12-2017

The Effect of Dietary Specialism and Generalism on Evolutionary Longevity in an Early Paleogene Mammalian Community

Samantha Glonek
Grand Valley State University

Recommended Citation

Glonek, Samantha, "The Effect of Dietary Specialism and Generalism on Evolutionary Longevity in an Early Paleogene Mammalian Community" (2017). *Masters Theses*. 871.
https://scholarworks.gvsu.edu/theses/871

The Effect of Dietary Specialism and Generalism on Evolutionary Longevity in an Early Paleogene Mammalian Community

Samantha Glonek

Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Masters of Health Science

Biomedical Sciences

December 2017

Dedication

I would like to dedicate this thesis to my mom, who continues to believe in me during every step of life. She has made me who I am and has supported me during every hardship I have had to endure. She is my best friend and someone I strive to be like someday. Without her, I would not have been able to get through this stage of science, knowledge and life. My life is better because of her.

I love you.

Acknowledgements

For all specimens and computer access, I would like to thank Grand Valley State University Science Laboratories. I also thank Melissa Tallman Ph.D. and Paul Keenlance Ph.D for their generous time and consideration for being on the committee of this research and their valuable comments to help improve the document.

I especially would like to thank Laura Stroik Ph.D and her expertise in this field that helped keep me motivated and focused through every stage of this research. I am deeply grateful for her invaluable help and guidance with this project. Her continued faith in me is what helped me finish this study.

Abstract

This study examines the relationship between relief index (RFI) on first and second mandibular molars and longevity of the genus. The molars were extracted from small-bodied, arboreal mammals during the late-Paleocene, early-Eocene in the Bighorn Basin in Wyoming. This study site is a well-known location to research and study fossil mammals of this time period. The study was conducted and analyzed at the genus level due to the relatively small number of specimens available and identifiable at the species level. Dietary breadth, or how broad or narrow a dietary preference is for a mammal, is an area of concentration within this study. Dental topography was used as a quantitative measure to study dietary breadth of fossils. Although there are many dental topographic measures, relief index has previously been identified as the best indicator for predicting diet in mammals. This research uses dietary niche breadth (measured as standard deviations of RFI values) to predict for longevity of the fossil genus. By comparing extant taxa and finding a significant difference between generalist and specialist species and their respective values of RFI breadth, this concept was then applied to the fossil sample. The longevities were taken from literature and a least-squared linear regression was conducted. The p-value of the correlation (P=0.465 and R=0.114) indicated that there was not a significant correlation between RFI and longevity. RFI cannot be used to predict longevity of fossil genera. Due to the results of this study, it is now known that there is more that goes into longevity than just dietary niche itself. Although dietary niche may play a part in the extinction of a genus, it is not the sole contributor and must be caused by a combination of other variables.

Table of Contents

List of Tables

List of Figures

Abbreviations

DNE- Dirichlet Normal Energy

OPCR-Orientation Patch Count Rotated

RFI-Relief Index

SD-Standard Deviation

SQ-Shearing Quotient

Introduction

Across the class Mammalia, generalist and specialist species and genera differ greatly and have several distinguishing characteristics (Vamosi et al., 2014). Members of generalist mammalian species and genera utilize a broad spectrum of resources in order to survive and are thus considered “generalized” (Griffith and Sultan, 2012). In contrast, members of specialist species or genera utilize a more restricted set of resources in order to survive and thus have more specialized resource preferences, and smaller, narrower niches (Loxdale and Harvey, 2016). Here, a niche is defined as a set of resources exploited by a taxon within its environment (Kostikova et al., 2013), and niche breadth can be defined as the amount of variation among these resources (Wilson and Hayek, 2015).

Generalists are known to be more versatile not only in their resource use but also in their ability to adapt to variable environmental conditions. Generalists are also known to be successful in environments that are heterogeneous and continuingly changing, whereas specialists tend to be restricted to environments that are stable and homogenous (Wilson and Hayek, 2015). Compared to specialists, generalists are less affected by natural disasters or community instability because they can use a wider range of resources available to them, including those outside their resource preferences (Xu et al., 2012; Loxdale and Harvey, 2016). The greater breadth in resource exploitation of generalists may also result in more frequent or far-ranging migration patterns compared to those of specialists, which are more constrained and localized (Loxdale and Harvey, 2016).

Furthermore, generalists are known to have more stable population structures (Colles et al., 2009). Generalist populations tend to be more genetically diverse than those of specialists, and lower genetic diversity is broadly associated with a higher extinction risk (Li et al., 2014).

As a result, specialists are more affected by population bottlenecks, particularly in the face of a significant environmental event (Angermeijer, 1995; Li et al., 2014). In the fossil record, generalists persist longer due to their decreased sensitivity to ecological and environmental change (Colles et al., 2009; Wilson and Hayek, 2015). For example, Price et al. (2012) state that in extant taxa, herbivores (a more specialized taxa) tend to become extinct faster when compared to omnivores (a more generalized taxa).

Extinction risk also increases when there is narrow access to resources and a limited ability to acquire those resources; thus, when resource availability is high, the evolutionary longevity of generalist lineages tends to be higher than that of specialists. Narrower dietary niche breadth can cause more intraspecific, and possibly interspecific competition, for the same, or similar resources (Bolnick et. al, 2003). As such, generalists may live longer because of less competition due to their broadened resources and variation in the feeding and hunting mechanisms that they utilize (Colles et al., 2009). Many species that are experiencing intraspecific competition could also experience less niche expansion due to the decreasing amount of competitive species as a whole due to the competition for resources (Smith, 1990). Thus, it has been shown that the broader niches of generalists can afford evolutionary benefits such as increased taxonomic longevity, as the more resources potentially available to a taxon, the more potentially successful it can be (Loxdale and Harvey, 2016).

This breadth in the environmental distribution size and need for resources between generalists and specialists has an impact on the species survival. Specifically, because generalists are less selective with resources, are more genetically diverse, have greater gene flow, and are able to withstand more significant environmental changes than specialist species, in an evolutionary context, generalist species are generally expected to have greater longevity than specialist species (Colles et al., 2009). When considering evolutionary changes, specialists are more easily affected by relatively minor paleoenvironmental changes (Wilson and Hayek, 2015).

In the mammalian fossil record, one of the most studied components of the mammal ecological niche is diet (Boyer, 2008). Due to their frequent preservation in the fossil record, teeth allow researchers the ability not only to reconstruct diet but also to study the evolution of taxa, and in this study, genus (Christenson, 2014). Thus, the dietary niche was examined in this study. Within this context, dietary generalists can utilize a wide range of food resources, have more generalized dietary preferences, and possess a larger dietary niche. On the other hand, dietary specialists have more specialized dietary preferences and thus have a relatively narrow spectrum of utilized food resources and a smaller dietary niche (Loxdale and Harvey, 2016).

