet) in *Paranthropus* ultimately led to its extinction.

A more diverse diet also explains evolutionary success in Potts's (1998) Variability Selection hypothesis, which proposed that large fluctuations in climate and habitat in Africa over short periods of time led to selection for flexible responses to these changes in mammalian species. Instead of adapting to a specific environmental condition, hominins were adapting to a range of conditions with an ability to move easily between different habitats. In response to increased climatic fluctuations in the Pleistocene, hominins experienced selection for a broader dietary niche in the form of a wider range of dietary items and a more flexible diet. Potts (1998) proposed that this dietary

expansion was one of the factors that led to the evolution of the genus *Homo* in contrast to earlier *Australopithecus* and *Paranthropus* species.

One hurdle to testing these, among other, hypotheses involving dietary diversity is the lack of a method to consistently determine this measure among closely related fossil species. Methods that have been used to approximate diet in fossil species include dental allometry (Kay, 1974, 1975), dental morphology (Kay, 1978, 1984; Benefit, 1999, 2000; Ungar and Bunn, 2009), stable isotope analyses (Codron et al., 2005, 2008; Sponheimer et al., 2009), and dental microwear analyses (Teaford and Walker, 1984; Grine et al., 2006; Scott et al., 2005; Ungar et al., 2010). However, in order to examine dietary diversity, it is necessary to 1) use a method that relies on what an animal actually ate rather than what it was adapted to eat, and 2) use a method that captures frequency and variation in diet. Because stable isotope and dental microwear analyses fulfill these two criteria, these two methods are appropriate for investigating inter- and intraspecific dietary variation and can potentially approximate dietary diversity (Teaford and Robinson, 1989; Teaford and Glander, 1991, 1996; Sponheimer et al., 2006, 2009; Merceron et al., 2010; Ungar et al., 2010; Cerling et al., 2011). However, while stable carbon isotope (δ13C) analyses capture the variation in δ13C in the diet, the results of these analyses do not distinguish between broader food categories (such as meat, leaves, or fruit) that comprise the diet. Thus, while the results capture the breadth of plants that make up the dietary niche (i.e., a range of C3 and C4 plants), they do not differentiate between hard, soft, or tough foods.

Dental microwear, the microscopic features left on the dentition by food and grit in the last days to weeks before an animal died (Teaford and Oyen, 1989), has traditionally been used to distinguish species that feed on hard objects from those that feed on tough leaves or grasses (Teaford and Walker, 1984; Grine, 1986; Teaford, 1988; Scott et al., 2005, 2006; Ungar et al., 2008, 2010). Studies of microwear formation related to diet in wild populations indicate similar patterns across orders and classes, demonstrating that this method is robust and thus can be used to infer diet in fossil species (e.g. Teaford and Walker, 1984; Teaford, 1988; Scott, 2012; Stynder et al., 2012; Ungar et al., 2012; Haupt et al., 2013). Additionally, short-term variation in microwear due to seasonal and ecological differences has been noted (Teaford and Robinson, 1989; Teaford and Glander, 1991, 1996; Teaford and Runestad, 1992; Mainland, 2003; Merceron et al., 2004, 2010), indicating that microwear can be used to distinguish intraspecific differences in season and ecology.

Documented dental microwear patterns are the result of both the fracture properties of food and the occlusal mechanics of mastication (Scott et al., 2012). The angles of approach of opposing occlusal facets are dictated by the fracture properties of food, and these angles result in different patterns when abrasives such as phytoliths or grit are moved across facet surfaces during mastication. How quickly wear is formed thus depends on both the abrasiveness of the diet and frequency of consumption of abrasive foods.

Some of the first quantitative studies of microwear on teeth used scanning electron microscopy (SEM) to capture images of wear features in two dimensions (Walker et al., 1978; Ryan, 1981; Gordon, 1982). Researchers found that scratches,

features that were longer and thinner, dominated the surfaces of animals that fed on tough foods such as leaves or grasses, while pits, features that were wider, dominated the surfaces of animals that fed on harder or grittier objects (Teaford and Walker, 1984). More recently, there has been a move to use dental microwear texture analysis (DMTA), a topographic analysis of worn surfaces that uses scale-sensitive fractal analysis to characterize the tooth's surface at different scales. This analysis is based on the principles of fractal geometry that the profile lengths, areas, and volumes of a rough surface change with the scale of observation (Scott et al., 2006). Benefits of DMTA over SEM include characterization of a worn surface in three dimensions, rather than two, and that it is fully automated, leading to lower inter-observer error rates (Scott et al., 2006; DeSantis et al., 2013). DMTA studies on molar occlusal surfaces have identified five variables that relate to diet: area-scale fractal complexity (complexity or *Asfc*), exact proportion Length-scale anisotropy of relief (anisotropy or *epLsar*), heterogeneity of area-scale fractal complexity (heterogeneity or *HAsfc*), scale of maximum complexity (*Smc*), and textural fill volume (*Tfv)*. Complexity measures the changes in relative area with scale such that more complex surfaces have greater relative areas as scale decreases. Complexity has been shown to be greater on molars of primates that eat more hard, brittle foods such as hard fruits (Scott et al., 2005, 2006, 2012). Anisotropy measures the directionality of surface roughness, such that surfaces that have more features in the same direction have greater anisotropy; it has been shown to be greater on molars of primates that eat tough foods, such as leaves or grass (Scott et al., 2005, 2006; Ungar et al., 2008a). Heterogeneity measures the variation in texture across the tooth's surface by breaking the surface into subregions of equal area, calculating the median absolute deviation of *Asfc* for each

subregion, and dividing by the median of *Asfc* (Scott et al., 2006). It has been suggested that this measure can distinguish frequent from less frequent hard/brittle object feeding or greater variation in diet (Scott et al., 2006, 2012). The scale of maximum complexity identifies the scale at which the surface is most complex, and corresponds to the size of wear-causing particles such that higher values correspond with larger features (Scott et al., 2006; Ungar et al., 2008). Textural fill volume measures "summed volumes of square cuboids of a given scale that fill a surface" (Ungar et al., 2008b: 402) and relates to both the shape and texture of a surface; higher values indicate a surface with more mid-scale features (See Chapter 1 for more detailed descriptions and figures).

Despite the long, well-documented history of microwear analyses, there is still controversy over the results of analyses in fossil species (Strait et al., 2013; Lucas et al., 2013). One recurrent question has been why microwear results are so different in *Paranthropus robustus* and *P. boisei* despite remarkably similar derived morphologies in these species. *P. robustus* has consistently shown highly pitted and complex microwear patterns (Grine, 1986, 1987; Scott et al., 2005), whereas *P. boisei* has low complexity and more anisotropic wear (Ungar et al., 2008b); these results have been interpreted to indicate a diet of harder objects for *P. robustus* and more tough objects such as leaves or grasses for *P. boisei* (Grine, 1986; Scott et al., 2005; Ungar et al., 2008b). Because of the potentially short time over which these patterns could have formed, there is some suggestion that these wear patterns may reflect seasonal use of mechanically difficult "fallback foods" and that the annual diets of these species may be more similar than is reflected in microwear analyses (Ungar et al., 2008b). However, analysis of extant primate mortality patterns suggests that it is unlikely that mortality would be higher

during times of fallback food use, and thus it is unlikely that fossil assemblages would be overrepresented by such a short-term seasonal diet (Gogarten and Grine, 2013). Other hominins also show increases in robust chewing morphology while lacking evidence of hard-object feeding in their microwear textures. In particular, *A. afarensis* demonstrates a trend in increased robustness of the masticatory system over time (Lockwood et al., 2000; Kimbel and Delezene, 2009); however, the microwear of *A. afarensis* shows no evidence of hard-object feeding and remains remarkably similar over 650,000 years (Grine et al., 2006). Taken together, these results suggest that *P. robustus* had a diet different from other hominins and was not the result of seasonal consumption of hard foods, but many details about the diet of *P. robustus* and other hominins remain undetermined.

One avenue that may help answer questions about the dietary diversity of fossil primates such as hominins is the intraspecifc variation in DMTA variables. Although central tendencies of DMTA variables have been shown to differ between species with diets differing in fracture properties, many individuals of different species overlap in these variables (for example see Scott et al., 2012). Thus, the range of variable values for each species of primate can be quite large. Because primate diets are generally diverse in comparison to those of other orders, this fact is not surprising. Because material properties of foods also select for dental morphology (Kay, 1978, 1984), and dental morphology has been shown to correlate well with diet in primates (Kay, 1978, 1984; Benefit, 1987, 1999, 2000), variation in the material properties of foods, and thus variation in dental microwear textures, appears to be a good variable to approximate dietary diversity, since species that consume foods with a wider range of material properties would be expected to have greater variation in their microwear. Additionally,

Scott et al. (2009) have shown that variation in dental microwear textures was greater in a species with a diverse diet (the yellow baboon, *Papio cynocephalus*) than in a species with a narrow diet (the gelada, *Theropithecus gelada*).

In this study, the approach of Scott et al. (2009) is expanded by examining intraspecific variation in DMTA variables among a group of African Old World monkeys (Cercopithecidae) with differences in dietary diversity. I tested three hypotheses based on the prediction that species with greater dietary diversity would have greater variation in microwear textures. Hypothesis A states that species with greater dietary diversity have greater variance in the individual microwear variables *Asfc*, *epLsar*, *HAsfc*, *Smc*, and *Tfv*, while species with lower dietary diversity have lower variance in these variables. The test for Hypothesis A follows the statistical method of Ungar and colleagues (Scott et al., 2005; Ungar et al., 2008, 2010) and has generally been used as evidence of variation in diet, but a strong link between variation in these individual variables and variation in diet has not yet been shown.

Since heterogeneity (*HAsfc*) measures how variable the surface texture is within each scan, Scott et al. (2005, 2006, 2012) suggest that heterogeneity may be greater in species with greater variation in diet. However, other researchers have found that heterogeneity may relate to frequency of hard-object feeding, with species that occasionally eat hard foods having higher heterogeneity values than species that either rarely or often eat hard foods (Calandra et al., 2012). In this study, I also test Hypothesis B, that species with greater dietary diversities have higher values of mean heterogeneity, while species with lower dietary diversities have lower heterogeneity.

Finally, although these hypotheses test the relationship between dietary diversity

and individual DMTA variables, they do not test whether dietary diversity is related to *overall* variation in microwear. To further examine whether dietary diversity is related to microwear variation, I also test Hypothesis C, that species with greater dietary diversity have greater *overall* variation in microwear.

Materials & Methods

Casts of eight species of African Old World monkeys that exhibited varying degrees of dietary diversity and distribution across Africa were used in this study. The species examined included three species of guenons, the blue monkey (*Cercopithecus mitis*), De Brazza's monkey (*Cercopithecus neglectus*), and the vervet (*Chlorocebus aethiops*); three papionins, the red-capped mangabey (*Cercocebus torquatus*), the anubis baboon (*Papio anubis*), and the gelada (*Theropithecus gelada*); and two colobines, the guereza (*Colobus guereza*) and the Eastern red colobus (*Procolobus rufomitratus*). These species were selected based on availability of specimens, their dietary diversity, and the number and quality of field studies examining feeding ecology in these species. There is little consensus on the taxonomy of the Cercopithecidae (Grubb et al., 2003; Butynski et al., 2013), and whether or not the individuals within each of the groups here are considered to be multiple species, a single species, or a subspecies will differ based on the taxonomy used. The two main groups of specimens that could be considered multiple species in this study are the vervet (*Ch. aethiops*) and the Eastern red colobus (*Pr. rufomitratus*).

The genus *Chlorocebus*, resurrected by Groves (2005) to contain the polytypic species previously recognized as *Cercopithecus aethiops*, a widespread taxon distributed

across most of sub-Saharan Africa, has been broken down into a number of species based on differences in, among other characteristics, cheek whisker form and male genitalia coloration (Dandelot, 1959; Grubb et al., 2003). However, Napier (1981) disagrees that these species can be easily distinguished and considers *Ch. aethiops* to be a highly polytypic species; the consensus of Grubb et al. (2003) follows this view, although Groves and Kingdon (2013) break *Chlorocebus* into six species. However, these *Chlorocebus* forms easily hybridize where their ranges meet and are ecologically similar, inhabiting savanna and riparian woodlands and consuming a variety of foods including leaves, fruits, insects, flowers, and gums, although the frequencies of consumption of each of these vary among sites (Kavanagh, 1978; Wrangham and Waterman, 1981; Harrison, 1982; Isbell et al., 1998). For these reasons, the view that *Ch. aethiops* represents a single, polytypic species with a widespread distribution is adopted here, and specimens are analyzed as a single group. Post-hoc comparisons among the (sub) species groups did not yield any differences in any microwear variables, further supporting the idea that these groups do not differ in their feeding ecology and can be considered together as a single species.

The taxonomy of red colobus has also changed greatly over the last few decades, often recognized as a single species (*Procolobus badius*), but broken down into several species groups, first by Dandelot (1968, 1974), then by a series of researchers beginning in the 1990s. Grubb et al. (2003) recognized at least four species of red colobus, which is supported by Ting's work on the molecular phylogeny of the group (Ting, 2008), while Groves (2001) recognized nine and then 16 species (2007). Although red colobus are found throughout equatorial Africa, the various species or subspecies are mostly

allopatric and differ in pelage and some morphological features, but they hybridize readily where their distributions overlap (Grubb et al., 2003, 2013; Groves, 2007). In particular, the red colobus of the eastern Congo Basin, which have been split into as many as eight species, are known to form "hybrid swarms" (Groves, 2007), and thus are difficult to place into a single species (or subspecies depending on taxonomic inclination). Overall, however, red colobus are ecologically similar, generally inhabiting lowland rainforests and consuming high frequencies of leaves with fruit and/or seed consumption as a secondary food source (Fashing, 2011). All samples in this study come from the eastern Congo Basin, attributed to *Pr. rufomitratus* based on the taxonomy used by Grubb et al. (2013), and are here considered to be a single species.

Additionally, some researchers consider all baboons (genus *Papio*) to be members of one polytypic species, and thus consider the olive baboon (*Papio anubis*) to be a subspecies of *P. hamadryas.* However, many recognize each regional variant as a separate species. This second view is accepted here, in part because the forms exhibit different morphologies and behaviors (Swedell, 2010).

The sample used for this study consisted of 309 specimens (see see Table 2.1 for a summary; a full list of all specimens is found in Appendix A). All specimens come from wild populations and most have associated locations and dates of collection. Museum specimens are from the collections of the National Museum of Natural History (U.S.), the Field Museum, the Museum of Vertebrate Zoology (UC Berkeley), the Royal Belgian Institute of Natural Sciences, and the Royal Museum of Central Africa; additionally, a sample of geladas (*Theropithecus gelada*) that had been collected from a field study site (Guassa Plateau, Ethiopia) were also included.

All original specimens were cleaned with alcohol-soaked cotton swabs before vinyl impressions were made of all usable upper and lower first and second molars using President's Jet Regular Body Dental Impression Material (Coltene-Whaledent). Casts were made using Epotek 301 epoxy resin and hardener (Epoxy Technologies). Following previous studies (Ungar et al., 2003; Scott et al., 2006; Scott et al., 2012), casts were scanned on Phase II occlusal facets (9, x, or 10n; Kay, 1977); lower second molars were preferentially selected for analysis, but when they did not yield good surfaces first molars or upper second molars were also examined. Scans were collected using a 100x objective on a Sensofar Plμ white-light scanning confocal profiler (Solarius, Sunnyvale, CA) housed at the University of Arkansas. Scans result in point clouds with a lateral sampling interval of 0.18 μm and a vertical resolution of 0.005 μm, and four adjoining fields were collected for a total area of 276 μm x 204 μm. Scans were leveled using Solarmap Universal software, and artifacts, such as dust particles, were excluded by thresholding and erase operators. Dental microwear texture parameters were calculated through two scale-sensitive fractal analysis programs (Toothfrax and Sfrax, Surfract). Six variables for each specimen were calculated: complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), and heterogeneity at the 3x3 (*HAsfc9*) and 9x9 (*HAsfc81*) scales.

Data on diet of each species came from published field studies of wild monkeys. Studies were selected that had collected data on the frequency of consumption of major food categories across a year. Unfortunately, these data were not always exactly comparable since categories varied from study to study. For example, some researchers collected frequencies of consumption of young leaves and mature leaves, while others

collected only frequencies of overall leaf consumption. To make the studies as comparable as possible, categories used in this research were selected that were more general and best reflected differences in mechanical properties of foods. The main categories used were total foliage (including all leaf material as well as herbs, forbs, and grasses), total fruit (including fruits, seeds, and pods), flowers, animal prey (including invertebrates and vertebrates), and other (including unidentified items as well as items not grouped into the preceding categories, such as gums and underground items). Annual food consumption frequencies were used in two ways to characterize the diet. Species average frequencies were calculated using data from all sites; for sites that had multiple years of data collection, either by the same or separate researchers, these data were first averaged so that one site did not skew the data for the species. Shannon Diversity indices (*H)* were then calculated for each site using the formula:

$$H = -(\Sigma\, p_i * \ln p_i)$$

where p_i = frequency of food category consumption. The frequencies used, the sources of the frequencies, and the associated indices are available in Appendix C.

For Hypothesis A, Levene's Test (Levene, 1960) was used to test for differences in the intraspecific variances in microwear variables among the species. Levene's Test has been shown to be robust to deviances from normality and performed the best out of 20 variance tests in simulations (Conover et al., 1981; Donnelly and Kramer, 1999). The raw data were first transformed for Levene's Test by using the residuals from the group median:

$$(r = | x - (\text{median } X)|)$$

and mean:

($r = | x - (\text{mean } X)|$).

The median Levene's Test is the more conservative test (Conover et al., 1981; Donnelly and Kramer, 1999) but can be overly so, hence the use of both median and mean Levene's Tests. The residuals were then used in MANOVA, single ANOVAs, and post-hoc Tukey's Honestly Significant Difference (HSD) and Fisher's Least Significant Difference (LSD) tests; the use of these two post-hoc tests has been shown to minimize Type I and Type II errors (Cook and Farewell, 1996). This method has been used by Ungar and colleagues (e.g. Ungar et al., 2010) to distinguish species with greater variances from those with smaller variances. All analyses were run in RStudio (v. 0.98.978).

For Hypothesis B, single ANOVAs and post-hoc tests were used to test for differences in mean heterogeneity of *HAsfc9* and *HAsfc81*. Since both of these heterogeneity variables were not normally distributed, the variables were ranked and ANOVAs were performed on the ranked data. This method, rather than Kruskal-Wallis Ranked Sums tests, allows for post-hoc tests to identify which group means are different. As with the Levene's Tests, both Tukey's HSD and Fisher's LSD post-hoc tests were performed. All analyses were run in RStudio (v. 0.98.978).

To test Hypothesis C, I used a method that compares the overall interspecific variation in all the variables simultaneously. This method was first developed by Wills et al. (1994) and previously used in primate communities by Kamilar (2006, Chapter 2) and Fleagle et al. (2010). The idea is to compare average distances of individuals from the total species morphospace; species that show greater variation will have greater distributions in the morphospace (Kamilar, 2006). A principal components analysis

(PCA) was run on the raw microwear data and the resulting principal components for each individual were weighted by the respective eigenvalue scores. The variances of all the weighted values for each component were then summed for each species, yielding a summed variance relating to how variant the species is overall (see Table 2.2 for an example). The formula is described as:

$$(s_i^2 * e_i + s_{i+1}^2 * e_{i+1} + \ldots)$$

where s_i^2 is the variance of the principle component scores for each species and e_i is the eigenvalue of the *i*th component (Kamilar, 2006). To see if overall variation in microwear variables was correlated with dietary variation, these summed variances were then compared to the diversity measure (*H*) and annual dietary frequency averages using Pearson's product-moment correlations. The PCA was conducted with the variables *Asfc, epLsar, Smc, Tfv, HAsfc9,* and *HAsfc81*; the PCA was run in JMP Pro 11, while subsequent analyses were run in RStudio (v. 0.98.978).

Results

The raw microwear values are available in Appendix A, and summary statistics appear in Appendix B.

Levene's Test (Hypothesis A)

The species differed in variances (median MANOVA: Pillai's Trace = 0.21, F (7, 301) = 1.57, $p < 0.01$; mean MANOVA: Pillai's Trace = 0.32, F (7, 301) = 2.41, $p < 0.001$). Individual ANOVAs identified differences in *Asfc*, *Smc*, *HAsfc9,* and *HAsfc81*; there were no differences detected in *epLsar* or *Tfv* (Table 2.3).

Complexity (*Asfc*). The species exhibited differences in their variances in complexity using both the median and mean Levene's Tests (median: F (7, 301) = 2.14, $p < 0.05$; mean: F (7, 301) = 2.77, $p < 0.01$; Figure 2.1, Tables 2.3-2.4). Tukey's HSD for the median Levene's Test identified one pair that differed in their variances: *P. anubis* had higher variance than *Pr. rufomitratus* ($p < 0.05$). With the mean Levene's Test, Tukey's HSD also showed *Ch. aethiops* and *C. neglectus* to have marginally greater variance in complexity than *Pr. rufomitratus* ($0.05 < p < 0.1$). Fisher's LSD test using the median and mean Levene's Test each identified two groups among which variance did not differ, but the species included in the groups differed. For both the median and mean, the high variance group contained all the species except for *Pr. rufomitratus*. The median Fisher's LSD identified the low variance group to include *Co. guereza, C. mitis*, *Ce. torquatus, Pr. rufomitratus,* and *T. gelada*, while the mean Fisher's LSD identified the low variance group to include only *Ce. torquatus, Pr. rufomitratus,* and *T. gelada.*

Scale of maximum complexity (*Smc*). The species exhibited no differences in *Smc* using the median Levene's Test (F (7, 301) = 1.42, $p > 0.1$) but did when using the mean Levene's Test (F (7, 301) = 4.68, $p < 0.001$; Fig. 2.2). Tukey's HSD identified greater variance in *P. anubis* than in *Co. guereza, Pr. rufomitratus,* and *T. gelada*; Fisher's LSD identified three groups within which variance did not differ: a highest variance group (*Ch. aethiops*, *C. mitis*, *Ce. torquatus*, and *P. anubis*), a medium variance group (*C. mitis*, *C. neglectus*, and *Pr. rufomitratus*), and a lowest variance group (*Co. guereza, C. neglectus, Pr. rufomitratus,* and *T. gelada*). However, it should be noted that *Smc* has a very right-skewed distribution; although Levene's Test is robust to deviations

from normality (Conover et al., 1981; Donnelly and Kramer, 1999), it does not perform well with strongly skewed data. When *Smc* was ln-transformed, Levene's Test showed no differences in *Smc* using either the median or mean tests.

Heterogeneity at the 3x3 scale (*HAsfc9*). The species exhibited differences in their variances in *HAsfc9* using both the median and mean Levene's Tests (median: F (7, 301) = 2.25, $p < 0.05$; mean: F (7, 301) = 2.94, $p < 0.01$; Fig. 2.3). For both tests, Tukey's HSD and Fisher's LSD identified *C. mitis* to have greater variance than *P. anubis*, but no other differences were found.

Heterogeneity at the 9x9 scale (*HAsfc81*). The species exhibited differences in their variances in *HAsfc81* using both the median and mean Levene's Tests (median: F (7, 301) = 2.32, $p < 0.05$; mean: F (7, 301) = 3.03, $p < 0.005$; Fig. 2.4). For both the median and mean Levene's Test, Tukey's HSD also identified greater variance in *C. mitis* than in *P. anubis*. Fisher's LSD identified two groups within which variance did not differ: a higher variance group, which included all species except *P. anubis*, and a lower variance group, which included *Co. guereza, P. anubis, Pr. rufomitratus,* and *T. gelada* with the median method, but only included *Co. guereza* and *P. anubis* with the mean method.

Mean Heterogeneity (Hypothesis B)

The ANOVA on the ranked data showed differences among the species in their mean ranks of *HAsfc9* (ANOVA: F (7, 301) = 3.61, $p < 0.001$) and *HAsfc81* (ANOVA: F

(7, 301) = 9.46, p <0.0001). Tukey's HSD showed that *C. neglectus* had lower mean *HAsfc9* ranks than *Ch. aethiops, Co. guereza, C. mitis,* and *Pr. rufomitratus*; Fisher's LSD identified three groups within which mean ranks did not differ: a highest ranking group including *Ch. aethiops*, *Co. guereza, Ce. torquatus,* and *Pr. rufomitratus*; a medium ranking group including all the species except *C. neglectus* and *Pr. rufomitratus*; and a lowest ranking group including *C. neglectus* and *T. gelada* (Fig. 2.3). Tukey's HSD also showed a number of differences in mean *HAsfc81* rank: *P. anubis* was lower than *Ch. aethiops, Co. guereza*, *C. mitis,* and *Pr. rufomitratus; C. neglectus* was lower than *C. mitis* and *Pr. rufomitratus*; and *T. gelada* was also lower than *C. mitis* and *Pr. rufomitratus*. Fisher's LSD identified three groups within which mean ranks did not differ: a highest ranking group (*Ch. aethiops, C. mitis, Co. guereza*, *Ce. torquatus*, and *Pr. rufomitratus*), a medium ranking group (*Co. guereza*, *C. neglectus*, *Ce. torquatus*, and *T. gelada*), and a lowest ranking group (*C. neglectus*, *P. anubis*, and *T. gelada*) (Fig. 2.4).

Summed Variance Method (Hypothesis C)

The results for the PCA and the resulting summed variances are shown in Table 2.5 and Figure 2.5. The summed variances were negatively correlated with annual frequency of foliage consumption (Pearsons' product-moment correlation: r (6) = -0.84, p < 0.01; Fig. 2.6) and positively correlated with annual frequency of fruit consumption (Pearsons' product-moment correlation: r (6) = 0.72, p < 0.05; Fig. 2.6). Additionally, the summed variances showed a positive trend with the Shannon Diversity index H (Pearsons' product-moment correlation: r (6) = 0.64, 0.05 < p < 0.1; Fig. 2.7) such that species with a high diversity also had greater summed variance, but the hypothesis of no

relationship could not be rejected. However, when the outlier *Ce. torquatus* was removed from the analyses, the correlations increased (Figures 2.6-2.7). Frequency of foliage consumption had a stronger negative correlation (Pearsons' product-moment correlation: r (5) = -0.91, $p < 0.005$; Fig. 2.6) and frequency of fruit consumption had a stronger positive correlation (Pearsons' product-moment correlation: r (5) = 0.92, $p < 0.005$; Fig. 2.6) with summed variance. When *C. torquatus* was removed, *H* was also positively correlated with summed variance (Pearsons' product-moment correlation: r (5) = 0.75, $p < 0.05$; Fig. 2.7).

Discussion

Levene's Test (Hypothesis A)

Levene's Test identified differences among the species in microwear variance of *Asfc*, *Smc*, *HAsfc9*, and *HAsfc81*. Both variance in *Asfc* and *Smc* appeared to distinguish some species with high dietary diversity from those with low diversity. Using the more conservative Tukey's HSD tests, *P. anubis* had greater variance in *Asfc* and *Smc* than *Pr. rufomitratus*, which would be expected given that *P. anubis* has a more diverse diet than the very specialized *Pr. rufomitratus.* With the less conservative Fisher's LSD tests, *Ch. aethiops*, *C. mitis,* and *P. anubis*, all of which have more diverse diets, were included in the highest variance groups for both *Asfc* and *Smc*, while *Co. guereza*, *Pr. rufomitratus*, and *T. gelada*, which have the least diverse diets, were included in the lowest variance groups for both *Asfc* and *Smc*. However, some results were not as expected for these variables. *C. neglectus* grouped with the most variant species in *Asfc*, while it grouped with the medium and least variant species in *Smc*; although *C. neglectus* is specialized

compared to the other guenons in this sample, it has a dietary breadth that is in the middle of those in this sample. *Ce. torquatus,* which has a low dietary diversity, also grouped with the most variant species in *Smc* but with the least variant species in *Asfc*. Additionally, *C. mitis,* with a high dietary diversity, grouped with the least variant species in *Asfc,* at least using the median Levene's Test and post-hoc Fisher's LSD. Thus, although the variance in *Asfc* and *Smc* did generally separate species based on dietary diversity, with species with the most diverse diets having greater variance and species with the least diverse diets having lower variance, species with variance in the middle were not separated as expected. Additionally, these results were generally only seen with the less conservative tests; with the more conservative median Levene's and post-hoc Tukey's HSD tests, only a few differences were noted. Although these did conform to expectations based on dietary diversity, the method did not distinguish species well based on dietary diversity.

Although differences in variance in *HAsfc9* and *HAsfc81* were also identified among the species, they did not appear to be drawn along the lines expected based on differences in dietary diversity. Contrary to expectations, *P. anubis* had lower variance in both heterogeneity variables than almost all the species. However, it was not necessarily expected that variance in heterogeneity would distinguish species based on dietary breadth, as mean heterogeneity may be greater in species with broader diets (discussed below).

No differences were found among the species in variance in anisotropy, which is surprising given that mean anisotropy has been one of the best predictors of diet in primates (Scott et al., 2005, 2006, 2012), with species that eat high frequencies of leaves

or grasses having high anisotropy. In this sample, all species showed a fairly broad range of anisotropy values (Fig. 2.8). These results suggest that, although mean anisotropy can distinguish species that consume a high frequency of leaves or grasses from those that do not, the variation around the mean is not different among species and thus is not indicative of dietary diversity.

Mean Heterogeneity (Hypothesis B)

Mean heterogeneity rank did not clearly separate the species based on dietary diversity. Although some species showed relationships in the expected direction, with *C. mitis* having a high dietary diversity and high mean heterogeneity rank and *T. gelada* having a low dietary diversity and low mean heterogeneity rank, many species did not show the expected relationships. *P. anubis*, which has a fairly diverse diet, had one of the lowest mean heterogeneity ranks, while *Pr. rufomitratus*, with a less diverse diet, showed one of the highest. These results suggest that heterogeneity may not be the best predictor of dietary diversity and may be indicative of other dietary behaviors. Research by Calandra et al. (2012) suggests that heterogeneity is negatively correlated with fruit consumption, such that species eating more fruit have lower heterogeneity values; however, there was great intraspecific variation in heterogeneity in their sample, particularly in species with intermediate frequencies of fruit consumption. Additionally, their sample of *T. gelada*, which would be predicted to have the highest heterogeneity values given its low frequencies of fruit consumption, was intermediate in heterogeneity, while their sample of *Pongo abelii* (the Sumatran orangutan) had much higher heterogeneity than would be expected given its high frequency of fruit consumption.

Overall, the relationship between heterogeneity and diet appears to be more complex than a simple correlation with fruit consumption or dietary diversity and should be investigated further.

Summed Variance method (Hypothesis C)

The summed variance method shows more promise in separating species by dietary diversity. Summed variances using all species were significantly correlated with annual average frequency of both foliage and fruit consumption, and showed a trend towards correlation with dietary diversity (*H*). Species that consume a high frequency of foliage have low summed variances in microwear, while those that consume low frequencies of foliage have high summed variances. Species with high dietary diversities also tended to have higher summed variances. The only species that was quite divergent from these relationships was *Ce. torquatus*, which had lower than expected summed variance given its low frequency of leaf consumption and high frequency of fruit consumption, but higher summed variance than expected given its low *H* value (Figs. 2.5-2.6). This result may be because *Ce. torquatus* consumes a diet unlike any other species examined here, with a high frequency of fruit consumption but low consumption frequencies of leaves and animal matter. High fruit consumption has been shown to be related to high complexity and heterogeneity (Daegling et al., 2011; Scott et al., 2006, 2012). *Ce. torquatus* in this sample had relatively high mean complexity and high to medium mean heterogeneity; additionally, *Ce. torquatus* had very high *Smc* compared to the other groups. However, the results may also be related to the small sample size (n = 9) of *Ce. torquatus*, lending each specimen a greater weight. Additionally, *Ce. torquatus*

is the subject of only two dietary studies that had good enough data to be used in this research (Mitani, 1989; Cooke, 2012). It is possible that the data from these studies do not reflect the actual diet of the animals used in this research. This possibility is enhanced by the fact that one study categorized 9.5% of the diet as "Other" and included no leaves in the diet, while the other study documented an average of 12% leaves (Mitani, 1989; Cooke, 2012). When *Ce. torquatus* was removed from the sample, this method looked more accurate at reflecting dietary diversity; however, it was much more strongly reflective of annual frequency of fruit and foliage in the diet.

The results of the Summed Variance method suggest that overall variation in DMTA variables is correlated with dietary breadth, since species that had higher summed variances also had higher *H* values; however, they also had lower frequencies of leaf consumption and higher frequencies of fruit consumption. The relationship between summed variances and these two annual dietary frequencies was present even when *Ce. torquatus* was included in analyses, and both correlations were stronger than that between dietary diversity and summed variance. These relationships suggest that variation in DMTA variables may be more closely linked to annual dietary frequencies than to dietary diversity. In particular, higher frequencies of foliage consumption are correlated with less variation in DMTA variables, while lower frequencies of foliage consumption are correlated with greater variation in DMTA variables. This relationship may be due to the amount of abrasion involved in the consumption of different food types. More abrasive diets may quickly and consistently overwrite microwear features, leading to low overall variation in microwear. This interpretation is consistent with experimental work by Schulz et al. (2013) in rabbits indicating that greater consumption of abrasives in the diet

leads to lower variance in dental microwear parameters; it is also consistent with ongoing work conducted by Karme et al. (2014), using an experimental chewing machine, that shows greater variation in microwear when wear is caused only by attrition but shows a decrease in variation as abrasiveness of masticated material increases. The only species in the sample examined in this paper that has a low dietary diversity and low frequency of foliage consumption is *Ce. torquatus*, which is a fruit specialist; the fact that this species does not conform to expectations of microwear variation based on dietary diversity but better conforms to expectations based on frequency of foliage and fruit consumption lends further support to the idea that variance in microwear is more indicative of these frequencies than of dietary diversity.

One concern in using these methods with fossil species would be the effect of small sample sizes on the ability to distinguish differences among the species. In these analyses, *Ce. torquatus* had the smallest sample size and was not as predicted in a number of ways. When using Levene's Test, it showed high variance in *Smc* but did not vary from any species in *Asfc*. However, it showed fairly high summed variance when compared to its calculated dietary breadth and leaf consumption in comparison to other species. It is possible these results are due to small sample size; however, *Ce. torquatus* showed similar levels of variation in these variables to a large (n = 55) sample of *Cercocebus atys* analyzed by Scott et al. (2012); if anything, this sample of *Ce. torquatus* showed low variation in *Asfc* compared to the larger sample, but no tests were significantly different between the two groups in either mean or variance of any variable. Since the two species are closely related and have similar diets (Mitani, 1989; Daegling et al., 2011; Cooke, 2012), the fact that they show similar amounts of variation likely

means that the sample of *Ce. torquatus* is not significantly biased, and thus it is possible to use a small sample size and achieve accurate results. Further analyses using bootstrapping may further support this conclusion. Additionally, the summed variance method was originally suggested as a method robust to small sample sizes and differences in sample size among species (Kamilar, 2006).

These methods have the ability to separate species based on dietary diversity and thus allow for testing hypotheses based on dietary diversity in fossil species. Further analyses using other mammalian groups should be completed in order to strengthen this link between DMTA variances, dietary diversity, and dietary frequencies. In particular, these methods should be used in analyzing the Hominidae to test for differences among hominins, a group where there is much contention over differences in dietary diversity. Furthermore, these methods can be used to explore macroecological relationships related to dietary breadth in the fossil record.

Conclusion

Overall, these results indicate that there is a relationship between variation in microwear and dietary breadth, but the relationship may not be a strong one. Although examining the differences in variance among groups in individual microwear variables may be informative of specific dietary behaviors, such as variation in hard object or fruit consumption, it appears that, for identifying overall dietary diversity, the summed variances method is more effective, since it correlates with *H* and separates all the species as expected (except for *Ce. torquatus*). However, the fact that the summed variances correlate better with frequencies of fruit and foliage consumption suggest that

reconstructions of dietary diversity may still need to be inferred based on these more general dietary categories.

In terms of interpreting fossil microwear textures, the results from these analyses suggest that comparisons of variance of individual DMTA variables may not indicate differences in dietary variation among species, although there is some support for these comparisons for *Asfc* and *Smc*. Furthermore, differences in mean heterogeneity appear to be more indicative of frequency of hard object feeding than of dietary diversity. The most promising avenue for inferring dietary diversity appears to be the summed variance method. Fossil DMTA variables can be entered in the PCA with the species examined here to infer their diets. Species with low summed variances can be interpreted to have high frequencies of foliage consumption, low frequencies of fruit consumption, and low dietary diversity; species with high summed variances can be interpreted to have high frequencies of fruit consumption and low frequencies of foliage consumption, but may have high or low dietary diversities (based on the position of *Ce. torquatus*). Other data, such as body size and dental morphology, may need to be used in concert with microwear analyses to infer dietary diversity in species with high summed variances of DMTA variables.

References

Benefit BR. 1999. Biogeography, dietary specialization and the diversification of African Plio-Pleistocene monkeys. In: Bromage TG, Schrenk F, eds. African Biogeography, Climate Change, and Human Evolution. Oxford: Oxford University Press, pp. 172-188.

Benefit BR. 2000. Old World monkey origins and diversification: an evolutionary study of diet and dentition. In: Whitehead PF, Jolly CJ, eds. Old World Monkeys. Cambridge:Cambridge University Press, pp. 133-179.

Bowman DM, Murphy BP, McMahon CR. 2010. Using carbon isotope analysis of the diet of two introduced Australian megaherbivores to understand Pleistocene megafaunal extinctions. J Biogeogr 37:499-505.

Boyles JG, Storm JJ. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLoS One 2(7):e672.

Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. J Hum Evol 63:85-98.

Cerling TE, Mbua E, Kirera FM, Kyalo Manthi F, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. Proc Nat Acad Sci USA 108:9337-9341.

Codron D, Luyt J, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J. 2005. Utilization of savanna-based resources by baboons during the Plio-Pleistocene. S Afr J Sci 101:254–248.

Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation? Int J Primatol 29:757-772.

Conover WJ, Johnson ME, Johnsons MM. 1981. A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. Technometrics 23:351-361.

Cook RJ, Farewell VT. 1996. Multiplicity considerations in the design and analysis of clinical trials. J R Statistic Soc A, 159: 93-110.

Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. PLoS One 6(8):e23095.

Dandelot P. 1959. Note sur la classificatlon des Cercopithèques du groupe *aethiops*. Mammalia, 23:357-368.

Dandelot P. 1968. Primates: Anthropoidea. In: Meester J, ed. Smithsonian Institution Preliminary Identification Manual for African Mammals, Part 24. Washington, D.C.: Smithsonian Institution, pp. 24:1-80.

Dandelot P. 1974. Order Primates. In: Meester J, Setzer H, eds. The Mammals of Africa: An Identification Manual, Part 3. Washington, D.C.: Smithsonian Institution Press, pp. 1–43.

DeSantis LR, Haupt RJ. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. Biol Lett 10(4):20140203.

DeSantis LR, Scott JR, Schubert BW, Donohue SL, McCray BM, Van Stolk CA, Winburn AA, Greshko MA, O'Hara MC. 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. PloS ONE 8(8):e71428.

Donnely SM, Kramer A. 1999. Testing for multiple species in fossil samples: an evaluation and comparison of tests for equal relative variation. Am J Phys Anthropol 108:507-529.

Fashing PJ. 2011. African colobine monkeys: their behavior, ecology, and conservation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective. Oxford: Oxford University Press, pp. 203-229.

Fleagle JG, Gilbert CC, Baden AL. 2010. Primate cranial diversity. Am J Phys Anthropol 142:565-578.

Gaston KJ, Blackburn TM. 2000. Pattern and Process in Macroecology. Oxford: Blackwell Science. 377 p.

Gogarten JF, Grine FE. 2013. Seasonal mortality patterns in primates: implications for the interpretation of dental microwear. Evol Anthropol 22:9-19.

Gordon KD. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am J Phys Anthropol 59:195-215.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. J Hum Evol 15:783-822.

Grine FE. 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. Scanning Microscopy 1:647-656.

Grine FE, Ungar PS, Teaford MF. 2006. Was the Early Pliocene hominin '*Australopithecus*' *anamensis* a hard object feeder? S Afr J Sci 102:301

Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297-319.

Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am J Phys Anthropol 148:285-317.

Groves CP. 2001. Primate Taxonomy. Washington D.C.: Smithsonian Institution Press, 350 pp.

Groves CP. 2005. Order Primates. In: Wilson DE, Reeder DM, eds. *Mammal Species of the World: a Taxonomic and Geographic Reference.* Baltimore: Johns Hopkins University Press, pp. 111-184.

Groves CP. 2007. The taxonomic diversity of the Colobinae of Africa. J Anthropol Sci 85:7-34.

Groves CP, Kingdon J. 2013. Genus *Chlorocebus*: Savanna Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 264-266.

Grubb P, Butynski TM, Oates JF, Bearder SK, Disotell TR, Groves CP, Struhsaker TT. 2003. Assessment of the diversity of African primates. Int J Primatol 24:1301-1357.

Grubb P, Struhsacker TT, Siex KS. 2013. Subgenus *Piliocolobus*: Red Colobus Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 125-128.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization, and extinction in primates. J Biogeogr 29:445-456.

Harrison MJ. 1982. The behavioural ecology of green monkeys (*Cercopithecus sabaeus*) at Mt. Assirik, Senegal. PhD Dissertation, University of Stirling.

Haupt RJ, DeSantis LR, Green JL, Ungar PS. 2013. Dental microwear texture as a proxy for diet in xenarthrans. J Mammal 94:856-866.

Isbell LA, Pruetz JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behav Ecol Sociobiol 42:123-133.

IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. <http://www.iucnredlist.org>. Downloaded on 27 January 2011.

Kamilar JM. 2006. Geographic variation in primate behavior and ecology: from populations to communities. PhD dissertation. Stony Brook, NY: State University of New York.

Karme A, Rannikko J, Bertin T, Clauss M, Fortelius M. 2014. Chewing machine and tooth wear: how plant materials and grit affect teeth. Podium presentation, Society of Vertebrate Paleontology 74th Annual Meetings.

Kavanagh, M. 1978. The diet and feeding behaviour of Cercopithecus aethiops tantalus. Folia Primatol 30:30-63.

Kay RF. 1974. Body size, molar structure and diet in primates. Am J Phys Anthropol 41:487-488.

Kay RF. 1975. Allometry and early hominids. Science 189:61-64.

Kay RF. 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.

Kay RF. 1978. Molar structure and diet in extant Cercopithecidae. In: Butler PM, Joysey KA, eds. Development, Function, and Evolution of Teeth. New York: Academic Press, pp. 309-339.

Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, eds. Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys and apes. New York: Columbia University Press, pp. 21-53.

Kimbel WH, Delezene LK. 2009. "Lucy" redux: A review of research on *Australopithecus afarensis*. Am J Phys Anthropol 140(S49):2-48.

Levene H. 1960. Robust tests for equality of variances. In: Olkin I, ed. Contributions to Probability and Statistics. Stanford: Stanford University Press, pp. 278-292.

Lockwood CA, Kimbel WH, Johanson DC. 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis.* J Hum Evol 39:23-55.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd edition. Sunderland, Mass: Sinauer Associates, Inc. 841 pp.

Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. J R Soc Interface 10:20120923.

Mainland IL. 2003. Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*) and its implications for dietary reconstruction. J Archaeol Sci 30:1513-1527.

Mbizah MM, Marino J, Groom RJ. 2012. Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*). S Afr J Wildlife Research 42:94-103.

Merceron G, Viriot L, Blondel C. 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*) from Chizé (Western France) and relation to food composition. Small Ruminant Res 53:125-132.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542.

Mitani M. 1989. *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of southwestern Cameroon. Primates 30:307-323.

Napier PH. 1981. Catalogue of Primates in the British Museum (Natural History) and elsewhere in the British Isles, part II: Family Cercopithecidae, subfamily Cercopithecinae. London: British Museum, 120pp.

Potts R. 1998. Variability selection in hominid evolution. Evol Anthropol 7:81-96.

Robinson JT. 1954. The genera and species of the Australopithecinae. Am J Phys Anthropol 12:181-200.

Robinson JT. 1956. The dentition of the Australopithecinae. Transvaal Mus Mem 9:1-185.

Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45:281-297.

Ryan AS. 1981. Anterior dental microwear and its relationship to diet and feeding behavior in three African primates (*Pan troglodytes troglodytes*, *Gorilla gorilla gorilla* and *Papio hamadryas*). Primates 22:533-550.

Schluter D. 2000. The ecology of adaptive radiation. Oxford: Oxford University Press, 296 pp.

Schulz E, Piotrowski V, Clauss M, Mau M, Merceron G, Kaiser TM 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS ONE 8:e56167.

Scott JR. 2012. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution. PhD Dissertation, University of Arkansas.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436:693-695.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51:339-349.

Scott RS, Teaford MF, Ungar PS. 2009. Dietary diversity and dental microwear variability in *Theropithecus gelada* and *Papio cynocephalus*. Am J Phys Anthropol (S48):234.

Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Sponheimer M, Passey B, de Ruiter D, Guatelli-Sternberg D, Cerling T, Lee-Thorp J. 2006. Isotopic evidence for dietary flexibility in the early hominin *Paranthropus robustus*. Science 314: 980-982.

Sponheimer M, Codron D, Passey BH, de Ruiter DJ, Cerling TE, Lee-Thorp JA. 2009. Using carbon isotopes to track dietary change in modern, historical, and ancient primates. Am J Phys Anthropol 140:661-670.

Strait DS, Constantino P, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA, Weber GW, Wang Q, Byron C, Slice DE, Chalk J, Smith AL, Smith LC, Wood S, Berthaume M, Benazzi S, Dzialo S, Tamvada K, Ledogar JA. 2013. Diet and dietary adaptations in early hominins: The hard food perspective. Am J Phys Anthropol 151:339-355.

Strait SG. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. J Mammal 74:391-402.

Stynder DD, Ungar PS, Scott JR, Schubert BW. 2012. A dental microwear texture analysis of the Mio-Pliocene hyaenids from Langebaanweg, South Africa. Acta Palaeontol Pol 57:485-496.

Swedell L. 2011. African papionins: diversity of social organization and ecological flexibility. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective, pp. 241-277.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. 2003. Responses of 'resistant'vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1-18.

Teaford MF. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microscopy 2:1167-1175.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Glander KE. 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk M, Rosenberger A, Garber P, eds. Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 433-449.

Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. Am J Phys Anthropol 80:447-460.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401.

Teaford MF, Runestad JA. 1992. Dental microwear and diet in Venezuelan primates. Am J Phys Anthropol 88:347-364.

Teaford MF, Walker AC. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am J Phys Anthropol 64:191-200.

Ting N. 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living colobus monkeys. J Hum Evol 55:312-325.

Ungar PS, Bunn JM. 2009. Dental topography and diets of four old world monkey species. Am J Primatol 71:466-477.

Ungar PS, Brown CA, Bergstrom TS, Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning Microscopy 25:185-193.

Ungar PS, Grine FE, Teaford MF. 2008a. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3:1-6.

Ungar PS, Scott RS, Scott JR, Teaford MF. 2008b. Dental microwear analysis: historical perspectives and new approaches. In: Irish JD, Nelson GC, eds. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press, pp 389-425.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis.* Phil Trans R Soc B 365:3345-3354.

Walker A, Hoeck HN, Perez L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201:908-910.

Wills MA, Briggs DE, Fortey, RA. 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. Paleobiology 20:93-130.

Wrangham RW, Waterman PG. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. J Anim Ecol 50:715-731.

Table 2.1
Summary of Cercopithecid Sample

Species	*n*	Localities	Geographic Region[a]
Cercocebus torquatus	9	2	C
Cercopithecus mitis	71	11	C, E, S
Cercopithecus neglectus	22	5	C
Chlorocebus aethiops	27	15	C, E, S, W
Colobus guereza	45	12	C, E
Papio anubis	45	10	C, E, W
Procolobus rufomitratus	74	5	C
Theropithecus gelada	16	4	E

[a] Geographic region of Africa (Central=C, Eastern=E, Southern=S, Western=W) from which the specimens come.

Table 2.2
Example of Calculating the Summed Weighted Variance

Step 1. Conduct Principal Components Analysis on raw data					
Taxon	PC1	PC2	PC3		
Ch. aethiops	1.17	1.21	-0.56		
Ch. aethiops	0.50	4.85	1.31		
Ch. aethiops	-1.04	0.40	-0.11		
Ch. aethiops	0.17	-1.67	0.52		
Co. guereza	1.61	-1.86	0.09		
Co. guereza	3.11	-2.56	0.74		
Co. guereza	-0.40	-1.40	-0.68		
Co. guereza	0.06	-3.07	0.74		
Eigenvalue of PC	2.13	1.44	0.94		
Step 2. Weight components (PC Score x Eigenvalue)					
	PC1 x	PC2 x	PC3 x		
Taxon	2.13	1.44	0.94		
Ch. aethiops	2.48	1.74	-0.53		
Ch. aethiops	1.06	6.99	1.23		
Ch. aethiops	-2.22	0.58	-0.10		
Ch. aethiops	0.36	-2.40	0.49		
Co. guereza	3.44	-2.68	0.08		
Co. guereza	6.62	-3.68	0.70		
Co. guereza	-0.85	-2.02	-0.64		
Co. guereza	0.13	-4.42	0.69		
Step 3. Calculate variance of weighted component for each species					
Ch. aethiops	3.89	15.33	0.59		
Co. guereza	11.51	1.13	0.40		
Step 4. Sum weighted components for each species					**Summed Weighted Variance**
Ch. aethiops	3.89	15.33	0.59	=	**19.80**
Co. guereza	11.51	1.13	0.40	=	**13.04**

Table 2.3
Levene's Test Results

Variable	Levene's Test	*F* (7, 301)	*p*
Asfc	Median	2.14	< 0.05
	Mean	2.77	< 0.01
Smc	Median	1.42	> 0.1
	Mean	4.68	< 0.001
HAsfc9	Median	2.25	< 0.05
	Mean	2.94	< 0.01
HAsfc81	Median	2.32	< 0.05
	Mean	3.03	< 0.005
epLsar	Median	0.6	> 0.1
	Mean	0.63	> 0.1
Tfv	Median	1.28	> 0.1
	Mean	1.54	> 0.1

Table 2.4
Post-hoc Test Results for Homogeneity of Variance

	Asfc			***Smc***		***HAsfc9***	***HAsfc81***		
Levene's Test[a]	MD/ M	MD	M	M	M	MD/ M	MD/ M	MD	M
Post-Hoc test [b]	HSD	LSD	LSD	HSD	LSD	HSD/ LSD	HSD	LSD	LSD
Species									
Ce. torquatus	AB	AB	AB	B	A	AB	AB	A	A
C. mitis	AB	AB	A	AB	AB	A	A	A	A
C. neglectus	AB	A	A	AB	BC	AB	AB	A	A
Ch. aethiops	AB	A	A	AB	A	AB	AB	A	A
Co. guereza	AB	AB	A	AB	C	AB	AB	AB	AB
P. anubis	A	A	A	A	A	B	B	B	B
Pr. rufomitratus	B	B	B	B	BC	AB	AB	AB	A
T. gelada	AB	AB	AB	B	C	AB	AB	AB	A

Note. Species with the same letter do not differ for the given test; A = greatest variance, C = lowest variance.
[a] Test type is Median (MD) or Mean (M) Levene's Test
[b] Post-hoc test is Tukey's Honestly Significant Difference (HSD) or Fisher's Least Significant Difference (LSD) test at the $\alpha = 0.05$ level.

Table 2.5
Summed Weighted Variances and Dietary Indices

Taxon	**SV1**	**SV2**	**Foliage**	**Fruit**	***H***
Cercocebus torquatus	10.85	*	0.06	0.83	0.65
Cercopithecus mitis	13.13	13.03	0.23	0.47	1.33
Cercopithecus neglectus	11.84	13.87	0.14	0.51	1.22
Chlorocebus aethiops	10.67	10.70	0.18	0.37	1.55
Colobus guereza	8.63	8.65	0.63	0.26	0.96
Papio anubis	10.61	10.71	0.32	0.43	1.27
Procolobus rufomitratus	8.87	9.02	0.71	0.09	0.86
Theropithecus gelada	4.97	6.13	0.80	0.02	0.65

Note. Summed weighted variances were calculated for a principle components analysis containing *Cercocebus torquatus* (SV1) and without *Ce. torquatus* (SV2). Foliage and Fruit indicate annual average frequencies of consumption of these items, and *H* is the Shannon Diversity Index for annual average diet (see Appendix C for references).

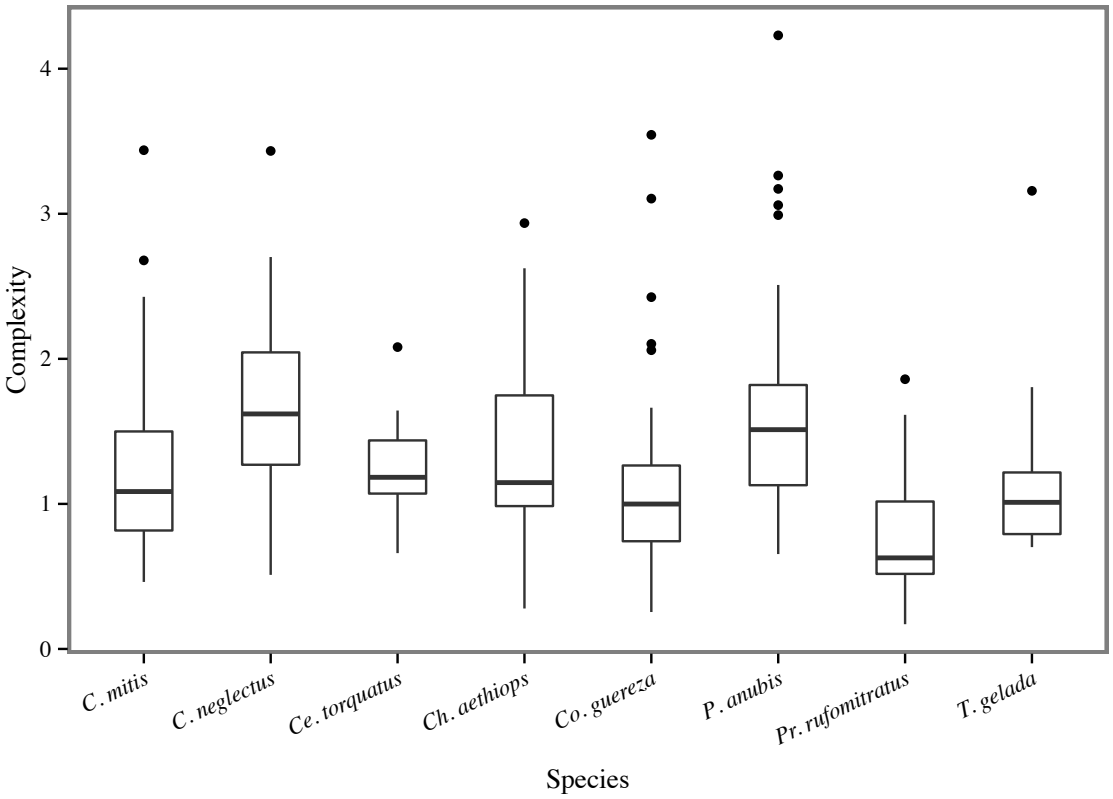

Figure 2.1. Box plot of complexity (*Asfc*) by species. Species differed in their variances in complexity (Levene's Test: median: F (7, 301) = 2.14, $p < 0.05$; mean: F (7, 301) = 2.77, $p < 0.01$).

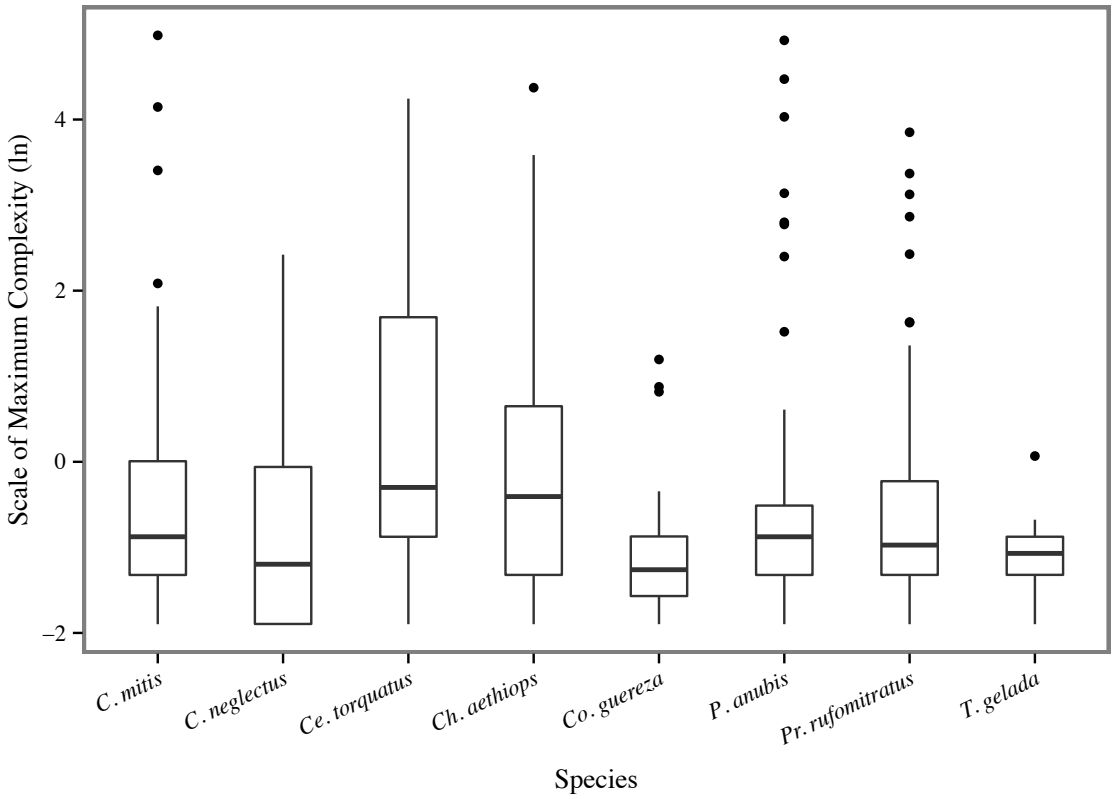

Figure 2.2. Box plot of scale of maximum complexity (*Smc*) by species. Scale of maximum complexity is natural-logarithm (ln) transformed. The species did not differ in variance in *Smc* when using the median Levene's Test (F (7, 301) = 1.42, $p > 0.1$) but did when using the mean Levene's Test (F (7, 301) = 4.68, $p < 0.001$).

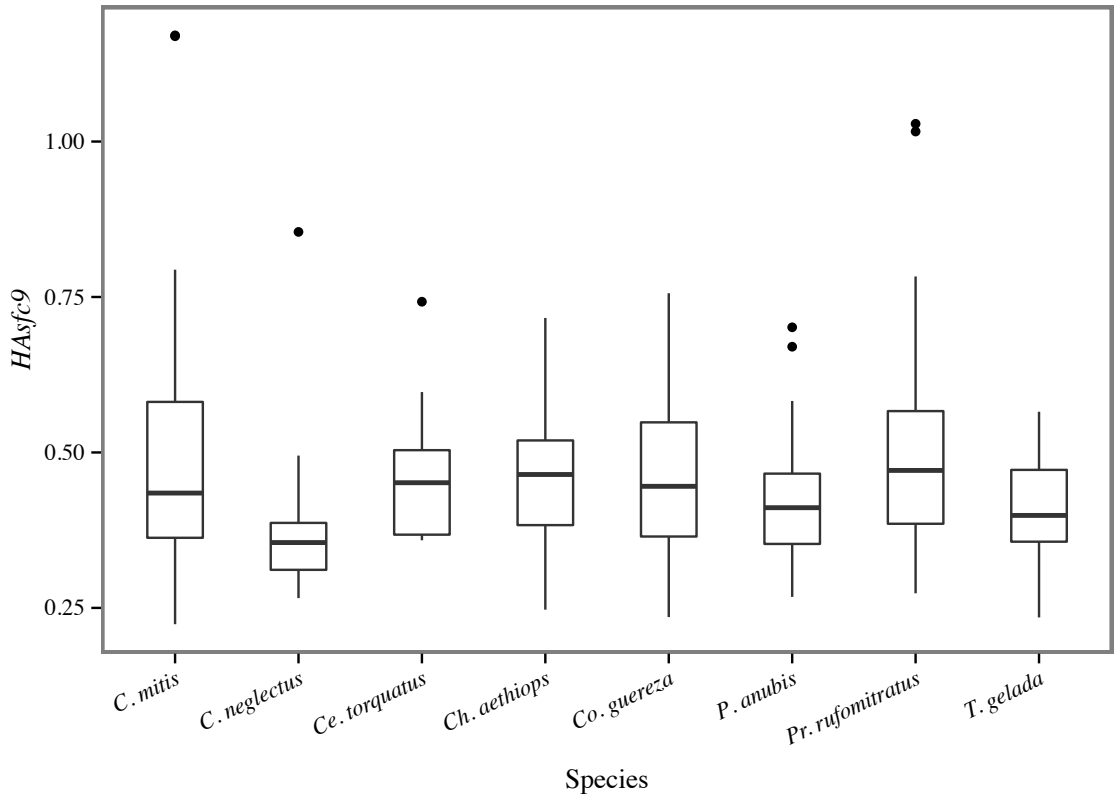

Figure 2.3. Box plot of heterogeneity at the 3 x 3 scale (*HAsfc9*) by species. The species differed in their mean *HAsfc9* ranks (ANOVA: F (7, 301) = 3.61, $p < 0.001$) and their *HAsfc9* variances (Levene's Test: median: F (7, 301) = 2.25, $p < 0.05$; mean: F (7, 301) = 2.94, $p < 0.01$).

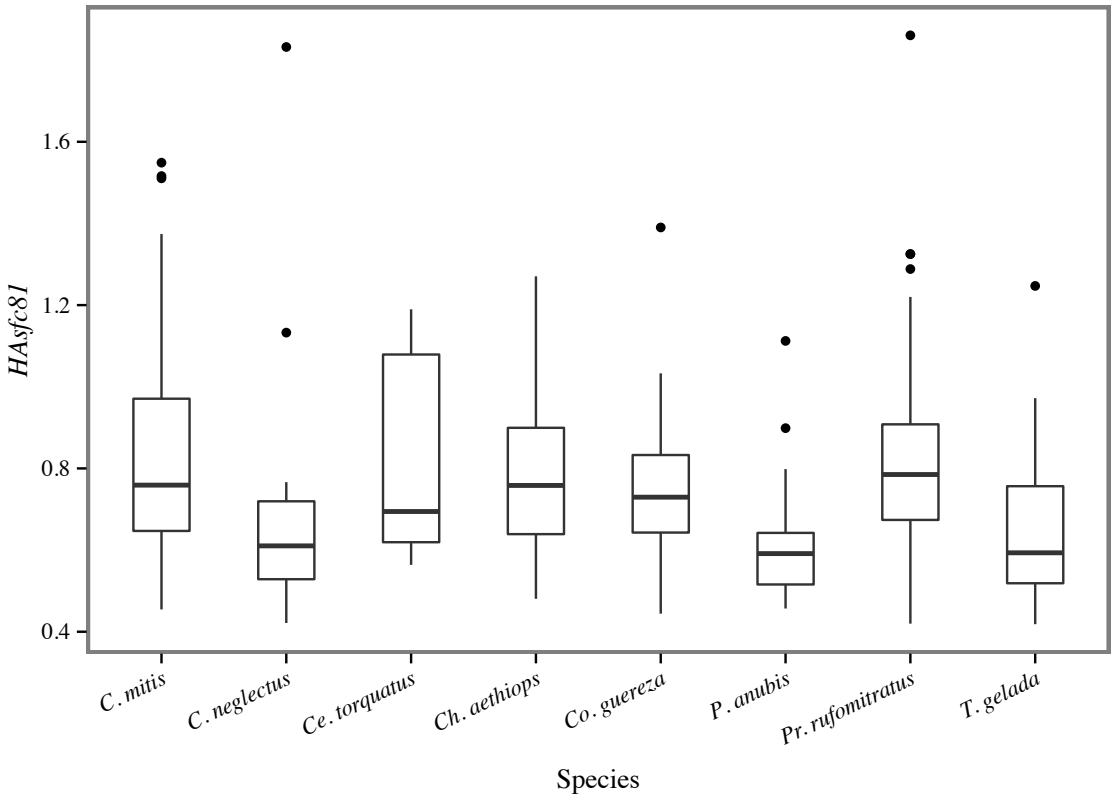

Figure 2.4. Box plot of heterogeneity at the 9 x 9 scale (*HAsfc81*) by species. Species differed in mean *HAsfc81* ranks (ANOVA: F (7, 301) = 9.46, p <0.0001) and in *HAsfc81* variance (median: F (7, 301) = 2.32, $p < 0.05$; mean: F (7, 301) = 3.03, $p < 0.005$).

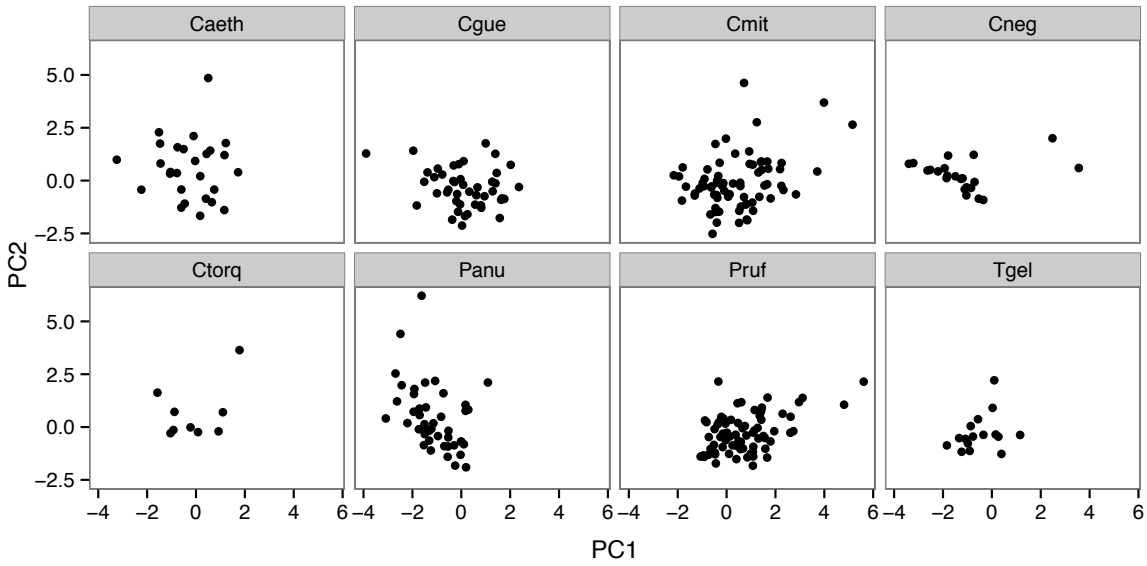

Figure 2.5. Principal components analysis by species. Scatter plots showing principal component 2 (PC2) by principal component 1 (PC1) for each species (given by the first letter of the genus name and first three or four letters of the species name). PC1 accounts for 32.9% of variation, while PC2 accounts for 24.1% of variation.

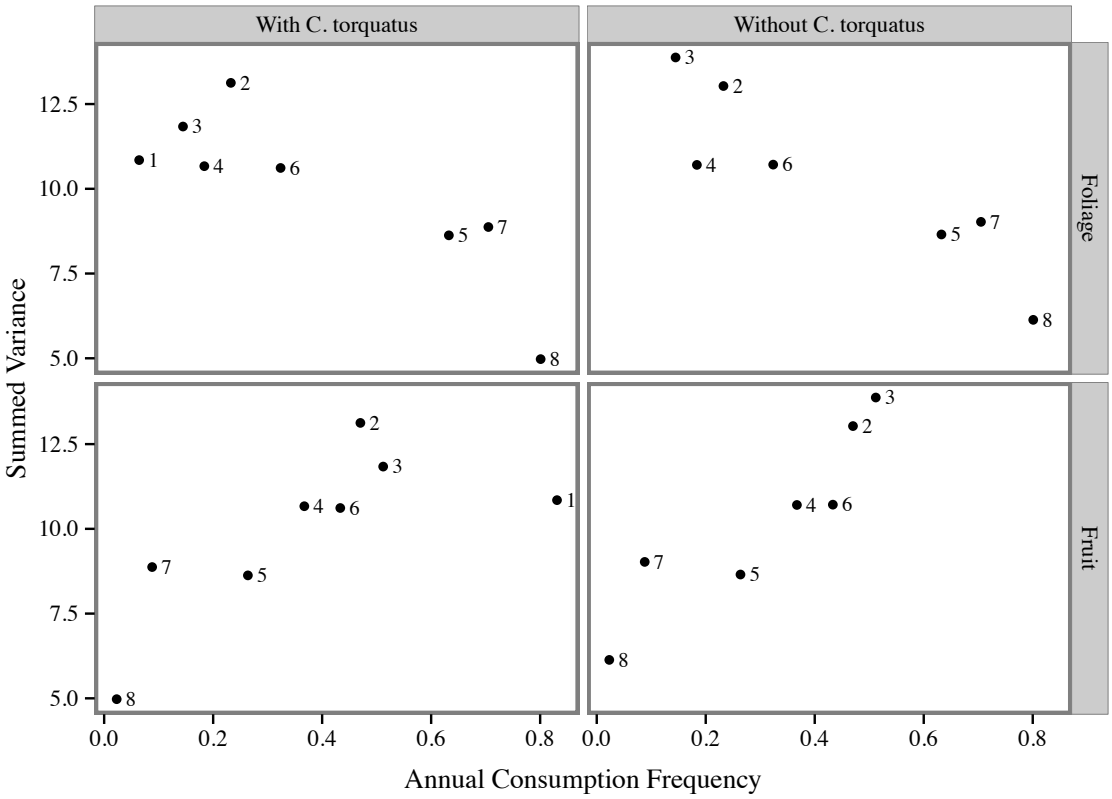

Figure 2.6. Summed variance correlations for foliage and fruit. Scatter plots of annual foliage and fruit consumption averages by the summed weighted variance of principal components analyses of six microwear variables for eight species (1 = *Cercocebus torquatus*, 2 = *Cercopithecus mitis*, 3 = *Cercopithecus neglectus*, 4 = *Chlorocebus aethiops*, 5 = *Colobus guereza*, 6 = *Papio anubis*, 7 = *Procolobus rufomitratus*, 8 = *Theropithecus gelada*). Both foliage and fruit consumption are correlated with summed variance, both with (Foliage: r (6) = -0.84, $p < 0.01$; Fruit: r (6) = 0.72, $p < 0.05$) and without *C. torquatus* (Foliage: r (5) = -0.91, $p < 0.005$; Fruit: r (5) = 0.92, $p < 0.005$).

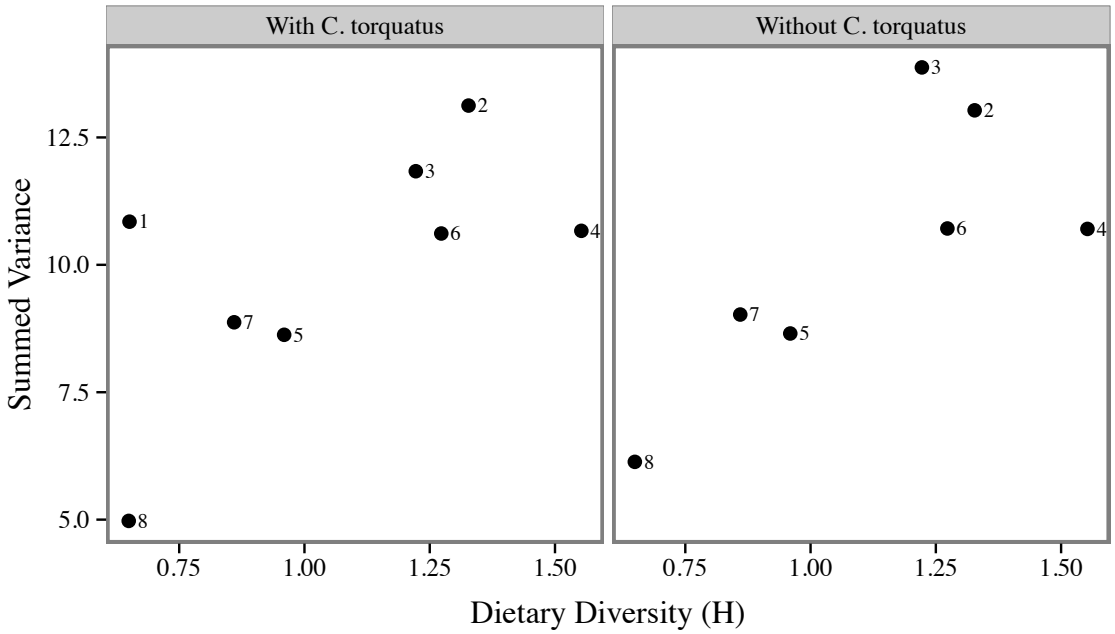

Figure 2.7. Summed variance correlations for dietary diversity. Scatter plots of the Shannon Diversity index (*H*) for annual diet by the summed weighted variance of principal components analyses of six microwear variables for eight species (1 = *Cercocebus torquatus*, 2 = *Cercopithecus mitis*, 3 = *Cercopithecus neglectus*, 4 = *Chlorocebus aethiops*, 5 = *Colobus guereza*, 6 = *Papio anubis*, 7 = *Procolobus rufomitratus*, 8 = *Theropithecus gelada*). The summed variances showed a positive trend with *H* (r (6) = 0.64, $0.05 < p < 0.1$); when *C. torquatus* was removed, *H* was positively correlated with summed variance (r (5) = 0.75, $p < 0.05$).

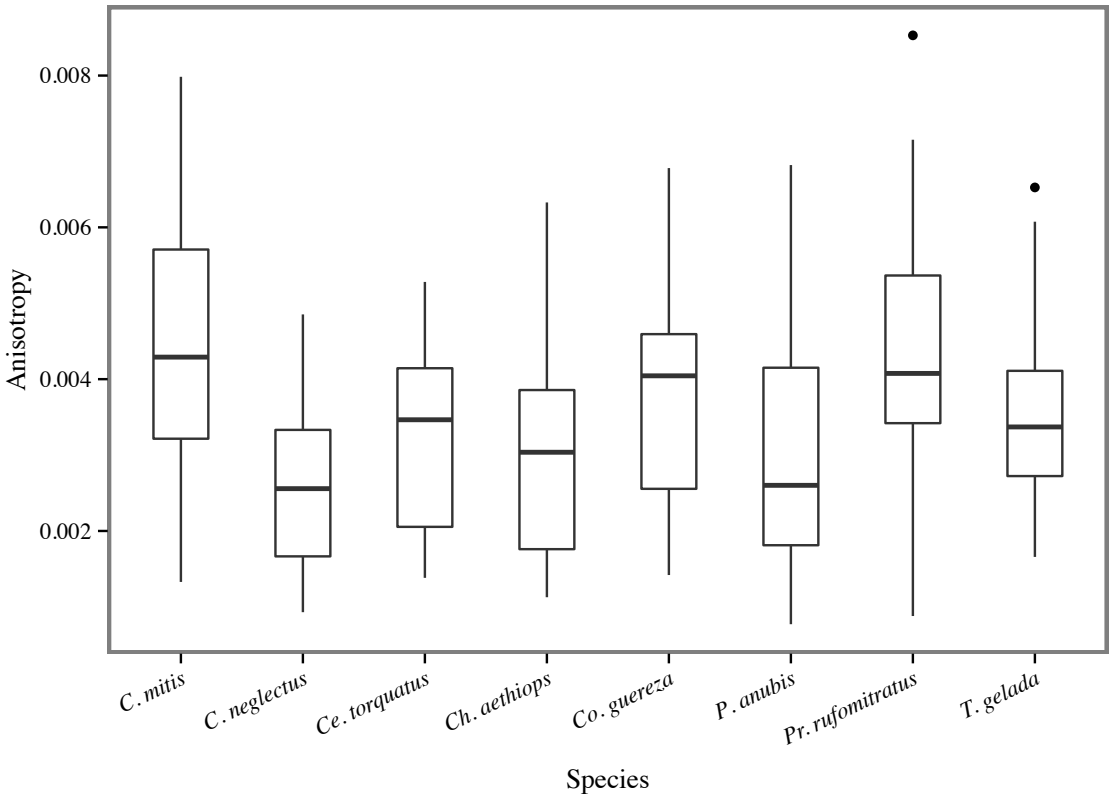

Figure 2.8. Box plot of anisotropy (*epLsar*) by species. No differences in variance exist among the species (Levene's Test: median: F (7, 301) = 0.60, $p > 0.10$; mean: F (7, 301) = 0.62, $p > 0.10$).