Resource preference and foraging ability has been tested in different groups of mammals. A study was conducted on marine mammals with different foraging strategies. Seasonal changes in foraging strategies and habitat use was measured within this study. Due to their narrower dietary niche, specialists had lowered hunting success caused by a shortage of resources, as they were less likely to encounter their prey. The narrower dietary niche (specialist) mammals were likely to wait until resources increased, or conditions were more optimal, in order to forage for their preferred resources (Breed et. al., 2006).

In a study by Wilder et. al (2013), research was conducted on various mammals within the database, “AnAge: The Animal Aging & Longevity Database,” which included specialists (herbivores and carnivores) and generalists (omnivores) from 86 different mammalian families. The mammals were separated into dietary categories based on percentages of their diet composed of different food resources. For example, if a mammal species had a dietary preference of at least 66.67% meat, then it was classified as a carnivore; mixed-diet mammals were classified as omnivores. Using this database, the study tested for a relationship between reproduction rates, life expectancy, and dietary breadth. When comparing the three categories (herbivores, carnivores, and omnivores), the omnivores held the longest life expectancies, and a significant correlation between the species life expectancy and dietary niche was found (P=0.008). This study also noted that there was no significant difference in reproductive success or life expectancy when comparing herbivores and carnivores, but a longer longevity and higher reproductive success within the omnivores (Wilder et al., 2013). These results help demonstrate that resource preference and availability can impact the life expectancy and reproductive rate of a species. Thus, these examples show that there is a correlation between how broad or narrow a diet is for each species (i.e., dietary niche breadth) and the life expectancy within a species. Although these examples are tested at the species level, and most studies only consider life expectancy, it is possible this concept can be extrapolated to the genus level. If overall life expectancy can impact the longevity of the genus, the emphasis of research can be focused on the life expectancy and reproductive success, and extrapolate that data to the evolutionary longevity. Thus, the main hypothesis of this study is that genera with larger dietary niches (i.e., generalists) will have greater evolutionary "success" (measured by longevity) than genera with smaller dietary niches (i.e., specialists).

In the fossil record, dietary niche breadth has to be reconstructed using dental anatomy. In mammals, dental morphology has a strong association with diet, as the biomechanics of eating behavior and dietary preference shape dental anatomy to maximize feeding efficiency in different species (Ungar, 2004). In general, molar strength and the resources consumed can have dramatic effects on occlusal, or chewing surface, morphological differences among genera and species (Evans and Sanson, 2005). This diet-dentition correlation in extant taxa is thus used by paleontologists as a template to reconstruct the dietary habits of similar or related extinct species (Allen et al, 2015). Molars have been used in most research studies to correlate with diet and what are mainly used for mastication during the mammals lifetime (Boyer, 2008). Specifically, distinct molar features have been found to be associated with living mammal dietary behaviors, including different number, positions, height, sharpness, and shapes of cusps (Evans, 2013), crest length, rake angle ("angle of leading face of a crest to a line perpendicular to the direction of movement"), approach angle, edge sharpness, and basin depth (Evans and Sanson, 2005). For example, mammals with sharper and pointed cusps and longer crests on their molars are more likely to need to shear or tear through food resources, such as those with high carbohydrate diets (Evans, 2005; Boyer, 2008). In contrast, mammals with blunter, rounded cusps use their molars for crushing, such as in a diet rich in nuts or fruits (Boyer, 2008; Winchester et al., 2014). This study focused on molars because they are frequently preserved in the fossil record and have been used previously to reconstruct dietary niches in fossil species (Boyer, 2008, 2010).

Several measures of dental morphology have been used widely in examining the diet-dentition relationship in mammals. For example, a common dental measure in living and fossil mammals is shearing quotient (SQ) (Boyer, 2008). SQ is a measurement of the shearing edges of a tooth (Allen et al., 2015), with emphasis on the shearing crest (Evans, 2013). Previous research concluded that frugivores tend to have lower SQ values (Strait, 2001), whereas folivores and insectivores have higher SQ values (Bunn et al., 2011). The restriction of SQ is that it must be measured with undamaged or unworn teeth and requires homologous crest morphology. As a result, studies that employ homology-free topographic measures can reduce this complication (Ungar, 2004).

When examining distantly related species with morphologically diverse dentitions (e.g., taxa within a guild or community), homology- and landmark-free measures are more appropriate. Thus, in recent years, dietary regimes in extinct species have been reconstructed using dental topography (Prufrock et al., 2016). Dental topography is quantitative measure of physical features on teeth through the examination of occlusal relief (Ungar, 2004). Dental topography is used in order to study the different projections of each tooth's surface and provide a function of each of those projections (Evans, 2013). In order to reconstruct dietary variation in fossil mammalian diets, researchers must use measures that will help differentiate dentitions from one another, such as "topographic relief, curvature, and complexity" (Winchester et al., 2014). By comparing the degree of three-dimensional complexity of molars, researchers can gather information about the types of foods that can be broken down via mastication and thus posit a hypothesis of the species' actual dietary niche during its lifetime (Prufrock et al., 2016). A number of studies using dental topography have been conducted on primate and non-primate mammals (Winchester et. al, 2014).

To date, three main dental topographic measures have been used to reconstruct diet in fossil mammalian taxa. First, orientation patch count rotated (OPCR) is a measure that calculates the complexity of the occlusal surface (Bunn et al., 2011). Specifically, OPCR measures occlusal surface via the curves, relief, and complexity variables and uses this information to determine the number of "tools," or the necessary molar dental anatomy, needed to break down the resources the animal consumes (Bunn et al., 2011; Prufrock et al. 2016). OPCR determines the number of 2.5D surface grid points that would point in the same direction in order to be considered a patch (Evans, 2013). The patches are created by taking adjacent points on each tooth facing the same direction in relation to a compass (Bunn et al., 2011). After the tooth is rotated, the mean is calculated from all of the patches totaled together (Prufrock et al., 2016). A high OPCR value signifies a diet rich in challenging or difficult resources to consume, for example, folivory or insectivory (diets that require molars to facilitate shearing) (Prufrock et al., 2016). On the other hand, a low OPCR value is indicative of a diet of crushing rather than shearing, for example in frugivores and bamboo specialists (Bunn et al., 2011). Alone, OPCR is not a perfect model in reconstructing diet, but alongside other topographic measures, it can be a helpful quantitative tool (Bunn et al., 2011).

Second, Dirichlet normal energy (DNE) can be computed to measure the curvature of a tooth. DNE was proposed as a way to quantify the occlusal surface by measuring the deviation away from the "normal" state of energy (Bunn et al., 2011). This computation is done by summing up the squares of surface curves on the occlusal surface (Evans, 2013). The higher the value, the more curves on the occlusal surface (Bunn et al., 2011). Low DNE values signify a lower degree of curvature of the occlusal surface, suggesting little necessity to shear foods, such as in frugivores and omnivores (Prufrock et al., 2016), whereas high DNE values are associated with taxa more capable of cleaving resources, for example in more insectivorous diets (Prufrock, et al., 2016). DNE measures the occlusal curvature of a tooth and is less sensitive to quantitative variations, such as cropping error or orientation, than other measures because DNE is not applied to the entire molar crown (Prufrock et al., 2016).