CHAPTER 3

INTRASPECIFIC DIFFERENCES IN DENTAL MICROWEAR TEXTURES AMONG AFRICAN OLD WORLD MONKEYS (CERCOPITHECIDAE) AND THEIR RELATIONSHIP TO SEASONAL AND GEOGRAPHIC VARIATION

Introduction

Dental microwear analyses are increasingly used to infer diet in fossil species, particularly hominins (Teaford and Walker, 1984; Grine, 1986; Scott et al., 2005; Ungar et al., 2010). Studies using traditional scanning electron microscopy (SEM), as well as those using the newer technique of dental microwear texture analysis, distinguish species that feed on hard, brittle objects such as hard fruit or seeds from those that feed on tough leaves or grasses (Teaford and Walker, 1984; Grine, 1986; Scott et al., 2005, 2012; Ungar et al., 2008, 2010). More subtle differences in diet among or within species have also been distinguishable using these methods (e.g. Teaford and Robinson, 1989; Merceron et al., 2010). In Chapter 2, I showed support for one method of analyzing intraspecific variation in microwear textures that could distinguish species with diverse diets, i.e. species that eat a wide variety of food resources, from those that have narrow diets, i.e. species that specialize on only a few foods or food categories. Species with diverse diets, however, also tend to live in more seasonal environments, to have greater geographic distributions, and to live in more habitat types (Brown, 1995; Cowlishaw and Hacker, 1997; Eeley and Foley, 1999; Eeley and Lawes, 1999; Gaston and Blackburn, 2000; Harcourt et al., 2002; Vazquez and Stevens, 2004). Thus, a question that emerges from dietary diversity research is: does variation in seasonality, geography, or habitat type

increase the microwear variation within species with broad diets, or is the variety in the diet of these species a greater source of microwear variability?

This question stems from the fact that intraspecific differences in microwear have been shown among sites, seasons, and habitat types for primates and other mammals. Teaford and Robinson (1989) showed a seasonal difference in size and frequency of pitting within *Cebus nigrivittatus* at dry tropical woodland sites, but did not show differences between sites of humid and dry forests or seasonal differences at humid forest sites. Teaford and Glander (1991, 1996) further demonstrated that habitat type could create intraspecific differences in microwear; they found differences in microwear features between *Aloutta palliata* who lived in tropical dry forests and those that lived in tropical moist forests, and by obtaining both samples during the wet season they controlled for seasonality. Merceron et al. (2010) showed differences in microwear based on the seasonality of resource use between and within different sexes of roe deer; the two sexes are observed to vary their diets during different seasons, and some of these distinctions are observable in the microwear textures of sexes by season. Galbany et al. (2009) revealed greater similarity in buccal microwear among different hominoid species living in the same environment than among the same species living in different environments. Withnell and Ungar (2013) showed differences in incisor microwear between shrews inhabiting grasslands and forests, but no differences among other habitats. Across all habitats, there were no differences in microwear among different dietary regimes; however, within a single habitat, there were differences among the different dietary regimes (Withnell and Ungar, 2013). Taken together, these results suggest that differences in habitat and season can lead to differences in microwear,

potentially increasing the variation in microwear among dietary regimes such that they mask differences related to discerning diet.

African monkeys (Cercopithecidae) are a particularly important group in which to consider the impact of habitat, season, and geography on microwear patterns. Cercopithecids are often used as analogs to fossil hominins (Elton, 2006; Jolly, 2009), which are the subject of many microwear studies (Grine, 1986; Scott et al., 2005; Ungar et al., 2006, 2008, 2010; Grine et al., 2012). Cercopithecids, particularly the cercopithecines, also have some of the most diverse and flexible diets of all primates (Jaffe and Isbell, 2011; Swedell, 2011; Fleagle, 2013). Coupled with these generally broad diets, cercopithecids inhabit a wide range of habitat types, spanning forests to bushland and semi-desert (Swedell, 2011; Butynski et al., 2013). This range of habitat types is in contrast to those of African apes (Hominidae), which tend to inhabit forests; even those apes, such as chimpanzees, that utilize more open habitats do not utilize the C4 foods found in these more open habitats (Sponheimer et al., 2003, 2006), unlike cercopithecids. This broad ecological niche and ability to exploit a range of food categoriess and habitats has made Cercopithecidae a particularly important comparative taxon for fossil hominins (e.g. Elton, 2006; Jolly, 2009), but the effects of seasonality, geographic location, and habitat on dental microwear variation have not as yet been widely examined in this group.

The ability to survive seasonal environmental changes has often been cited as crucial to the move from forest to open habitats in hominins (Foley, 1993; Potts, 1998; Klein, 1999; Reed and Fish, 2005). However, all primates are affected by changes to their habitat due to season; these changes, in varying degrees of intensity, have been reported

in all types of habitats where primates range (Hemingway and Bynum, 2005). Diet is most affected by seasonal changes, and during certain seasons, primates often face food scarcity. In a review of seasonality in primate diets, Hemingway and Bynum (2005) showed over 70% of all identified responses to food scarcity were shifts in diet, involving either an increased or decreased dietary breadth (here the number of species consumed). Hemingway and Bynum (2005) also found a significant relationship between the number of species consumed and how variable the diet was; dietary variability decreased as the number of species increased. In contrast to these findings, Chapman and Chapman (1990) found no relationship between seasonality (measured as the CV of rainfall) and dietary variability in food category use in African cercopithecids. Thus, although cercopithecids vary their diet across the year in response to seasonal changes, there may not be a specific rule to how they do so.

One of the major issues in paleoanthropology in the last decade, which relates to seasonality, has been the relative importance of "fallback foods" in the diet and evolution of primates, particularly of hominins (see Lambert, 2009, and other articles from Special Issue on Fallback Foods (2009), Am J Phys Anth 140(4)). The definition of fallback foods is quite generalized (Hemingway and Bynum 2005; Lambert 2009, and references therein), but indicates a dietary resource that is less preferred and critical to species survival during food scarcity (Altmann, 1998; Lambert, 2007). Thus, utilization of fallback foods is one example of a dietary shift during food scarcity. The relative importance of fallback foods in the shaping of primate morphology and adaptation is a topic that has being hotly debated (e.g. Lambert, 2009). However, the relationship between fallback foods and dietary breadth is not clear. Since Hemingway and Bynum

(2005) found that primates that incorporated more species into their diets (one measure of dietary breadth) had less dietary variability, we might expect that species with greater dietary breadth would be less likely to rely on fallback foods during times of scarcity. More seasonal environments may encourage greater dietary variability, but they may also encourage greater dietary breadth.

Not only do species with broader diets tend to encounter more seasonal environments, they also tend to have wider distributions and to encounter more habitat types (Brown, 1984, 1995; Brown et al., 1995; Lomolino et al., 2006). The causal relationship among these factors has been debated for the last few decades (i.e. Gaston and Blackburn, 2000; Vazquez and Stevens, 2004), but this general rule has been supported within primates, particularly on the African continent (Cowlishaw and Hacker, 1997; Eeley and Foley, 1999; Harcourt, 2000; Harcourt et al., 2002). Cowlishaw and Hacker (1997) demonstrated that the latitudinal range of African primates (i.e. how far North/South they were distributed) was related to their ability to withstand seasonal variation, particularly seasonal variation in rainfall. Harcourt (2000) also supported this finding and further demonstrated a relationship between latitudinal range and both dietary breadth (how many food categories a primate eats) and habitat breadth (how many habitats a primate lives in), where species with larger latitudinal ranges had broader dietary and habitat breadths. Eeley and Foley (1999) and Harcourt et al. (2002) also found relationships between the absolute size of primate ranges in Africa and their habitat and dietary breadth, again with primates that had large ranges having greater dietary and habitat breadths.

Overall, these relationships among dietary breadth, seasonality in diet, primate distribution, and habitat breadth caution against the conclusion that dietary breadth or dietary diversity is the main or only cause of greater microwear variation in the sample of African monkeys examined (Chapter 2). Here I examine the potential effects of season, geographic distribution, and habitat differences on microwear variation in a previously studied sample of African Cercopithecidae (Chapter 2). The goal is to identify if the greater variation in microwear variables in species with more diverse diets is an outcome of sampling more seasons, more sites, and more widely distributed sites in these species, or if the variation seen reflects the true dietary variability of each species.

Materials & Methods

Species and Specimens

Casts of five species of African Old World monkeys (Cercopithecidae) that exhibited varying degrees of dietary breadth, seasonality, and distribution across Africa were used in this study. The species examined included three cercopithecines (*Chlorocebus aethiops*, *Cercopithecus mitis,* and *Papio anubis*) and two colobines (*Colobus guereza* and *Procolobus rufomitratus*). These species were selected based on the dietary breadth exhibited, the number and quality of field studies examining feeding ecology in these species, and the available museum specimens. Small sample sizes, lack of collection information on specimens, and/or lack of detailed seasonal dietary studies excluded three species used in the original analyses (*Cercocebus torquatus, Cercopithecus neglectus*, and *Theropithecus gelada*).

The sample used for this study consisted of 262 specimens, mostly wild shot and with associated locations and dates of collection. A summary of sites and seasons for each species is given in Table 3.1. A full list of specimens used in this study with associated localities is available in Appendix A. A small number of *P. anubis* specimens were collected from cave sites; since the season of death was unknown for these specimens, they were not included in analyses of season but were included in analyses of geography.

Dental Microwear Textures

All original specimens were cleaned with alcohol-soaked cotton swabs and vinyl impressions were made of all usable upper and lower first and second molars using President's Jet Regular Body Dental Impression Material (Coltene-Whaledent). Casts were made using Epotek 301 epoxy resin and hardener (Epoxy Technologies). Following previous studies (Ungar et al., 2003; Scott et al., 2006; Scott et al., 2012), casts were scanned on Phase II occlusal facets (9, x, or 10n; Kay, 1977); lower second molars were preferentially selected for analysis, but when they did not yield good surfaces first molars or upper second molars were also examined. Scans were collected using a 100x objective on a Sensofar Plμ white-light scanning confocal profiler (Solarius, Sunnyvale, CA) housed at the University of Arkansas. The resulting point clouds had a lateral sampling interval of 0.18 μm and a vertical resolution of 0.005 μm, and four adjoining fields were collected for a total area of 276 μm x 204 μm. Scans were leveled using Solarmap Universal software, and artifacts, such as dust particles, were excluded by thresholding and erase operators.

Dental microwear texture parameters were calculated through Toothfrax (Surfract), a scale-sensitive fractal analysis program. Four variables for each specimen were calculated: area-scale fractal complexity (*Asfc*), anisotropy (*epLsar*), and heterogeneity of *Asfc* at the 3x3 (*HAsfc9*) and 9x9 (*HAsfc81*) scales. These variables have been linked to different dietary parameters (e.g. Scott et al., 2006). Complexity measures changes in relative area with scale and has been shown to be greater on molars of primates that eat more hard, brittle foods such as fruit and seeds, while anisotropy measures the directionality of surface roughness, and has been shown to be greater on molars of primates that eat tough foods such as grass and leaves (Scott et al., 2005, 2006, 2012). Heterogeneity measures the similarity of textures across the tooth's surface and should be greater in primates that have greater variation in diet, particularly greater variation in consumption of foods that create complexity (Scott et al., 2006, 2012). However, there is some evidence that high frequencies of fruit consumption are correlated with low heterogeneity (Calandra et al., 2012).

Seasonal Dietary Expectations

To test whether microwear variables matched what would be predicted based on seasonal dietary differences, I compiled information on monthly consumption of food categories at as many sites as possible for each species, collected from publications of field studies. Many seasonal consumption frequencies were not listed in the texts but were found in graphs published in the texts; in these cases, I used the WebPlotDigitizer application (Version 3.3; Rohatgi, 2014) to extract data estimates of consumption frequencies from two-dimensional frequency plots and bar graphs. Although there is

great variation in dietary frequencies, some differences may not be statistically significant and thus would not be expected to cause detectable differences in microwear between seasons. Therefore, I used dietary frequencies to test for differences in diet between or among seasons; seasons were categorized as dry or rainy based on rainfall records from the publications or nearby weather stations, but sometimes I also broke the rainy season into early rainy (first half) or late rainy (second half), since some sites had marked differences in phenology within the rainy season and/or few months of dry season which were swamped by the more numerous rainy season months. Each month was categorized into one or two of these seasons and had dietary variables associated with them. Dietary variables that were examined were frequencies of food category consumption and dietary diversity. The food categories used were total foliage (all leaf material as well as grasses, herbs, and forbs), seeds (when provided), fruits, total fruit (fruits plus seeds and seed pods), and subterranean items (for *P. anubis*). Dietary diversity was calculated for each month using Shannon's Diversity Index *H:*

$H = -(\sum p_i * \ln p_i)$ where p_i=frequency of food category consumption for each *i* category).

The frequencies used, the sources of the frequencies, and the associated indices are available in Appendix C. Based on the compilation of data and statistical analyses, I made predictions for what I would expect in the microwear sample based on the geographic location and distribution of seasons sampled. Each species is discussed separately in the results section below.

Geographic Location and Habitat

The sites where museum specimens were collected were categorized into four locations, eastern, western, central, and southern, according to the general area of Africa from which they came. These groups generally correspond to the broader biogeographic regions that have been used to characterize Africa (e.g. Linder et al., 2012). Differences in climate, vegetation, distribution of habitats, and soil types occur among regions, and these differences may lead to intraspecific differences in microwear textures among the individuals in the sample. Differences in microwear textures may exist among sites as well, since individual sites may differ in these factors. By testing for differences among geographic locations, at both a broad scale and the scale of the site, we can identify if and how much the intraspecific variation in microwear is affected by geography. Differences in the geographic distribution of the species led to differences in how widespread the sites were from which the specimens came; species with small geographic distributions (i.e. *Pr. rufomitratus*) had sites from only a small geographic area (< 250,000 km^2), while species with large distributions, such as *Ch. aethiops*, had sites from a large geographic area (> 1,000,000 km^2).

Unfortunately, most museum specimens do not have habitat information associated with the site of collection. However, museum specimens are the most easily accessible specimens for a study such as this one that uses a number of different species from many sites. Thus, for this study, geographic location is an important proxy for environmental variables such as climate and soil type that contribute to habitat formation. Although habitat types can be the same across different geographic locations, factors such as seasonality that affect these habitats differently due to location would likely lead

to differences in microwear if in fact habitat is a large contributor to microwear variation in this sample. Thus, if there are few differences in microwear found among different geographic locations, it is likely that both geographic location and habitat do not play a large role in the intraspecific microwear differences in this sample.

A final consideration is that the link between diet observed in wild population and the diet consumed by the museum specimens before they died may not be strong. Diet can differ from year to year in the same population (Hemingway and Bynum, 2005), so field studies that record the annual diet of a population may differ from the actual diet consumed by that population. Additionally, the same plant parts can have very different fracture properties depending on the species of plant or time of year they are consumed (Teaford et al., 2006). This fact indicates a potentially large variation in fracture properties within dietary categories. These facts need to be considered as potential reasons for a lack of resolution between microwear differences and seasonal and geographic variation in the samples. These issues are potentially unresolvable, however, when using a museum sample.

Statistical Analyses

Statistical analyses were conducted on the dietary data compiled from field studies as well as the microwear data collected from the cercopithecid sample. For tests of dietary data, two-tailed *t*-tests, Welch's *t*-tests, and ANOVAs were used. For microwear data, comparisons between two regions or two seasons included one- or two-tailed *t*-tests, Welch's *t*-tests, or Mann-Whitney *U* tests based on the distribution of the data. For comparisons among three seasons, ANOVA or Kruskal-Wallis tests were used,

followed by post-hoc Tukey's Honestly Significant Difference (HSD) and Fisher's Least Significant Difference (LSD) tests to control for Type 1 and 2 errors (Cook and Farewell, 1996). For comparisons among three or more regions and for comparisons among sites, MANOVA including the four variables was used first to control for experiment-wise error (Ungar et al., 2010). Following a significant MANOVA, individual ANOVAs and Tukey's HSD and Fisher's LSD tests were used. Levene's Test for homogeneity of variance was used to test for differences in variance; for comparisons among three or more groups, MANOVA and/or ANOVA on residuals was used in order for use of post-hoc tests. All analyses were conducted in RStudio (version 0.98.978).

Results

Seasonal Dietary Differences

***Chlorocebus aethiops*.** The genus *Chlorocebus* has one of the broadest distributions of monkeys in Africa. It lives in habitats ranging from dry bushland to forest, and can be encountered generally throughout sub-Saharan Africa barring desert and deep forest, although it is most often found in riparian forests and the neighboring habitats (Groves and Kingdon, 2013). The sample used here consists of specimens covering central, eastern, and southern Africa and across both dry and wet seasons (Table 3.1).

Perhaps related to the success of the species in many habitats and climates, the diet of *Ch. aethiops* is varied and adaptable. Although much work has been conducted on vervet behavioral ecology (e.g. Cheney and Seyfarth, 1981; Pruetz and Isbell, 2000), many studies do not report food part consumption on a seasonal or monthly basis. Kavanagh (1978) recorded seasonal dietary variation at two savanna sites in Cameroon;

however, no differences in seasonal consumption of resources were apparent. At Mount Assirik, Harrison (1982,1983) recorded that *Ch. aethiops* averaged more fruit consumption during the wet season but more seed consumption during the dry season; he also recorded a greater variation in fruit and total fruit (fruit and seed) consumption during the dry season. Although consumption of leaf material was low overall, there was greater average consumption during the rainy season as well as a greater variance in consumption. Overall, I also found that the population showed a greater dietary breadth, as measured by *H*, during the dry season. However, *t*-tests and Levene's Tests showed no significant differences in consumption in this sample between dry and rainy seasons. Wrangham and Waterman (1981) showed that *Ch. aethiops* in Amboseli relied heavily on two species of *Acacia*; in a single dry season, over 75% of its diet came from these two species. Parts used included a high frequency of gums (no apparent difference between seasons), young leaves (consumed more in the dry season), flowers (consumed more in the dry season), and seeds (consumed only in the dry season). Ripe fruit from other species and insects appeared to be consumed more in the wet season; however, the data available from this study were not suitable for use in statistical tests. Lee and Hauser (1998), working at Amboseli as well, confirmed the high proportion of *Acacia* consumption. However, they also found significant differences in monthly part consumption between different years of their study and among populations living in different habitats at the site. Their work shows a link between the availability of foods, due to seasonal production cycles and rainfall, and the frequency at which the foods were consumed.

Overall, no clear pattern of seasonal dietary change is apparent in *Ch. aethiops*. Populations at Mount Assirik showed greater variation in fruit consumption and dietary diversity in the dry season, and Amboseli appears to show greater seed consumption and variation in seed consumption during the dry season. Thus, microwear predictions for the sample were 1) no significant difference in mean complexity, anisotropy, or heterogeneity between dry and rainy seasons and 2) greater variance in complexity and heterogeneity in the dry season.

As predicted, *Ch. aethiops* showed no difference in means of any microwear variable between dry and rainy seasons, but did show greater variance in complexity during the dry season (Levene's Test: F (1,25) = 4.89, $p < 0.05$; Figure 3.1). In contrast to predictions, the microwear did not show greater variance in either *HAsfc9* or *HAsfc81* in the dry season.

***Colobus guereza*.** The guereza has been one of the most well-studied African colobine species; it is distributed throughout the central and eastern African forests, inhabiting lowland and montane moist forest, swamp forest, dry forest, and gallery forest (Kingdon et al., 2008; Fashing and Oates, 2013). Although, like most colobines, *C. guereza* subsists primarily on leaves, it also incorporates fruit, particularly fleshy fruit, into their diets, though the amount they do so varies by site and season (Fashing and Oates, 2013). Extensive field studies of *C. guereza* have shown a range of folivory, with Kibale, Uganda showing the highest amounts of folivory (Oates, 1974, 1977). Oates (1974, 1977) also found greater dietary diversity during the dry season at Kanyawara, Kibale Forest, Uganda. At Kakamega Forest, Uganda, Fashing (1999) recorded greater

fruit and total fruit consumption during the rainy season and greater leaf consumption during the dry season. My tests confirmed that these were significant differences (fruit: t (10) = 2.62, $p < 0.05$; total fruit: t (10) = 2.61, $p < 0.05$; leaves: t (10) = 2.99, $p < 0.05$). Bocian (1997) recorded data on seasonal consumption of resources in Ituri Forest, Democratic Republic of Congo (DRC). When examined by rainy versus dry season, no differences were observed; however, when the rainy season was broken down into an earlier and later section, there were differences among the seasons in consumption of leaves, seeds, and total fruit, with fewer leaves and more seeds and total fruit consumed in the later rainy season (Kruskal-Wallis Tests: leaves: $X^2 = 7.60$; seeds: $X^2 = 8.48$; total fruit: $X^2 = 7.00$; df=2, $p < 0.05$ for all). Based on data from Plumptre (2006) at Budongo Forest, Uganda, I found greater consumption of fruit and total fruit in the rainy season (fruit [Welch's t-test]: t (12.93) = 3.95, $p < 0.01$; total fruit [t-test]: t (13) = 2.87, $p < 0.05$), greater variance in fruit consumption in the rainy season (Levene's Test: F (1,13) = 4.76, $p < 0.05$), and greater variance in dietary diversity in the dry season (Levene's Test: F (1,13) = 6.64, $p < 0.05$). When broken down into early rainy and later rainy seasons, Tukey's HSD showed differences between early rainy and dry seasons for fruit consumption and late rainy and dry seasons for total fruit consumption. Overall, these studies suggested microwear differences in complexity, anisotropy, and heterogeneity between rainy and dry seasons, and particularly between the late rainy season and the dry season. I predicted that 1) complexity should be greater during the rainy season, particularly the later rainy season, and should be more variant in the dry season, 2) anisotropy should be greater during the dry season, and 3) heterogeneity should be greater and more variant in the dry season.

C. guereza did not show any differences in microwear when rainy season was considered as one season, although results were in the direction predicted for all variables and complexity did approach significance (One-tailed *t*-test: t (42) = 1.41, $0.05 < p < 0.1$). When divided into early and late rainy seasons, however, there were differences among the groups in complexity (ANOVA: F (2,41) = 4.12, $p < 0.05$; Fig. 3.2) and *HAsfc9* (ANOVA: F (2,41) = 3.40, $p < 0.05$; Fig. 3.3). Tukey's HSD and Fisher's LSD tests showed the dry season to have lower complexity than the late rainy season, while the early rainy season was not different from either of these groups (Fig. 3.2). Tukey's HSD showed no differences greater than the alpha level of 0.05 for *HAsfc9*, but did show that the late rainy season showed lower *HAsfc9* than both the early rainy and dry seasons at $0.05 < p < 0.1$; Fisher's LSD test also showed that the late rainy season showed lower *HAsfc9* than the other two seasons (Fig. 3.3). There was also greater variance in complexity in the late rainy season than in the dry season (Levene's Test: F (2,41) = 3.51, $p < 0.05$; Tukey's HSD, Fisher's LSD; Fig. 3.2), contrary to predictions; however, neither heterogeneity variable differed in variance among the seasons.

***Cercopithecus mitis*.** Similar to *Ch. aethiops*, *C. mitis* has a large distribution across Africa; however, it is restricted mainly to the eastern coast, from southern Ethiopia to South Africa, although a population exists in western Angola. It is mainly found in forest habitats, although its tolerance of habitats of poor quality has been cited as a factor in its widespread distribution (Lawes, 1990; Thomas, 1991). It is an omnivore that mainly feeds on fruit, but also includes a sizable portion of leaves and insects in its diet. Data from a population in Malawi (Beeson, 1989) show greater fruit consumption during the

rainy season and greater *H* values during the dry season, although these differences were not significant; the population also showed greater variation in *H* during the rainy season (Levene's Test: $F(1,9) = 5.33$, $p < 0.05$). Using data from Nyungwe Forest Reserve in Rwanda (Kaplin et al., 1998), I found greater fruit consumption in the dry season (*t* test: $t(6)=2.92$, $p < 0.05$), greater leaf consumption in the rainy season (*t* test: $t(6)= 2.69$, $p < 0.05$), and greater *H* values in the rainy season (Welch's *t* test: $t(4.22) = 7.48$, $p < 0.001$); I also found greater variance in *H* in the rainy season (Levene's Test: $F(1,6) = 6.67$, $p < 0.05$). At Kakamega Forest in Kenya, Cords (1986) found a bimodal distribution of consumption frequency, with fruit consumption highest in the middle of the rainy and dry seasons. There was also no difference in *H* values between the different seasons. Data from Tesfaye et al. (2013) show that *C. mitis* in Jibat Forest, Ethiopia ate more total fruit during the dry season ($t(8) = 2.59$, $p < 0.05$) and more leaf material during the rainy season ($t(8) = 6.31$, $p < 0.001$).

These results show no clear patterns in seasonal consumption of food categories for *C. mitis*; two studies show greater fruit consumption in the dry season, while two show greater fruit consumption in the rainy season. The most concordant results are greater consumption of leaf material during the rainy seasons, since two of these studies showed this significant result; there is no consensus on differences in fruit consumption, but there is a slightly more well-supported incidence of greater fruit consumption during dry seasons. With these results, predictions were 1) greater anisotropy during rainy season and 2) greater complexity during the dry season. However, overall the variation among sites suggests no clear predictions in *C. mitis*.

C. mitis did not show greater anisotropy during the rainy season; it also did not show greater complexity during the dry season. Thus, no seasonal differences in microwear textures were found in this sample.

Papio anubis. *Papio anubis* is also a widespread and generalized primate. It is the most widespread of the baboons, being found across the northern part of Sub-Saharan Africa, from southern Mauritania to Sudan and south to Tanzania and the DRC (Kingdon et al., 2008; Palombit, 2013). As with other species of *Papio*, *P. anubis* also eats a broad diet consisting of fruit, leaves, and animal matter. One interesting aspect of the diet is that some *Papio* species eat high frequencies of subterranean items, such as corms and roots (Daegling and Grine, 1999). At Laikipia Plateau, Kenya, Barton (1990) recorded a diverse diet across the year for *P. anubis* but focused on a limited number of food categories at any one time. At the end of the long rainy season (July-August), this population consumed high frequencies (~80%) of fruits and grass seeds; in September, over 80% of the diet was acacia flowers, while in March and December over 50% of the diet was foliage (leaves and grass blades). There was greater consumption of seeds (grass seeds and acacia seeds/pods) and leaves in the wet season, but I did not find these to be significant; I did however find greater variation in leaf consumption in the wet season (Levene's Test: $F\,(1,8) = 7.64$, $p < 0.05$). In Budongo Forest, Uganda, Okecha and Newton-Fisher (2006) found greater consumption of fruits in the wet season (Mann-Whitney U Test: $U = 22$, $p < 0.05$, in Okecha and Newton-Fisher, 2006) but no differences among other food categories.

These results do not point to clear dietary differences between seasons across different sites. However, since vegetation, particularly grass blades, was consumed at a greater frequency and was more variably consumed in the rainy season, I predicted that there would be greater mean and variance in anisotropy during the rainy season. Seeds and fruits were also consumed more during the rainy season, but underground items were consumed more during the dry season; these results suggest that complexity would not differ among seasons, since all of these food categoriess are associated with higher complexity. Based on the prediction of higher anisotropy during the rainy season and high complexity throughout, as well as the fact that dietary diversity is greater in the rainy season, I also predicted greater heterogeneity in the rainy season.

P. anubis results did not show any significant differences based on season; the differences in mean *HAsfc9* and *HAsfc81* were in the expected direction, with greater heterogeneity in the rainy season, but the results were not significant. Similarly, the mean and variance of anisotropy was greater in the rainy season, but again the results were not significant. Thus, no differences in microwear textures were seen based on season.

Procolobus rufomitratus. The red colobus supergroup (*Procolobus* genus) ranges across tropical Sub-Saharan Africa, although populations in West and East Africa are often isolated, which has probably led to the wide variation in morphology and pelage seen in the group (Kingdon, 2013). Disagreement over taxonomy has led to a wide array of taxonomic systems to categorize red colobus; however, they are primarily folivorous at all sites, although they consume high frequencies of fruits and flowers at some sites (Kingdon, 2013). Steel (2012) recorded three months of rainy season and four months of

dry season food consumption for *Pr. gordonorum* at Mwanihana and Magombera Forests in Uganda. There were no significant differences between the seasons in fruit or leaf consumption frequencies or in dietary breadth; however, there was great variation in consumption frequencies among months. In the Niger Delta, Werre (2000) found greater consumption of leaves by *Pr. pennantii* during the rainy season (t (10) = 2.82, $p < 0.05$); when broken down into early and later rainy season, no significant differences were found, but a pattern did emerge of greater dietary diversity in the dry season, decreasing to the late rainy season. In *Pr. rufomitratus*, Clutton-Brock (1975) found greater consumption of fruit during the late rainy season at Gombe, Tanzania, although I did not find significant differences in consumption frequencies or *H* among seasons. Decker (1989) noted great seasonal and yearly variation in plant consumption in *Pr. rufomitratus* at the Tana River Primate National Reserve in Kenya. Although frequency of consumption of different food parts was not available, Decker noted that *Pr. rufomitratus* consumed a broader diet, in terms of more species, during the dry season. Maisels et al. (1994) collected data at Salonga National Park, DRC; results indicated greater leaf consumption during the dry season and the early rainy season (ANOVA: F (2,9) = 19.15, $p < 0.001$, followed by Tukey's HSD), greater seed and total fruit consumption during the late rainy season (ANOVA: seed: F (2,9) = 6.61, $p < 0.05$; total fruit: F (2,9) = 21.33, $p < 0.001$, followed by Tukey's HSD), and greater dietary diversity during the late rainy season than the early rainy season (ANOVA: F (2,9) = 6.46, $p < 0.05$, followed by Tukey's HSD). Leaf consumption at Salonga was seasonally different from consumption in the Niger Delta (Werre, 2000), likely due to the fact that red colobus at Salonga subsisted mostly on seeds for four months, while red colobus in the Niger Delta subsisted

primarily on leaves for all but two months, at which time they primarily subsisted on flowers.

The sample of red colobus used in this study came exclusively from five sites in the DRC; although there are no long-term studies on populations from the exact area where the specimens were collected, they are most likely to resemble the population studied at Salonga, since they are both from the Congo Basin and are likely exposed to similar seasonal habitat effects. Additionally, all populations are considered members of the same species under one of the stricter taxonomies, that used by Groves and Kingdon (2013). Thus, predictions for this regionally-restricted species follow from Maisels et al. (1994): 1) lower anisotropy in the late rainy season, 2) greater complexity in the late rainy season, 3) greater heterogeneity in the late rainy season, and 4) greater variation in complexity and anisotropy in the late rainy season.

There were no differences in anisotropy among the seasons. There were significant differences among the seasons in complexity (ANOVA: F (2,71) = 7.35, $p <$ 0.01); the late rainy season was greater than the early rainy season, as predicted, but so was the dry season, and the late rainy and dry seasons were not different from each other (Tukey's HSD and Fisher's LSD; Fig. 3.4). There were also differences among the seasons in heterogeneity (ANOVA: *HAsfc9*: F (2,71) = 7.04, $p < 0.01$; *HAsfc81*: F (2,71) = 3.81, $p < 0.05$), but, contrary to predictions, Tukey's HSD and Fisher's LSD showed lower heterogeneity in the late rainy season than in the early rainy season (the dry season was not different from either rainy season; Fig. 3.5). Additionally, although complexity showed more variation in the late rainy season, it did not reach the alpha level for

significance (Levene's Test: F (2,71) = 2.54, $0.05 < p < 0.1$; Fig. 3.4); anisotropy also showed no differences in variation among the seasons.

Geographic Area

Chlorocebus aethiops. Since there were only two specimens of *Ch. aethiops* from West Africa in the sample, these were left out of the geographic analyses. *Ch. aethiops* showed no differences among central, eastern, and southern regions in means (MANOVA: Pillai's Trace = 0.42, F (2,22) = 1.31, $p > 0.1$) but approached significance in variances (MANOVA: Pillai's Trace = 0.57, F (2,22) = 1.99, $0.05 < p < 0.1$). Single ANOVAs showed differences in variance among the regions only in complexity (ANOVA: F (2,22) = 4.87, $p < 0.05$); both Tukey's HSD and Fisher's LSD showed that the central region showed lower variance in complexity than either the eastern or southern regions (Fig. 3.6). There were also no differences among localities in means (MANOVA: Pillai's Trace = 1.29, F (5,12) = 1.15, $p > 0.1$).

***Colobus guereza*.** There were differences between central and eastern regions in microwear means (MANOVA: Pillai's Trace = 0.27, F (1,42) = 3.56, $p < 0.05$); individual t-tests identified differences between the regions only in complexity (t (42) = 3.79, $p < 0.001$), with the central region showing greater complexity. However, the sample from central Africa is sampled mostly from the rainy season (early and late), while the sample from east Africa is mostly from the dry season; as *Co. guereza* also shows differences in complexity among the seasons, this result could be due to uneven sampling in season within each geographic area. No differences in variances were found

between the regions (MANOVA: Pillai's Trace = 0.15, F (1,42) = 1.78, $p > 0.1$). When analyzed by site, MANOVA showed marginal differences among localities (Pillai's Trace = 1.01, F(6,28) = 1.57, $0.05 < p < 0.1$). Individual ANOVAs showed only a difference in complexity among localities (F (6,28) = 4.66, $p < 0.01$), with specimens from Mount Kenya showing lower complexity than specimens from Molidi River and Mauda, and Molidi River also showing higher complexity than Kahe (Tukey's HSD). Fisher's LSD test showed four groups of localities that did not differ in complexity (Fig. 3.7).

Cercopithecus mitis. *Cercopithecus mitis* did not differ among central, eastern, and southern regions in means (MANOVA: Pillai's Trace = 0.17, F (2,69) = 1.57, $p > 0.1$), but it did in variances (MANOVA: Pillai's Trace = 0.25, F (2,69) = 2.41, $p < 0.05$). The only difference identified with individual Levene's Tests was a difference in variance in *HAsfc9* (Levene's Test: F (2,69) = 8.47, $p < 0.001$) Interestingly, even though the central region had by far the most specimens (n = 58), it had the lowest variance in *HAsfc9*, significantly lower than both the eastern and southern regions by both the Tukey's HSD and Fisher's LSD methods (Fig. 3.8). There were no differences in microwear among localities (MANOVA: Pillai's Trace = 0.58, F (8,59) = 1.24, $p > 0.1$).

Papio anubis. There were no differences among western, central, and eastern regions in means (MANOVA: Pillai's Trace = 0.25, F (2,42) = 1.43, $p > 0.1$). MANOVA identified differences among the regions in variances (MANOVA: Pillai's Trace = 0.39, F (2,42) = 2.41, $p < 0.05$), but no individual Levene's Tests were significant. No

differences in means among localities were found (MANOVA: Pillai's Trace = 0.96, F (8,35) =1.38, $p > 0.1$).

Procolobus rufomitratus. *Procolobus rufomitratus* specimens were only collected from the central region, so they were not tested for differences among regions. No differences among localities were found in means (MANOVA: Pillai's Trace = 0.19, F (4,67)=0.85, $p > 0.1$).

Discussion

The degree of seasonal dietary patterning differed among species. The cercopithecines *Ch. aethiops*, *C. mitis*, and *P. anubis* showed differences among field sites in how seasonality affected their diets, and therefore showed few seasonal dietary patterns that held across sites. In contrast, the colobines *Co. guereza* and *Pr. rufomitratus* showed a more consistent pattern of seasonal dietary responses across sites. No differences in means between seasons were found for the cercopithecines, while some differences in means were found among seasons for the colobines, although the differences were not as great as the dietary data would suggest. One consistent result was that variation in anisotropy was great in all samples, and no differences in means or variances in anisotropy were found among any groups; this result agrees with results from Chapter 2 that showed no differences among species in their variances in anisotropy. Only two species showed differences in variance between or among seasons: *Ch. aethiops* showed greater variance in complexity in the dry season and *Co. guereza*

showed greater variance in complexity in the late rainy season than in the dry season.

Overall, fewer differences in microwear means and variances were found between or among seasons for each species than would be expected given the significant differences found among seasons using dietary studies. Colobines differed the most in diet and microwear among seasons, indicating that season of collection of specimens would be more important for these species than for the cercopithecines when attempting to characterize the yearly diet in a microwear study. For cercopithecines, season of collection does not appear to contribute a large amount of variation, since the variation within seasons is so great. In terms of overall variation, these results suggest that the greater overall microwear variation in *Ch. aethiops*, *C. mitis*, and *P. anubis* (Chapter 2) is not due to more seasonal variation in diet. In contrast, *Co. guereza* and *Pr. rufomitratus*, which show less overall variation (Chapter 2), appear to be more affected by season, and therefore greater care should be placed in making sure microwear studies sample specimens across seasons when referencing annual diets.

Although seasonal differences in diet appear to contribute to microwear variation in some species, there were few distinctions in microwear among geographic areas, either among the broader African regions or among localities. Complexity was the only variable that differed in means among regions or sites, and only in *C. guereza* populations, but as stated earlier, this difference reflected that found among seasons. This result suggests that either 1) seasonal variation in *C. guereza* microwear was due to regional variation and unequal seasonal sampling of regions, or 2) regional variation in microwear was due to dietary variation and unequal regional sampling of seasons. When *C. guereza* was analyzed by locality, differences in microwear emerged among localities within the same

region; based on this fact, it is most likely that the seasonal differences in microwear are real, while the differences among regions are simply reflecting the fact that the sample from eastern Africa is almost exclusively from the dry season. If we accept this interpretation, no real distinctions in means were found among the regions.

There were also few distinctions among regions in variance. MANOVA only identified marginal differences for *Ch. aethiops*, with the central region showing lower variance in complexity. For *C. mitis*, the central region also showed lower variance in *HAsfc9* and *HAsfc81*. Given that greater variance in microwear is moderately related to greater variation in diet, particularly in complexity (Chapter 2), these results might suggest that the central region shows less variation in diet for *Ch. aethiops* and *C. mitis* than the eastern and southern regions; this interpretation corresponds with general ecological data that suggest greater dietary variation in more seasonal environments, such as those in eastern and southern, but not central, Africa (Brown, 1995; Cowlishaw and Hacker, 1997; Eeley and Foley, 1999; Harcourt et al., 2002; Vazquez and Stevens, 2004).

Although there are documented differences in diet among sites for all species that might lead to differences in microwear among the localities sampled here, the only differences in microwear identified among localities were in complexity for *Co. guereza*. It is possible that these differences are related to dietary or habitat differences among the individuals at these localities; in fact, *Co. guereza* does show variability in fruit consumption among sites, with high annual frequencies of fruit consumption (39%) at Kakamega Forest (Fashing, 1999) and low frequencies (5-15%) at Kanyawara and Kibale (Oates, 1977,1994; Wasserman and Chapman, 2003). However, the fact that complexity in *Co. guereza* is the only microwear variable that differs among localities for all species

suggests that intraspecific differences in microwear related to subtle differences in diet among sites are probably not a large contributor to intraspecific variation in this sample.

Overall, these results suggest that the variation in microwear seen at each locality is as great as that among localities; thus, geographic location introduces negligible variation in these species. For example, *P. anubis* appears to show differences among individual localities in anisotropy (Fig. 3.9), but overall, the range in anisotropy seen at other individual localities encompasses these differences. One aspect to note, however, is that sample sizes for each locality tended to be small ($n = 4$ for many), so it is possible that larger sample sizes from each locality would show differences in microwear among individual localities. Thus, this sample is not ideal for examining differences among individual localities, and these results are provisional for the conclusion that the number of individual localities introduces negligible variation in this sample.

Conclusion

The goal of this study was to identify whether differences among species in intraspecific variation in microwear can be explained by sampling of different seasons, habitats, and geograpy in species with broader diets; overall, these results suggest that although variation in microwear in a sample can be increased due to greater sampling of seasons and localities, there is generally more variation sampled within seasons and localities than among them. Colobines, which have narrower dietary breadths, also appear to differ more in mean complexity among seasons, but the cercopithecine species, with greater dietary breadths, differ more in microwear variances among regions, at least within this sample. Since the ultimate goal of microwear studies in extant species is to

better infer diet in fossil species, the results from this study suggest two main conclusions for interpreting variation in fossil samples. First, in terms of microwear means, interpretations of fossil species with narrow diets are more likely to be affected by small sample sizes, since small sample sizes are more likely to sample season unevenly. Second, in terms of variance in microwear, species with broader diets are more likely to be affected by geographic sampling area; a single site is less likely to show a range of microwear values for a species with a broad diet that accurately reflects the range of diet for that species than including multiple sites. Overall, however, season and geographic location appear to contribute negligible variation in this sample of Cercopithecidae in contrast to the overall intraspecific variation in microwear. Given this conclusion, these results also validate the use of the methods described in Chapter 2 to interpret dietary diversity in fossil cercopithecids and potentially hominins.

References

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press, 608pp.

Barton RA. 1990. Foraging Strategies, Diet And Competition In Olive Baboons. PhD Dissertation, University of St. Andrews.

Beeson M. 1989. Seasonal dietary stress in a forest monkey (*Cercopithecus mitis*). Oecologia 78:565-570.

Bocian CM. 1997. Niche separation of black-and-white colobus monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri Forest. PhD Dissertation, City University of New York.

Brown JH. 1984. On the relationship between abundance and distribution of species. Am Nat 124:255-279.

Brown JH. 1995. Macroecology. Chicago: University of Chicago Press, 284 pp.

Brown JH, Mehlman DW, Stevens GC. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

Butynski TM, Kingdon J, Kalina J, eds. 2013. Mammals of Africa: Volume 2, Primates. London: Bloomsbury, 560 pp.

Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. J Hum Evol 63:85-98.

Chapman CA, Chapman LJ. 1990. Dietary variability in primate populations. Primates 31:121-128.

Cheney DL, Seyfarth RM. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, *76*(1), 25-60.

Clutton-Brock TH. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. Folia Primatol 23:165-207.

Cook RJ, Farewell VT. 1996. Multiplicity considerations in the design and analysis of clinical trials. J R Statistic Soc A, 159:93-110.

Cords M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. J Anim Ecol 55:811-827.

Cowlishaw G, Hacker JE. 1997. Distribution, diversity, and latitude in African primates. Am Nat 150:505–512.

Daegling DJ, Grine FE. 1999. Occlusal microwear in *Papio ursinus*: The effects of terrestrial foraging on dental enamel. Primates 40:559-572.

Decker BS. 1989. Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus *(Colobus badius rufomitratus*). PhD Dissertation, Emory University.

Eeley HAC, Foley RA. 1999. Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodivers Conserv 8:1033–1056.

Eeley HAC, Lawes MJ. 1999. Large scale patterns of species richness and species range size in anthropoid primates. In: Fleagle JG, Janson CH, Reed KE, eds. Primate Communities. Cambridge: Cambridge University Press, pp. 191-219.

Elton S. 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. J R Anthropol Inst 12:19-38.

Fashing PJ. 1999. The Behavioral Ecology of an African Colobine Monkey: Diet, Range Use, and Patterns of Intergroup Aggression in Eastern Black and White Colobus Monkeys *(Colobus guereza)*. PhD Dissertation, Columbia University.

Fashing PJ, Oates JF. 2013. *Colobus guereza*. In: Kingdon J, Happold D, Butynski T, eds. Mammals of Africa. London: Bloomsbury Publishing, pp. 111-119.

Fleagle JG. 2013. Primate Adaptation and Evolution: 3rd Edition. San Diego: Academic Press, 464 pp.

Foley RA. 1993. African terrestrial primates: the comparative evolutionary biology of *Theropithecus* and the Hominidae. In: Jablonski N, ed. Theropithecus: The Rise and Fall of a Primate Genus. Cambridge: Cambridge Univeristy Press, pp. 245-270.

Galbany J, Estebaranz F, Martínez LM, Pérez-Pérez A. 2009. Buccal dental microwear variability in extant African Hominoidea primates: taxonomy versus ecology. Primates 50:221-230.

Gaston KJ, Blackburn TM. 2000. Pattern and process in macroecology. Oxford: Blackwell Science, 377 pp.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. J Hum Evol 15:783-822.

Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am J Phys Anthropol 148:285-317.

Groves CP, Kingdon J. 2013. Genus *Chlorocebus*: Savanna Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 264-266.

Grubb P, Struhsacker TT, Siex KS. 2013. Subgenus *Piliocolobus*: Red Colobus Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 125-128.

Harcourt AH. 2000. Latitude and latitudinal extent: a global analysis of Rapoport effect in a tropical mammalian taxon: Primates. J Biogeog 27:1169-1182.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization, and extinction in primates. J Biogeogr 29:445-456.

Harrison MJ. 1982. The behavioural ecology of green monkeys (*Cercopithecus sabaeus*) at Mt. Assirik, Senegal. PhD Dissertation, University of Stirling.

Harrison, M. J. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Anim Behav 31:969-977.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 57-103.

Kingdon J, Butynski TM, De Jong Y. 2008. *Papio anubis*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 December 2014.

Kingdon J, Struhsaker T, Oates JF, Hart J, Groves CP. 2008. *Colobus guereza*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 December 2014.

Jaffe KE, Isbell LA. 2011. The guenons: polyspecific associations in socioecological perspective. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective. Oxford: Oxford University Press, pp. 277-300.

Jolly CJ. 2009. Fifty years of looking at human evolution: backward, forward, and sideways. Curr Anthropol 50:187-199.

Kaplin BA, Munyaligoga V, Moermond TC. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). Biotropica 30:56-71.

Kavanagh, M. 1978. The diet and feeding behaviour of Cercopithecus aethiops tantalus. Folia Primatol 30:30-63.

Kay RF. 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.

Klein RG. 1999. The Human Career: Human Biological and Cultural Origins. Chicago: University of Chicago Press, 840 pp.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee versus cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar P, ed. Evolution of Human Diet: The Known, the Unknown, and the Unknowable, University of Oxford Press, pp. 324-343.

Lambert JE. 2009. Primate fallback strategies as adaptive phenotypic plasticity: scale, process, and pattern. Am J Phys Anthropol 140:759-766.

Lawes MJ. 1990. The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. J Biogeogr 17:669-680.

Lee PC, Hauser MD. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. J Anim Ecol 67:347-358.

Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldså J, Rahbek C. 2012. The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. J Biogeogr 39:1189-1205.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd edition. Sunderland, Mass: Sinauer Associates, Inc. 841 pp.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. Int J Primatol 15:681-701.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542

Oates JF. 1974. The Ecology and Behaviour of the Black and White Colobus Monkey (*Colobus guereza* Rueppell) in East Africa. PhD Dissertation, University of London.

Oates JF. 1977. The social life of a black-and-white colobus monkey, *Colobus guereza.* Zeitschrift für Tierpsychologie 45:1-60.

Okecha AA, Newton-Fisher NE. 2006. The diet of olive baboons (*Papio anubis*) in the Budongo Forest Reserve, Uganda. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, eds. Primates of Western Uganda. New York: Springer, pp. 61-73.

Palombit, RA. 2013. *Papio anubis*. In: Kingdon J, Happold D, Butynski T, eds. Mammals of Africa. London: Bloomsbury Publishing, pp. 233-239.

Plumptre A. 2006. The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda: Effects of logging on primate diets. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, eds. Primates of Western Uganda. New York: Springer, pp. 345-371.

Potts R. 1998. Variability selection in hominid evolution. Evol Anthropol 7:81-96.

Pruetz JD, Isbell LA. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. Behav Ecol Sociobiol 49:38-47.

Reed KE, Fish JL. 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 489-518.

Rohatgi A. 2014. WebPlotDigitizer, Version 3.3. <http://arohatgi.info/WebPlotDigitizer>.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436:693-695.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51:339-349.
Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D, Ehleringer J. 2003. Nitrogen isotopes in mammalian herbivores: hair δ15N values from a controlled feeding study. Int J Osteoarchaeol 13:80-87.

Sponheimer M, Loudon JE, Codron D, Howells ME, Pruetz JD, Codron J, de Ruiter DJ, Lee-Thorp JA. 2006. Do "savanna" chimpanzees consume C_4 resources? J Hum Evol 51:128-133.

Steel R. 2012. The Effects of Habitat Parameters on the Behavior, Ecology, and Conservation of the Udzungwa Red Colobus Monkey (*Procolobus gordonorum*). PhD Dissertation, Duke University.

Swedell L. 2011. African papionins: diversity of social organization and ecological flexibility. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective, pp. 241-277.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Glander KE. 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk M, Rosenberger A, Garber P, eds. Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 433-449.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401.

Teaford MF, Walker AC. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am J Phys Anthropol 64:191-200.

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 129: 99-104.

Tesfaye D, Fashing PJ, Bekele A, Mekonnen A, Atickem A. 2013. Ecological flexibility in Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest, Ethiopia: a comparison of habitat use, ranging behavior, and diet in intact and fragmented forest. Int J Primatol 34:615-640.

Thomas SC. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. Biotropica 23:68-83

Ungar PS, Brown CA, Bergstrom TS, Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning Microscopy 25:185-193.

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3:1-6.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis.* Phil Trans R Soc B 365:3345-3354.

Vazquez D, Stevens RD. 2004. The latitudinal gradient in niche breadth: concepts and evidence. Am Nat164:E1-E19.

Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. J Anim Ecol 72:650-659.

Werre JLR. 2000. Ecology and behavior of the Niger Delta red colobus (*Procolobus badius epieni*). PhD Dissertation, City University of New York.

Withnell CB, Ungar PS. 2014. A preliminary analysis of dental microwear as a proxy for diet and habitat in shrews. Mammalia 78:409-415.

Wrangham RW, Waterman PG. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. J Anim Ecol 50:715-731.

Table 3.1
Summary of Cercopithecid Sample: Region, Season, and Localities

Species	***n***	**Geographic Region**[a]				**Season**[b]		**Localities**[c]
		E	C	S	W	D	R (LR)	
Ch. aethiops	27	9	8	8	2	16	9	5
Co. guereza	45	24	21	0	0	23	22 (12)	7
C. mitis	71	10	57	4	0	33	38	7
P. anubis	45	14	20	0	11	8	33	8
Pr. rufomitratus	74	0	74	0	0	20	54 (21)	5

[a] For Geographic Region, E = East, C = Central, S = South, W = West.
[b] Season refers to number of specimens coming from dry (D) and rainy (R) season; for species where season was broken down into early and late rainy season, the number of specimens from late rainy season (LR) is given in parantheses.
[c] Localities refers to the number of localities with $n > 3$ specimens.

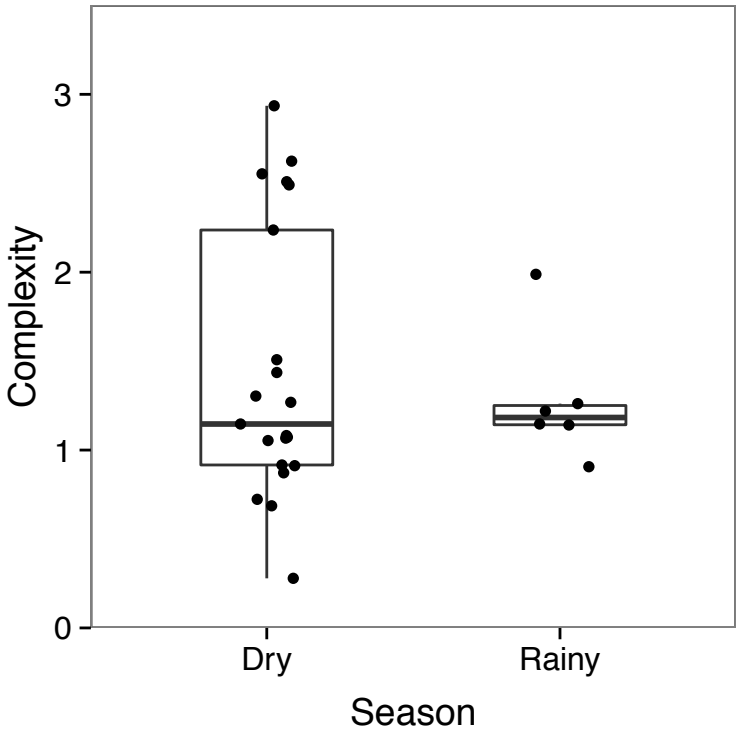

Figure 3.1. Box plot of complexity by season for *Ch. aethiops.* Box plot and individual distribution points of complexity by season for *Chlorocebus aethiops*. The dry season shows greater variance in complexity than the rainy season (Levene's Test: F (1,25) = 4.89, $p < 0.05$).

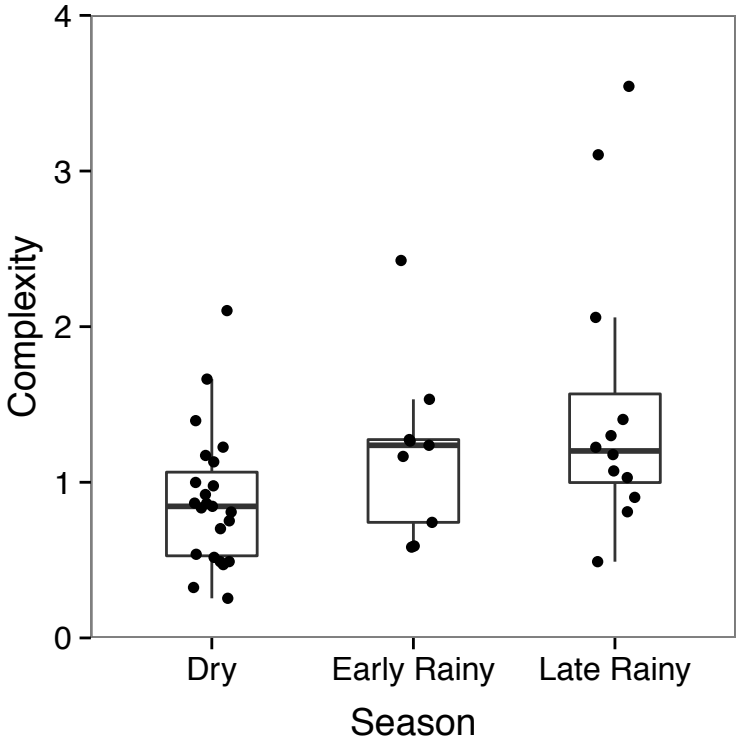

Figure 3.2. Box plot of complexity by season for *Co. guereza*. The dry season shows lower complexity than the late rainy season (ANOVA: F (2,41) = 4.12, $p < 0.05$; Tukey's HSD) as well as lower variance in complexity than the late rainy season (Levene's Test: F (2,41) = 3.51, $p < 0.05$; Tukey's HSD).

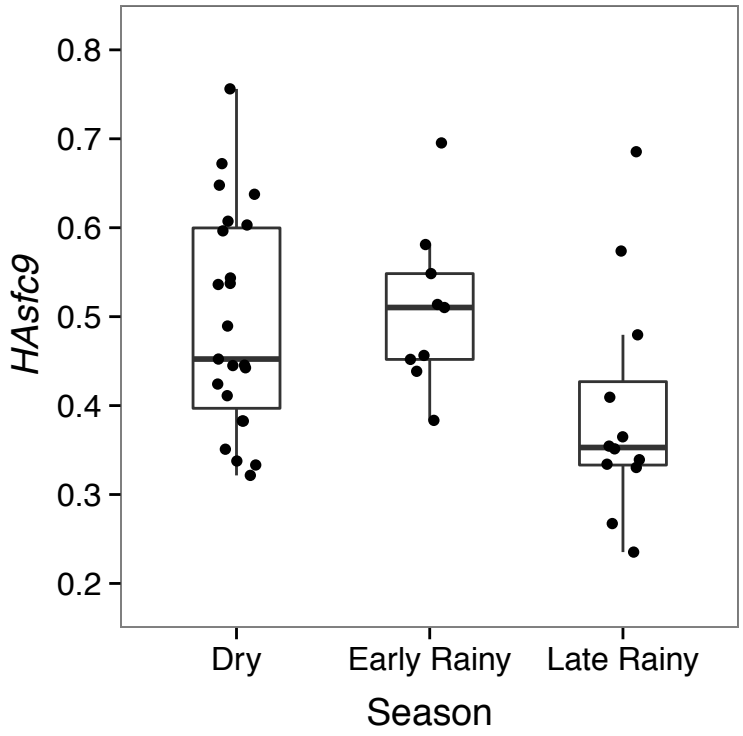

Figure 3.3. Box plot of heterogeneity at the 3x3 scale (*HAsfc9*) by season for *Co. guereza*. The dry season shows greater *HAsfc9* than the late rainy season (ANOVA: $F_{(2,41)} = 3.40$, $p < 0.05$; Tukey's HSD), but early rainy season does not differ from either dry or late rainy seasons.

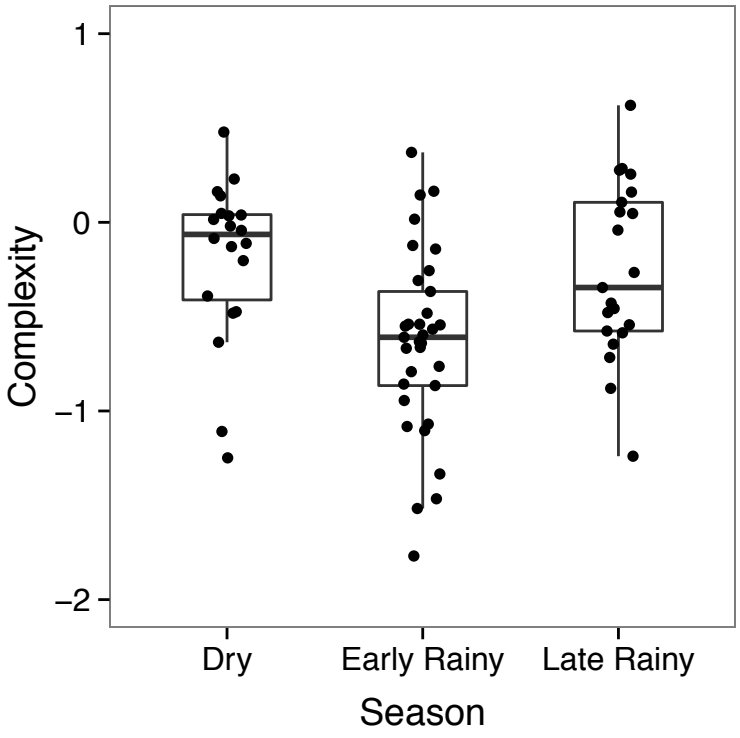

Figure 3.4. Box plot of complexity by season for *Pr. rufomitratus*. Complexity (*Asfc*) is natural-log (ln) transformed. Early rainy season shows lower complexity than dry season and late rainy season (ANOVA: F (2,71) = 7.35, $p < 0.01$; Tukey's HSD).

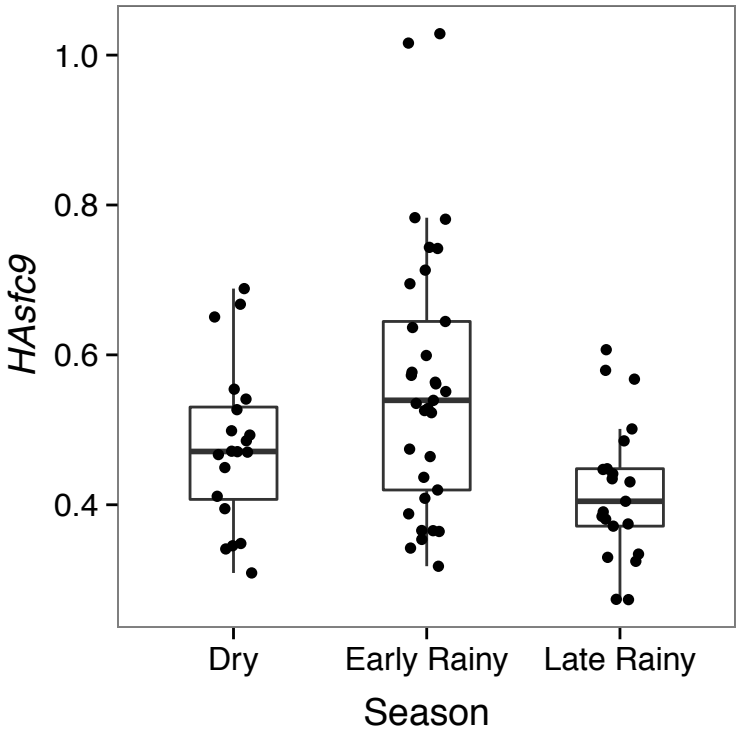

Figure 3.5. Box plot of heterogeneity at the 3x3 scale (*HAsfc9*) by season for *Pr. rufomitratus*. The early rainy season shows greater *HAsfc9* than the late rainy season (ANOVA: *HAsfc9*: F (2,71) = 7.04, $p < 0.01$; Tukey's HSD).

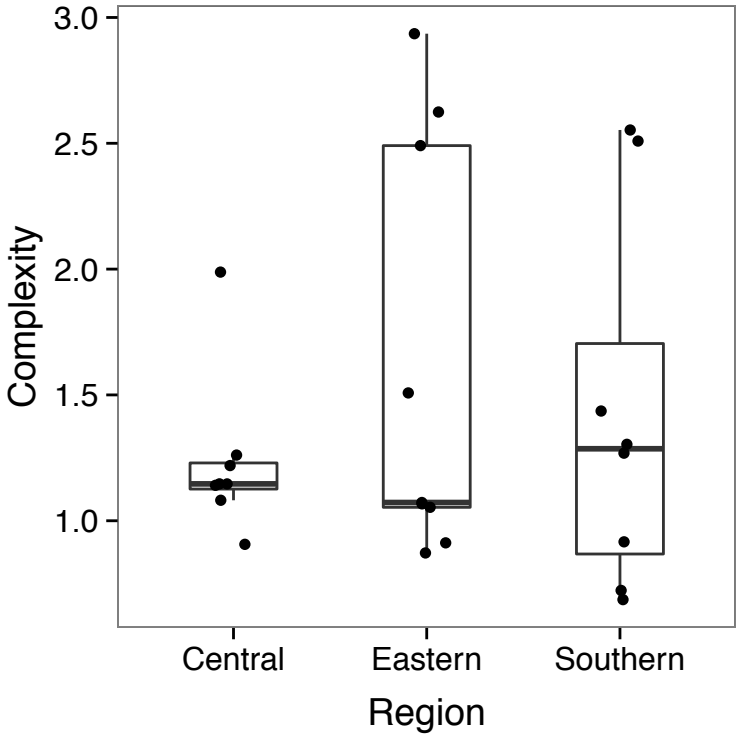

Figure 3.6. Box plot of complexity by geographic region for *Ch. aethiops*. The central region shows lower variance than the eastern or southern regions (Levene's Test: F (2,22) = 4.87, $p < 0.05$; Tukey's HSD).

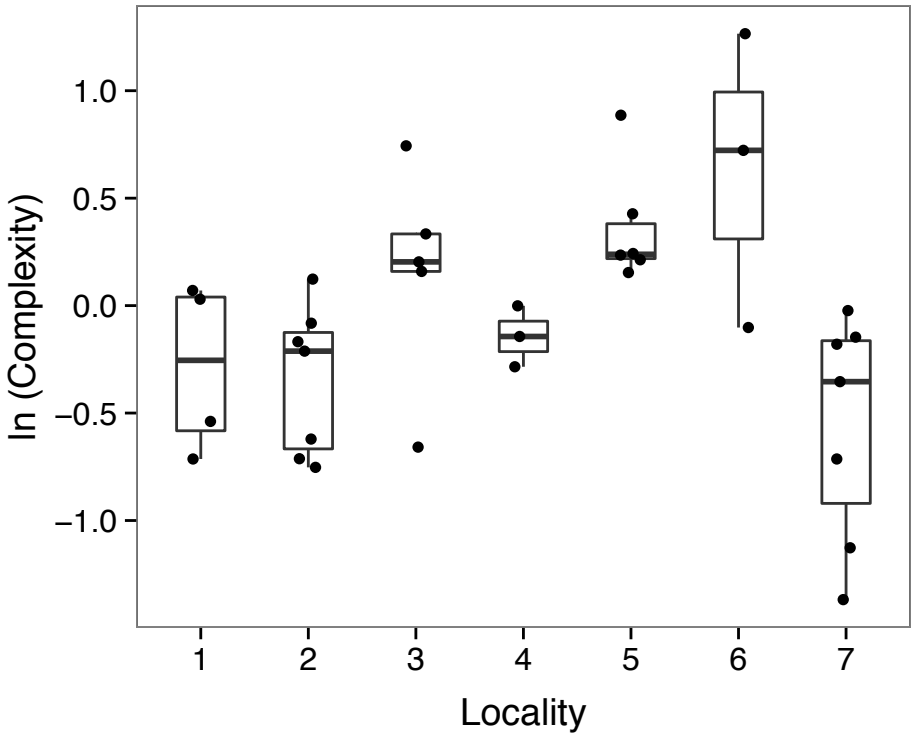

Figure 3.7. Box plot of complexity by locality for *Co. guereza.* Complexity is ln-transformed; localities are from central and eastern Africa (1 = Gangala no Bodio, 2 = Kahe, 3 = Kisumu, 4 = Marindas Forest Reserve, 5 = Mauda, 6 = Molidi River, 7 = Mount Kenya; see Appendix A for detailed locality information). Localities differed in complexity (ANOVA: F (6, 28) = 4.66, $p < 0.01$); Molidi River (6) had higher complexity than Kahe (2) and Mount Kenya (7), and Mauda (5) also had higher complexity than Mount Kenya (7; Tukey's HSD).

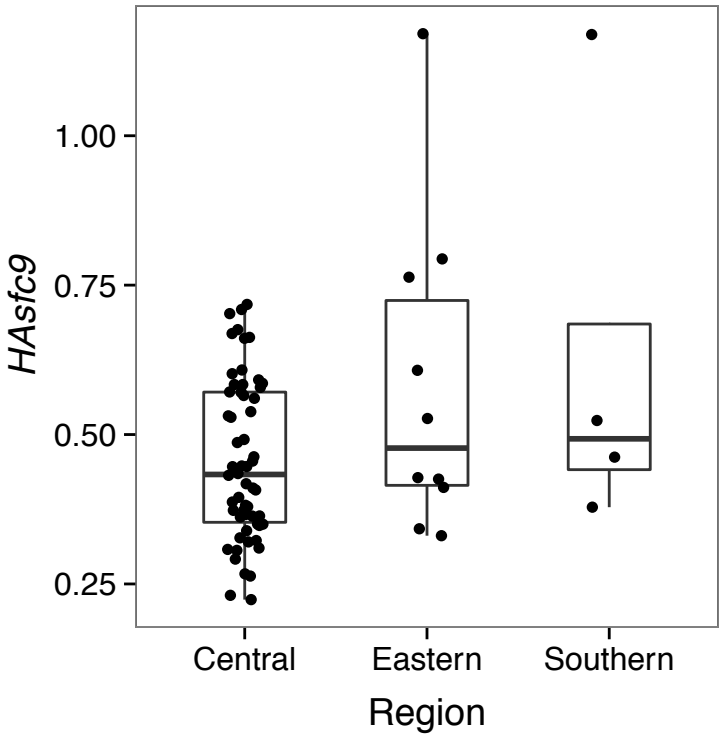

Figure 3.8. Box plot of heterogeneity at the 3x3 scale (*HAsfc9*) by geographic region for *C. mitis*. The central region shows lower variance in *HAsfc9* than the eastern and southern areas (Levene's Test: F (2,69) = 8.47, $p < 0.001$; Tukey's HSD).

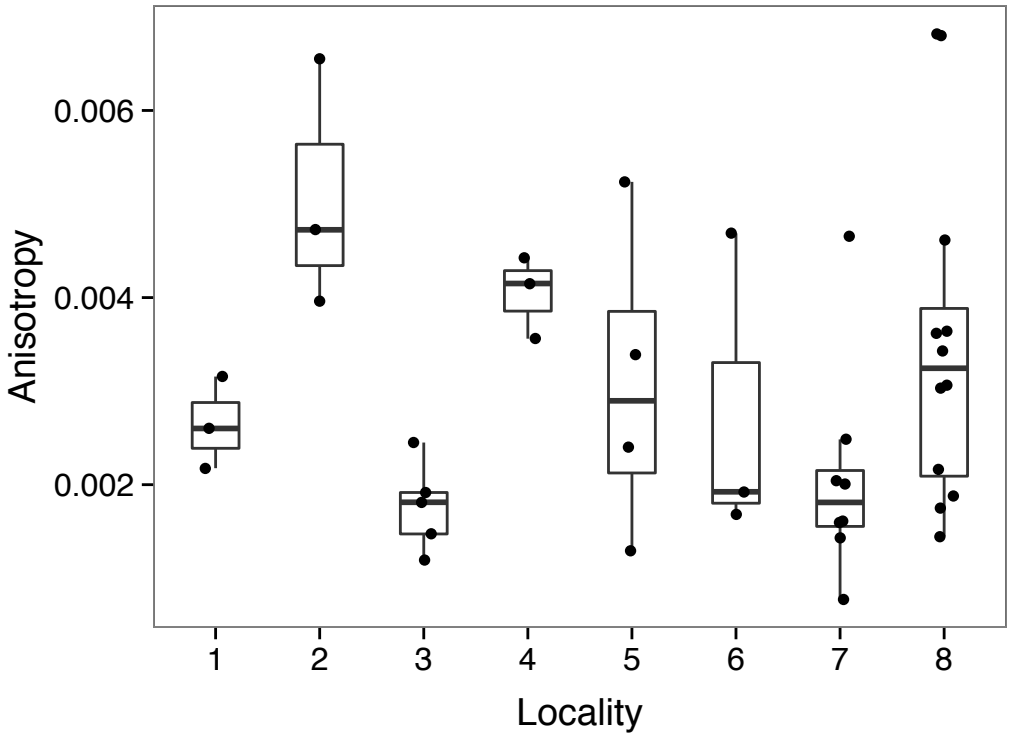

Figure 3.9. Box plot of anisotropy by locality for *P. anubis*. Localities come from central, eastern, and western geographic regions (1 = Aledjo, 2 = Kimani, 3 = Kisangani, 4 = Mahagi Lac, 5 = Marigot, 7 miles S.E., Lake Baringo, 6 = Mount Lukenya, 7 = Park W, 8 = Tshopo; see Appendix A for detailed locality information). No differences were found in anisotropy among localities.

CHAPTER 4

THE RELATIONSHIP BETWEEN MONTHLY DIETARY VARIATION AND VARIATION AN DENTAL MICROWEAR TEXTURES AN AFRICAN OLD WORLD MONKEYS (CERCOPITHECIDAE)

Introduction

A major issue in paleoanthropology in the last decade has been the relative importance of fallback foods to the evolution of primate morphologies, particularly those of hominins (see Constantino and Wright, 2009, and other articles from Special Issue on Fallback Foods, Am J Phys Anth 140(4)). The use of the term "fallback foods" has been varied (Hemingway and Bynum, 2005; Constantino and Wright, 2009) but indicates a dietary resource that is eaten when preferred foods are unavailable and that is critical to species survival during food scarcity (Altmann, 1998; Lambert, 2007; Constantino and Wright, 2009). Fallback foods tend to be mechanically challenging to process, often falling into the "hard object" category (Lucas et al., 2009), leading to potential selective pressure on morphologies that enhance processing efficiency of these foods (Marshall and Wrangham, 2007; Constantino and Wright, 2009). However, since fallback foods constitute an infrequent addition to the annual diet of a species, they may not be detectable in fossil species using methods that are dependent on how often an item is consumed, such as dental microwear and isotope analyses.

This disconnect between the results of dental microwear analyses and morphologies, which respond to evolutionary pressure and are not necessarily dependent on frequency of dietary item use, has been particularly apparent in dietary reconstructions of early hominins. An increased robustness in the masticatory system over time in

Australopithecus and *Paranthropus* species was originally explained by an increase in feeding on hard objects (Kay, 1981; Ward et al., 1999; Teaford and Ungar, 2000; Ungar et al., 2008; Lee-Thorp et al., 2012; Strait et al., 2013). However, dental microwear analyses have suggested that only *Paranthropus robustus* included such hard objects in its diet, while *Australopithecus afarensis* and *P. boisei* lacked evidence of hard object consumption (Scott et al., 2005; Grine et al., 2006a, b; Ungar et al., 2008, 2010). The difference between the apparent morphological selection for a robust masticatory system and the microwear results suggesting less reliance on hard items in *A. afarensis* and *P. boisei* was explained by the seasonal use of hard objects as fallback foods (Wood and Strait, 2004; Scott et al., 2005; Grine et al., 2006a, b; Ungar et al., 2008). These hard foods would have been crucial for survival in times of food scarcity and would thus lead to morphological change reflecting the processing needs of hard foods. However, a lack of any microwear indicating hard objects in the diet of these species even as sample sizes have increased (Ungar et al., 2010; Grine et al., 2012), and in *A. afarensis* the fact that these microwear patterns hold over geographic location and through time (Grine et al., 2006b), indicate that the morphology of these species may be responding to other dietary pressures and not those related to hard object feeding. This conclusion is supported by recent research by Scott et al. (2014) demonstrating that evolution of such a robust morphology in *P. boisei* from a less robust ancestral condition is only consistent with gnathic loading across the year, most likely with repetitive processing of tough foods. Additionally, isotopic evidence showing high C4 content in the diet of *P. boisei* is likely consistent with a year-round consumption of C4 dietary resources (Cerling et al., 2011;

Grine et al., 2012; Sponheimer et al., 2013), potentially indicating a diet dominated by low-quality vegetation (Cerling et al., 2001).

The relative importance of fallback foods in the shaping of non-hominin primate morphology and adaptation has also been hotly debated (e.g. Lambert, 2009). Lambert et al. (2004) implicated the infrequent consumption of hard seeds in grey-cheeked mangabeys (*Lophocebus albigena*) in the evolution of thick dental enamel; however, McGraw et al. (2014) have demonstrated a year-round consumption of hard seeds in the sooty mangabey (*Cercocebus atys*) and propose that the year-round consumption of this dietary item has led to the evolution of some of the thickest enamel in extant primates. Other extant primates such as orangutans (*Pongo pygmaeus*) and New World monkeys (Platyrhini) also demonstrate hard object feeding that has likely led to their robust morphologies (Kinzey and Norconk, 1990, 1993; Wright, 2005; Vogel et al., 2008).

These studies highlight how the ability to identify annual versus short-term consumption of items with different mechanical properties in the diets of fossil primates would allow further investigation of the role of fallback foods in the adaptation and evolution of primates. Of particular importance is whether robust morphologies evolved due to the infrequent short-term consumption of fallback foods or to the full annual diet. However, identifying the frequency of consumption of a dietary item in a fossil species is quite difficult. Primate species that have similar annual diets are usually difficult to discriminate using dental morphological methods of dietary reconstruction (e.g. allometry: Hylander, 1975; Corruccini and Henderson, 1978; Goldstein et al., 1978; Ungar, 1996; dental topography: Ungar and M'Kirera, 2003; Boyer, 2008; molar shearing: Kay, 1984; Benefit and McCrossin, 1990; Strait, 1997). Since dental microwear

captures information about the diet of an animal in the few weeks before it died (Teaford and Oyen, 1989), it has the ability to differentiate between groups or individuals that differ their diets seasonally (Teaford and Robinson, 1989; Teaford and Glander, 1991, 1996; Merceron et al., 2004). It is therefore possible that microwear differs among species that eat the same annual frequency of food types but differ in how often they consume them. For example, it is possible that a species that eats a high frequency of seeds only at certain times of the year can be discerned using microwear analyses from a species that eats a lower frequency of seeds throughout the year. Here I present data investigating whether dental microwear texture analysis can be used as a method to distinguish species that have similar annual diets but different monthly variations in consumption frequencies of food categories with different mechanical properties.

My goal was to examine whether species that have similar annual dietary diversities but vary their monthly reliance on food categories can be distinguished from one another. Dietary diversity is an index that reflects the number, frequency, and evenness of use of food categories consumed by a species (Krebs, 1999). I focused on broad food categories, such as fruit and foliage, since these are most closely linked to food mechanical properties, are often recorded in studies of wild primate dietary ecology, and are generally comparable among studies and species. Additionally, it is important to test whether differences in specific microwear textures were linked to differences in the frequencies of hard object consumption among species with similar dietary diversity.

My predictions rely on the observation that species that consume hard foods, such as seeds, fruit, and grit-laden underground items such as tubers, have higher values of the microwear texture variable area-scale fractal complexity (*Asfc*), while species that rely on

more tough foods, such as leaves and grasses, have higher values of anisotropy (*epLsar*) (Scott et al., 2005, 2006, 2012). Another texture variable that has been linked to diet is heterogeneity of area-scale fractal complexity (heterogeneity or *HAsfc*); this variable is related to both the size and variability in wear-causing particles (Scott et al., 2006), and thus has been suggested to be greater in species with a more diverse or varying diet (Scott et al., 2012). However, Calandra et al. (2012) have shown support for a negative correlation between heterogeneity and frequency of fruit consumption in primates, although the species with intermediate fruit consumption had heterogeneity values that were as high or higher than species with low frequencies of fruit consumption.

Based on these links between microwear and diet, I predict that species with greater monthly variation in dietary diversity will have greater variation in complexity and anisotropy. Species with greater monthly variation in dietary diversity are expected to switch between a more generalized diet, incorporating more food types, to a more specialized diet incorporating fewer food types. This switch will lead to a pattern of greater variation in microwear textures in comparison to species that consume a more constant diet throughout the year. Predictions for heterogeneity are more complex; since heterogeneity has been proposed to relate to either dietary diversity or to the frequency of fruit and/or hard object feeding (Scott et al., 2006; Calandra et al., 2012), two separate hypotheses are proposed. The first hypothesis states that 1) species with greater dietary diversity have greater mean heterogeneity than species with less dietary diversity and 2) species with greater variation in dietary diversity across the year have greater variance in heterogeneity than species with less variation in dietary diversity. The second hypothesis states that 1) species that eat higher frequencies of fruit and/or hard objects will have

lower mean heterogeneity and 2) species with greater variation in fruit and/or hard object feeding will have greater variance in heterogeneity.

Materials & Methods

These hypotheses were tested using six species of African Old World monkeys (Cercopithecidae). The species examined included four cercopithecines (*Chlorocebus aethiops*, *Cercopithecus mitis, Papio anubis*, and *Theropithecus gelada*) and two colobines (*Colobus guereza* and *Procolobus rufomitratus*). These species were selected based on the available museum specimens and the number and quality of field studies examining feeding ecology in these species.