Finally, relief index (RFI) is the ratio of the enamel's surface area to the crown's occlusal plane projection, or the amount of morphological relief, or topography, of the tooth (Boyer, 2008). RFI is a measurement of high and low projections of the surface of a crown (Winchester, 2016). In M'kiera and Ungar, (2003), RFI was calculated for a group of primate molars (using only the occlusal surface), and the results were analyzed to differentiate dietary preferences and mechanical demands. However, Boyer (2008) included the entire crown in his measure of relief index, the logic behind this being that the functional part of the crown is more than just the occlusal surface (Pampush et al., 2016; Boyer, 2008). High RFI values are associated with molars with longer crests (Boyer, 2008), higher crowns, and taller cusps (e.g., in folivores), whereas low RFI values are associated with relatively featureless molars with lower crowns and shorter cusps (e.g., in frugivores) (Ledogar et al., 2013; Prufrock et al., 2016). In conjunction with a consideration of the phylogenetic relationships among species, RFI tends to be the most useful measurement to study variance in diet (Winchester et al., 2014).

In contrast to OPCR, RFI calculates the steepness of the slope of the crown (Pampush et al., 2016), and compared to SQ, RFI is a better predictor of dietary reconstruction in most cases, due to its ability to distinguish relief changes with wear (Ozaki and Yamada, 2014). In another study conducted by Plyusnin et al. (2008), a ranking system of 100 dental variables that have been shown to reflect diet was created, and RFI was ranked within the top ten (Plysusin et al., 2008). Finally, Boyer (2008) evaluated a sample similar in composition to that examined in this study, and RFI was found to be a useful predictor of dietary behavior (Boyer, 2008). Thus, RFI was used to reconstruct diet in this study.

Table 2. Raw RFI variation, RFI standard deviation, and longevity for each genus included in this study

Genus	RFI Variation	Standard Deviation	Longevity (Ma)
Absarokius	0.153	0.108	5.70
Acritoparamys	0.405	0.154	9.00
Anemorhysis	0.611	0.316	4.90
Apatemys	0.712	0.298	18.10
Arapahovis	0.012	0.008	1.90
Arctodontomys	0.639	0.279	2.10
Cantius	0.187	0.070	5.80

Copelemur	0.461	0.326	4.80
Diacochoerus	0.529	0.374	4.50
Didelphodus	1.342	0.568	18.00
Eoryctes	1.182	0.836	0.80
Ignacius	0.225	0.151	24.50
Knightomys	0.508	0.256	7.90
Labidolemur	0.953	0.523	7.60
Leipsanolestes	0.496	0.351	4.80
Leptacodon	0.649	0.459	14.20
Leptotomus	0.242	0.171	6.10
Macrocranion	0.906	0.325	18.10
Microparamys	0.429	0.164	20.00
Microsyops	0.502	0.235	12.20
Mimoperadectes	0.694	0.361	2.40
Niptomomys	0.817	0.343	4.00
Palaeictops	0.747	0.376	18.00
Palaeoryctes	1.601	1.10	9.00
Paradectes	0.683	0.307	34.80
Paramys	0.349	0.135	19.20
Phenacolemur	0.668	0.243	17.20
Plagioctenodon	0.760	0.337	7.30
Plagioctenoides	0.297	0.210	1.50
Plagiomene	0.042	0.030	2.40
Prodiacodon	1.259	0.555	50.10
Pseudotetonius	0.309	0.218	1.50
Reithroparamys	0.249	0.129	14.90
Scenopagus	0.012	0.008	10.50
Teilhardina	0.575	0.295	2.00
Tetonius	0.191	0.103	1.90
Tetonoides	0.168	0.119	1.90
Worlandia	0.608	0.430	0.80
Wyonycteris	0.702	0.388	2.80

Materials and Methods

Study Sample

The fossil sample is composed of 129 specimens, spanning a 4.5 million-year interval, from approximately 55.5 to 60 million years ago (late-Paleocene-early Eocene), representing 10 orders, 13 families, and 39 mammalian genera from a community within the Bighorn Basin (Table 1).

Table 1. Fossil sample used in this study (N=129)

Order	Family	Genus	N
APATOTHERIA	Apatemyidae	*Apatemys*	5
		Labidolemur	3
DIDELPHIMORPHIA	Peradectidae	*Mimoperadectes*	3
		Peradectes	5
DIDELPHODONTA	Palaeoryctidae	*Didelphodus*	4
		Eoryctes	2
		Palaeoryctes	2
ERINACEOMORPHA	Amphilemuridae	*Diacochoerus*	2
		Leipsanolestes	2
		Macrocranion	5
		Scenopagus	2
EUPRIMATES	Adapidae	*Cantius*	5
		Copelemur	2
	Omomyidae	*Absarokius*	2
		Anemorhysis	4
		Arapahovis	2
		Pseudotetonius	2
		Teilhardina	3
		Tetonius	3
		Tetonoides	2
LEPTICIDA	Leptictidae	*Palaeictops*	3
		Prodiacodon	3
PLESIADAPIFORMES	Microsyopidae	*Arctodontomys*	4
		Microsyops	4
		Niptomomys	5
	Paromomyidae	*Ignacius*	4
		Phenacolemur	5
RODENTIA	Paramyidae	*Acritoparamys*	6
		Leptotomus	2
		Microparamys	6

		Paramys	6
		Reithroparamys	3
	Sciuravidae	*Knightomys*	3
SORICOMORPHA	Nesophontidae	*Leptacodon*	2
		Plagioctenodon	3
		Plagioctenoides	2
		Wyonycteris	3
INCERTAE SEDIS	Plagiomenidae	*Plagiomene*	3
		Worlandia	2

Specimens included in this study are from a single guild: small-bodied, arboreal mammals. This sample is analyzed at the genus level due to the relatively small number of specimens available which are identifiable at the species level. The Bighorn Basin provides one of the most complete sequences of late Paleocene- early Eocene mammalian fossils (Gingerich et al., 1982). From the discovery of the site, it is estimated that around 100,000 fossil specimens have been found in the Bighorn Basin (Chew, 2005). This site is thus abundant in mammalian fossils, and previous researchers have used this sample extensively to identify evolutionary changes within single lineages (e.g., Gingerich, 1980). Thus, after a century of data collection in the Bighorn Basin, there have been countless documented cases of temporally precise evolutionary change in this mammal community (Chew, 2005). These data are therefore ideal to determine the correlation between dietary niche breadth and longevity across multiple mammal groups.

Data Collection

Relief index (RFI) of the first and second mandibular molars (m1 and m2) was calculated as the natural log of the ratio of two different measurements taken from digital tooth images: (1) the enamel crown surface area *(3da)* and (2) “the surface area of the crown’s projection onto the occlusal plane” *(2da):* RFI = (3da/2da) x 100 (Boyer, 2008; Bunn et al., 2011). This measure is resistant to different stages of molar wear (Ozaki and Yamada, 2014), although only unworn or slightly worn molars are used in this study. RFI values were collected from microCT scans of mounted tooth casts using a ScancoMedical μCT machine at 10μm resolution. The scanning protocol followed Boyer (2008) wherein approximately 12-15 molars were mounted on ~1cm-diameter discs, and the image processing protocol followed Boyer (2008) and Prufrock et al (2016).

Each individual tooth was first digitally isolated from the other molars within the microCT scan (each scan included 4-6 discs) using ImageJ 1.6.0. Specimen scans were imported and rotated to align all scans with the occlusal surfaces facing up. The complete ImageJ protocol is listed in Appendix 1.

The resulting set of microCT images were then used to create three-dimensional surface reconstructions of each molar using the image-processing software, Amira 5.2.0. Amira is a software program that takes CT (or microCT) images and allows the user to manipulate, conceptualize, and reconstruct two- and three-dimensional data. This software was used for image segmentation and surface generation. The set of microCT scans pertaining to each molar specimen was uploaded into Amira and was labeled and segmented in order to isolate each individual molar from any surrounding material. After isolating each molar, a surface was created for each tooth using the SurfaceGen function. Each tooth was then cropped at the cementoenamel junction (Figure 1). In order for relief index to be analyzed, the tooth was then smoothed and simplified following Prufrock et al. (2016). The image was saved as a .ply image for importing into MorphoTester for RFI data collection (Figure 2). The complete Amira protocol is listed in Appendix 2. Each genus included at least two specimens so that a range of RFI values and standard deviation would be able to be analyzed for each taxon.

Taxonomic longevities (measured in tenths of millions of years) were collected at the genus level from the literature (Janis, 2008). In this study, the variation in RFI values (measured as standard deviations) were used as a proxy for the degree of dietary specialism or generalism of the genus (Table 2). For example, a larger range of RFI values would indicate a larger dietary niche, and thus a more generalist diet.

Table 2. Raw RFI variation, RFI standard deviation, and longevity for each genus included in this study.

Genus	RFI Variation	Standard Deviation	Longevity (Ma)
Absarokius	0.153	0.108	5.70
Acritoparamys	0.405	0.154	9.00
Anemorhysis	0.611	0.316	4.90
Apatemys	0.712	0.298	18.10
Arapahovis	0.012	0.008	1.90
Arctodontomys	0.639	0.279	2.10
Cantius	0.187	0.070	5.80
Copelemur	0.461	0.326	4.80
Diacochoerus	0.529	0.374	4.50
Didelphodus	1.342	0.568	18.00
Eoryctes	1.182	0.836	0.80
Ignacius	0.225	0.151	24.50
Knightomys	0.508	0.256	7.90
Labidolemur	0.953	0.523	7.60
Leipsanolestes	0.496	0.351	4.80
Leptacodon	0.649	0.459	14.20
Leptotomus	0.242	0.171	6.10
Macrocranion	0.906	0.325	18.10
Microparamys	0.429	0.164	20.00
Microsyops	0.502	0.235	12.20
Mimoperadectes	0.694	0.361	2.40
Niptomomys	0.817	0.343	4.00
Palaeictops	0.747	0.376	18.00
Palaeoryctes	1.601	1.10	9.00
Paradectes	0.683	0.307	34.80
Paramys	0.349	0.135	19.20

Phenacolemur	0.668	0.243	17.20
Plagioctenodon	0.760	0.337	7.30
Plagioctenoides	0.297	0.210	1.50
Plagiomene	0.042	0.030	2.40
Prodiacodon	1.259	0.555	50.10
Pseudotetonius	0.309	0.218	1.50
Reithroparamys	0.249	0.129	14.90
Scenopagus	0.012	0.008	10.50
Teilhardina	0.575	0.295	2.00
Tetonius	0.191	0.103	1.90
Tetonoides	0.168	0.119	1.90
Worlandia	0.608	0.430	0.80
Wyonycteris	0.702	0.388	2.80

Analytical Methods

To validate the relationship between variation in RFI values and dietary breadth, an extant mammalian sample derived from Boyer (2008) and Bunn et al. (2011) was evaluated. Dietary classifications were taken directly from these two sources. Species with strict insectivorous, folivorous, or frugivorous diets (9 genera) were classified as specialists, and the omnivores (9 genera) were classified as generalists. Unknown dietary classifications were disregarded from this study. Standard deviations of RFI values were collected from Boyer (2008; Table 5) and Bunn et al. (2011; Table 4) (see Table 3). A two-tailed, non-paired t-test between generalist and specialist extant genera and their respective standard deviations in RFI values was performed.

To examine the relationship between breadth of RFI values (independent variable) and longevity (dependent variable) within the fossil sample, an ordinary least squared regression was performed in Excel 2010 (v.14.0).

Table 3. RFI standard deviations (SDs) of extant generalist and specialist species (collected from Boyer (2008) and Bunn (2011)).

Generalist Genera	SD
Eulemur	0.030
Lemur	0.025
Microcebus	0.021
Nycticebus	0.024
Perodicticus	0.025
Cheirogaleus	0.017
Daubentonia	0.010
Varecia	0.010
Tupaia	0.037

Specialist Genera	SD
Tarsius	0.005
Galago	0.015
Loris	0.017
Cynocephalus	0.002
Indri	0.022
Hapalemur	0.008
Lepilemur	0.008
Propithecus	0.010
Prolemur	0.004

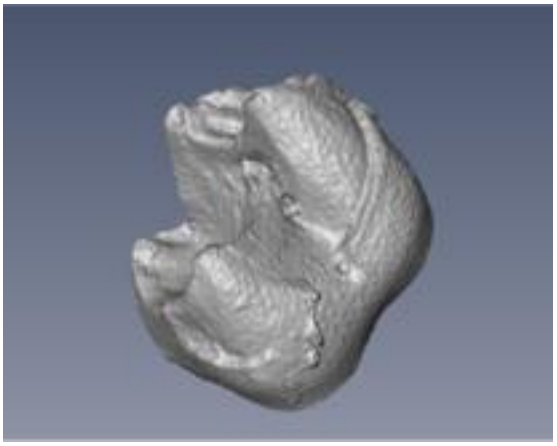

Figure 1. *Cantius* m2 after image cropping. Image from Amira.

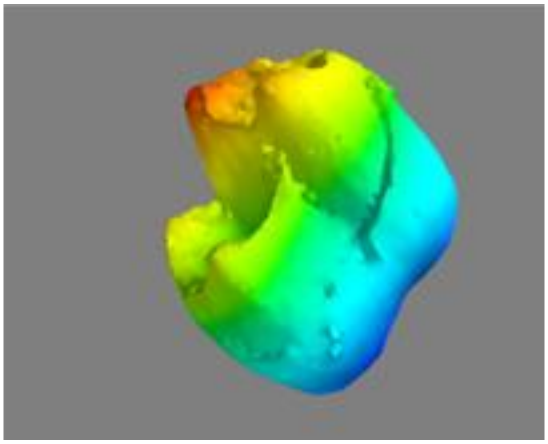

Figure 2. *Cantius* m2 after input into MorphoTester.