To determine the variation in diet across the year for each species, I first compiled information on monthly consumption of food categories at as many sites as possible for each species (see Table 4.1 and Appendix D). Many monthly consumption frequencies were not listed in the texts but were found in graphs published in the texts; in these cases, I used the WebPlotDigitizer application (Version 3.3; Rohatgi, 2014) to extract data estimates of consumption frequencies from two-dimensional frequency plots and bar graphs. I then calculated the coefficient of variation (CV) for each site for each food type examined as well as the overall dietary diversity (discussed below). The food types used were foliage (encompassing young and mature leaves, leaf buds, leaf stems, and grass blades), seeds (when recorded by researchers), fruits (when recorded by researchers), and total fruit (fruits plus seeds and seed pods). For *P. anubis* and *T. gelada*, underground item consumption, including roots, tubers, and corms, was also examined. Dietary diversity was calculated for each month using Shannon's Diversity Index *H:*

$H = -(\sum p_i * \ln p_i)$ where p_i=frequency of food category consumption for each *i* category.

For calculation of *H*, I used the same categories for each species to control for differences in data collection categories (e.g., some authors only collected data on total fruit, while others collected data on both fruits and seeds). Categories used were foliage, total fruit, flowers, animal material (invertebrates and vertebrates), and other (unidentified items plus items not recorded by all authors, including underground items and gums). The frequencies used, the sources of the frequencies, and the associated indices and CVs are given in Table 4.1.

To collect microwear data, casts were made from 278 wild-caught museum specimens (see Appendix A). All specimens were cleaned with alcohol-soaked cotton swabs before vinyl impressions were made of all usable upper and lower first and second molars using President's Jet Regular Body Dental Impression Material (Coltene-Whaledent). Casts were made using Epotek 301 epoxy resin and hardener (Epoxy Technologies). Following previous studies (Ungar et al., 2003; Scott et al., 2006, 2012), casts were scanned on Phase II occlusal facets (9, x, or 10n; Kay, 1977); lower second molars were preferentially selected for analysis, but when they did not yield good surfaces first molars or upper second molars were also examined. Scans were collected using a 100x objective on a Sensofar Plμ white-light scanning confocal profiler (Solarius, Sunnyvale, CA) housed at the University of Arkansas. The resulting point clouds had a lateral sampling interval of 0.18 μm and a vertical resolution of 0.005 μm, and four adjoining fields were collected for a total area of 276 μm x 204 μm. Scans were leveled

using Solarmap Universal software, and artifacts, such as dust particles, were excluded by thresholding and erase operators.

Dental microwear texture parameters were calculated through Toothfrax (Surfract), a scale-sensitive fractal analysis program. Four variables for each specimen were calculated: area-scale fractal complexity (*Asfc*), anisotropy (*epLsar*), and heterogeneity at the 3x3 (*HAsfc9*) and 9x9 (*HAsfc81*) scales. These variables have been linked to different dietary parameters (i.e. Scott et al., 2006). Complexity measures changes in relative area with scale and has been shown to be greater on molars of primates that eat more hard, brittle foods such as fruit and seeds, as well as gritty items such as underground foods; anisotropy measures the directionality of surface roughness, and has been shown to be greater on molars of primates that eat tough foods such as grass and leaves (Scott et al., 2005, 2006, 2012). Heterogeneity measures the similarity of textures across the tooth's surface by breaking the scan area into smaller, equal-size quadrants and taking the median complexity value of these quadrants; two scales of heterogeneity that are commonly used are those at the 3x3 quadrant (*HAsfc9*) and 9x9 quadrant (*HAsfc81*) scales. Heterogeneity may be greater in primates that have greater variation in diet, particularly greater variation in consumption of foods that create complexity (Scott et al., 2006, 2012), or may be greater in primates that have lower frequencies of fruit and/or hard object consumption (Calandra et al., 2012). These differing interpretations of the link between heterogeneity and diet demonstrate that this link may be more complex than that between complexity, anisotropy, and diet.

For statistical tests, two groups were examined separately: a high dietary diversity group consisting of *Ch. aethiops*, *C. mitis*, and *P. anubis* and a low dietary diversity

group consisting of *Co. guereza, Pr. rufomitratus*, and *T. gelada*. The high dietary diversity group exhibits annual dietary diversities greater than one ($H > 1$), while the low dietary diversity group exhibits annual dietary diversities less than one ($H < 1$). An additional set of comparisons was made using all six species in order to test for further relationships between the CVs of dietary parameters and microwear (discussed below). The low number of sites with comparable quantitative data on full annual cycles of dietary frequencies did not allow for informative statistical tests of dietary diversity and variation at each site. Therefore, I compared the calculated CVs of dietary diversity and food categories qualitatively. These comparisons yielded predictions for mean heterogeneity and variance in complexity, anisotropy, and heterogeneity among the species. I used Levene's Test for homogeneity of variance to test for differences among the species in their variance in complexity, anisotropy, and heterogeneity. I transformed the data using the formula:

$$X' = | x - (\text{mean } X) |$$

and used these data in an ANOVA; this reflects the formula for the mean version of Levene's Test but allows for post-hoc testing of the data and has previously been used by other researchers (e.g., Ungar et al., 2010). I also tested for differences among the species in mean heterogeneity (*HAsfc9* and *HAsfc81*) using ANOVA and Kruskal-Wallis tests. Post-hoc Tukey's Honestly Significant Difference (HSD) and Fisher's Least Significant Difference (LSD) tests were used after significant ANOVAs or Kruskal-Wallis tests. Finally, I tested for a relationship between the dietary CVs from each site and microwear variable CVs of the six species to see if monthly variation in diet was related to intraspecific variation in microwear variables. I used Pearson's product- moment

correlations and Spearman's rank correlations to test for a relationship between the CVs of the dietary parameters (dietary diversity (*H)*, foliage, and total fruit) and the CVs of microwear variables (complexity, anisotropy, *HAsfc9*, and *HAsfc81*). All statistical tests were conducted in RStudio (version 0.98.978).

Results

High dietary diversity group

The vervet (*Ch. aethiops*), blue monkey (*C. mitis*), and olive baboon (*P. anubis*) showed differences in the variation in diet across the year based on field studies (Table 4.1, Appendix D). *Ch. aethiops* had relatively high CVs of *H* at the sites examined (0.31 at Mount Assirik (Harrison, 1982) and 0.40 at Cameroon savannah sites (Kavanagh, 1978; note that this data point is not exactly comparable since it encompassed eight months total, four from each of two savannah sites)). At Mount Assirik, *Ch. aethiops* showed great variation in total fruit consumption, from 32% of the diet in January to over 90% of the diet in October (Harrison, 1982). At the savanna sites examined in Cameroon, Kavanagh (1978) noted a low of 2% fruit consumption and a high of 98% fruit consumption. These studies show that *Ch. aethiops* varies its diet greatly, subsisting almost entirely on fruit at certain times of year and almost entirely on other items, such as flowers and exudates, at other times of the year. Indeed, this ability to subsist on locally abundant resources in times of preferred resource scarcity has been noted as an adaptation that has allowed *Ch. aethiops* to inhabit much of sub-Saharan Africa, particularly in seasonal environments (Kingdon, 2013).

In contrast to *Ch. aethiops*, *C. mitis* showed a more evenly distributed diet over much of the year. Although the average dietary diversity ($H = 1.00$) among the sites examined is close to that of *Ch. aethiops* ($H = 1.03$), *C. mitis* shows a more consistent dietary diversity across the year, represented by a lower average CV of dietary diversity (0.16) across sites. At each site examined, the CV of dietary diversity remained low, indicating a high dietary diversity maintained across the year at each site. *C. mitis* at Jibat Forest, Ethiopia (Tesfaye et al., 2013) and Nyungwe Forest Reserve (Kaplin et al., 1998) showed similar consumption frequencies of different food types throughout the year, as well as similar dietary diversities. Tesfaye et al. (2013) observed fruit to make up the largest portion of the *C. mitis* diet in most months, but a few months showed the highest portion to switch either to flowers, foliage, or insects. Although total fruit was always the most-consumed food at Nyungwe Forest Reserve, flowers, foliage, and insects all contributed significant amounts in certain months (Kaplin et al., 1998). At Kakamega Forest, Kenya, Cords (1986) found that fruit made up the largest portion of the *C. mitis* diet in every month examined, with foliage and insects contributing most of the remaining portion. This evenly distributed diet led to a very low CV of dietary diversity (0.07) at Kakamega Forest. Overall, *C. mitis* showed low monthly variation in both dietary diversity and food category consumption frequencies, indicating a less seasonally variable diet.

Unfortunately, only one study of *Papio anubis* feeding ecology that included monthly frequencies of food consumption was available (Barton, 1990). This study, on the Laikipia Plateau, Kenya, recorded an eclectic diet across the year, with *P. anubis* subsisting on foliage (grass blades and leaves) at around 50% of the diet for four months

of the year; in other months, *P. anubis* subsisted primarily on fruit or acacia flowers. Underground items were eaten at low frequencies, as were seeds. The varied diet of *P. anubis* yielded a higher average dietary diversity ($H = 1.09$) than either *Ch. aethiops* or *C. mitis*, but a CV of dietary diversity (0.20) that was only slightly higher than that of *C. mitis*. Comparing the CVs of dietary categories, *P. anubis* had the highest CV of total fruit consumption (0.83), higher than the average of *Ch. aethiops* (0.50) and *C. mitis* (0.24). In terms of foliage consumption, *Ch. aethiops* showed the highest average CV (1.22), *P. anubis* had an intermediate CV (0.72), and *C. mitis* the lowest average CV (0.60) (Table 4.1).

Based on these data supporting greater variation in dietary diversity in *Ch. aethiops*, coupled with high variation in both total fruit and foliage consumption, I predicted that *Ch. aethiops* would have greater variance in complexity and anisotropy than *C. mitis* and *P. anubis*. However, none of the species differed in their variance in complexity (Levene's Test: $F(2,140)=1.39$, $p > 0.1$) or anisotropy (Levene's Test: $F(2,140)=0.16$, $p > 0.1$).

The first hypothesis for heterogeneity yields the prediction that species with similar dietary diversity, including these three species, should not differ in mean heterogeneity, but since *Ch. aethiops* has greater variation in dietary diversity, it should have greater variance in heterogeneity. The second hypothesis is that species with higher annual frequencies of fruit and/or hard object consumption should have lower mean heterogeneity, and species that have greater variation in hard object consumption should have greater variance in heterogeneity. Since *P. anubis* has lower annual total fruit consumption than *Ch. aethiops* and *C. mitis*, *P. anubis* should have the highest mean

heterogeneity, while *Ch. aethiops* and *C. mitis* should have similar mean heterogeneity. Because *C. mitis* has the lowest variation in total fruit consumption, *Ch. aethiops* has intermediate variation, and *P. anubis* has the highest variation, *C. mitis* should have the lowest variation in heterogeneity and *P. anubis* should have the highest variation.

Although the species did not differ in mean *HAsfc9* (ANOVA: F (2, 140) =1.60, $p > 0.1$), they did differ in mean *HAsfc81* (Kruskal-Wallis $X^2 = 33.74$, df = 2, $p < 0.0001$; Figure 4.1). Contrary to both hypotheses, *P. anubis* showed lower mean *HAsfc81* than both *Ch. aethiops* and *C. mitis*, while these two species did not differ in *HAsfc81* (Tukey's HSD and Fisher's LSD tests). The three species also differed in variance in both *HAsfc9* (Levene's Test: F (2,140) = 6.85, $p < 0.001$) and *HAsfc81* (Levene's Test: F (2,140) = 11.99, $p < 0.0001$; Fig. 4.1). For *HAsfc9*, *C. mitis* had the greatest variation, which was significantly higher than that of *P. anubis* (Tukey's HSD and Fisher's LSD), but *Ch. aethiops* did not differ from either species. For *HAsfc81*, both *Ch. aethiops* and *C. mitis* had greater variation than *P. anubis*, though neither differed from each other (Fig. 4.1). Thus, the results from mean heterogeneity do not fully support either hypothesis; the first hypothesis is supported by results of mean *HAsfc9* but not by results of mean *HAsfc81*, while the second hypothesis is not supported by mean results of either heterogeneity variable. Additionally, results of variance in heterogeneity were contrary to both hypotheses.

Low dietary diversity group

Although there was great intraspecific variation among sites in monthly consumption frequencies, overall the species in the low dietary diversity group did not

differ greatly in their monthly variation in dietary diversity (Table 4.1).

The guereza (*Co. guereza*) showed the most diverse diets, with an average dietary diversity of $H = 0.94$, and had a low average CV of dietary diversity (0.24), demonstrating a more even distribution across dietary categories throughout the year and low seasonal variation in dietary diversity. However, *Co. guereza* did show a range from 94% foliage consumption in a single month at Budongo Forest, Uganda (Plumptre, 2006), to only 8% at the Okapi Reserve, DRC (Bocian, 1997). This range went along with a total fruit consumption range from 86% to 0% at the Okapi Reserve (Bocian, 1997). *Co. guereza* also varied among the sites in whether it consumed fruits or seeds, with mostly fruit consumed at Kakamega Forest (Fashing, 1999), mostly seeds consumed in the Okapi Reserve, DRC (Bocian, 1997), and a mix of fruits and seeds consumed at Budongo Forest, Uganda (Plumptre, 2006).

The Eastern red colobus (*Pr. rufomitratus*) showed a slightly higher average CV of dietary diversity (0.29), which went along with a higher reliance on foliage in most months. At Gombe, Tanzania, Clutton-Brock (1975) noted a relatively high frequency of leaf consumption, with a nine-month mean of 82% and a range of 66-97%. Here, leaves made up the most eaten food category for each month of the year. In contrast, Maisels et al. (1994) recorded more monthly variation in diet at Salonga Forest, DRC, with red colobus subsisting primarily on seeds for four months of the year but primarily on leaves for the rest of the year. This regimen yielded a CV of 0.52 for foliage consumption and 0.86 for total fruit consumption. On average, however, *Pr. rufomitratus* showed lower CVs of total fruit (0.65) and foliage (0.28) consumption than did *Co. guereza*, indicating a less seasonally varying diet. However, it should be noted that the sample of *Pr.*

rufomitratus that I used in this study comes exclusively from the DRC and might be expected to have a diet most similar to that of the population studied by Maisels et al. (1994).

In contrast to the two colobine monkeys, the gelada (*T. gelada*) consumes a fundamentally different diet, with the majority of its food coming from grasses rather than leaf material. Additionally, out of the studies of gelada feeding ecology, only one (Fashing et al., 2014) has been long-term. Thus, monthly dietary frequencies from the study site of Guassa (Fashing et al., 2014) are not directly comparable to the studies of Dunbar (1977) and Iwamoto (1979), which published some monthly frequencies, making these last two studies not directly comparable to the data from the other two species. Additionally, since a large number of the *T. gelada* specimens used in this study come directly from the site of Guassa, it makes sense to compare the dietary data from this site directly to those of the other species. As with other sites, Guassa geladas consume a high frequency of foliage, with an annual average of 80% and a range of 67-91%, most of this coming from grass blades with the addition of forbs. This high frequency of grass and forb consumption throughout the year yields a low CV of foliage consumption (0.10), a relatively low annual dietary diversity ($H = 0.63$), and a low CV of dietary diversity (0.23). These data show Guassa geladas to have less monthly variation in consumption frequencies than the other two species examined in this group. However, it should be noted that at the site of Sankabar, Iwamoto (1979) noted 71% consumption of grass seeds in a single month and 67% consumption of underground items in another month.

Since the three species had similar CVs of dietary diversity, I based my predictions for microwear textures on their CVs of foliage and fruit consumption. Since

Co. guereza had the highest CVs for these, I predicted that they would have greater variation in complexity and anisotropy than *Pr. rufomitratus* and *T. gelada.* The low dietary diversity group approached significance in their variation in complexity (Levene's Test: F (2,132) = 3.02, $0.05 < p < 0.1$), with *Co. guereza* showing greater variation than *Pr. rufomitratus* (Tukey's HSD, Fisher's LSD) but neither of these species differing from *T. gelada*. However, the species did not differ in their variation in anisotropy (Levene's Test: F (2,132) = 0.52, $p > 0.1$).

If the first heterogeneity hypothesis holds true, *Co. guereza* should have higher mean heterogeneity since it has higher *H* values than the other two species; since *Pr. rufomitratus* had the greatest variation in *H* values, it would also be predicted to have the greatest variation in heterogeneity. If the second hypothesis holds true, *Pr. rufomitratus* and *Co. guereza* should have lower mean heterogeneity than *T. gelada*, since they had higher annual frequencies of total fruit consumption, while *Co. guereza* should have greater variation in heterogeneity since it had the greatest CV of total fruit consumption. The species did approach significance in their mean *HAsfc9* (ANOVA: F (2,132) = 2.95, $0.05 < p < 0.1$) and did differ in mean *HAsfc81* (ANOVA: F (2,132) = 5.76, $p < 0.01$; Fig. 4.2). Contrary to both predictions, however, post-hoc tests showed *Pr. rufomitratus* had greater *HAsfc81* than *T. gelada* (Tukey's HSD and Fisher's LSD) and marginally greater *HAsfc81* than *Co. guereza* (Fisher's LSD only); however, *Co. guereza* did not differ in *HAsfc81* from *T. gelada.* Additionally, the species did not differ in their variation in heterogeneity (Levene's Test; *HAsfc9:* F (2,132) = 1.61, $p > 0.1$; *HAsfc81*: F (2,132) = 0.63, $p > 0.1$), contrary to both hypotheses.

Correlations

The CVs of microwear variables and dietary parameters for each species are given in Table 4.2. If variation in microwear is related to monthly variation in dietary parameters, there should be a relationship between these variables. However, the only CV of any dietary parameter that was significantly correlated with a CV of microwear variables was the CV of total fruit consumption and the CV of *HAsfc81* (Pearson's product-moment correlation: $r = -0.70$, $t\,(11) = 3.28$, $p < 0.01$; Fig. 4.3). Additionally, the CV of anisotropy was positively correlated with the CV of foliage consumption, but the hypothesis of no relationship could not be rejected (Spearman's rank correlation: $r = 0.53$, $S = 169.50$, $0.05 < p < 0.10$).

Discussion

Overall, these results show only mild support for the hypothesis that greater monthly variation in dietary diversity yields greater variation in the microwear textures of complexity and anisotropy. Within the high dietary diversity group, no differences were found among the species in their variation in either of these texture variables; within the low dietary diversity group, *Co. guereza* did have marginally greater variation in complexity than *Pr. rufomitratus*, as predicted, but not greater than *T. gelada*, nor did it differ from either species in variation in anisotropy. In particular, it should be noted that anisotropy showed great variation in all the species examined here and yielded no distinctions among the species.

Additionally, the relationship between heterogeneity and diet was not strongly supported. Though it has been suggested that heterogeneity relates to dietary diversity

(Scott et al., 2006, 2012) or to frequency of hard object feeding (Calandra et al., 2012), neither relationship was strongly supported in either the high or low dietary diversity groups. The high dietary diversity group did not differ in the coarser heterogeneity variable *HAsfc9*, as predicted by the first hypothesis, but it did differ in the finer heterogeneity variable *HAsfc81*, although not in the way predicted by the second hypothesis. Since *P. anubis* has the lowest annual frequency of total fruit consumption, it should have the highest heterogeneity as predicted by the second hypothesis. However, it had the lowest heterogeneity, significantly lower than both *Ch. aethiops* and *C. mitis*. In fact, *P. anubis* had the lowest mean fine-scale heterogeneity (*HAsfc81*) value out of eight cercopithecid species (Chapter 2). If heterogeneity is negatively correlated with fruit consumption, as is suggested by Calandra et al. (2012), *P. anubis* would be expected to have higher values than *Ch. aethiops* and *C. mitis*, as it consumes less fruit than either of these species. However, another component of the diet that potentially contributes to hard object consumption is subterranean items (e.g. roots, tubers, and corms), which makes up a significant portion of *P. anubis* diet at certain times of the year. If subterranean items are grouped with total fruit, this "hard object" category makes up 50% of the annual diet of *P. anubis* averaged across all sites (Appendix C), putting *P. anubis* much closer to the annual frequencies of the other two species. However, *P. anubis* still has lower average annual frequencies of fruit/hard object consumption than either *Ch. aethiops* or *C. mitis*, and thus the low heterogeneity values are still unexpected given the combined fruit and subterranean item annual frequencies if heterogeneity is negatively correlated with consumption of these items.

The low dietary diversity group also did not differ in mean heterogeneity in the way predicted by either hypothesis, since *Pr. rufomitratus* had the highest heterogeneity and *Co. guereza* had intermediate heterogeneity. Although the species in the low dietary diversity group subsist primarily on foliage, they had similar mean heterogeneity values to those in the high diversity group (Fig. 4.1); this outcome is unexpected given either hypothesis for the relationship between diet and heterogeneity. Additionally, neither group showed the expected predictions for variation in heterogeneity for either hypothesis.

Thus, results within each dietary diversity group showed little support for a relationship between heterogeneity and either dietary diversity or fruit consumption. A further result that does not support the negative relationship between heterogeneity and frequency of fruit consumption is the negative correlation that was found between the CV of monthly fruit consumption and CV of fine-scale heterogeneity (*HAsfc81*; Fig. 4.2). This relationship suggests that species that have greater variation in fruit consumption among months have less variation in heterogeneity, actually the opposite of the second hypothesis, which stated that species with greater variation in fruit consumption would have greater variation in heterogeneity. Greater variation in fruit consumption can be achieved through either high annual frequencies of fruit consumption with some months of low consumption or low annual frequencies of fruit consumption with some months with high consumption; however, because CVs are calculated by dividing the standard deviation by the mean, the second scenario will generally yield higher CVs since the mean is low. The two species in the sample that have the highest CVs of fruit consumption are *P. anubis* and *Co. guereza*, which both have relatively low annual fruit

consumption but subsist on fruit and/or seeds at high frequencies (> 74%) during a few months of the year (Table 4.1). They also both have the lowest CVs of *HAsfc81*, driven mainly by low standard deviations, although *P. anubis* has a low mean as well. If low heterogeneity is related to high frequencies of fruit consumption, species such as *P. anubis* and *Co. guereza* that have greater variation in fruit consumption should show a distribution with higher means and some specimens with low heterogeneity values related to the few periods of high fruit consumption. However, the opposite distribution is seen in this sample, with low mean heterogeneity seen in both species and a few specimens with high heterogeneity values (Fig. 4.1). At the other end of the spectrum is *T. gelada*, which also has a low annual frequency of fruit consumption but does not subsist on fruit/seeds at high frequencies at any time. Thus, *T. gelada* has a low CV of fruit consumption. It also has the highest CV of *HAsfc81*, likely due in part to a small sample size but also to a low mean and high standard deviation of *HAsfc81*. Due to its low fruit consumption, and no periods of high fruit consumption, *T. gelada* would be predicted to display an overall high mean heterogeneity and lower range of heterogeneity values if low fruit consumption was associated with high heterogeneity. Again, the opposite distribution is seen, with a low mean heterogeneity and a relatively greater range of heterogeneity values. Thus, the negative correlation between the CV of fruit consumption and the CV of *HAsfc81* does not support the hypothesis of a negative correlation between frequency of fruit consumption and mean heterogeneity. However, the negative correlation found by Calandra et al. (2012) was low (r = -0.42), suggesting that fruit consumption is a small driver of the variation in *HAsfc81* and that other factors contribute to the variation as well.

Overall, these results do not show support for using variation in the dental microwear texture variables complexity and anisotropy to distinguish differences in monthly variation in dietary diversity among fossil species with similar annual dietary diversities. Within the groups with high and low annual diversity, the species were similar in their variation in these texture variables. Additionally, both mean heterogeneity and variation in heterogeneity do not appear to distinguish the species in these groups along dietary lines. Although there were differences among the species in mean heterogeneity and variance in heterogeneity, the differences were not in the expected direction for either hypothesis for heterogeneity and diet. The relationship between the CV of monthly fruit consumption and the CV of *HAsfc81* does not support either hypothesis as well.

Although these results do not support the use of variation in microwear as a method of distinguishing short-term use of dietary items with different mechanical properties among species with similar annual diets, they do highlight the difference in nature of the diet between species that fall into the high and low dietary diversity groups and how this nature is reflected in the species's dental microwear. The high dietary diversity group is in general quite variable in diet across the year and among sites, and this overall diversity in diet seems to obscure any differences among the species in microwear variation due to changes in dietary diversity throughout the year. In effect, the great diversity in these species's diets masks any monthly differences that might occur due to changes in this diversity. In contrast, the low dietary diversity group shows more of the effect of monthly changes in dietary diversity on microwear, possibly because any changes will be better represented against a backdrop of overall lower diversity. Perhaps

because of its more frequent reliance on fruit, *Co. guereza* appears different in its microwear than the other two species in this group. *Co. guereza* does display marginally greater variation in complexity than the other two species, which goes along with the species's greater variation in total fruit and leaf consumption; however, *Co. guereza* also displays greater annual dietary diversity than the other two species, which has been moderately associated with greater variation in complexity (Chapter 2), so it's not clear if this greater variation in complexity is related to the greater monthly variation in fruit and leaf consumption in *Co. guereza* or simply a greater annual dietary diversity. *Pr. rufomitratus* also shows marginally greater heterogeneity than *Co. guereza*, although these species have similar average total fruit consumption; this may be due to the higher frequency of seed consumption in *Pr. rufomitratus*, while *Co. guereza* varies among sites in whether it consumes fruits or seeds. However, since it has been suggested that hard objects of a larger size yield greater heterogeneity than objects of a smaller size (Calandra et al., 2012), it is unclear if seed eating would lead to higher heterogeneity in *Pr. rufomitratus*. *T. gelada* also shows lower heterogeneity than *Pr. rufomitratus*, potentially because of the low frequency of consumption of seeds and underground items.

There are a few reasons why the results of this study may not show a relationship between seasonal consumption of dietary resources and variation in microwear. First, it is possible that the dietary categories used in this study are too broad to make fine-grained predictions about the relationships between dental microwear textures and diet in these species. In order to compare data from multiple field sites and species, it was necessary to use categories that were consistent across studies, which led to the use of broader categories than would be ideal. The variation in mechanical properties within each

dietary category can be large, and therefore it might be easier to link specific microwear signals to dietary variation by using a greater number of dietary categories, each more refined than the ones used in this research. Second, the specimens (except for the Guassa gelada sample) were not collected from the field sites from which these dietary data come, so their diets could be different from the published studies. For this reason, studies of microwear in populations where diets have been directly observed (e.g. Teaford and Glander, 1996; Ungar, 1996; Daegling and Grine, 1999; Nystrom et al., 2004) or experimentally controlled (e.g. Teaford and Oyen, 1989; Schulz et al., 2013) are so important to refining the link between diet and microwear. Finally, the variation due to seasonal dietary changes among species with similar diets may simply be too small to detect within the natural variation in microwear. Since some seasonal differences linked to diet have been identified within species in this sample (Chapter 2), examining the species as a whole may make these differences undetectable. Hopefully, as further research is conducted on controlled samples, such as those in experimental settings (e.g. Schulz et al., 2013; Karme et al., 2014), the ability to detect more refined dietary regimes will increase.

Conclusion

The goal of this research was to identify whether analyzing variation in dental microwear textures could distinguish differences in consumption frequencies of food categories across the year among primate species with similar dietary diversities. While the results from this study suggest that species with similar annual diets do not differ in microwear texture variation, they do suggest that species that differ greatly in their

microwear variation likely differ greatly in their diets. Since cercopithecid species with similar annual dietary diversities are mostly indistinguishable from each other in terms of their microwear variation, it is likely that fossil species with different variation in microwear textures have fundamentally different diets. This supports conclusions by Ungar et al. (2008, 2010) that *P. robustus*, which shows very high variance in microwear textures in comparison to other hominins, consumed a diet that was quite different from that consumed by other *Australopithecus* and *Paranthropus* species. Whether this variation was due to a seasonally changing diet or to other factors cannot yet be determined, however. Further research into microwear texture variation in experimentally controlled samples and populations where diet has been directly observed may help to elucidate further causes of microwear variation and allow us to better interpret diet in fossil primates.

References

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press, 608pp.

Barton RA. 1990. Foraging Strategies, Diet And Competition In Olive Baboons. PhD Dissertation, University of St. Andrews.

Benefit BR, McCrossin ML. 1990. Diet, species diversity and distribution of African fossil baboons. Kroeber Anthropol Soc Pap 71:79-93.

Bocian CM. 1997. Niche separation of black-and-white colobus monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri Forest. PhD Dissertation, City University of New York.

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. J Hum Evol 63:85-98.

Cerling TE, Mbua E, Kirera FM, Kyalo Manthi F, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of Paranthropus boisei in the early Pleistocene of East Africa. Proc Nat Acad Sci USA 108: 9337-9341.

Clutton-Brock TH. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. Folia Primatol 23:165-207.

Constantino PJ, Wright BW. 2009. The importance of fallback foods in primate ecology and evolution. Am J Phys Anthropol 140:599-602.

Cords M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. J Anim Ecol 55:811-827.

Corruccini RS, Henderson AM. 1978. Multivariate dental allometry in primates. Am J Phys Anthropol 48:203-208.

Daegling DJ, Grine FE. 1999. Occlusal microwear in *Papio ursinus*: The effects of terrestrial foraging on dental enamel. Primates 40:559-572.

Dunbar RIM. 1977. Feeding ecology of gelada baboons: a preliminary report. In: Clutton-Brock TH, ed. Primate Ecology. London: Academic Press, pp. 250–273.

Fashing PJ. 1999. The Behavioral Ecology of an African Colobine Monkey: Diet, Range Use, and Patterns of Intergroup Aggression in Eastern Black and White Colobus Monkeys *(Colobus guereza)*. PhD Dissertation, Columbia University.

Fashing PJ, Nguyen N, Venkataraman VV, Kerby JT. 2014. Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropith and hominin dietary evolution. Am J Phys Anthropol 155:1-16.

Goldstein S, Post D, Melnick D. 1978. An analysis of cercopithecoid odontometrics. I. The scaling of the maxillary dentition. Am J Phys Anthropol 49:517-532.

Grine FE, Ungar PS, Teaford MF. 2006. Was the Early Pliocene hominin '*Australopithecus*' *anamensis* a hard object feeder? S Afr J Sci 102:301

Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297-319.

Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am J Phys Anthropol 148:285-317.

Groves CP, Kingdon J. 2013. Genus *Chlorocebus*: Savanna Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 264-266.

Harrison MJ. 1982. The behavioural ecology of green monkeys (*Cercopithecus sabaeus*) at Mt. Assirik, Senegal. PhD Dissertation, University of Stirling.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 57-103.

Hylander WL. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science 189:1095-1098.

Iwamoto T. 1979. Feeding ecology. In: Kawai M, ed. Ecological and Sociological Studies of Gelada Baboons. Basel: Springer, pp. 279–330.

Kaplin BA, Munyaligoga V, Moermond TC. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). Biotropica 30:56-71.

Karme A, Rannikko J, Bertin T, Clauss M, Fortelius M. 2014. Chewing machine and tooth wear: how plant materials and grit affect teeth. Podium presentation, Society of Vertebrate Paleontology 74th Annual Meetings.

Kavanagh, M. 1978. The diet and feeding behaviour of Cercopithecus aethiops tantalus. Folia Primatol 30:30-63.

Kay RF. 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.

Kay RF. 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141-151.

Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, eds. Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys and apes. New York: Columbia University Press, pp. 21-53.

Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. Am J Phys Anthropol 81:5-15.

Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int J Primatol 14:207-227.

Krebs CJ. 1999. Ecological Methodology. Menlo Park, CA: Benjamin/Cummings, 624 pp.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee versus cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar P, ed. Evolution of Human Diet: The Known, the Unknown, and the Unknowable, University of Oxford Press, pp. 324-343.

Lambert JE. 2009. Primate fallback strategies as adaptive phenotypic plasticity: scale, process, and pattern. Am J Phys Anthropol 140:759-766.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am J Phys Anthropol 125:363-368.

Lee-Thorp J, Likius A, Mackaye HT, Vignaud P, Sponheimer M, Brunet M. 2012. Isotopic evidence for an early shift to C4 resources by Pliocene hominins in Chad. Proc Natl Acad Sci USA 109:20369–20372.

Lucas PW, Constantino PJ, Chalk J, Ziscovici C, Wright BW, Fragaszy DM, Hill DA, Lee JJW,Chai H, Darvell BW, Lee PKD, Yuen TDB. 2009. Indentation as a technique to assess the mechanical properties of fallback foods. Am J Phys Anthropol 140:643-652.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. Int J Primatol 15:681-701.

Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219-1235.

McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. Am J Phys Anthropol 154:413-423.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542

Nystrom P, Phillips-Conroy JE, Jolly CJ. 2004. Dental microwear in anubis and hybrid baboons (*Papio hamadryas*, s.l.) living in the Awash National Park, Ethiopia. Am J Phys Anthropol 125:279-291.

Plumptre A. 2006. The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda: Effects of logging on primate diets. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, eds. Primates of Western Uganda. New York: Springer, pp. 345-371.

Schulz E, Piotrowski V, Clauss M, Mau M, Merceron G, Kaiser TM. 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS ONE 8:e56167.

Scott JE, McAbee KR, Eastman MM, Ravosa MJ. 2014. Experimental perspective on fallback foods and dietary adaptations in early hominins. Biol Lett 10:20130789.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436:693-695.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51:339-349.

Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Sponheimer M, Alemseged Z, Cerling TE, Grine FE, Kimbel WH, Leakey M G, Lee-Thorp JA, Manthi FK, Reed KE, Wood BW, Wynn JG. 2013. Isotopic evidence of early hominin diets. Proc Natl Acad Sci USA 110:10513-10518.

Strait SG. 1997. Tooth use and the physical properties of food. Evol Anthropol 5:199-211.

Strait DS, Constantino P, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA, Weber GW, Wang Q, Byron C, Slice DE, Chalk J, Smith AL, Smith LC, Wood S, Berthaume M, Benazzi S, Dzialo S, Tamvada K, Ledogar JA. 2013. Diet and dietary adaptations in early hominins: The hard food perspective. Am J Phys Anthropol 151:339-355.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Glander KE. 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk M, Rosenberger A, Garber P, eds. Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 433-449.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401

Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. Am J Phys Anthropol 80:447-460.

Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. Proc Natl Acad Sci USA 97:13506-13511.

Tesfaye D, Fashing PJ, Bekele A, Mekonnen A, Atickem A. 2013. Ecological flexibility in Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest, Ethiopia: a comparison of habitat use, ranging behavior, and diet in intact and fragmented forest. Int J Primatol 34:615-640.

Ungar PS. 1996. Relationship of incisor size to diet and anterior tooth use in sympatric Sumatran anthropoids. Am J Primatol 38:145-156.

Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. Proc Natl Acad Sci USA 100:3874–3877.

Ungar PS, Brown CA, Bergstrom TS, Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning Microscopy 25:185-193.

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3:1-6.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis.* Phil Trans R Soc B 365:3345-3354.

Vogel ER, van Woerden JT, Lucas PW, Atmoko SSU, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55:60-74.

Ward C, Leakey M, Walker A. 1999. The new hominid species *Australopithecus anamensis*. Evol Anthropol 7:197-205.

Wood B, Strait D. 2004. Patterns of resource use in early *Homo* and *Paranthropus.* J Hum Evol 46:119-162.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473-492.

Table 4.1
Summary of Means and Coefficients of Variation (CVs)

Species	Site / Reference	Type	Fruit	Foliage	*H*
Chlorocebus aethiops	Mount Assirik, Senegal Harrison (1982)	Mean	0.64	0.07	1.09
		CV	0.32	1.17	0.31
	Buffle Noir and Kalamaloue, Kavanagh (1978)	Mean	0.46	0.10	0.97
		CV	0.69	1.26	0.40
Ch. aethiops	All Sites (Average)	Mean	0.55	0.09	1.03
		CV	0.50	1.22	0.36
Cercopithecus mitis	Kakamega Forest, Kenya Cords (1986)	Mean	0.54	0.18	0.93
		CV	0.13	0.35	0.07
	Jibat Forest, Ethiopia Tesfaye et al. (2013)	Mean	0.53	0.23	1.02
		CV	0.34	0.66	0.22
	Nyungwe Forest Reserve, Kaplan et al. (1998)	Mean	0.54	0.15	1.04
		CV	0.24	0.79	0.19
C. mitis	All Sites (Average)	Mean	0.54	0.19	1.00
		CV	0.24	0.60	0.16
Colobus guereza	Kakamega Forest, Kenya Fashing (1999)	Mean	0.41	0.51	0.88
		CV	0.38	0.29	0.10
	Budongo Forest, Uganda Plumptre (2006)	Mean	0.29	0.63	0.77
		CV	0.66	0.29	0.31
	Ituri Forest, DRC Bocian (1997)	Mean	0.24	0.55	1.06
		CV	1.14	0.52	0.32
Co. guereza	Average (All Sites)	Mean	0.31	0.56	0.91
		CV	0.73	0.37	0.24
Papio anubis	Laikipia Plateau, Kenya Barton (1990)	Mean	0.28	0.28	1.09
		CV	0.85	0.72	0.20
Procolobus rufomitratus	Salonga Forest, DRC Maisels et al. (1994)	Mean	0.38	0.61	0.50
		CV	0.86	0.52	0.28
	Tana River, Kenya Marsh (1981)	Mean	0.22	0.64	0.89
		CV	0.49	0.19	0.19
	Gombe, Tanzania Clutton-Brock (1975)	Mean	0.12	0.82	0.52
		CV	0.61	0.12	0.41
Pr. rufomitratus	Average (All Sites)	Mean	0.24	0.69	0.64
		CV	0.65	0.28	0.29
Theropithecus gelada	Guassa, Ethiopia Fashing et al. (2014)	Mean	0.02	0.80	0.63
		CV	1.58	0.10	0.23

Note. See Appendix D for a detailed list of monthly data from each site.