Results

In the extant sample, results showed a significant difference between generalist and specialist dietary groups (P=.0049). Given this result, it was determined that RFI variation could be used to discriminate generalist and specialist taxa in the fossil record. Figure 3 demonstrates a positive linear relationship between the standard deviation of RFI values and longevity measured in millions of years, in the fossil sample. The R-value is 0.114, indicating that the linear relationship between RFI variation and longevity is weak. The p-value of the correlation was 0.465, meaning there was not a significant correlation between RFI and longevity.

Table 4. Results of regression analyses of RFI standard deviation against longevity (Ma).

	R-Value	R-Squared Value	Adjusted R-Squared Value	P-Value	Lower 95%	Upper 95%
RFI SD	0.114	0.01342	0.013	0.465	-9.472	20.360

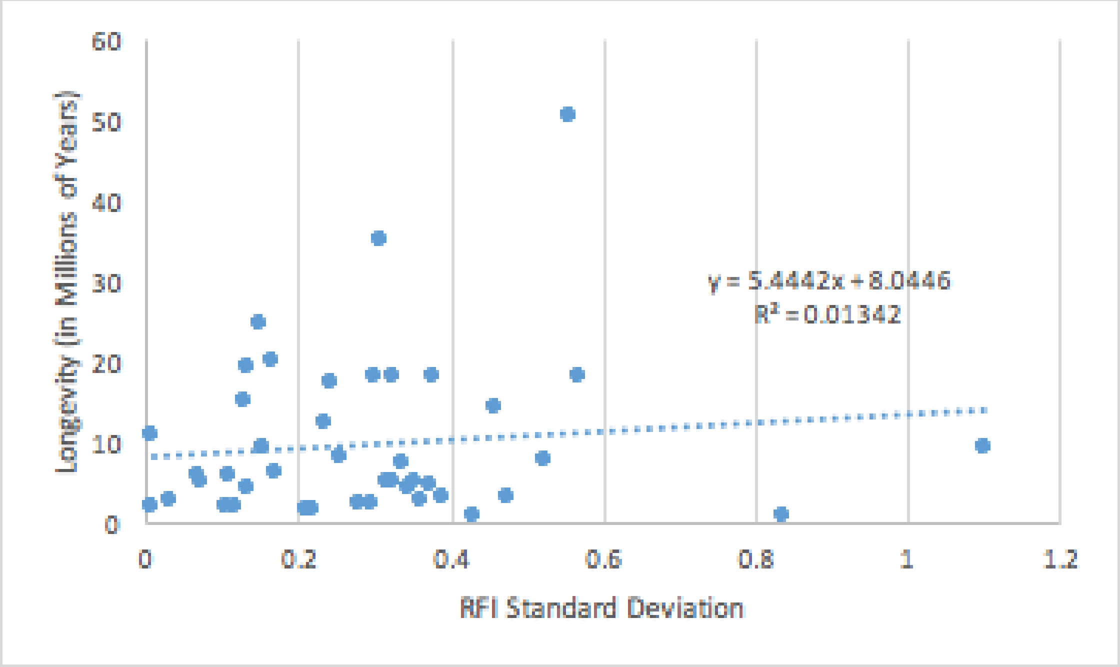

Figure 3. Results of ordinary least-squares linear regression of RFI standard deviation and longevity (P=0.465).

In a graphs shown in Figure 4 and Figure 5, there is not a strong visual connection between time periods of the longevity of the genus. Thus, the RFI's are not different based on the time period in which each genus lived. Within figure 6, there is not a strong visual connection between RFI values and the Mammalian Family, however there are certain families, such as Adapidae, in which could produce a stronger correlation of similarities as the specimens are clustered in a similar formation. Perry, St Clair and Hartstone-Rose, (2015) researched the Adapidae family and stated that their diet was mainly folivory, meaning more specialized. They also mentioned that this specific family had "great adductor muscle leverage" which signified a firm chewing force (Perry, St Clair and Hartstone-Rose, 2015). Due to this discovery, it is possible that with this specific sub-classification of dietary preference within the specialist family, the folivorous mammals would have a stronger RFI clustering and correlate with their longevity of around 5 Ma (4.8 and 5.3 within this study). On the other hand, the Palaeoryctidae family varies significantly with its respective RFI values. This family is strictly insectivore (Behrensmeyer and Turner, 2013). A thing to note is that the longevity between the Palaeoryctidae family is vastly different from one another (18 Ma, 9 Ma and as low as .9 Ma). This may be an indicator that the longevity does play some role into the RFI equation. In figure 7, a solid visual connection is found, specifically with the group of specimens with a longevity under 7 Ma, which also includes the Adapidae family. The standard deviation for this group of specimen is .185, signifying that 68% of the standard deviation of RFI values are between .077 and .447 and close to the mean.

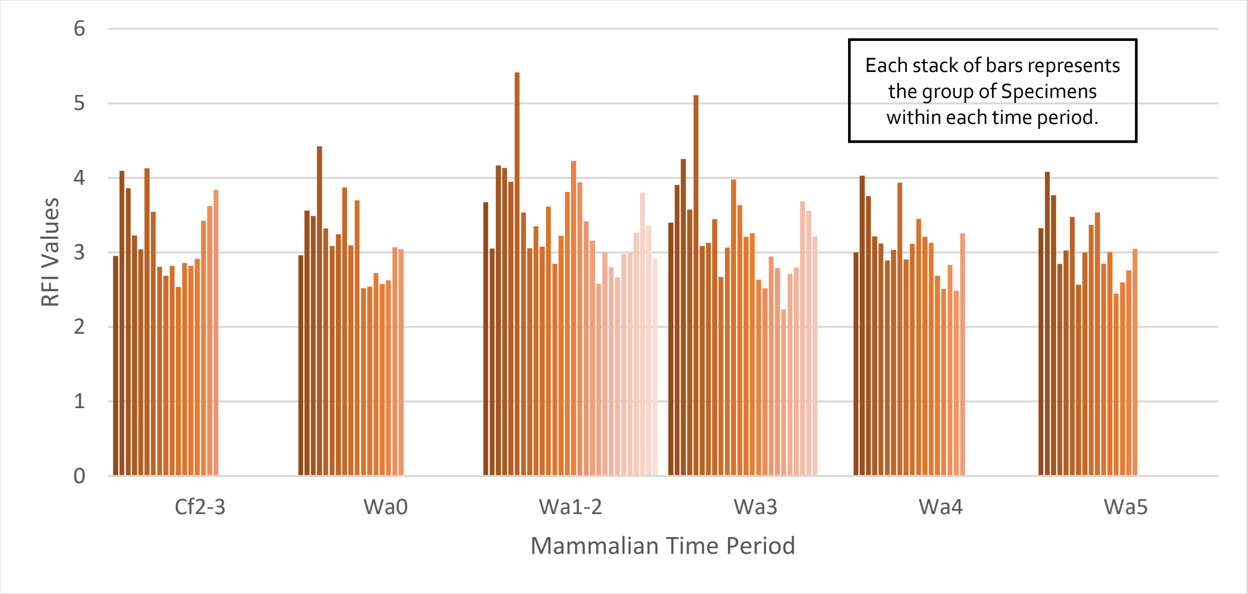

Figure 4. Visual representation of the group of RFI specimens within each genus separated by time interval.

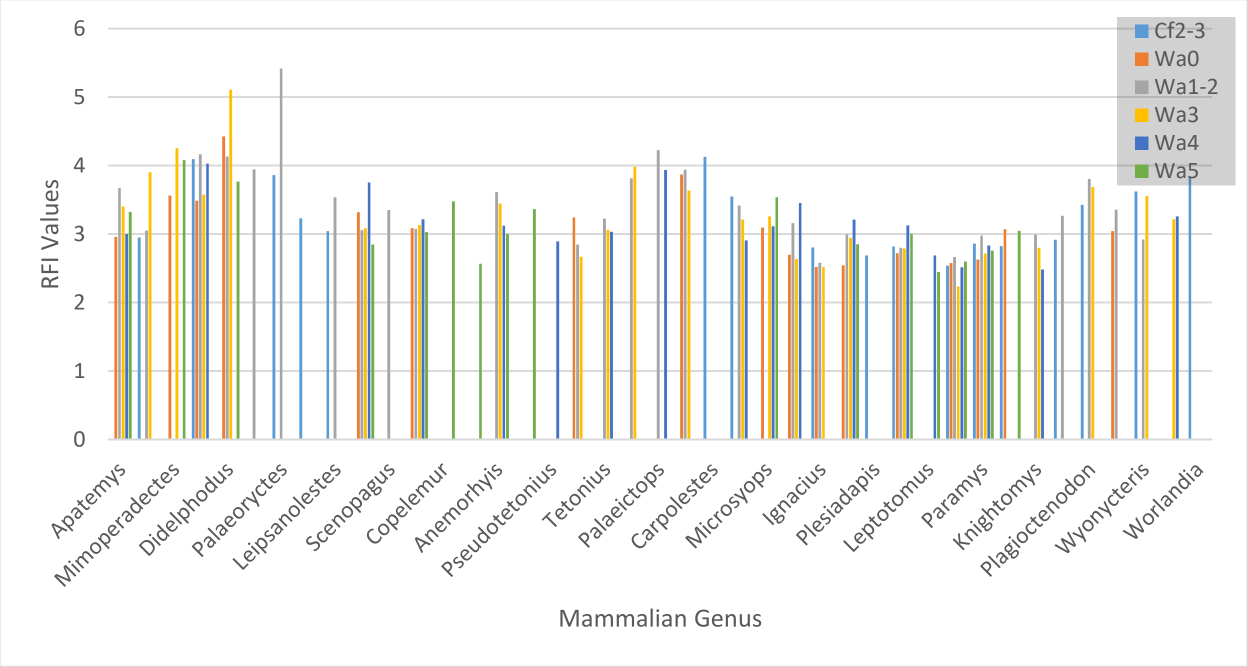

Figure 5. Visual representation of the RFI values within each genus separated by time interval.

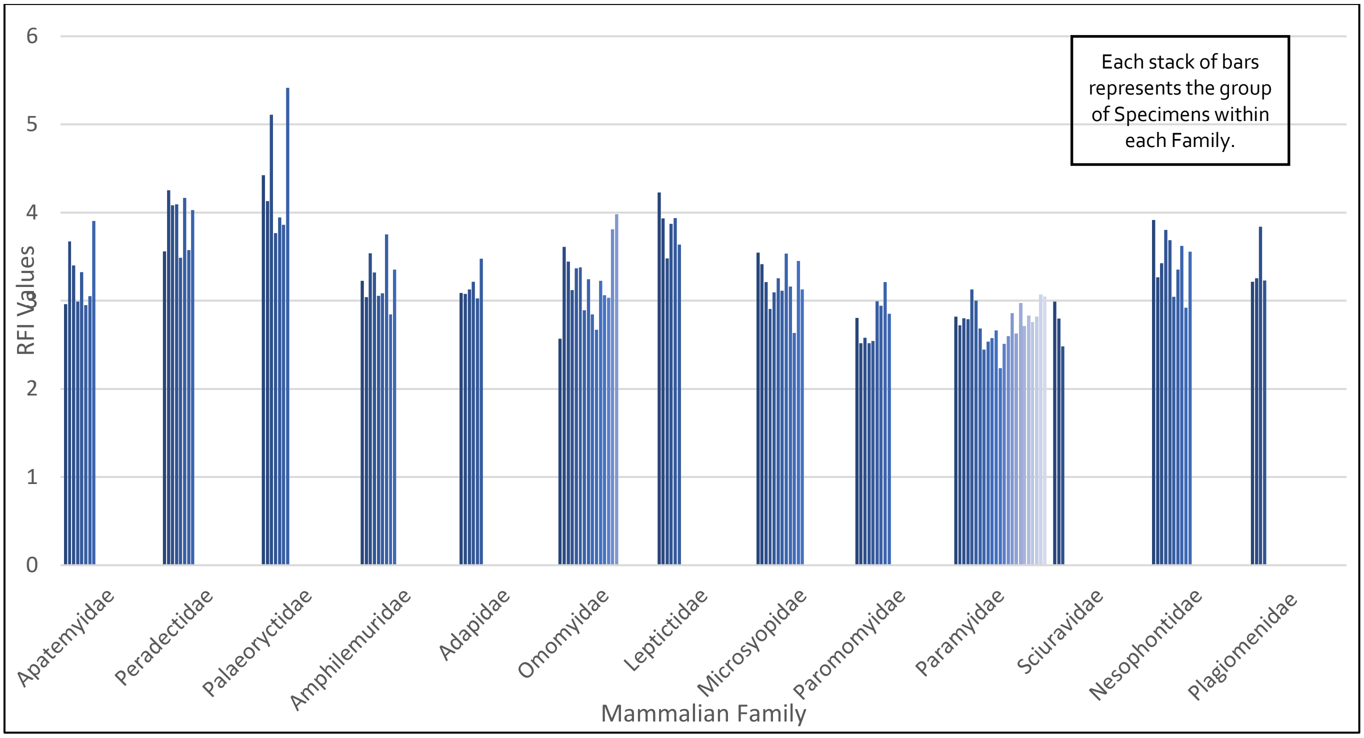

Figure 6. Visual representation of the RFI values within each Mammalian family.