Table 4.2
Coefficients of Variation (CVs) for Microwear Texture and Dietary Variables

Species	***HAsfc9***	***HAsfc81***	***Asfc***	***epLsar***	***H*[a]**	**FR[b]**	**FOL[c]**
Ch.aethiops	0.27	0.28	0.49	0.47	0.36	0.50	1.22
Co. guereza	0.27	0.24	0.59	0.37	0.25	0.72	0.37
C. mitis	0.37	0.30	0.46	0.36	0.12	0.28	0.53
P. anubis	0.22	0.20	0.46	0.51	0.20	0.85	0.72
Pr. rufomitratus	0.30	0.28	0.47	0.35	0.29	0.65	0.28
T. gelada	0.22	0.34	0.52	0.37	0.01	0.04	0.08

[a] Shannon Diversity Index
[b] Total fruit
[c] Total foliage

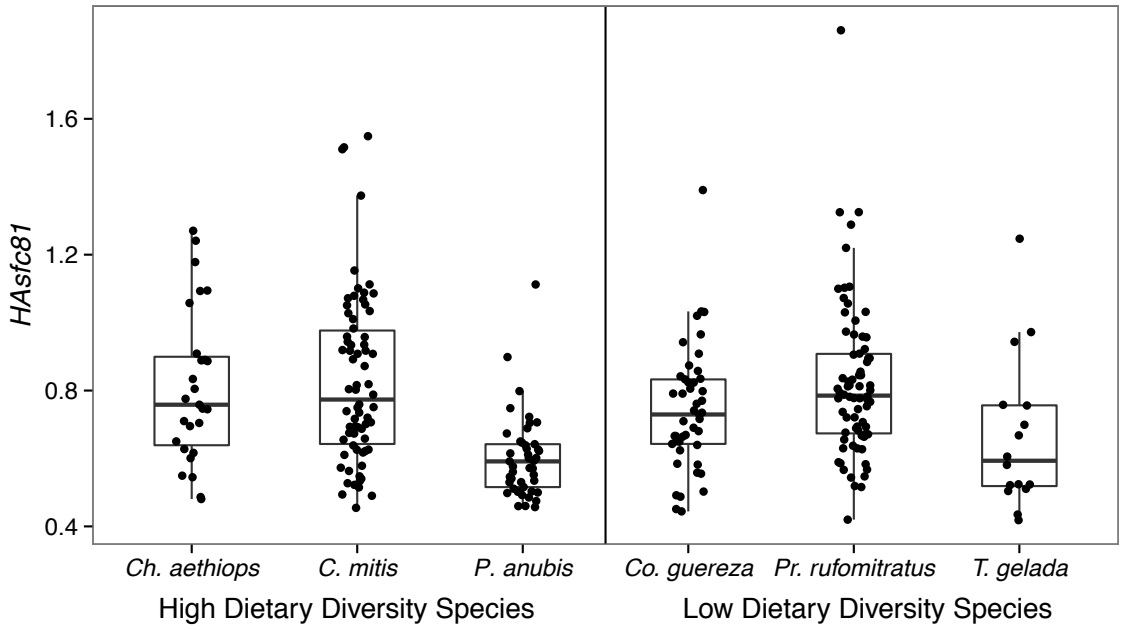

Figure 4.1. Box plots of heterogeneity at the 9x9 scale (*HAsfc81*) by species. Box plots and individual distribution points for the high dietary diversity group of *Ch. aethiops, C. mitis*, and *P. anubis* and the low dietary diversity group of *Co. guereza*, *Pr. rufomitratus,* and *T. gelada.* The high dietary diversity species differed in mean *HAsfc81* (Kruskal-Wallis $X^2 = 33.74$, df = 2, $p < 0.0001$) and variance in *HAsfc81* (Levene's Test: F (2,140) = 11.99, $p < 0.0001$). *Papio anubis* showed lower mean and variance in *HAsfc81* than both *Ch. aethiops* and *C. mitis*, while these two species did not differ in *HAsfc81* from each other (Tukey's HSD and Fisher's LSD tests). The low dietary diversity species differed in mean *HAsfc81* (ANOVA: F (2,132) = 5.76, $p < 0.01$); post-hoc tests show *Pr. rufomitratus* had greater *HAsfc81* than *T. gelada* (Tukey's HSD and Fisher's LSD) and marginally greater *HAsfc81* than *Co. guereza* (Fisher's LSD only).

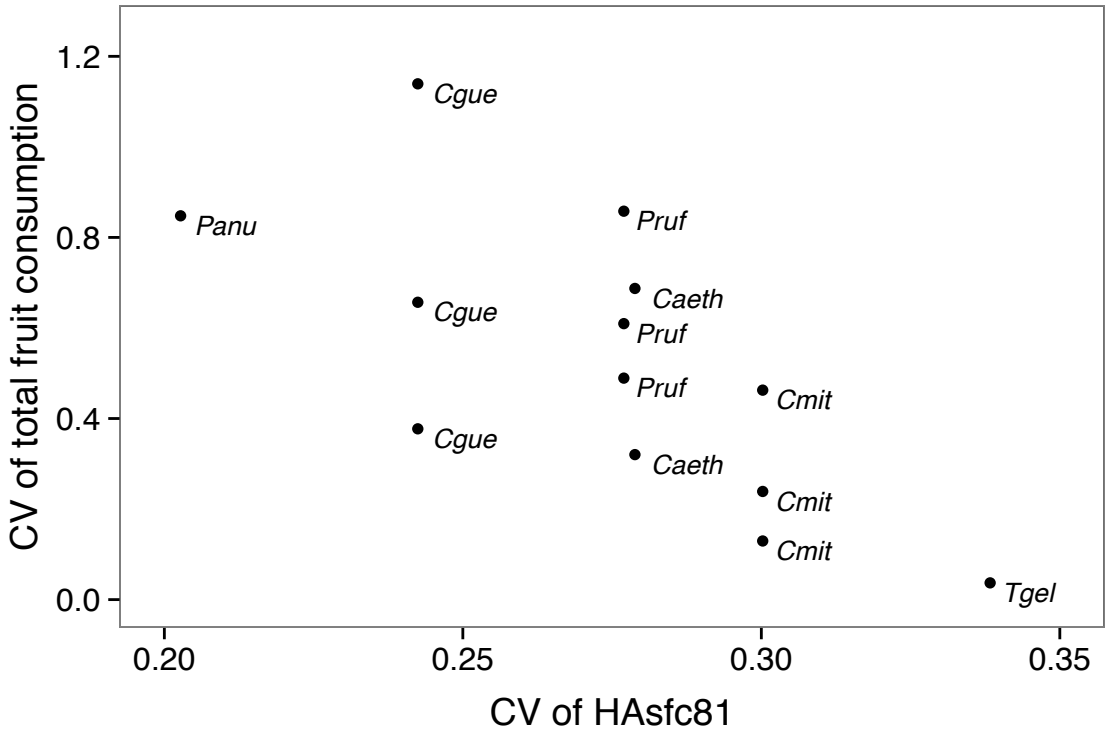

Figure 4.2. Correlation of the coeffecients of variation of fruit consumption by heterogeneity at the 9x9 scale (*HAsfc81*). Scatter plot of the coefficient of variation (CV) of total fruit consumption for each site against the CV of heterogeneity at the 9x9 scale (*HAsfc81*) for each species. The two variables were negatively correlated (Pearson product-moment correlation: $r\,(11) = -0.70$, $p < 0.01$). Species labeled with the first letter of the genus and first three or four letters of the species name.

CHAPTER 5

CONCLUSIONS

Summary

Numerous methods exist for reconstructing the diets of fossil mammals, many of which can classify a species into a broad dietary category or determine the amount of a specific dietary item an animal eats. However, dietary diversity or dietary breadth is another important but less studied component of the dietary ecology of a species. Diverse diets have been linked to greater geographic range size, greater range from the equator, and evolutionary success in relation to competitors (Potts, 1998; Gaston and Blackburn, 2000; Harcourt et al., 2002; Swihart et al., 2003; Lomolino et al., 2006; Boyles and Storm, 2007; Bowman et al., 2010; IUCN, 2010; Mbizah et al., 2012; DeSantis and Haupt, 2014). An understanding of dietary diversity in fossil species complements other dietary reconstructions of these species and clarifies their place in the larger mammalian community. Reconstructions of dietary diversity also allow for testing of macroecological patterns in fossil groups.

Dietary diversity has also played an important role in the foundations of paleoanthropology, in particular because modern humans exhibit such a diverse and flexible diet. Robinson, one of the founders of modern paleoanthropology, hypothesized that dietary expansion (i.e. a more diverse diet) had allowed the survival of the *Australopithecus* lineage, ultimately leading to *Homo*, while dietary specialization (i.e. a less diverse diet) in *Paranthropus* ultimately led to its extinction (Robinson, 1954, 1956). Potts expanded on this idea in his Variability Selection hypothesis (1998), which proposed that increased climatic fluctuations in the Pleistocene led to selection in

hominins for a broader dietary niche in the form of a wider range of dietary items and a an ability to vary the diet when needed. Potts (1998) proposed that this dietary expansion was one of the factors that led to the evolution of the *Homo* genus in contrast to earlier *Australopithecus* and *Paranthropus* species.

Reconstructions of fossil hominin diets have been greatly enhanced by dental microwear analyses. Analyses using scanning electron microscopy and microwear textures have been successful in linking specific diets to particular wear profiles (Teaford and Walker, 1984; Scott et al., 2005, 2006, 2012) and have identified strong differences in wear in *Paranthropus* species long thought to have had similar diets (Ungar et al., 2008). Some of these analyses have also identified differences among hominin species in the variance of microwear variables (Scott et al., 2005; Ungar et al., 2008, 2010). These researchers have suggested that differences in variance are related to differences among species in how varied their diets are. This interpretation makes logical sense, as the material properties of food cause microwear patterns; the more variable the material properties of foods eaten, the more variable the microwear patterns should be. Although research has shown some support for this interpretation (Scott et al., 2009), a broader association between dietary variation and variation in dental microwear should be established before using difference in variance to infer dietary diversity in fossil taxa.

The main goal of this dissertation was to provide a test of the association between dietary variation and dental microwear variation in Cercopithecidae, a group that has a broad array of diets and geographic ranges in Africa (Campbell et al., 2011; Butynski et al., 2013) and has long been used as analogs to fossil hominins (Jolly, 1970, 2009; Elton, 2006). However, different types of dietary variation exist in this group. Annual dietary

diversity, that is, how frequently a species consumes a range of dietary items and how evenly across categories this consumption occurs, is the most widely considered type of dietary diversity. Species that specialize on a particular food category consume high annual frequencies of this food and low annual frequencies of other foods, while species that are more generalized will consume more food categories at a moderate annual frequency. However, many species could be considered seasonal specialists, subsisting on a specific category of food at a high frequency for a few months of the year, particularly when this type of food is abundant. This high frequency of consumption can change monthly or seasonally, providing either a species that eats a wide variety of foods, each at a high frequency during certain months of the year, or a species that consumes fallback foods at times of preferred food scarcity. The different ways primates consume these types of foods are important to the interpretation of diets using microwear, since microwear accumulates over a short period of time. Although one individual may not be indicative of the full annual diet of a species, its microwear produces a data point reflective of the diet at a particular time within that annual cycle. As the number of individuals in a sample increases, the average of the sample should approximate the average of the species if the date of collection is random. If the date of collection is known, a more nuanced evaluation of the link between diet and microwear can be evinced.

The different chapters of this dissertation attempted to evaluate the link between variation in dental microwear and dietary variation at these different dietary levels: annually, seasonally, and monthly. In Chapter 2, "Variation in dental microwear textures as a proxy for interspecific differences in annual dietary diversity in African monkeys," I

examined the link between annual variation in diet and variation in six dental microwear texture variables within a diverse group of extant African cercopithecids. This group included 309 wild-caught specimens from eight species: three species of guenons, the blue monkey (*Cercopithecus mitis*), De Brazza's monkey (*Cercopithecus neglectus*), and the vervet (*Chlorocebus aethiops*); three papionins, the red-capped mangabey (*Cercocebus torquatus*), the anubis baboon (*Papio anubis*), and the gelada (*Theropithecus gelada*); and two colobines, the guereza (*Colobus guereza*) and the Eastern red colobus (*Procolobus rufomitratus*). I used this sample to test three hypotheses that related annual dietary diversity to dental microwear texture variation. The first hypothesis, that variance in dental microwear textures was greater in species with greater dietary diversity, was only partially supported. Two variables, complexity (*Asfc*) and scale of maximum complexity (*Smc*) were more variable in species that had high dietary diversity and less variable in species that had low dietary diversity; however, most species were not distinguishable from each other in their variance, even in these two variables. There was also little support for the second hypothesis, that species with greater dietary diversity had greater mean heterogeneity (*HAsfc*), since only a few of the species showed the expected magnitude of mean heterogeneity given their dietary diversities. There was much greater support for the third hypothesis, that overall variance in all six microwear variables was greater in species that had greater dietary diversity. Using the summed variance of the weighted principal components for each species, I found that species with greater annual dietary diversities had greater summed variances. Summed variance in microwear variables was positively correlated with dietary diversity when the one outlier, *Ce. torquatus*, was removed from the sample. However, even with

Ce. torquatus left in the analyses, summed variance was more strongly correlated with the annual frequencies of foliage and fruit consumption for each species. Species with high frequencies of foliage consumption and low frequencies of fruit consumption had low summed variances, and summed variance increased as fruit consumption increased and foliage consumption decreased.

One concern in the results of Chapter 2 was that species that had greater dietary variation also tended to have greater range size, to have greater latitudinal range, to live in more habitat types, and to live in more seasonal environments. Primates are known to vary their diet among habitats, seasons, and sites (Hemingway and Bynum, 2005); since differences microwear due to seasonal and ecological differences have been noted (Teaford and Robinson, 1989; Teaford and Glander, 1991, 1996; Teaford and Runestad, 1992; Mainland, 2003; Merceron et al., 2004, 2010), the greater variation in microwear found in species with greater dietary diversity may be due to sampling a species from more habitats, a larger geographic area, more localities, or better reflecting the annual diet by sampling the full annual cycle. Chapter 3, "Intraspecific differences in dental microwear textures among African Old World Monkeys (Cercopithecidae) and their relationship to seasonal and geographic variation", attempted to test for variation in microwear textures due to season of collection and two types of geographic location, locality and broad geographic area, in five of the species examined in Chapter 2: *Ch. aethiops*, *Co. guereza*, *C. mitis*, *P. anubis*, and *Pr. rufomitratus*. Because the specimens come from a range of sites and their diets were not observed in the weeks before their collection, it was important first to understand what expectations for microwear patterns were based on other field studies of diet. I compiled seasonal dietary data from a number

of field sites for each species, which showed differences among sites in how the primates varied their diet due to season. The cercopithecines, *Ch. aethiops*, *C. mitis*, and *P. anubis,* varied among sites in their dietary responses to seasonal change, i.e. there was no consistent pattern in any species in dietary differences among seasons. They showed few differences in their microwear textures among seasons, thus following expectations. In contrast, the colobines, *Co. guereza* and *Pr. rufomitratus*, had more consistent differences among sites in their dietary shifts due to seasonal change. They also showed predicted differences in their microwear among seasons, specifically in complexity and heterogeneity. This suggests that more care should be taken to make sure a sample includes a range of seasons when selecting specimens of colobines, and potentially other folivorous monkeys, in order to sample the full variation present in the species, particularly since they have low microwear variation overall as seen in Chapter 2. Few differences among geographic locations, either at a regional scale or among sites, were found. Additionally, differences in microwear means among geographic locations were small and only seen in *Co. guereza,* while differences in microwear variances were found among regions for *Ch. aethiops* and *C. mitis*.

The results from Chapter 3 show that, although differences exist in microwear textures among seasons for some of the species, these differences are small and are actually found in the species with lower dietary variation; differences due to geographic location also exist, but are small in comparison to the overall variation in each species. Overall, intraspecific variation is affected very little by season and geographic location. This finding indicates that, although the variation in species with high dietary diversity may be greater because they are from a wider geographic range and more seasonal

environments, the amount of variation due to this sampling is likely very small in comparison to the overall variation in each species. Thus, the greater variation in species with greater dietary diversity found in Chapter 2 is supported.

The final relationship that I examined in this dissertation was the relationship between monthly variation in diet and variation in microwear. A major question in studies of fossil hominins has been the importance of fallback foods to the morphological evolution of these species. Fallback foods are eaten at high frequencies for short periods at certain times of the year. Chapter 4, "The relationship between monthly dietary variation and variation in dental microwear textures in African Old World Monkeys (Cercopithecidae)", examined whether monthly variation in different food categories related to overall variation in microwear textures. The goal was to test if species that had similar annual dietary diversities, but varied their diets monthly, could be distinguished from each other through microwear texture analyses. In particular, I was interested in whether species that varied their dietary diversity, i.e. specialized on a food category for a short time but otherwise had diverse diets, could be distinguished from species that maintained a more even use of dietary items across the year. I used six species, the same five from Chapter 3 plus *T. gelada*, and compared them in two groups, a high dietary diversity group consisting of *Ch. aethiops*, *C. mitis*, and *P. anubis*, and a low dietary diversity group consisting of *Co. guereza, Pr. rufomitratus,* and *T. gelada*. None of the species differed in ways expected given the variation in their diets; thus, the results do not support the use of variation in microwear as a method of distinguishing monthly variation in dietary items with different mechanical properties among species with similar annual diets.

There are a few main conclusions from this dissertation. First, the variation in microwear textures found in the species examined in this dissertation was fairly high for all species, and in particular anisotropy showed great variation in each species. Second, although some variation was likely due to season, habitat, and geographic location, this variation was small in comparison to overall variation in each species. Third, heterogeneity does not closely reflect dietary diversity, and its relationship to diet is likely more complex and deserves further research. Fourth, variation in each microwear variable did not always match expected differences due to annual and seasonal dietary diversity as well. This conclusion throws some doubt on whether variation in microwear variables should be used to infer differences in dietary variation, as some researchers have done (i.e. Scott et al., 2005; Ungar et al., 2010). Although complexity (*Asfc*) and scale of maximum complexity (*Smc*) appear to best reflect differences in dietary variation, they may only account for variation in particular food categories. This result, in addition to results using overall microwear variation, support the final conclusion: comparisons using multivariate methods that incorporate all six conventional microwear texture variables appear better at distinguishing differences in dietary diversity. Since each texture variable describes something different about the topography of the dental wear, and different foods affect wear in different ways, it makes sense that incorporating all of the variables simultaneously into an analysis may yield better results. This fact is particularly true for comparisons of dietary diversity, since dietary diversity is a measure that involves all the food categories consumed. However, other researchers have also found the most distinctive results when using multivariate methods (i.e. Merceron et al., 2009; Scott, 2012). These results call for greater use of multivariate techniques in

analyzing dental microwear textures in the future, rather than only single comparisons of texture variables.

Future Directions

The results from this dissertation suggest a few directions for future research in the area of dental microwear texture analysis and its relationship to dietary variation. The first direction is to test the statistical method of the summed variances of principal components analyses and its relationship to dietary diversity in a wider array of species. Although the results from this paper suggest a link between the summed variance and dietary diversity, it also suggests stronger relationships between summed variance and the annual frequencies of fruit and foliage in the diet. Testing this relationship in other species will help to verify its validity in inferring dietary diversity in fossil species.

The fact that multivariate methods show promise for better connections between diet and microwear patterns suggests the second direction for further research into reconstructing dietary diversity: using multiple lines of evidence using the same specimens. Because dietary diversity reflects a range of dietary parameters, the best way to approximate it may be through a multi-proxy approach, as different dietary proxies may record different aspects of the diet that relate to dietary diversity. Methods such as stable isotope analyses, topographic analyses, and microwear analyses of both anterior and posterior dentition might as a whole be able to separate species based on dietary diversity.

Another clear avenue for further research is examining microwear in individuals where diet has been directly observed. A number of researchers are currently conducting

this type of analysis in laboratory settings (e.g. Karme et al., 2014; Teaford et al., 2015) where foods can be experimentally controlled. However, it is also important to continue this type of research in wild populations where diet reflects what might be expected in fossil primates.

The final direction suggested by the results of this dissertation is further investigation into the relationship between abrasiveness and variation in microwear. Results from Chapter 2 suggested a relationship between high frequencies of foliage consumption and low variation in microwear; these results support work by Schulz et al. (2013) and ongoing work by Karme et al. (2014) that have suggested that abrasive diets yield less variant microwear patterns, while less abrasive diets yield more variant microwear patterns. Further research into the causes of this relationship will help to identify whether variation in microwear should be used to infer dietary parameters in fossil species.

References

Bowman DM, Murphy BP, McMahon CR. 2010. Using carbon isotope analysis of the diet of two introduced Australian megaherbivores to understand Pleistocene megafaunal extinctions. J Biogeogr 37:499-505.

Boyles JG, Storm JJ. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLoS One 2(7):e672.

Butynski TM, Kingdon J, Kalina J, eds. 2013. Mammals of Africa: Volume 2, Primates. London: Bloomsbury, 560 pp.

Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. 2011. Primates in Perspective. Oxford: Oxford University Press, 864 pp.

DeSantis LR, Haupt RJ. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. Biol Lett 10(4):20140203.

Elton S. 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. J R Anthropol Inst 12:19-38.

Gaston KJ, Blackburn TM. 2000. Pattern and process in macroecology. Oxford: Blackwell Science, 377 pp.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization, and extinction in primates. J Biogeogr 29:445-456.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 57-103.

IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. <http://www.iucnredlist.org>. Downloaded on 27 January 2011.

Jolly CJ. 1970. The seed eaters: A new model of hominid differentiation based on a baboon analogy. Man, 5: 5-26.

Jolly CJ. 2009. Fifty years of looking at human evolution: backward, forward, and sideways. Curr Anthropol 50:187-199.

Karme A, Rannikko J, Bertin T, Clauss M, Fortelius M. 2014. Chewing machine and tooth wear: how plant materials and grit affect teeth. Podium presentation, Society of Vertebrate Paleontology 74th Annual Meetings.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd edition. Sunderland, Mass: Sinauer Associates, Inc. 841 pp.

Mainland IL. 2003. Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*) and its implications for dietary reconstruction. J Archaeol Sci 30:1513-1527.

Mbizah MM, Marino J, Groom RJ. 2012. Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*). S Afr J Wildlife Research 42:94-103.

Merceron G, Viriot L, Blondel C. 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*) from Chizé (Western France) and relation to food composition. Small Ruminant Res 53:125-132.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542.

Merceron G, Scott J, Scott RS, Geraads D, Spassov N, Ungar PS. 2009. Folivory or fruit/seed predation for *Mesopithecus*, an earliest colobine from the late Miocene of Eurasia? J Hum Evol 57:732-8.

Potts R. 1998. Variability selection in hominid evolution. Evol Anthropol 7:81-96.

Robinson JT. 1954. The genera and species of the Australopithecinae. Am J Phys Anthropol 12:181-200.

Robinson JT. 1956. The dentition of the Australopithecinae. Transvaal Mus Mem 9:1-185.

Schulz E, Piotrowski V, Clauss M, Mau M, Merceron G, Kaiser TM. 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS ONE 8:e56167.

Scott JR. 2012. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution. PhD Dissertation, University of Arkansas.

Scott RS, Ungar PS, Bergstromb TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436: 693-695

Scott RS, Ungar PS, Bergstromb TS, Brown CA, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51: 339-349

Scott RS, Teaford MF, Ungar PS. 2009. Dietary diversity and dental microwear variability in *Theropithecus gelada* and *Papio cynocephalus*. Am J Phys Anthropol (S48):234.

Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. 2003. Responses of 'resistant'vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1-18.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Glander KE. 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk M, Rosenberger A, Garber P, eds. Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 433-449.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401.

Teaford MF, Runestad JA. 1992. Dental microwear and diet in Venezuelan primates. Am J Phys Anthropol 88:347-364.

Teaford MF, Walker AC. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am J Phys Anthropol 64:191-200.

Teaford MF, Taylor AB, Iriarte-Diaz J, Ross CF, Vinyard CJ. 2015. Rates of dental microwear in laboratory primates track changes in food items consumed. Am J Phys Anthropol 156(S60):302.

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3:1-6.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis.* Phil Trans R Soc B 365:3345-3354.

REFERENCES

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press, 608pp.

Anapol F, Lee S. 1994. Morphological adaptation to diet in platyrrhine primates. Am J Phys Anthropol 94:239-261.

Barton RA. 1990. Foraging Strategies, Diet And Competition In Olive Baboons. PhD Dissertation, University of St. Andrews.

Beeson M. 1989. Seasonal dietary stress in a forest monkey (*Cercopithecus mitis*). Oecologia 78:565-570.

Beeson M, Tame S, Keeming E, Lea SEG. 1996. Food habits of guenons (*Cercopithecus* spp.) in Afro-montane forest. Afr J Ecol 34:202-210.

Benefit BR. 1987. The Molar Morphology, Natural History, and Phylogenetic Position of the Middle Miocene Monkey *Victoriapithecus*, and Their Implications for Understanding the Evolution of the Old World Monkeys. PhD Dissertation, New York University.

Benefit BR. 1999. Biogeography, dietary specialization and the diversification of African Plio-Pleistocene monkeys. In: Bromage TG, Schrenk F, eds. African Biogeography, Climate Change, and Human Evolution. Oxford: Oxford University Press, pp. 172-188.

Benefit BR. 2000. Old World monkey origins and diversification: an evolutionary study of diet and dentition. In: Whitehead PF, Jolly CJ, eds. Old World Monkeys. Cambridge:Cambridge University Press, pp. 133-179.

Benefit BR, McCrossin ML. 1990. Diet, species diversity and distribution of African fossil baboons. Kroeber Anthropol Soc Pap 71:79-93.

Birchette M. 1981 Postcranial remains of *Cercopithecoides*. Am J Phys Anthropol 54:201

Blackburn TM, Gaston KJ. 1996. A sideways look at patterns in species richness, or why there are so few species outside the tropics. Biodivers Lett 3:44-53.

Bocian CM. 1997. Niche separation of black-and-white colobus monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri Forest. PhD Dissertation, City University of New York.

Bohm M, Mayhew PJ. 2005. Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata: Cercopithecidae). Biol J Linn Soc 85:235-246.

Bowman DM, Murphy BP, McMahon CR. 2010. Using carbon isotope analysis of the diet of two introduced Australian megaherbivores to understand Pleistocene megafaunal extinctions. J Biogeogr 37:499-505.

Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. J Hum Evol 55:1118-1137.

Boyles JG, Storm JJ. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLoS One 2(7):e672.

Brown JH. 1984. On the relationship between abundance and distribution of species. Am Nat 124:255-279.

Brown JH. 1995. Macroecology. Chicago: University of Chicago Press, 284 pp.

Brown JH, Maurer BA. 1989. Macroecology: the division of food and space among species on continents. Science 243:1145-1160.

Brown JH, Sax DF. 2004. Geographic gradients in diversity. In: Lomolino MV, Sax DF, Brown JH, eds. Foundations of Biogeography: Classic Works with Commentaries. The University of Chicago Press, Chicago, 1328 pp.

Brown JH, Mehlman DW, Stevens GC. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-and low-density subpopulations. Ecol Monogr 60:1-26.

Butynski TM, Kingdon J, Kalina J, eds. 2013. Mammals of Africa: Volume 2, Primates. London: Bloomsbury, 560 pp.

Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. J Hum Evol 63:85-98.

Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. 2011. Primates in Perspective. Oxford: Oxford University Press, 864 pp.

Cartmill M. 2002. Paleoanthropology — science or mythological charter? Anthropol Res 58:183-201.

Cerling TE, Mbua E, Kirera FM, Kyalo Manthi F, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. Proc Nat Acad Sci USA 108: 9337-9341.

Chapman CA, Chapman LJ. 1990. Dietary variability in primate populations. Primates 31:121-128.

Chapman CA, Gautier-Hion A, Oates JF, Onderdonk DA. 1999. African primate communities: determinants of structure and threats to survival. In: Fleagle JG, Janson CH, Reed KE, eds. Primate Communities. Cambridge: Cambridge University Press, pp 1-37.

Cheney DL, Seyfarth RM. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. Behaviour, 76(1), 25-60.

Clutton-Brock TH. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa. Folia Primatol 23:165-207.

Codron D, Luyt J, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J. 2005. Utilization of savanna-based resources by baboons during the Plio-Pleistocene. S Afr J Sci 101:254–248.

Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation? Int J Primatol 29:757-772.

Conover WJ, Johnson ME, Johnsons MM. 1981. A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. Technometrics 23:351-361.

Constantino PJ, Wright BW. 2009. The importance of fallback foods in primate ecology and evolution. Am J Phys Anthropol 140:599-602.

Cook RJ, Farewell VT. 1996. Multiplicity considerations in the design and analysis of clinical trials. J R Statistic Soc A, 159:93-110.

Cooke CA. 2012. The Feeding, Ranging, and Positional Behaviors of *Cercocebus torquatus*, the Red-Capped Mangabey, in Sette Cama, Gabon: A Phylogenetic Perspective. PhD Dissertation, The Ohio State University.

Cords M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. J Anim Ecol 55:811-827.

Corruccini RS, Henderson AM. 1978. Multivariate dental allometry in primates. Am J Phys Anthropol 48:203-208.

Cowlishaw G, Hacker JE. 1997. Distribution, diversity, and latitude in African primates. Am Nat 150:505-512.

Daegling DJ, Grine FE. 1999. Occlusal microwear in *Papio ursinus*: The effects of terrestrial foraging on dental enamel. Primates 40:559-572.

Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. PLoS One 6(8):e23095.

Dandelot P. 1959. Note sur la classificatlon des Cercopithèques du groupe *aethiops*. Mammalia, 23:357-368.

Dandelot P. 1968. Primates: Anthropoidea. In: Meester J, ed. Smithsonian Institution Preliminary Identification Manual for African Mammals, Part 24. Washington, D.C.: Smithsonian Institution, pp. 24:1-80.

Dandelot P. 1974. Order Primates. In: Meester J, Setzer H, eds. The Mammals of Africa: An Identification Manual, Part 3. Washington, D.C.: Smithsonian Institution Press, pp. 1–43.

Darwin C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray, 502 pp.

Decker BS. 1989. Effects of habitat disturbance on the behavioral ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratus*). PhD Dissertation, Emory University.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125:152-161.

DeSantis LR, Haupt RJ. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. Biol Lett 10(4):20140203.

DeSantis LR, Scott JR, Schubert BW, Donohue SL, McCray BM, Van Stolk CA, Winburn AA, Greshko MA, O'Hara MC. 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivorous mammals. PloS ONE 8(8):e71428.

Dobzhansky T. 1950. Evolution in the tropics. Reprinted in: Lomolino MV, Sax DF, Brown JH, eds. Foundations of Biogeography: Classic Works with Commentaries. Chicago: The University of Chicago Press, 1328 pp.

Donnely SM, Kramer A. 1999. Testing for multiple species in fossil samples: an evaluation and comparison of tests for equal relative variation. Am J Phys Anthropol 108:507-529.

Dunbar RIM. 1977. Feeding ecology of gelada baboons: a preliminary report. In: Clutton-Brock TH, ed. Primate Ecology. London: Academic Press, pp. 250–273.

Dunbar RIM, Dunbar EP. 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. Folia Primatol 21:36-60.

Eeley HAC, Foley RA. 1999. Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodivers Conserv 8:1033-1056.

Eeley HAC, Lawes MJ. 1999. Large scale patterns of species richness and species range size in anthropoid primates. In: Fleagle JG, Janson CH, Reed KE, eds. Primate Communities. Cambridge: Cambridge University Press, pp. 191-219.

El-Zaatari S, Grine FE, Teaford MF, Smith HF. 2005. Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. J Hum Evol 49:1–26.

Elton C. 1927. Animal Ecology. London: Sidgwick and Jackson, 207 pp.

Elton S. 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. J R Anthropol Inst 12:19-38.

Fashing PJ. 1999. The Behavioral Ecology of an African Colobine Monkey: Diet, Range Use, and Patterns of Intergroup Aggression in Eastern Black and White Colobus Monkeys (*Colobus guereza*). PhD Dissertation, Columbia University.

Fashing PJ. 2011. African colobine monkeys: their behavior, ecology, and conservation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective. Oxford: Oxford University Press, pp. 203-229.

Fashing PJ, Oates JF. 2013. *Colobus guereza*. In: Kingdon J, Happold D, Butynski T, eds. Mammals of Africa. London: Bloomsbury Publishing, pp. 111-119.

Fashing PJ, Nguyen N, Venkataraman VV, Kerby JT. 2014. Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropith and hominin dietary evolution. Am J Phys Anthropol 155:1-16.

Fleagle JG. 2013. Primate Adaptation and Evolution: 3rd Edition. San Diego: Academic Press, 464 pp.

Fleagle JG, Gilbert CC, Baden AL. 2010. Primate cranial diversity. Am J Phys Anthropol 142:565-578.

Foley RA. 1993. African terrestrial primates: the comparative evolutionary biology of Theropithecus and the Hominidae. In: Jablonski N, ed. Theropithecus: The Rise and Fall of a Primate Genus. Cambridge: Cambridge Univeristy Press, pp. 245-270.

Franklin J. 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge: Cambridge University Press, 338 pp.

Galat G, Galat-Luong A. 1977. Démographie et régime alimentaire d'une troupe de *Cercopithecus aethiops sabaeus* en habitat marginal au nord Sénégal. Rev Ecol-Terre Vie 31:557-577.

Galbany J, Estebaranz F, Martínez LM, Pérez-Pérez A. 2009. Buccal dental microwear variability in extant African Hominoidea primates: taxonomy versus ecology. Primates 50:221-230.

Gaston KJ, Blackburn TM. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. J Animal Ecol 66:579-601.

Gaston KJ, Blackburn TM. 2000. Pattern and process in macroecology. Oxford: Blackwell Science, 377 pp.

Gaston KJ. 1994. Rarity. Population and Community Biology Series 13. London; New York: Chapman and Hall, 205 pp.

Gaston KJ. 1998. Species-range size distributions: products of speciation, extinction and transformation. Phil Trans R Soc B 353:219-230.

Gaston KJ, Blackburn TM. 2000. Pattern and Process in Macroecology. Oxford: Blackwell Science, 377 pp.

Gautier-Hion A, Gautier JP. 1978. Le singe de Brazza: une strategic originale. Z Tierpsychol 46:84-104.

Gogarten JF, Grine FE. 2013. Seasonal mortality patterns in primates: implications for the interpretation of dental microwear. Evol Anthropol 22:9-19.

Goldstein S, Post D, Melnick D. 1978. An analysis of cercopithecoid odontometrics. I. The scaling of the maxillary dentition. Am J Phys Anthropol 49:517-532.

Gordon KD. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am J Phys Anthropol 59:195-215.

Gregory RD, Gaston KJ. 2000. Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. Oikos 88:515-526.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. J Hum Evol 15:783-822.

Grine FE. 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. Scanning Microscopy 1:647-656.

Grine FE, Ungar PS, Teaford MF. 2006. Was the Early Pliocene hominin '*Australopithecus*' anamensis a hard object feeder? S Afr J Sci 102:301

Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006. Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. J Hum Evol 51:297-319.

Grine FE, Sponheimer M, Ungar PS, Lee-Thorp J, Teaford MF. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. Am J Phys Anthropol 148:285-317.

Grinnell J. 1917. The niche-relationships of the California Thrasher. Auk 34:427–433.

Groves CP. 2001. Primate Taxonomy. Washington D.C.: Smithsonian Institution Press, 350 pp.

Groves CP. 2005. Order Primates. In: Wilson DE, Reeder DM, eds. Mammal Species of the World: a Taxonomic and Geographic Reference. Baltimore: Johns Hopkins University Press, pp. 111-184.

Groves CP. 2007. The taxonomic diversity of the Colobinae of Africa. J Anthropol Sci 85:7-34.

Groves CP, Kingdon J. 2013. Genus *Chlorocebus*: Savanna Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 264-266.

Grubb P, Butynski TM, Oates JF, Bearder SK, Disotell TR, Groves CP, Struhsaker TT. 2003. Assessment of the diversity of African primates. Int J Primatol 24:1301-1357.

Grubb P, Struhsacker TT, Siex KS. 2013. Subgenus Piliocolobus: Red Colobus Monkeys. In: Butynski TM, Kingdon J, Kalina J, eds. Mammals of Africa, Vol. 2: Primates. London: Bloomsbury, pp. 125-128.

Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210-221.

Hanski I. 1994. A practical model of metapopulation dynamics. J Animal Ecol 63: 151-162.

Hanski I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. In: Hanski I, Gilpin ME, eds. Metapopulation Biology: Ecology, Genetics, and Evolution. San Diego: Academic Press, pp 69-91.

Hanski I, Kouki J, Halkka A. 1993. Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs RE, Schluter D, eds. Species Diversity in Ecological Communities. Chicago: University of Chicago Press, pp. 108-116.

Harcourt AH. 2000. Latitude and latitudinal extent: a global analysis of Rapoport effect in a tropical mammalian taxon: Primates. J Biogeog 27:1169-1182.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization, and extinction in primates. J Biogeogr 29:445-456.

Harding RS. 1981. An order of omnivores: nonhuman primate diets in the wild. In: Harding RS, Teleki G, eds. Omnivorous Primates: Gathering and hunting in human evolution. New York: Columbia University Press, pp. 191-214.

Harrison MJ. 1982. The Behavioural Ecology of Green Monkeys (*Cercopithecus sabaeus*) at Mt. Assirik, Senegal. PhD Dissertation, University of Stirling.

Harrison MJ. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Anim Behav 31:969-977.

Haupt RJ, DeSantis LR, Green JL, Ungar PS. 2013. Dental microwear texture as a proxy for diet in xenarthrans. J Mammal 94:856-866.

Heino J. 2005. Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. Freshwater Biol 50: 1578-1587.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 57-103.

Hernández Fernández, M. 2001. Discriminant bioclimatic capacity of terrestrial mammal faunas. Global Ecol Biogeogr 10:113-128.

Hernández Fernández M, Vrba ES. 2005a. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. J Biogeogr 32:903-918.

Hernández Fernández M, Vrba ES. 2005b. Body size, biomic specialization and range size of African large mammals. J Biogeogr 32:1243-1256.

Hernández Fernández M, Vrba ES. 2005c. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. Evol Ecol 19:199-219.

Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415–427.

Hylander WL. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science 189:1095-1098.

Isbell LA, Pruetz JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behav Ecol Sociobiol 42:123-133.

IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. <http://www.iucnredlist.org>. Downloaded on 27 January 2011.

Iwamoto T. 1979. Feeding ecology. In: Kawai M, ed. Ecological and Sociological Studies of Gelada Baboons. Basel: Springer, pp. 279–330.

Jablonski D. 1986. Background and mass extinctions: The alternation of macroevolutionary regimes. Science 231:129-133.

Jablonski D. 1987. Heritability at the species level: Analysis of geographic ranges of Cretaceous mollusks. Science 238:360-363.

Jablonski D, Roy K. 2003. Geographical range and speciation in fossil and living mollusks. Proc R Soc Lond B 270:401-406.

Jaffe KE, Isbell LA. 2011. The guenons: polyspecific associations in socioecological perspective. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective. Oxford: Oxford University Press, pp. 277-300.

Jernvall J, Selänne L. 1999. Laser confocal microscopy and geographic information systems in the study of dental morphology. Palaeontol Electron 2:18.

Jolly CJ. 1970. The seed eaters: A new model of hominid differentiation based on a baboon analogy. Man, 5: 5-26.

Jolly CJ. 2009. Fifty years of looking at human evolution: backward, forward, and sideways. Curr Anthropol 50:187-199.

Kamilar JM. 2006. Geographic Variation in Primate Behavior and Ecology: from populations to communities. PhD dissertation. Stony Brook, NY: State University of New York.

Kaplin BA, Munyaligoga V, Moermond TC. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). Biotropica 30:56-71.

Kaplan and Moermond 2000

Karme A, Rannikko J, Bertin T, Clauss M, Fortelius M. 2014. Chewing machine and tooth wear: how plant materials and grit affect teeth. Podium presentation, Society of Vertebrate Paleontology 74th Annual Meetings.