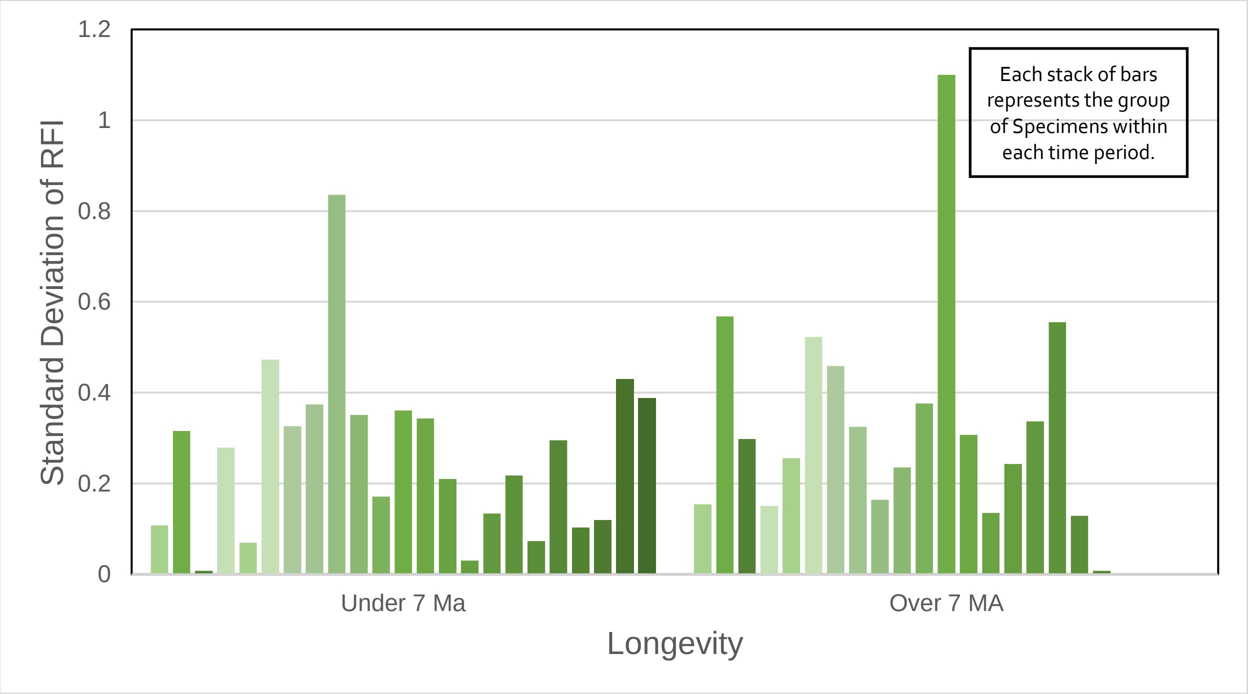

Figure 7. Visual representation of the specimens with longevity below 7 Ma and over 7 Ma.

Discussion

Although there was a correlation between dietary niche breadth and RFI variation in extant genera, this study could not confirm a correlation between longevity and dietary niche breadth (as measured by standard deviation in RFI values) in the fossil sample. These results indicate that although relief index can be used as a dental topographic measure to separate species based on dietary preference, it cannot be used to predict longevity of fossil genera.

By visualizing the lack of association between diet and longevity within the fossil taxa, diets were collected by Fossilworks fossil data base for all genera within the study (Behrensmeyer and Turner, 2013) to test the difference between generalists and specialists. If the ecological diet was classified as omnivore or a combination of dietary measures, the genus was deemed a generalist for the t-test. If the genus was classified as insectivore, folivore, carnivore, frugivore or herbivore, the genera was deemed a specialist. There were 25 specialist genera and 14 generalist genera (Table 5). From there, the t-test separated these genera and their respective standard deviation of RFI values. The results showed a P=.7530, a very insignificant value.

Table 5. RFI standard deviations (SDs) of fossils obtained from the generalist and specialist species within study sample (collected from Behrensmeyer and Turner, 2013).

Genera	Ecological Diet	Classification
Apatemys	Herbivore	Specialist
Absarokius	Insectivore	Specialist
Anemorhysis	Insectivore	Specialist
Arapahovis	Insectivore/Frugivore	Generalist
Acritoparamys	Herbivore	Specialist
Arctodontomys	Omnivore	Generalist
Cantius	Omnivore	Generalist
Copelemur	Omnivore	Generalist
Didelphodus	Carnivore	Specialist
Diacochoerus	Omnivore	Generalist
Eoryctes	Insectivore	Specialist

Ignacius	Omnivore	Generalist
Knightomys	Herbivore	Specialist
Leptotomus	Herbivore	Specialist
Leptacodon	Insectivore	Specialist
Labidolemur	Herbivore	Specialist
Leipsanoleste	Insectivore/Carnivore	Generalist
Microparamys	Herbivore	Specialist
Macrocranion	Insectivore	Specialist
Mimoperadecte	Omnivore	Generalist
Microsyops	Omnivore	Generalist
Niptomomys	Omnivore	Generalist
Peradectes	Omnivore	Generalist
Palaeoryctes	Insectivore	Specialist
Pseudotetonius	Insectivore	Specialist
Palaeictops	Insectivore/Carnivore	Generalist
Prodiacodon	Insectivore/Carnivore	Generalist
Phenacolemur	Omnivore	Generalist
Paramys	Herbivore	Specialist
Plagioctenodon	Insectivore	Specialist
Plagioctenoides	Insectivore	Specialist
Plagiomene	Folivore	Specialist
Reithroparamys	Herbivore	Specialist
Scenopagus	Insectivore	Specialist
Teilhardina	Insectivore	Specialist
Tetonius	Insectivore	Specialist
Tetonoides	Insectivore	Specialist
Wyonycteris	Insectivore	Specialist
Worlandia	Folivore	Specialist

In a study done by Navarro-Lopez et al. (2014), researchers focused on multiple generalist and specialist kestrels, a raptor species. They concluded that generalists that possessed a broader dietary niche had a higher life expectancy and greater overall fitness (Navarro-Lopez et al., 2014). However, this study showed evidence of this association by using birds rather than mammals, which could signify a lack of association between the mammalian population. This study also shows the relationship between lifespan being associated with diet, rather than longevity and would have to be investigated further to see whether or not evolutionary longevity was affected by the longer lifespan.

There have been a few studies that also indicate a lack of association between evolutionary success and dietary preference. For example, Crowley et al. (2016) tested for fitness function using two specialist strategies and two generalist strategies of insects. The study focused on generalist vs. specialist fitness when the surrounding environment conditions are stressed or changed. This relationship between overall fitness and stressed conditions is known as bet-hedging. Results from this study showed that even when exposed to random environments (classified as relatively wet or relatively dry years), both generalist and specialist dietary niches declined throughout time. In another test during this study, there were certain circumstances, such as when variation in the environment was low, in which specialists actually thrived over generalists (Crowley et. al., 2016).