Kavanagh, M. 1978. The diet and feeding behaviour of *Cercopithecus aethiops tantalus*. Folia Primatol 30:30-63.

Kay RF. 1974. Body size, molar structure and diet in primates. Am J Phys Anthropol 41:487-488.

Kay RF. 1975. Allometry and early hominids. Science 189:61-64.

Kay RF. 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. Am J Phys Anthropol 46:327-352.

Kay RF. 1978. Molar structure and diet in extant Cercopithecidae. In: Butler PM, Joysey KA, eds. Development, Function, and Evolution of Teeth. New York: Academic Press, pp. 309-339.

Kay RF. 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. Am J Phys Anthropol 55:141-151.

Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, eds. Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys and apes. New York: Columbia University Press, pp. 21-53.

Kay RF, Hiiemae KM. 1974. Jaw movement and tooth use in recent and fossil primates. Am J Phys Anthropol 40:227-256.

Kay RF, Hylander WL. 1978. The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In: Montgomery GG, ed. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution, pp. 173–191.

Kimbel WH, Delezene LK. 2009. “Lucy” redux: A review of research on *Australopithecus afarensis*. Am J Phys Anthropol 140(S49):2-48.

Kingdon J, Butynski TM, De Jong Y. 2008. *Papio anubis*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 December 2014.

Kingdon J, Struhsaker T, Oates JF, Hart J, Groves CP. 2008. *Colobus guereza*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 December 2014.

Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. Am J Phys Anthropol 81:5-15.

Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int J Primatol 14:207-227.

Klein RG. 1999. The Human Career: Human Biological and Cultural Origins. Chicago: University of Chicago Press, 840 pp.

Krebs CJ. 1999. Ecological Methodology. Menlo Park, CA: Benjamin/Cummings, 624 pp.

Kunz BK, Linsenmair KE. 2008. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. Folia Primatol 79:31-51.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee and Cercopithecoid model for interpreting the evolution of the hominin diet. In: Ungar PS, ed. Evolution of the human diet: the known, the unknown, and the unknowable. Oxford: Oxford University Press, pp. 324-343.

Lambert JE. 2009. Primate fallback strategies as adaptive phenotypic plasticity: scale, process, and pattern. Am J Phys Anthropol 140:759-766.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am J Phys Anthropol 125:363-368.

Lappalainen J, Soininen J. 2006. Latitudinal gradients in niche breadth and position - regional patterns in freshwater fish. Naturwissenschaften 93:246-250.

Lawes MJ. 1990. The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. J Biogeogr 17:669-680.

Lee PC, Hauser MD. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. J Anim Ecol 67:347-358.

Lee-Thorp J, Likius A, Mackaye HT, Vignaud P, Sponheimer M, Brunet M. 2012. Isotopic evidence for an early shift to C4 resources by Pliocene hominins in Chad. Proc Natl Acad Sci USA 109:20369–20372.

Lehman SM. 2004. Biogeography of the primates of Guyana: effects of habitat use and diet on geographic distribution. Int J Primatol 25:1225-1242.

Lennon JJ, Turner JRG, Connell D. 1997. A metapopulation model of species boundaries. Oikos 78:486-502.

Levene H. 1960. Robust tests for equality of variances. In: Olkin I, ed. Contributions to Probability and Statistics. Stanford: Stanford University Press, pp. 278-292.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15: 237-240.

Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldså J, Rahbek C. 2012. The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. J Biogeogr 39:1189-1205.

Lockwood CA, Kimbel WH, Johanson DC. 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. J Hum Evol 39:23-55.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd edition. Sunderland, Mass: Sinauer Associates, Inc. 841 pp.

Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, eds. Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge: Cambridge University Press, pp. 173-203.

Lucas PW, Constantino PJ, Chalk J, Ziscovici C, Wright BW, Fragaszy DM, Hill DA, Lee JJW,Chai H, Darvell BW, Lee PKD, Yuen TDB. 2009. Indentation as a technique to assess the mechanical properties of fallback foods. Am J Phys Anthropol 140:643-652.

Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. J R Soc Interface 10:20120923.

MacArthur RH. 1972. Geographical Ecology: Patterns in the Distribution of Species. New York: Harper and Row, 269 pp.

Mainland IL. 2003. Dental microwear in grazing and browsing Gotland sheep (*Ovis aries*) and its implications for dietary reconstruction. J Archaeol Sci 30:1513-1527.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. Int J Primatol 15:681-701.

Marsh CW. 1981. Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana River, Kenya. Folia Primatolog 35:147-178.

Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219-1235.

Mbizah MM, Marino J, Groom RJ. 2012. Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog (*Lycaon pictus*). S Afr J Wildlife Research 42:94-103.

McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): Implications for fallback foods and dental adaptation. Am J Phys Anthropol 154:413-423.

Merceron G, Viriot L, Blondel C. 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*) from Chizé (Western France) and relation to food composition. Small Ruminant Res 53:125-132.

Merceron G, Blondel C, De Bonis L, Koufos GD, Viriot L. 2005. A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). Palaios 20:551-561.

Merceron G, Scott J, Scott RS, Geraads D, Spassov N, Ungar PS. 2009. Folivory or fruit/seed predation for *Mesopithecus*, an earliest colobine from the late Miocene of Eurasia? J Hum Evol 57:732-8.

Merceron G, Escarguel G, Angibault JM, Verheyden-Tixier H. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5(3):e9542.

Mitani M. 1989. *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of southwestern Cameroon. Primates 30:307-323.

Napier PH. 1981. Catalogue of Primates in the British Museum (Natural History) and elsewhere in the British Isles, part II: Family Cercopithecidae, subfamily Cercopithecinae. London: British Museum, 120pp.

Nunes A. 1995. Foraging and ranging patterns in white-bellied spider monkeys. Folia Primatol 65:85–99.

Nystrom P, Phillips-Conroy JE, Jolly CJ. 2004. Dental microwear in anubis and hybrid baboons (*Papio hamadryas*, s.l.) living in the Awash National Park, Ethiopia. Am J Phys Anthropol 125:279-291.

Oates JF. 1974. The Ecology and Behaviour of the Black and White Colobus Monkey (*Colobus guereza* Rueppell) in East Africa. PhD Dissertation, University of London.

Oates JF. 1977. The social life of a black-and-white colobus monkey, *Colobus guereza*. Zeitschrift für Tierpsychologie 45:1-60.

Oates JF. 1994. The natural history of African colobines. In: Oates JF, Davies AG, eds. Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge: Cambridge University Press, pp. 75-128.

Okecha AA, Newton-Fisher NE. 2006. The diet of olive baboons (*Papio anubis*) in the Budongo Forest Reserve, Uganda. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, eds. Primates of Western Uganda. New York: Springer, pp. 61-73.

Palombit, RA. 2013. *Papio anubis*. In: Kingdon J, Happold D, Butynski T, eds. Mammals of Africa. London: Bloomsbury Publishing, pp. 233-239.

Passy SI. 2012. A hierarchical theory of macroecology. Ecol Lett 15:923-934.

Pianka ER. 1966. Latitudinal gradients in species diversity: a review of concepts. Am Nat 100: 33-46.

Plumptre A. 2006. The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda: Effects of logging on primate diets. In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, eds. Primates of Western Uganda. New York: Springer, pp. 345-371.

Potts R. 1998. Variability selection in hominid evolution. Evol Anthropol 7:81-96.

Pruetz JD, Isbell LA. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. Behav Ecol Sociobiol 49:38-47.

Rapoport EH. 1982. Areography: Geographical Strategies of Species. Oxford: Pergamon Press, 286 pp.

Reed DNO. 1997. Contour mapping as a new method for interpreting diet from tooth morphology. Am J Phys Anthropol (S24):194.

Reed KE, Fish JL. 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman DA, van Schaik CP, eds. Seasonality in Primates: Studies of Living and

Extinct Human and Non-Human Primates. Cambridge: Cambridge University Press, pp. 489-518.

Robinson, JT. 1954. The genera and species of the Australopithecinae. Am J Phys Anthropol 12:181-200.

Robinson JT. 1956. The dentition of the Australopithecinae. Transvaal Mus Mem 9:1-185.

Rohatgi A. 2014. WebPlotDigitizer, Version 3.3. <http://arohatgi.info/WebPlotDigitizer>.

Rohde K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514-527.

Rose JC, Ungar PS. 1998. Gross dental wear and dental microwear in historical perspective. In: Alt KW, Rosing FW, Teschler-Nicola M, eds. Dental Anthropology: Fundamentals, Limits, and Prospects. Vienna: Springer, pp. 349-386.

Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45:281-297.

Rowe N. 1996. The pictorial guide to the living primates. Charlestown, RI: Pogonias Press.

Ryan AS. 1981. Anterior dental microwear and its relationship to diet and feeding behavior in three African primates (*Pan troglodytes troglodytes*, *Gorilla gorilla gorilla* and *Papio hamadryas*). Primates 22:533-550.

Ryan AS, Johanson DC. 1989. Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and nonhuman primates. J Hum Evol 18:235-268.

Schluter D. 2000. The ecology of adaptive radiation. Oxford: Oxford University Press, 296 pp.

Schulz E, Piotrowski V, Clauss M, Mau M, Merceron G, Kaiser TM. 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS ONE 8:e56167.

Scott JE, McAbee KR, Eastman MM, Ravosa MJ. 2014. Experimental perspective on fallback foods and dietary adaptations in early hominins. Biol Lett 10:20130789.

Scott JR. 2012. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution. PhD Dissertation, University of Arkansas.

Scott RS, Ungar PS, Bergstromb TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436: 693-695.

Scott RS, Ungar PS, Bergstromb TS, Brown, CA, Grine FE, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. J Hum Evol 51:339-349.

Scott RS, Teaford MF, Ungar PS. 2009. Dietary diversity and dental microwear variability in *Theropithecus gelada* and *Papio cynocephalus*. Am J Phys Anthropol (S48):234.

Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551-579.

Semprebon GM, Godfrey LR, Solounias N, Sutherland MR, Jungers WL. 2004. Can low-magnification stereomicroscopy reveal diet? J Hum Evol 47:115-144.

Simpson GG. 1964. Species density of North American recent mammals. Syst Zool 13:57-73.

Slatyer RA, Hirst M, Sexton JP. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol Lett 16:1104-1114.

Slove J, Janz N. 2010. Phylogenetic analysis of the latitude-niche breadth hypothesis in the butterfly subfamily Nymphalinae. Ecol Entomol 35:768-774.

Snaith TV, Chapman CA. 2008. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. Behav Ecol 19:1289-1296.

Solounias N, Hayek LC. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. J Zool 229: 421-445.

Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling T, Dearing D, Ehleringer J. 2003. Nitrogen isotopes in mammalian herbivores: hair δ15N values from a controlled feeding study. Int J Osteoarchaeol 13:80-87.

Sponheimer M, Loudon JE, Codron D, Howells ME, Pruetz JD, Codron J, de Ruiter DJ, Lee-Thorp JA. 2006. Do “savanna” chimpanzees consume C4 resources? J Hum Evol 51:128-133.

Sponheimer M, Passey B, de Ruiter D, Guatelli-Sternberg D, Cerling T, Lee-Thorp J. 2006. Isotopic evidence for dietary flexibility in the early hominin *Paranthropus robustus*. Science 314: 980-982.

Sponheimer M, Codron D, Passey BH, de Ruiter DJ, Cerling TE, Lee-Thorp JA. 2009. Using carbon isotopes to track dietary change in modern, historical, and ancient primates. Am J Phys Anthropol 140:661-670.

Sponheimer M, Alemseged Z, Cerling TE, Grine FE, Kimbel WH, Leakey M G, Lee-Thorp JA, Manthi FK, Reed KE, Wood BW, Wynn JG. 2013. Isotopic evidence of early hominin diets. Proc Natl Acad Sci USA 110:10513-10518.

Steel R. 2012. The Effects of Habitat Parameters on the Behavior, Ecology, and Conservation of the Udzungwa Red Colobus Monkey (*Procolobus gordonorum*). PhD Dissertation, Duke University.

Stehli FG, Douglas RG, Newell ND. 1969. Generation and maintenance of gradients in taxonomic diversity. Science 164:947-949.

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240-256.

Strait DS, Constantino P, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA, Weber GW, Wang Q, Byron C, Slice DE, Chalk J, Smith AL, Smith LC, Wood S, Berthaume M, Benazzi S, Dzialo S, Tamvada K, Ledogar JA. 2013. Diet and dietary adaptations in early hominins: The hard food perspective. Am J Phys Anthropol 151:339-355.

Strait SG. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. J Mammal 74:391-402.

Strait SG. 1997. Tooth use and the physical properties of food. Evol Anthropol 5:199-211.

Struhsaker TT. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. Recent Adv Primatol 1:225-248.

Stynder DD, Ungar PS, Scott JR, Schubert BW. 2012. A dental microwear texture analysis of the Mio-Pliocene hyaenids from Langebaanweg, South Africa. Acta Palaeontol Pol 57:485-496.

Swedell L. 2011. African papionins: diversity of social organization and ecological flexibility. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Primates in Perspective, pp. 241-277.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. 2003. Responses of 'resistant'vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1-18.

Teaford MF. 1985. Molar microwear and diet in the genus *Cebus*. Am J Phys Anthropol 66:363-370.

Teaford MF. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microscopy 2:1167-1175.

Teaford MF. 1993. Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In: Jablonski NG, ed. *Theropithecus*: the Life and Death of a Primate Genus. Cambridge: Cambridge University, pp. 331-349.

Teaford MF. 2007. What do we know and not know about dental microwear and diet? In: Ungar PS, ed. Evolution of the human diet: the known, the unknown, and the unknowable. Oxford: Oxford University Press, pp. 106-131.

Teaford MF, Glander KE. 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 85:313-319.

Teaford MF, Glander KE. 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk M, Rosenberger A, Garber P, eds. Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 433-449.

Teaford MF, Oyen OJ. 1989. In vivo and in vitro turnover in dental microwear. Am J Phys Anthropol 80:447-460.

Teaford MF, Robinson JG. 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. Am J Phys Anthropol 80:391-401.

Teaford MF, Runestad JA. 1992. Dental microwear and diet in Venezuelan primates. Am J Phys Anthropol 88:347-364.

Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. Proc Natl Acad Sci USA 97:13506-13511.

Teaford MF, Walker AC. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am J Phys Anthropol 64:191-200.

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 129: 99-104.

Teaford MF, Ungar PS, Kay RF. 2008. Molar shape and molar microwear in the Koobi Fora monkeys: ecomorphological implications. In: Jablonski NG, Leakey MG, eds. Koobi Fora Research Project. Volume 6. The Fossil Monkeys. San Francisco: Occasional Paper of the California Academy of Sciences, pp. 337-358.

Teaford MF, Taylor AB, Iriarte-Diaz J, Ross CF, Vinyard CJ. 2015. Rates of dental microwear in laboratory primates track changes in food items consumed. Am J Phys Anthropol 156(S60):302.

Tesfaye D, Fashing PJ, Bekele A, Mekonnen A, Atickem A. 2013. Ecological flexibility in Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest, Ethiopia: a comparison of habitat use, ranging behavior, and diet in intact and fragmented forest. Int J Primatol 34:615-640.

Thomas SC. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. Biotropica 23:68-83

Thorn JS, Nijman V, Smith D, Nekaris KAI. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). Divers Distrib 15:289–298.

Ting N. 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living colobus monkeys. J Hum Evol 55:312-325.

Tokeshi M. 1999. Species Coexistence. Cambridge: Cambridge University Press, 454 pp.

Ungar PS. 1996. Relationship of incisor size to diet and anterior tooth use in sympatric Sumatran anthropoids. Am J Primatol 38:145-156.

Ungar PS. 1998. Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evol Anth 6:205-217.

Ungar PS. 2002. Reconstructing the diets of fossil primates. In: Plavcan JM, Kay RF, Jungers W, van Schaik CP, eds. Reconstructing behavior in the primate fossil record. New York: Kluwer Academic/Plenum, pp. 261-296.

Ungar PS. 2014. Some musing on the history of dental microwear research and the role of texture analysis. Podium Presentation. Inferring Diet and Dental Function from Dental Microwear Textures: Society of Vertebrate Paleontology 74th Annual Meetings Workshop.

Ungar PS, Bunn JM. 2009. Dental topography and diets of four old world monkey species. Am J Primatol 71:466-477.

Ungar PS, Grine FE. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. J Hum Evol 20:313-340.

Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. Proc Natl Acad Sci USA 100:3874–3877.

Ungar PS, Teaford MF. 1996. A preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. Am J Phys Anthropol 100:101-113.

Ungar PS, Simons J-C, Cooper JW. 1991. A semiautomated image analysis procedure for the quantification of dental microwear. Scanning 13:31-36.

Ungar PS, Brown CA, Bergstrom TS, Walker A. 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. Scanning Microscopy 25:185-193.

Ungar PS, Grine FE, Teaford MF. 2008a. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS ONE 3(4):e2044.

Ungar PS, Scott RS, Scott JR, Teaford MF. 2008b. Dental microwear analysis: historical perspectives and new approaches. In: Irish JD, Nelson GC, eds. Technique and Application in Dental Anthropology. Cambridge: Cambridge University Press, pp 389-425.

Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Phil Trans R Soc B 365:3345-3354.

Vazquez D, Stevens RD. 2004. The latitudinal gradient in niche breadth: concepts and evidence. Am Nat164:E1-E19.

Vogel ER, van Woerden JT, Lucas PW, Atmoko SSU, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55:60-74.

Wahome JM, Rowell TE, Tsingalia HM. 1993. The natural history of de Brazza's monkey in Kenya. Int J Primatol 14:445-466.
Walker A, Hoeck HN, Perez L. 1978. Microwear of mammalian teeth as an indicator of diet. Science 201:908-910.

Ward C, Leakey M, Walker A. 1999. The new hominid species *Australopithecus anamensis*. Evol Anthropol 7:197-205.

Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. J Anim Ecol 72:650-659.

Werre JLR. 2000. Ecology and behavior of the Niger Delta red colobus (*Procolobus badius epieni*). PhD Dissertation, City University of New York.

Whitten PL. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am J Primatol 5:139-159.

Willig MR, Kaufmann DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu Rev Ecol Syst 34:273-309.
Wills MA, Briggs DE, Fortey, RA. 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. Paleobiology 20:93-130.

Withnell CB, Ungar PS. 2014. A preliminary analysis of dental microwear as a proxy for diet and habitat in shrews. Mammalia 78:409-415.

Wood B, Strait D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. J Hum Evol 46:119-162.

Wrangham RW, Waterman PG. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. J Anim Ecol 50:715-731.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473-492.

Zeeve SR. 1991. Behavior and ecology of primates in the Lomako forest, Zaire. PhD Dissertation, State University of New York at Stony Brook.

APPENDIX A

RAW MICROWEAR TEXTURE DATA

Species	Specimen #[a]	Country	Locality	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc9*	*HAsfc81*
C. mitis	FMNH127793	Tanzania	Lake Manyara, Moto Umbu, nr	0.56	0.0043	0.27	0.0	0.61	1.09
C. mitis	FMNH127794	Tanzania	Lake Manyara, Moto Umbu, nr	1.22	0.0027	0.34	6097.8	0.43	0.63
C. mitis	FMNH127795	Tanzania	Lake Manyara, Moto Umbu, nr	0.87	0.0064	0.34	0.0	0.41	0.69
C. mitis	FMNH27534	DRC	Walikali, Buruku, Ituri	2.43	0.0044	0.15	14916.1	0.34	0.67
C. mitis	FMNH27538	DRC	Walikali, Buruku, Ituri	1.08	0.0018	0.71	5595.3	0.54	1.11
C. mitis	FMNH27539	DRC	Walikali, Buruku, Ituri	1.68	0.0049	0.21	7955.1	0.66	1.08
C. mitis	RBINS10598	DRC	Katanga, Parc Nat Upembe, Lufira Riv Senze	1.12	0.0017	6.15	9329.5	0.58	0.92
C. mitis	RBINS10600	DRC	Katanga, Parc Nat Upembe, Lufira Riv Senze	0.97	0.0013	1.37	8110.7	0.37	0.70
C. mitis	RBINS10601	DRC	Katanga, Parc Nat Upembe, Lufira Riv Senze	1.32	0.0051	2.40	12168.1	0.29	0.53
C. mitis	RBINS10604	DRC	Katanga, Parc Nat Upembe, Lufira Riv Senze	1.65	0.0028	30.13	9998.0	0.53	0.92
C. mitis	RBINS34669	DRC	Kisangani	1.52	0.0040	0.27	12248.4	0.66	1.01
C. mitis	RBINS34670	DRC	Kisangani	1.01	0.0036	0.27	0.0	0.67	0.89
C. mitis	RBINS34673	DRC	Kisangani	0.91	0.0040	5.42	6623.7	0.59	1.03
C. mitis	RBINS34674	DRC	Kisangani	1.45	0.0059	0.15	9512.7	0.32	0.75
C. mitis	RBINS34675	DRC	Kisangani	2.68	0.0048	0.15	3313.2	0.27	0.51
C. mitis	RBINS34676	DRC	Kisangani	1.43	0.0055	0.27	167.5	0.36	0.98
C. mitis	RBINS34677	DRC	Kisangani	1.58	0.0038	0.43	6484.5	0.60	1.05

C. mitis	RBINS34678	DRC	Kisangani	0.92	0.0053	0.15	4948.3	0.35	0.55
C. mitis	RBINS34682	DRC	Kisangani	1.94	0.0024	0.21	3690.5	0.41	0.92
C. mitis	RBINS34692	DRC	Kisangani	0.71	0.0027	0.60	9076.0	0.38	0.64
C. mitis	RBINS34693	DRC	Kisangani	0.81	0.0069	2.55	16551.5	0.72	0.91
C. mitis	RBINS34694	DRC	Kisangani	0.91	0.0059	1.07	223.6	0.23	0.45
C. mitis	RBINS34695	DRC	Kisangani	1.60	0.0066	63.22	11640.9	0.61	1.03
C. mitis	RMCA37524	DRC	Katauleko, Kalonge	1.35	0.0043	0.21	3231.7	0.57	1.37
C. mitis	RMCA37525	DRC	Katauleko, Kalonge	1.05	0.0057	0.21	10414.6	0.58	0.68
C. mitis	RMCA83006M235	DRC	Tshopo	1.31	0.0080	2.02	272.0	0.68	1.09
C. mitis	RMCA83006M239	DRC	Tshopo	1.26	0.0050	0.27	8225.0	0.36	0.82
C. mitis	RMCA83006M242	DRC	Tshopo	0.46	0.0058	0.21	13182.7	0.36	0.75
C. mitis	RMCA83006M249	DRC	Tshopo	1.92	0.0040	1.85	14786.9	0.22	0.69
C. mitis	RMCA83006M251	DRC	Tshopo	1.34	0.0031	1.04	2563.7	0.57	1.10
C. mitis	RMCA83006M253	DRC	Tshopo	1.20	0.0063	0.27	2344.4	0.39	0.74
C. mitis	RMCA83006M254	DRC	Tshopo	2.11	0.0039	0.15	4408.6	0.49	0.72
C. mitis	RMCA83006M257	DRC	Tshopo	1.81	0.0043	0.42	4528.5	0.53	0.62
C. mitis	RMCA83006M258	DRC	Tshopo	1.14	0.0033	0.71	6874.1	0.71	0.96
C. mitis	RMCA83006M259	DRC	Tshopo	0.49	0.0041	0.43	83.9	0.70	1.51
C. mitis	RMCA83006M261	DRC	Tshopo	0.81	0.0041	0.43	0.0	0.43	0.82
C. mitis	RMCA83006M262	DRC	Tshopo	0.86	0.0049	0.51	1604.8	0.59	1.15
C. mitis	RMCA83006M263	DRC	Tshopo	0.82	0.0057	0.94	4702.2	0.31	0.91

C. mitis	RMCA83006M265	DRC	Tshopo	1.13	0.0068	1.21	2463.6	0.49	1.05
C. mitis	RMCA83006M268	DRC	Tshopo	1.77	0.0038	0.15	5961.5	0.31	0.57
C. mitis	RMCA83006M270	DRC	Tshopo	1.56	0.0047	0.27	121.9	0.35	0.49
C. mitis	RMCA91060M236	DRC	Marche de Kisangani	0.49	0.0042	0.27	8980.5	0.56	0.66
C. mitis	RMCA91060M238	DRC	Marche de Kisangani	0.78	0.0042	4.61	2431.7	0.45	0.80
C. mitis	RMCA91060M239	DRC	Marche de Kisangani	0.77	0.0068	146.00	12843.6	0.57	0.69
C. mitis	RMCA91060M240	DRC	Marche de Kisangani	1.02	0.0066	0.42	497.8	0.33	0.72
C. mitis	RMCA91060M242	DRC	Tshopo	1.08	0.0068	0.34	0.0	0.41	0.71
C. mitis	RMCA91060M244	DRC	Tshopo	2.33	0.0039	0.43	8941.2	0.43	0.80
C. mitis	RMCA91060M245	DRC	Tshopo	1.48	0.0016	0.71	830.3	0.46	0.79
C. mitis	RMCA91060M246	DRC	Tshopo	1.48	0.0039	0.15	2836.3	0.37	0.69
C. mitis	RMCA91060M248	DRC	Tshopo	0.55	0.0033	0.27	2415.8	0.58	0.96
C. mitis	RMCA91060M250	DRC	Tshopo	0.97	0.0051	0.27	1147.2	0.26	0.58
C. mitis	RMCA91060M256	DRC	Marche de Kisangani	0.91	0.0039	0.21	13032.6	0.32	0.66
C. mitis	RMCA91060M257	DRC	Marche de Kisangani	2.41	0.0035	0.21	11826.5	0.31	0.56
C. mitis	USNM182243	Kenya	Mount Mbololo	1.06	0.0027	1.07	1373.9	0.79	1.07
C. mitis	USNM182248	Kenya	Mount Mbololo	1.52	0.0032	0.51	374.6	0.76	0.94
C. mitis	USNM182361	Kenya	Kisumu, Lukosa River	1.27	0.0026	0.27	12173.5	1.17	1.52
C. mitis	USNM182369	Kenya	Kisumu, Lukosa River	3.44	0.0046	0.15	11076.3	0.53	1.07

C. mitis	USNM182376	Kenya	Kisumu, Lukosa River	1.08	0.0048	0.21	3224.3	0.34	0.54
C. mitis	USNM182377	Kenya	Kisumu, Lukosa River	1.06	0.0020	0.27	12359.4	0.43	0.93
C. mitis	USNM182378	Kenya	Kisumu, Lukosa River	1.37	0.0046	0.42	2274.2	0.33	0.63
C. mitis	USNM236988	Uganda	Budongo Forest	0.48	0.0028	0.97	11030.1	0.45	0.61
C. mitis	USNM236990	Uganda	Budongo Forest	0.78	0.0058	0.94	13829.1	0.46	0.76
C. mitis	USNM236991	Uganda	Budongo Forest	1.16	0.0028	0.15	8277.7	0.38	0.53
C. mitis	USNM236992	Uganda	Budongo Forest	0.66	0.0030	0.27	13134.8	0.42	0.49
C. mitis	USNM236994	Uganda	Budongo Forest	0.72	0.0016	0.60	3344.8	0.39	0.62
C. mitis	USNM236995	Uganda	Budongo Forest	0.69	0.0074	0.74	5907.7	0.37	0.87
C. mitis	USNM236996	Uganda	Budongo Forest	2.04	0.0028	0.27	5979.5	0.35	0.52
C. mitis	USNM425424	Zimbabwe	Chirinda Forest	0.77	0.0065	2.81	6146.2	0.46	0.94
C. mitis	USNM425427	Zimbabwe	Chirinda Forest	0.79	0.0045	8.04	5422.6	1.17	1.55
C. mitis	USNM425429	Zimbabwe	Chirinda Forest	1.07	0.0065	1.21	3438.9	0.52	0.74
C. mitis	USNM425430	Zimbabwe	Chirinda Forest	0.56	0.0058	0.34	11827.9	0.38	0.70
C. neglectus	RBINS39696	DRC	Kisangani	1.53	0.0017	0.15	3710.0	0.33	0.71
C. neglectus	RBINS39700	DRC	Kisangani	2.01	0.0022	0.15	7220.5	0.44	0.52
C. neglectus	RBINS39701	DRC	Kisangani	1.34	0.0019	0.21	5567.0	0.39	0.73
C. neglectus	RBINS39702	DRC	Kisangani	2.52	0.0009	0.15	6003.7	0.34	0.60
C. neglectus	RBINS39703	DRC	Kisangani	1.54	0.0042	0.15	7343.2	0.28	0.68
C. neglectus	RBINS39704	DRC	Kisangani	1.95	0.0011	1.31	11787.2	0.29	0.53
C. neglectus	RBINS39705	DRC	Kisangani	2.70	0.0034	0.15	4515.7	0.36	0.77
C. neglectus	RBINS39706	DRC	Kisangani	2.04	0.0016	0.27	12975.9	0.27	0.53

C. neglectus	RMCA14253	DRC	Lisala Bokweli	1.70	0.0048	0.82	13590.1	0.43	0.50
C. neglectus	RMCA28731	DRC	Env Boende, Mount Beha	2.13	0.0044	0.94	464.9	0.37	0.70
C. neglectus	RMCA83006M40	DRC	Tshopo	1.86	0.0028	9.94	15879.3	0.38	0.62
C. neglectus	RMCA83006M43	DRC	Tshopo	1.18	0.0034	0.51	9535.1	0.36	0.55
C. neglectus	RMCA83006M44	DRC	Tshopo	2.05	0.0011	0.15	6545.9	0.28	0.71
C. neglectus	RMCA83006M45	DRC	Tshopo	1.38	0.0023	8.34	13348.3	0.48	0.76
C. neglectus	RMCA83006M46	DRC	Tshopo	2.64	0.0014	0.15	14384.0	0.27	0.42
C. neglectus	RMCA83006M47	DRC	Tshopo	1.46	0.0017	0.15	10388.7	0.37	0.47
C. neglectus	RMCA83006M50	DRC	Tshopo	1.25	0.0023	4.54	16286.1	0.31	0.56
C. neglectus	RMCA83006M51	DRC	Tshopo	3.43	0.0030	0.15	12732.3	0.31	0.46
C. neglectus	RMCA8407	DRC	Mount Uele, Mauda	0.64	0.0029	0.34	10892.5	0.35	0.60
C. neglectus	RMCA8409	DRC	Mount Uele, Mauda	1.13	0.0030	0.94	1938.7	0.34	0.72
C. neglectus	RMCA8413	DRC	Mount Uele, Mauda	0.51	0.0049	0.34	4795.0	0.49	1.83
C. neglectus	RMCA8642	DRC	Mount Uele, Mauda	0.61	0.0032	11.26	10188.8	0.85	1.13
Ce. torquatus	FMNH29812	Cameroon	Edea	1.33	0.0050	0.74	13642.7	0.37	0.62
Ce. torquatus	FMNH29813	Cameroon	Edea	1.44	0.0041	5.42	1717.5	0.36	1.19
Ce. torquatus	FMNH29815	Cameroon	Edea	1.07	0.0014	0.94	11874.8	0.45	0.69
Ce. torquatus	FMNH29816	Cameroon	Edea	1.64	0.0025	0.27	2264.4	0.60	1.09

Ce. torquatus	USNM220350	Gabon	Fernan Vaz, Nytonga	0.66	0.0015	0.42	3931.2	0.41	0.84
Ce. torquatus	USNM220351	Gabon	Fernan Vaz, Nytonga	2.08	0.0021	10.34	14338.2	0.50	0.60
Ce. torquatus	USNM220352	Gabon	Fernan Vaz, Nytonga	1.00	0.0035	0.15	9426.3	0.50	0.63
Ce. torquatus	USNM220353	Gabon	Fernan Vaz, Nytonga	1.07	0.0038	0.42	11706.7	0.36	0.56
Ce. torquatus	USNM220370	Gabon	Fernan Vaz, Nytonga	1.18	0.0053	69.68	12933.1	0.74	1.08
Ch. aethiops	FMNH127781	Tanzania	Serengeti Plains, Seronera	1.51	0.0041	0.54	10225.3	0.66	1.06
Ch. aethiops	FMNH127787	Tanzania	Serengeti Plains, Seronera	2.62	0.0016	79.23	7199.7	0.65	1.24
Ch. aethiops	FMNH127790	Tanzania	Serengeti Plains, Seronera	1.07	0.0025	0.21	13303.8	0.46	0.54
Ch. aethiops	FMNH127792	Tanzania	Serengeti Plains, Seronera	0.91	0.0053	0.72	1248.0	0.37	0.62
Ch. aethiops	FMNH27063	Ethiopia	Ziway Hayk ("Lake Zwai"), S of, Suksuk R	0.87	0.0037	0.60	4141.7	0.41	0.49
Ch. aethiops	MVZ117269	South Africa	Vrede Farm, 27 mi W Graaff Reinet	2.51	0.0025	0.15	4002.8	0.29	0.48
Ch. aethiops	MVZ117270	South Africa	Vrede Farm, 27 mi W Graaff Reinet	1.44	0.0013	0.21	12954.0	0.41	0.65
Ch. aethiops	RMCA11371	DRC	Moba	1.08	0.0038	0.21	3323.8	0.25	0.70
Ch. aethiops	RMCA37477	DRC	Ngamba	1.15	0.0015	2.17	10416.7	0.45	1.27
Ch. aethiops	RMCA37478	DRC	Ngamba	1.15	0.0056	0.27	3044.7	0.48	0.71
Ch. aethiops	RMCA5771	DRC	N'gombe	1.99	0.0052	1.49	14014.3	0.39	0.70
Ch. aethiops	RMCA8457	DRC	Mahagi Lac	1.26	0.0011	1.07	8243.2	0.53	1.09

Ch. aethiops	RMCA8458	DRC	Mahagi Lac	1.14	0.0037	13.66	11837.3	0.53	0.75
Ch. aethiops	RMCA8459	DRC	Mahagi Lac	0.91	0.0033	1.69	3895.0	0.57	1.18
Ch. aethiops	RMCA8460	DRC	Mahagi Lac	1.22	0.0019	0.43	10222.1	0.72	1.09
Ch. aethiops	USNM182163	Kenya	Nguaso Nyiro	2.49	0.0030	36.04	12502.8	0.49	0.63
Ch. aethiops	USNM182164	Kenya	Nguaso Nyiro	2.94	0.0023	0.15	15613.3	0.25	0.55
Ch. aethiops	USNM182165	Kenya	Nguaso Nyiro	1.07	0.0036	0.71	9290.1	0.48	0.83
Ch. aethiops	USNM182166	Kenya	Nguaso Nyiro	1.05	0.0063	0.27	482.6	0.49	0.76
Ch. aethiops	USNM351931	South Africa	Eshowe, 6 Mi E	0.72	0.0028	0.67	1296.8	0.36	0.89
Ch. aethiops	USNM351933	South Africa	Eshowe, 6 Mi E	1.27	0.0042	2.85	14467.6	0.37	0.74
Ch. aethiops	USNM351937	South Africa	Eshowe, 6 Mi E Buxton	2.55	0.0017	0.15	13646.7	0.48	0.80
Ch. aethiops	USNM367894	Botswana	Maun, 6 Mi N	0.92	0.0017	23.42	12348.1	0.40	0.89
Ch. aethiops	USNM367898	Botswana	Maun, 6 Mi N	0.69	0.0039	0.34	11503.5	0.38	0.60
Ch. aethiops	USNM367911	Botswana	Maun, 6 Mi N	1.30	0.0013	0.27	16093.6	0.71	0.78
Ch. aethiops	USNM381442	Gambia	Toniataba	2.24	0.0018	3.33	10693.1	0.51	0.89
Ch. aethiops	USNM381452	Gambia	Toniataba	0.28	0.0037	0.71	7609.4	0.42	0.91
Co. guereza	FMNH17696	Kenya	Kijabe	0.74	0.0046	0.27	139.9	0.51	0.64
Co. guereza	FMNH17699	Kenya	Kijabe	0.59	0.0067	0.15	55.8	0.46	0.82
Co. guereza	RMCA19798	DRC	Gangala na Bodio	1.03	0.0024	0.21	0.0	0.41	0.64
Co. guereza	RMCA25552	DRC	Gangala na Bodio	0.49	0.0052	0.34	1142.4	0.34	0.50
Co. guereza	RMCA27262	DRC	Gangala na Bodio	1.07	0.0059	0.21	2338.6	0.35	0.69

Co. guereza	RMCA27264	DRC	Gangala na Bodio	0.58	0.0035	0.27	5675.7	0.58	0.67
Co. guereza	RMCA2800	DRC	Moera	0.81	0.0044	0.42	27.9	0.33	0.68
Co. guereza	RMCA2801	DRC	Moera	1.18	0.0022	0.27	2605.0	0.48	0.77
Co. guereza	RMCA37559	DRC	Molidi River	0.90	0.0042	0.60	6635.8	0.69	0.87
Co. guereza	RMCA37605	DRC	Molidi River	3.54	0.0014	0.15	14509.8	0.27	0.45
Co. guereza	RMCA37611	DRC	Djilube	3.10	0.0017	0.15	10526.3	0.33	0.91
Co. guereza	RMCA37619	DRC	Molidi River	2.06	0.0033	0.15	690.7	0.35	0.79
Co. guereza	RMCA37633	DRC	Mamudioma	1.22	0.0044	0.15	27.9	0.36	0.62
Co. guereza	RMCA37634	DRC	Mamudioma	1.30	0.0024	0.21	768.1	0.57	1.39
Co. guereza	RMCA37637	DRC	Djilube	1.40	0.0020	0.71	2605.0	0.24	0.44
Co. guereza	RMCA8404	DRC	Mauda	1.24	0.0039	2.40	13843.9	0.55	0.82
Co. guereza	RMCA8411	DRC	Mauda	1.53	0.0022	0.27	8110.7	0.45	0.56
Co. guereza	RMCA8415	DRC	Mauda	2.43	0.0039	0.15	6812.1	0.38	0.86
Co. guereza	RMCA8416	DRC	Mauda	1.17	0.0019	0.27	12084.2	0.44	0.67
Co. guereza	RMCA8417	DRC	Mauda	1.26	0.0068	0.42	9998.0	0.51	0.65
Co. guereza	RMCA8418	DRC	Mauda	1.27	0.0026	3.31	11710.4	0.70	1.03
Co. guereza	USNM163123	Kenya	Mount Kenya	0.86	0.0041	0.15	12578.0	0.45	0.66
Co. guereza	USNM163125	Kenya	Mount Kenya	0.49	0.0035	0.42	2221.6	0.54	0.74
Co. guereza	USNM163266	Kenya	Mount Kenya	0.70	0.0054	0.42	1326.4	0.64	0.73
Co. guereza	USNM163267	Kenya	Mount Kenya	0.84	0.0058	0.71	1450.1	0.54	0.94
Co. guereza	USNM163274	Kenya	Mount Kenya	0.32	0.0064	0.34	12604.3	0.49	0.65
Co. guereza	USNM163278	Kenya	Mount Kenya	0.25	0.0044	0.42	7870.8	0.38	0.58
Co. guereza	USNM164844	Kenya	Mount Kenya	0.98	0.0040	0.27	10690.6	0.33	0.56
Co. guereza	USNM182362	Kenya	Kisumu, Lukosa River	1.40	0.0032	0.28	1858.2	0.42	0.71
Co. guereza	USNM182363	Kenya	Kisumu, Lukosa River	1.23	0.0016	0.27	11866.2	0.32	0.72
Co. guereza	USNM182365	Kenya	Kisumu, Lukosa River	1.17	0.0042	2.27	9778.4	0.44	0.79

Co. guereza	USNM182366	Kenya	Kisumu, Lukosa River	0.52	0.0041	0.51	6915.0	0.61	0.83
Co. guereza	USNM182375	Kenya	Kisumu, Lukosa River	2.10	0.0039	0.21	9422.5	0.44	1.02
Co. guereza	USNM18922	Tanzania	Kahe	1.13	0.0025	0.15	7656.0	0.76	0.97
Co. guereza	USNM18923	Tanzania	Kahe	0.47	0.0044	0.42	13756.0	0.38	0.58
Co. guereza	USNM18924	Tanzania	Kahe	0.49	0.0034	0.27	0.0	0.41	0.83
Co. guereza	USNM18925	Tanzania	Kahe	0.81	0.0050	0.60	27.9	0.60	0.84
Co. guereza	USNM18926	Tanzania	Kahe	0.85	0.0037	0.51	614.7	0.60	0.81
Co. guereza	USNM236983	Uganda	Budongo Forest	1.66	0.0063	0.15	1173.4	0.45	0.76
Co. guereza	USNM25863	Tanzania	Kahe	0.54	0.0014	0.27	12648.9	0.54	0.67
Co. guereza	USNM25864	Tanzania	Kahe	1.20	0.0046	0.34	11115.6	0.42	0.73
Co. guereza	USNM25865	Tanzania	Kahe	0.92	0.0053	0.71	672.5	0.67	1.03
Co. guereza	USNM452624	Kenya	Marindas Forest Reserve	1.00	0.0029	0.42	13691.1	0.35	0.49
Co. guereza	USNM452625	Kenya	Marindas Forest Reserve	0.75	0.0050	0.60	6514.8	0.65	0.80
Co. guereza	USNM452627	Kenya	Marindas Forest Reserve	0.87	0.0045	0.34	709.9	0.34	0.49
P. anubis	FMNH135055	Kenya	Mt Suswa, Cave 36E	1.02	0.0051	0.34	5286.5	0.35	0.49
P. anubis	FMNH135056	Kenya	Mt Suswa, Cave 36E	1.65	0.0032	0.42	4914.0	0.32	0.46
P. anubis	FMNH135059	Kenya	Mt Suswa, Cave 36E	1.08	0.0049	0.51	233.6	0.30	0.61
P. anubis	FMNH29588	Kenya	Mt Lukenya	1.54	0.0017	16.43	18474.5	0.47	0.69
P. anubis	FMNH29589	Kenya	Mt Lukenya	0.86	0.0047	0.42	7513.1	0.47	0.59
P. anubis	FMNH29591	Kenya	Mt Lukenya	1.71	0.0019	0.27	12226.4	0.36	0.63
P. anubis	MVZ149503	Niger	Park W	3.26	0.0016	0.15	10418.1	0.37	0.63
P. anubis	MVZ149504	Niger	Park W	2.51	0.0008	0.21	17220.4	0.48	0.57
P. anubis	MVZ149506	Niger	Park W	4.23	0.0020	0.15	14970.8	0.48	0.75
P. anubis	MVZ149508	Niger	Park W	0.92	0.0016	0.34	5424.9	0.47	0.59
P. anubis	MVZ149512	Niger	Park W	1.82	0.0014	0.43	11613.8	0.44	0.53

P. anubis	MVZ149513	Niger	Park W	1.75	0.0020	0.60	14007.3	0.43	0.56
P. anubis	MVZ149514	Niger	Park W	0.87	0.0047	0.42	7513.1	0.47	0.59
P. anubis	MVZ149515	Niger	Park W	1.48	0.0025	0.27	10336.2	0.34	0.50
P. anubis	RBINS34933	DRC	Kisangani	3.06	0.0018	87.54	12840.9	0.46	0.55
P. anubis	RBINS34934	DRC	Kisangani	1.39	0.0019	0.21	6861.4	0.57	0.90
P. anubis	RBINS34935	DRC	Kisangani	2.08	0.0015	137.76	14976.5	0.51	0.67
P. anubis	RBINS34936	DRC	Kisangani	1.93	0.0012	0.27	8502.3	0.32	0.52
P. anubis	RBINS34937	DRC	Kisangani	1.37	0.0025	0.27	9913.8	0.67	0.72
P. anubis	RMCA73009M47	Togo	Aledjo	1.61	0.0022	11.01	8891.5	0.70	1.11
P. anubis	RMCA73009M48	Togo	Aledjo	0.77	0.0026	0.42	3789.3	0.40	0.53
P. anubis	RMCA73009M49	Togo	Aledjo	1.27	0.0032	0.51	13474.1	0.42	0.70
P. anubis	RMCA83006M1	DRC	Tshopo	1.90	0.0022	0.21	13785.9	0.37	0.58
P. anubis	RMCA83006M11	DRC	Tshopo	0.90	0.0068	4.57	13469.1	0.34	0.49
P. anubis	RMCA83006M2	DRC	Tshopo	1.72	0.0036	0.21	12596.8	0.32	0.64
P. anubis	RMCA83006M3	DRC	Tshopo	1.14	0.0046	0.42	12149.5	0.33	0.46
P. anubis	RMCA83006M4	DRC	Tshopo	2.99	0.0014	0.15	12306.5	0.53	0.65
P. anubis	RMCA83006M5	DRC	Tshopo	1.36	0.0030	0.27	10155.9	0.41	0.51
P. anubis	RMCA83006M6	DRC	Tshopo	1.24	0.0034	1.84	11461.8	0.35	0.53
P. anubis	RMCA83006M7	DRC	Tshopo	1.99	0.0036	23.06	11915.6	0.52	0.71
P. anubis	RMCA83006M9	DRC	Tshopo	1.51	0.0019	0.21	14499.4	0.45	0.60
P. anubis	RMCA8461	DRC	Mahagi lac	1.50	0.0042	0.15	11741.7	0.58	0.80
P. anubis	RMCA8462	DRC	Mahagi lac	1.76	0.0044	0.82	12400.2	0.47	0.50
P. anubis	RMCA8464	DRC	Mahagi lac	1.30	0.0036	56.32	13875.5	0.42	0.61
P. anubis	RMCA90042M224	DRC	Tshopo	0.73	0.0068	0.51	4545.5	0.36	0.55
P. anubis	RMCA90042M2	DRC	Tshopo	1.81	0.0031	0.21	495.0	0.33	0.50

	27								
P. anubis	RMCA90042M228	DRC	Tshopo	2.12	0.0018	16.03	13468.8	0.39	0.64
P. anubis	USNM384219	Kenya	Kimani	1.13	0.0066	0.60	9258.1	0.46	0.60
P. anubis	USNM384221	Kenya	Kimani	1.73	0.0040	0.21	11997.3	0.40	0.46
P. anubis	USNM384222	Kenya	Kimani	1.81	0.0047	0.34	11347.1	0.32	0.54
P. anubis	USNM384234	Kenya	Mau Narok, Site A	0.65	0.0013	0.27	669.3	0.39	0.65
P. anubis	USNM395433	Kenya	Marigot, 7 Mi S. E., Lake Baringo	3.17	0.0013	0.27	6649.9	0.27	0.50
P. anubis	USNM395435	Kenya	Marigot, 7 Mi S. E., Lake Baringo	0.84	0.0024	0.60	5899.1	0.40	0.62
P. anubis	USNM395436	Kenya	Marigot, 7 Mi S. E., Lake Baringo	1.40	0.0052	0.60	11702.7	0.42	0.47
P. anubis	USNM395437	Kenya	Marigot, 7 Mi S. E., Lake Baringo	0.70	0.0040	0.27	2750.3	0.40	0.57
Pr. rufomitratus	RBINS34766	DRC	Kisangani	0.92	0.0038	1.21	11444.7	0.41	0.66
Pr. rufomitratus	RBINS34777	DRC	Kisangani	0.98	0.0064	11.32	10307.4	0.50	0.77
Pr. rufomitratus	RBINS34816	DRC	Kisangani	0.33	0.0031	0.60	6771.9	0.78	1.29
Pr. rufomitratus	RBINS34819	DRC	Kisangani	0.52	0.0036	22.77	12569.8	0.53	0.81
Pr. rufomitratus	RBINS34820	DRC	Kisangani	0.45	0.0072	0.60	3411.0	0.56	0.71
Pr. rufomitratus	RBINS34827	DRC	Kisangani	1.16	0.0029	0.27	12485.5	0.41	0.67
Pr. rufomitratus	RBINS34828	DRC	Kisangani	1.33	0.0040	1.08	7842.5	0.37	0.63
Pr. rufomitratus	RBINS34831	DRC	Kisangani	0.56	0.0030	5.12	3352.8	0.33	0.69
Pr. rufomit	RBINS34832	DRC	Kisangani	1.05	0.0066	2.02	2704.1	0.43	0.81

ratus									
Pr. rufomitratus	RBINS34871	DRC	Kisangani	0.58	0.0023	0.42	11917.1	0.46	0.78
Pr. rufomitratus	RBINS39938	DRC	Kisangani	0.52	0.0021	47.05	13877.4	0.43	0.82
Pr. rufomitratus	RBINS39940	DRC	Kisangani	0.82	0.0054	0.62	1602.7	0.47	0.81
Pr. rufomitratus	RBINS39943	DRC	Kisangani	0.53	0.0038	0.21	8121.0	0.35	0.52
Pr. rufomitratus	RBINS39947	DRC	Kisangani	1.18	0.0034	0.27	8931.0	0.47	0.79
Pr. rufomitratus	RBINS39952	DRC	Kisangani	1.03	0.0061	0.51	1090.0	0.49	0.67
Pr. rufomitratus	RBINS39954	DRC	Kisangani	0.62	0.0037	0.27	7783.2	0.47	0.67
Pr. rufomitratus	RBINS39961	DRC	Kisangani	0.58	0.0050	0.43	5779.2	0.37	0.64
Pr. rufomitratus	RBINS39965	DRC	Kisangani	0.96	0.0056	0.15	4578.4	0.40	0.84
Pr. rufomitratus	RBINS39972	DRC	Kisangani	0.71	0.0039	1.35	14374.3	0.45	0.69
Pr. rufomitratus	RBINS39980	DRC	Kisangani	0.33	0.0025	0.21	6957.0	0.53	1.11
Pr. rufomitratus	RBINS39982	DRC	Kisangani	1.05	0.0043	0.15	4579.6	0.54	1.01
Pr. rufomitratus	RBINS39983	DRC	Kisangani	1.26	0.0046	0.27	3548.8	0.49	0.89
Pr. rufomitratus	RBINS39989	DRC	Kisangani	0.58	0.0034	0.21	8224.0	0.53	0.86
Pr. rufomitratus	RBINS39997	DRC	Kisangani	1.06	0.0016	0.74	9155.1	0.38	0.74
Pr. rufomitratus	RBINS40024	DRC	Kisangani	0.96	0.0045	0.34	5572.9	0.34	0.57
Pr. rufomitratus	RBINS40025	DRC	Kisangani	0.62	0.0030	0.71	14404.2	0.45	0.78
Pr. rufomit	RBINS40028	DRC	Kisangani	0.88	0.0035	0.34	9828.2	0.67	0.91

ratus									
Pr. rufomitratus	RBINS40030	DRC	Kisangani	0.17	0.0056	3.90	3433.1	1.03	1.33
Pr. rufomitratus	RBINS40031	DRC	Kisangani	0.58	0.0044	0.42	13201.6	0.69	0.92
Pr. rufomitratus	RBINS40032	DRC	Kisangani	0.55	0.0054	0.21	7690.0	0.78	1.03
Pr. rufomitratus	RBINS40038	DRC	Kisangani	0.39	0.0038	0.34	6381.4	0.36	0.78
Pr. rufomitratus	RBINS40039	DRC	Kisangani	0.34	0.0048	0.51	11743.9	0.44	0.59
Pr. rufomitratus	RBINS40040	DRC	Kisangani	0.53	0.0046	0.34	13160.9	0.71	0.85
Pr. rufomitratus	RBINS40066	DRC	Kisangani	0.58	0.0085	0.51	14279.6	0.54	0.79
Pr. rufomitratus	RBINS40067	DRC	Kisangani	0.26	0.0051	1.51	3636.7	0.60	1.22
Pr. rufomitratus	RBINS40069	DRC	Kisangani	0.77	0.0063	0.34	10572.4	0.54	0.85
Pr. rufomitratus	RBINS40070	DRC	Kisangani	0.73	0.0063	0.21	7392.8	1.02	1.86
Pr. rufomitratus	RBINS40071	DRC	Kisangani	0.23	0.0027	0.71	4800.5	0.42	0.80
Pr. rufomitratus	RBINS40073	DRC	Kisangani	0.22	0.0032	0.82	408.5	0.39	0.66
Pr. rufomitratus	RMCA27102	DRC	Kabobo Mt	1.02	0.0046	0.15	822.2	0.35	1.10
Pr. rufomitratus	RMCA27103	DRC	Kabobo Mt	1.15	0.0014	0.15	5180.3	0.47	0.72
Pr. rufomitratus	RMCA27105	DRC	Kabobo Mt	0.89	0.0039	0.21	4195.9	0.55	0.91
Pr. rufomitratus	RMCA37640	DRC	Tungudu	0.88	0.0040	0.21	1000.8	0.56	0.96
Pr. rufomitratus	RMCA37643	DRC	Tungudu	1.18	0.0053	0.15	2802.5	0.37	0.90
Pr. rufomit	RMCA83006M3	DRC	Tshopo	0.54	0.0045	0.51	0.0	0.74	0.97

ratus	21								
Pr. rufomit ratus	RMCA8 3006M3 22	DRC	Tshopo	0.69	0.0040	0.15	11020.4	0.55	0.75
Pr. rufomit ratus	RMCA8 3006M3 24	DRC	Tshopo	1.32	0.0055	0.27	9702.1	0.49	0.68
Pr. rufomit ratus	RMCA8 3006M3 25	DRC	Tshopo	0.62	0.0009	0.71	38.1	0.52	0.72
Pr. rufomit ratus	RMCA8 3006M3 34	DRC	Tshopo	0.68	0.0037	0.28	9783.8	0.65	0.96
Pr. rufomit ratus	RMCA8 3006M3 36	DRC	Tshopo	0.51	0.0040	0.97	11745.0	0.35	0.78
Pr. rufomit ratus	RMCA8 3006M3 37	DRC	Tshopo	1.02	0.0033	5.09	12645.9	0.57	0.96
Pr. rufomit ratus	RMCA8 3006M3 45	DRC	Tshopo	0.49	0.0026	0.27	11663.6	0.44	0.88
Pr. rufomit ratus	RMCA8 3006M3 48	DRC	Tshopo	0.41	0.0057	0.34	515.7	0.39	0.77
Pr. rufomit ratus	RMCA8 3006M3 52	DRC	Tshopo	0.29	0.0048	0.27	10665.1	0.69	1.10
Pr. rufomit ratus	RMCA8 3006M3 56	DRC	Tshopo	1.17	0.0024	0.27	0.0	0.27	0.54
Pr. rufomit ratus	RMCA8 3006M3 60	DRC	Tshopo	1.45	0.0038	0.15	0.0	0.34	0.63
Pr. rufomit ratus	RMCA8 3006M3 62	DRC	Tshopo	0.62	0.0028	0.88	6982.0	0.57	1.07
Pr. rufomit ratus	RMCA8 3006M3 74	DRC	Tshopo	0.65	0.0046	0.42	3738.3	0.50	0.63
Pr. rufomit ratus	RMCA8 3006M3 80	DRC	Tshopo	0.77	0.0038	0.27	4765.9	0.33	0.59
Pr. rufomit ratus	RMCA8 3006M3 81	DRC	Tshopo	0.56	0.0034	0.27	6062.6	0.32	0.42
Pr. rufomit ratus	RMCA8 3006M3 83	DRC	Tshopo	1.04	0.0051	0.27	10548.0	0.39	0.69
Pr. rufomit ratus	RMCA8 3006M3 98	DRC	Tshopo	0.42	0.0038	2.21	2522.8	0.58	1.06
Pr. rufomit	RMCA8 3006M4	DRC	Tshopo	1.29	0.0068	0.27	656.3	0.61	0.78

ratus	00								
Pr. rufomitratus	RMCA83006M403	DRC	Tshopo	0.34	0.0070	0.43	6967.5	0.47	0.68
Pr. rufomitratus	RMCA83006M409	DRC	Tshopo	0.29	0.0066	0.27	10201.1	0.58	0.82
Pr. rufomitratus	RMCA83006M411	DRC	Tshopo	0.57	0.0047	17.54	6223.6	0.74	1.32
Pr. rufomitratus	RMCA83006M414	DRC	Tshopo	0.63	0.0069	1.73	11972.1	0.38	0.83
Pr. rufomitratus	RMCA83006M422	DRC	Tshopo	1.11	0.0046	0.42	2628.6	0.45	0.75
Pr. rufomitratus	RMCA83006M431	DRC	Tshopo	1.86	0.0061	0.54	4290.5	0.27	0.58
Pr. rufomitratus	RMCA83006M442	DRC	Tshopo	1.61	0.0067	1.33	2729.3	0.31	0.57
Pr. rufomitratus	RMCA91060M86	DRC	Banalia	0.42	0.0039	0.34	152.6	0.64	0.83
Pr. rufomitratus	RMCA91060M88	DRC	Banalia	0.87	0.0043	0.27	5740.3	0.32	0.52
Pr. rufomitratus	RMCA91060M89	DRC	Banalia	0.53	0.0023	29.04	4048.2	0.64	1.03
Pr. rufomitratus	RMCA91060M91	DRC	Banalia	0.47	0.0042	0.21	10220.8	0.37	0.55
T. gelada	FMNH27039	Ethiopia	Lake Tana, 25 mi W, Ambo Mineral Springs	0.81	0.0023	0.42	7910.1	0.36	0.51
T. gelada	FMNH27184	Ethiopia	Simien Mts, Devark, 20 mi NE, Mt Geech	0.73	0.0028	0.34	8826.3	0.41	0.52
T. gelada	FMNH27185	Ethiopia	Simien Mts, Devark, 20 mi NE, Mt Geech	0.74	0.0034	0.15	6459.9	0.30	0.52
T. gelada	FMNH27186	Ethiopia	Simien Mts, Devark, 20 mi NE, Mt Geech	1.17	0.0061	0.42	9482.9	0.54	0.61
T. gelada	FMNH27234	Ethiopia	Mugher R, N bank, Mulu, 20 mi NW	1.80	0.0065	0.15	9175.8	0.23	0.58

T. gelada	GUA001	Ethiopia	Guassa	0.75	0.0026	0.27	6954.3	0.35	0.50
T. gelada	GUA003	Ethiopia	Guassa	0.94	0.0042	0.34	3226.6	0.50	0.97
T. gelada	GUA202	Ethiopia	Guassa	3.16	0.0041	0.15	12428.4	0.57	1.25
T. gelada	GUA203	Ethiopia	Guassa	1.00	0.0023	0.42	7888.0	0.37	0.43
T. gelada	GUA204	Ethiopia	Guassa	1.10	0.0033	0.27	14206.9	0.47	0.94
T. gelada	MCA442	Ethiopia	Guassa	1.62	0.0017	0.51	2422.0	0.30	0.42
T. gelada	MCA444	Ethiopia	Guassa	1.37	0.0034	0.27	5547.2	0.39	0.76
T. gelada	MCA601	Ethiopia	Guassa	1.08	0.0029	0.42	11844.7	0.47	0.67
T. gelada	MCA604	Ethiopia	Guassa	0.84	0.0044	0.34	1501.8	0.38	0.76
T. gelada	SMF1011	Ethiopia	None	0.70	0.0034	0.51	7009.2	0.47	0.70
T. gelada	SMF16665	Ethiopia	None	1.03	0.0034	1.07	12132.9	0.46	0.52

[a] Museums include the Field Museum of Natural History (FMNH), Royal Belgian Institute of Natural Sciences (RBINS), Royal Museum of Central Africa (RMCA), Senkenberg Museum Frankfurt (SMF), Smithsonian Museum of Natural History (USNM), and UC Berkeley Museum of Vertebrate Zoology (MVZ); specimens also come from the Guassa Gelada Research Project (GUA or MCA).

APPENDIX B

SPECIES MICROWEAR TEXTURE SUMMARY STATISTICS

Cercocebus torquatus

n = 9	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.275	0.00322	0.477	0.813	9.819	9092.77
SD	0.412	0.00146	0.128	0.246	22.708	5065.94
Median	1.183	0.00347	0.451	0.694	0.741	11706.72
Trimmed	1.275	0.00322	0.477	0.813	9.819	9092.77
MAD	0.276	0.00209	0.124	0.194	0.704	3380.88
Min	0.661	0.00138	0.359	0.564	0.150	1717.52
Max	2.081	0.00528	0.742	1.190	69.676	14338.15
Range	1.420	0.00390	0.384	0.626	69.526	12620.63
Skew	0.485	0.04668	0.838	0.409	1.988	-0.45
Kurtosis	-0.722	-1.72396	-0.615	-1.788	2.383	-1.76
SE	0.137	0.00049	0.043	0.082	7.569	1688.65

Cercopithecus mitis

n = 71	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.233	0.00441	0.483	0.827	4.242	6216.90
SD	0.569	0.00157	0.180	0.248	18.951	4745.36
Median	1.085	0.00429	0.435	0.759	0.417	5907.67
Trimmed	1.167	0.00440	0.463	0.805	0.642	5995.80
MAD	0.456	0.00179	0.154	0.237	0.309	5387.03
Min	0.462	0.00133	0.224	0.455	0.150	0.00
Max	3.438	0.00798	1.171	1.549	146.002	16551.48
Range	2.976	0.00666	0.947	1.094	145.852	16551.48
Skew	1.282	0.10086	1.577	0.900	6.348	0.30
Kurtosis	2.099	-0.76775	3.722	0.619	42.465	-1.18
SE	0.067	0.00019	0.021	0.029	2.249	563.17

Cercopithecus neglectus

n = 22	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.709	0.00264	0.376	0.687	1.869	9095.13
SD	0.724	0.00119	0.125	0.298	3.408	4551.69
Median	1.620	0.00256	0.355	0.610	0.304	9861.97
Trimmed	1.686	0.00258	0.355	0.626	1.090	9195.77
MAD	0.628	0.00131	0.065	0.152	0.229	5348.09
Min	0.511	0.00093	0.266	0.421	0.150	464.85
Max	3.433	0.00485	0.855	1.832	11.257	16286.07
Range	2.922	0.00392	0.589	1.411	11.107	15821.22
Skew	0.337	0.36555	2.515	2.624	1.811	-0.15
Kurtosis	-0.339	-1.05605	7.103	7.242	1.694	-1.21
SE	0.154	0.00025	0.027	0.064	0.727	970.42

Chlorocebus aethiops

n = 27	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.420	0.00309	0.463	0.809	6.353	9022.96
SD	0.696	0.00144	0.124	0.226	16.705	4766.17
Median	1.147	0.00304	0.465	0.758	0.666	10225.28
Trimmed	1.383	0.00301	0.460	0.798	2.433	9138.37
MAD	0.356	0.00165	0.100	0.195	0.678	4564.16
Min	0.279	0.00113	0.247	0.481	0.150	482.59
Max	2.936	0.00633	0.716	1.270	79.230	16093.58
Range	2.657	0.00520	0.469	0.790	79.080	15610.99
Skew	0.759	0.46600	0.348	0.512	3.293	-0.36
Kurtosis	-0.646	-0.80313	-0.410	-0.805	10.839	-1.27
SE	0.134	0.00028	0.024	0.043	3.215	917.25

Colobus guereza

n = 45	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.122	0.00389	0.469	0.743	0.491	5943.80
SD	0.665	0.00146	0.124	0.180	0.620	5131.84
Median	0.999	0.00404	0.446	0.730	0.283	6514.84
Trimmed	1.021	0.00386	0.463	0.732	0.346	5719.31
MAD	0.394	0.00146	0.140	0.140	0.197	7919.23
Min	0.255	0.00142	0.235	0.444	0.150	0.00
Max	3.544	0.00678	0.756	1.390	3.307	14509.78
Range	3.290	0.00536	0.521	0.946	3.157	14509.78
Skew	1.741	0.10054	0.369	0.936	3.211	0.21
Kurtosis	3.458	-0.82579	-0.750	1.908	10.015	-1.60
SE	0.099	0.00022	0.019	0.027	0.092	765.01

Papio anubis

n = 45	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.635	0.00308	0.423	0.602	8.157	9967.63
SD	0.760	0.00158	0.092	0.122	25.239	4390.28
Median	1.512	0.00260	0.411	0.591	0.416	11461.83
Trimmed	1.541	0.00294	0.414	0.586	1.669	10236.57
MAD	0.568	0.00151	0.084	0.090	0.272	3578.51
Min	0.654	0.00077	0.268	0.457	0.150	233.63
Max	4.230	0.00682	0.701	1.112	137.761	18474.46
Range	3.576	0.00605	0.434	0.655	137.611	18240.82
Skew	1.294	0.69643	0.932	1.885	3.837	-0.54
Kurtosis	1.738	-0.42789	0.902	5.077	14.931	-0.44
SE	0.113	0.00024	0.014	0.018	3.762	654.46

Procolobus rufomitratus

n = 74	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	0.747	0.00435	0.499	0.822	2.377	6758.75
SD	0.354	0.00150	0.152	0.228	7.111	4317.86
Median	0.628	0.00408	0.471	0.785	0.380	6576.66
Trimmed	0.723	0.00432	0.483	0.799	0.615	6718.14
MAD	0.364	0.00137	0.135	0.171	0.254	5466.98
Min	0.171	0.00088	0.273	0.420	0.150	0.00
Max	1.859	0.00853	1.029	1.861	47.048	14404.17
Range	1.689	0.00765	0.755	1.441	46.898	14404.17
Skew	0.691	0.27048	1.207	1.573	4.523	0.07
Kurtosis	0.049	-0.18929	1.885	4.451	21.953	-1.21
SE	0.041	0.00018	0.018	0.026	0.827	501.94

Theropithecus gelada

n = 16	*Asfc*	*epLsar*	*HAsfc9*	*HAsfc81*	*Smc*	*Tfv*
Mean	1.177	0.00354	0.410	0.667	0.377	7938.56
SD	0.618	0.00130	0.091	0.226	0.218	3658.90
Median	1.011	0.00337	0.399	0.593	0.343	7899.06
Trimmed	1.070	0.00346	0.412	0.643	0.344	7950.59
MAD	0.346	0.00113	0.107	0.145	0.113	2917.55
Min	0.702	0.00166	0.235	0.418	0.150	1501.83
Max	3.158	0.00653	0.565	1.247	1.070	14206.90
Range	2.456	0.00487	0.331	0.829	0.920	12705.07
Skew	2.027	0.89675	-0.109	1.095	1.790	-0.10
Kurtosis	3.781	0.04115	-1.011	0.318	3.582	-1.02
SE	0.154	0.00033	0.023	0.056	0.055	914.72

Note. MAD = mean absolute deviation

APPENDIX C

ANNUAL DIETARY DATA

Species	Site	Reference	FOL	TF	(SD)	FL	AN	OT	(Sub)	H
C. mitis	Cape Vidal, South Africa	Lawes (1991)	0.26	0.57	0.00	0.13	0.06	0.00		1.10
C. mitis	Kakamega Forest, Kenya	Cords (1986)	0.19	0.57	0.03	0.04	0.17	0.04		1.17
C. mitis	Kanyawara, Uganda	Butynski (1990)	0.33	0.28		0.07	0.38	0.01		1.30
C. mitis	Ngogo, Uganda	Butynski (1990)	0.23	0.30		0.10	0.36	0.01		1.35
C. mitis	Nyungwe Forest, Rwanda	Kaplin et al. (1998); Kaplin and Moermond (2000)	0.06	0.57	0.09	0.06	0.25	0.06		1.19
C. mitis	Zomba Plateau, Malawi	Beeson et al. (1996)	0.33	0.54		0.10	0.01	0.03		1.08
C. neglectus	Kisere, Kenya	Wahome et al. (1993)	0.34	0.46	0.01	0.06	0.10	0.07		1.30
C. neglectus	Lomako, DRC	Zeeve (1991)	0.00	0.33	0.00	0.00	0.00	0.67		0.64
C. neglectus	Mpassa, Gabon	Gautier-Hion and Gautier (1978)	0.09	0.74		0.03	0.05	0.04		0.81
Ce. torquatus	Campo Animal Reserve, Cameroon	Mitani (1989)	0.12	0.83	0.20	0.02	0.03	0.00		0.58
Ce. torquatus	Sette Cama, Gabon	Cooke (2012)	0.01	0.83	0.53	0.00	0.02	0.14		0.54
Ch. aethiops	Amboseli, Kenya	Wrangham and Waterman (1981)	0.23	0.20	0.08	0.16	0.08	0.26		1.51
Ch. aethiops	Bole, Ethiopia	Dunbar and Dunbar (1974)	0.19	0.51		0.18	0.07	0.00		1.15

Ch. aethiops	Buffle Noir & Kalamaloue, Cameroon	Kavanagh (1978)	0.11	0.46	0.02	0.23	0.18	0.02		1.19
Ch. aethiops	Mt Assirik, Senegal	Harrison (1982)	0.07	0.63	0.13	0.13	0.13	0.02		1.09
Ch. aethiops	River Senegal, Senegal	Galat and Galat-Luong (1977)	0.42	0.27		0.30	0.08	0.11		1.52
Ch. aethiops	Samburu-Isiolo Reserve, Kenya	Whitten (1983)	0.17	0.33	0.20	0.49	0.02	0.00		1.08
Ch. aethiops	Segera Ranch, Kenya	Isbell et al. (1998)	0.10	0.18	0.08	0.08	0.23	0.39		1.45
Co. guereza	Budongo Forest, Uganda	Plumptre (2006)	0.58	0.31	0.11	0.09	0.00	0.04		1.01
Co. guereza	Ituri Forest, DRC	Bocian (1997)	0.58	0.25	0.22	0.03	0.00	0.15		1.05
Co. guereza	Kakamega Forest, Kenya	Fashing (1999)	0.54	0.39	0.01	0.01	0.00	0.08		0.95
Co. guereza	Kibale, Uganda (average)	Oates (1977, 1994), Wasserman and Chapman (2003)	0.84	0.11		0.03	0.00	0.03		0.60
P. anubis	Bole, Ethiopia	Dunbar and Dunbar (1974)	0.33	0.55		0.07	0.03	0.03	0.02	1.09
P. anubis	Budongo Forest, Uganda	Okecha and Newton-Fisher (2006)	0.24	0.47	0.13	0.00	0.00	0.20	0.01	1.02
P. anubis	Comoe,	Kunz and Linsenmair (2008)	0.41	0.47	0.18	0.06	0.01	0.11		1.18

P. anubis	Laikipia Plateau, Kenya	Barton (1990)	0.32	0.24	0.11	0.30	0.00	0.17	0.17	1.37
Pr. rufomitratus	Baomo S., Kenya	Decker (1989)	0.47	0.27		0.26	0.00	0.01		1.10
Pr. rufomitratus	Gombe, Tanzania	Clutton-Brock (1975)	0.79	0.07		0.11	0.00	0.03		0.72
Pr. rufomitratus	Kanyawara, Uganda (average)	Struhsaker (1978), Wasserman and Chapman (2003), Snaith and Chapman (2008)	0.84	0.06		0.06	0.00	0.03		0.59
Pr. rufomitratus	Kibale, Uganda (average)	Wasserman and Chapman (2003)	0.88	0.02		0.07	0.00	0.04		0.50
Pr. rufomitratus	Mchelelo, Kenya (average)	Marsh (1981), Decker (1989)	0.64	0.10		0.24	0.00	0.03		0.96
Pr. rufomitratus	Salongo, DRC	Maisels et al. (1994)	0.61	0.01	0.31	0.38	0.00	0.00		0.72
T. gelada	Gich, Ethiopia	Iwamoto (1979)	0.84	0.05		0.00	0.00	0.10	0.10	0.47
T. gelada	Guassa, Ethiopia	Fashing et al. (2014)	0.80	0.02		0.00	0.03	0.15	0.13	0.59
T. gelada	Sankabar, Ethiopia	Dunbar (1977)	0.52	0.17		0.01	0.00	0.30	0.30	0.61

Note. FOL = total foliage (leaves and leaf parts, herbs, grasses, forbs); TF = total fruit (fruits, seeds, seed pods, nuts); (SD) = seeds and seed pods (when noted; counted in TF); FL = flowers; AN = animal matter (invertebrates, vertebrates); OT = other (gums, subterranean items, unidentified items, all other items); (SUB) = subterranean items (when noted; counted in OT); *H* = Shannon Diversity index, calculated from FOL, TF, FL, AN, and OT.

APPENDIX D

MONTHLY DIETARY DATA

Species	Site/Reference	Food Category	Mean	Med	Min	Max	CV
C. mitis	Kakamega Forest, Kenya	Total Fruit	0.54	0.53	0.41	0.69	0.13
	Cords (1986)	Leaves	0.18	0.18	0.07	0.26	0.35
		H	0.93	0.93	0.78	1.00	0.07
C. mitis	Jibat Forest, Ethiopia	Fruit	0.53	0.54	0.25	0.81	0.34
	Tesfaye et al. (2013)	Seeds	0.01	0.00	0.00	0.05	2.60
		Total Fruit	0.53	0.55	0.25	0.81	0.34
		Leaves	0.23	0.23	0.02	0.49	0.66
		H	1.02	1.02	0.61	1.32	0.22
C. mitis	Nyungwe Forest Reserve, Rwanda	Fruit	0.50	0.49	0.29	0.73	0.32
	Kaplan et al. (1998)	Seeds	0.04	0.02	0.00	0.15	1.20
		Total Fruit	0.54	0.51	0.39	0.74	0.24
		Leaves	0.15	0.13	0.02	0.37	0.79
		H	1.04	1.09	0.80	1.34	0.19
C. mitis	All Sites (Average)	Fruit	0.51		0.27	0.77	0.33
		Seeds	0.02		0.00	0.10	1.90
		Total Fruit	0.54		0.35	0.75	0.24
		Leaves	0.19		0.04	0.37	0.60
		H	1.00		0.73	1.22	0.16
C. mitis	Mount Assirik, Senegal	Fruit	0.51	0.56	0.19	0.83	0.46
	Harrison (1982)	Seeds	0.13	0.06	0.00	0.51	1.37
		Total Fruit	0.64	0.70	0.32	0.91	0.32

		Leaves	0.07	0.04	0.00	0.28	1.17
		H	1.09	1.01	0.57	1.77	0.31
Ch. aethiops	Buffle Noir and Kalamaloue, Cameroon	Total Fruit	0.46	0.48	0.02	0.98	0.69
	Kavanagh (1978)	Leaves	0.10	0.06	0.00	0.41	1.26
		H	0.97	1.04	0.13	1.45	0.40
Ch. aethiops	All Sites (Average)	Total Fruit	0.55		0.17	0.94	0.50
		Leaves	0.09		0.00	0.34	1.22
		H	1.03		0.35	1.61	0.36
Co. guereza	Kakamega Forest, Kenya	Fruit	0.40	0.41	0.19	0.74	0.41
	Fashing (1999)	Seeds	0.01	0.01	0.00	0.07	1.43
		Total Fruit	0.41	0.41	0.24	0.74	0.38
		Leaves	0.51	0.51	0.20	0.71	0.29
		H	0.88	0.88	0.72	1.01	0.10
Co. guereza	Budongo Forest, Uganda	Fruit	0.17	0.16	0.01	0.34	0.69
	Plumptre (2006)	Seeds	0.12	0.08	0.00	0.44	1.05
		Total Fruit	0.29	0.31	0.04	0.62	0.66
		Leaves	0.63	0.62	0.38	0.94	0.29
		H	0.77	0.81	0.26	1.11	0.31
Co. guereza	Ituri Forest, DRC	Fruit	0.03	0.01	0.00	0.11	1.29
	Bocian (1997)	Seeds	0.21	0.08	0.00	0.84	1.30
		Total Fruit	0.24	0.10	0.00	0.86	1.14
		Leaves	0.55	0.64	0.08	0.80	0.52

		H	1.06	0.96	0.57	1.56	0.32
Co. guereza	Average (All Sites)	Fruit	0.20		0.07	0.40	0.80
		Seeds	0.11		0.00	0.45	1.26
		Total Fruit	0.31		0.09	0.74	0.73
		Leaves	0.56		0.22	0.82	0.37
		H	0.91		0.51	1.22	0.24
P. anubis	Laikipia Plateau, Kenya	Fruit	0.15	0.06	0.01	0.51	1.31
	Barton (1990)	Seeds	0.13	0.14	0.00	0.32	0.72
		Total Fruit	0.28	0.21	0.06	0.83	0.85
		Leaves	0.28	0.20	0.05	0.58	0.72
		Subterranean	0.15	0.17	0.03	0.25	0.54
		H	1.09	1.15	0.65	1.36	0.20
Pr. rufomitratus	Salonga Forest, DRC	Fruit	0.07	0.03	0.00	0.32	1.38
	Maisels et al. (1994)	Seeds	0.31	0.17	0.02	0.71	0.96
		Total Fruit	0.38	0.25	0.05	0.84	0.86
		Leaves	0.61	0.73	0.14	0.92	0.52
		H	0.50	0.48	0.27	0.76	0.28
Pr. rufomitratus	Tana River, Kenya	Total Fruit	0.22	0.22	0.08	0.46	0.49
	Marsh (1981)	Leaves	0.64	0.67	0.43	0.80	0.19
		H	0.89	0.87	0.64	1.18	0.19
Pr. rufomitratus	Gombe, Tanzania	Total Fruit	0.12	0.14	0.01	0.23	0.61
	Clutton-Brock (1975)	Leaves	0.82	0.84	0.66	0.97	0.12

		H	0.52	0.50	0.15	0.80	0.41
Pr. rufomitratus	Average (All Sites)	Total Fruit	0.24		0.05	0.51	0.65
		Leaves	0.69		0.41	0.90	0.28
		H	0.64	0.50	0.36	0.92	0.29
T. gelada	Guassa, Ethiopia	Seeds	0.02	0.01	0.00	0.13	1.58
	Fashing et al. (2014)	Total Fruit	0.02	0.01	0.00	0.13	1.58
		Leaves	0.80	0.82	0.67	0.91	0.10
		Subterranean	0.13	0.10	0.02	0.28	0.77
		H	0.63	0.61	0.43	0.91	0.23

Note. Med = Median; *H* = Shannon Diversity Index