In another study, Safi and Kerth (2004) conducted a study on bats. The goal of the study was to correlate dietary niche breadth with extinction risk. The research stated that there was not only a lack of association between diet and fitness but that extinction risk was actually heavily influenced by the wing morphology of the bat. This research indicated that diet was not the obvious cause of decreased fitness, and thus dietary specialists were not more or less vulnerable to extinction than bats that had a broader dietary resource preference (Safi and Kerth, 2004). Although life expectancy is not synonymous with evolutionary longevity, it is possible that a longer mammalian evolutionary longevity may be related to longer life expectancies among individuals. For instance, in Bonsall and Mangel (2009), a study was conducted on previous research from adult and juvenile animals to examine the relationship between life expectancy and the dynamics of evolutionary longevity by mathematical study. In this study, researchers examined changes in fitness and its effects on evolutionary longevity. The study was focused on ecological trade offs, or losing a part of the environmental interaction and gaining another. Due to the selective trade offs, natural selection of these animals favored mutations that lengthened the overall fitness. The mutations of interest had an influence on the process of reproduction, which impacted the evolutionary longevity as a whole. Results showed that overall evolutionary longevity was increased by numerous factors that included density-dependence within a certain area, age-structure, and life-expectancy (Bonsall and Mangel, 2009). Vera et al. (2012) tested for lifespan lengthening and longevity using telomeres in humans and mice. Based on the research, it was found that by increasing the shortening of telomeres over time, the shorter the lifespan. The study also showed that by through longitudinal telomere studies, the shortening of telomeres had a direct outcome on decreased longevity over time (Vera et al., 2012). Also, the study conducted by Lahdenper, Mar, and Lummaa (2014) tested 3037 elephants and 8943 humans and the overall conclusion was that with with longer lifespan and ability to reproduce will cause the more reproduction that will occur through the decades, leaving more offspring to lengthen the longevity of the taxon (Lahdenper, Mar, and Lummaa, 2014). Overall, most previous research has indicated an increased lifespan for dietary generalists, but it is possible that RFI and dietary niche could potentially have an opposite effect on longevity (i.e., a narrow dietary niche could result in a longer longevity).

It is also possible that variables such as environmental change can have an impact on longevity (Boyer, 2008). For example, the environment can have a profound effect on both the dietary niche and longevity. Typically, specialists will relocate when environmental change is continuous. The evolution and migratory patterns of a species may be influenced by surrounding environmental conditions (Colles et al., 2009). In Wilf (2000), it was found that during the late-

Paleocene, early-Eocene, the Bighorn Basin held two major turnover events. Both of these events showed that over 80% of the plants had become extinct (Wilf, 2000), which would have impacted the folivorous Adapidae family.

With this information and the continuous climatic change in the Bighorn Basin during the time period examined, it is possible that a narrow dietary niche could potentially be more utilized than the broad dietary niche preference at certain points in time. In addition, body mass can also impact longevity (Boyer, 2008). Molar size is generally correlated with body mass (Winchester, 2014), and the sample of this study consisted of only small-bodied mammals. Gingerich et al., (1982) concluded that within primates and other mammals, the body weight is a strong indicator of molar size. Within the study, the correlation for molar teeth and body size was above .90, where the premolars were just above .55, which further demonstrates the need to test molars compared to other teeth (Gingerich et al., 1982). Thus, the inclusion of mammalian body size (estimated by molar size) or mammals spanning a wider range of body masses in future studies may result in a stronger correlation between dietary niche and longevity in fossil taxa.

I would also like to note that in Figure 7, there may be a potential area of study with the genera that have a lower longevity (under 7 Ma). Although this would limit the sample size even further, there may be a connection between RFI and a tighter data set pertaining to longevity. If there is a ceiling of which this concept is applied (i.e. after 7 Ma), then the possibilities still stands that under certain circumstances, the RFI may impact longevity, just not with the complete set that I used in my study.

Furthermore, the terms “generalist” and “specialist” are not always concrete. In Costa et al. (2015), a study was conducted on *Salamandria perspicillata*, a species of salamanders that is known to be a dietary specialist. However, during the course of the study, the environment changed throughout the year, and during the fall season, the “specialist” salamander turned into more of a “generalist” due to the scarcity of food resources (Costa et al., 2015). In another example on Ungulates, the mammals were separated into two categories: browsing springbok (generalists) and grazing gemsbok (specialists). The investigation took nineteen months and had two periods of drought, meaning that resource availability was low. During this drought, the specialist gemsbok actually held a significantly larger dietary flexibility and were able to access fallback foods easier than the generalist springboks (Lehmann et al., 2013). This demonstrates that the current environment of the Bighorn Basin played a part in dietary niche breadth within genera and species. It is also worth mentioning that diet is only one partial aspect that goes into what determines a specialist mammal from a generalist. There are many other factors, such as environmental preference, that leads to the classification as a generalist or specialist. In addition, although the Bighorn Basin is a well-known location to study and research mammalian fossils, this study only represents the mammals at a single site. The RFI values at this site and time period could be entirely different from those of another community. By studying a location that has less climatic change, the RFI correlation with evolutionary longevity may be stronger. Thus, this research should be applied to multiple fossil sites over different periods of time.

There were a few more potential caveats or room for error within this study. As for dietary measures, RFI was used as it was the best representation of dietary niche (Boyer, 2008). However, if RFI was used in combination with SQ, DNE, or OPCR, it is possible that dietary niche breadth could be more precisely reconstructed (Winchester, 2014). According to Bunn et al., (2011), the most advantageous combination of dental topographic measures would be RFI, OPCR, and DNE because it yields a higher modal and overall success (Bunn et al., 2011). Longevity values were collected from the literature to the tenth of millions of years; however, with further investigation into each genus, data could be taken to the hundredth of millions of years, yielding a more precise estimate of genus lifespan. Another potential source of error is intra-observer error. Although the protocol was the same for each specimen, cropping each molar at the cemento-enamel junction is somewhat subjective. Thus, it is possible that if cropping was repeated, the resulting RFI values may be different (although see Boyer (2008)). Given that there were only 2-5 specimens representing each genus, even a small change in cropping could have impacted the study results. The smaller number of specimens could also impact the complication of a skewed RFI distribution due to the extreme difference in just 2 RFI values. With only two values, the RFI standard deviations likely don't represent true RFI variation for those genera. More specimens per genus could help create a more accurate standard deviation for the genus. By having a relatively small sample size of 129 specimens, the data set and thus analyses could be skewed. The lack of statistical power could have impacted the overall results. A larger sample (specifically, more specimens per genus) would be beneficial to analyze this on a broader scale. Thus, I suggest future investigation into testing RFI with a larger sample size or different subset of mammals, and more precise measures of dietary niche breadth and longevity as this may yield different results.

Overall, mammalian communities seem to be gradually declining due to ecosystems that are being genetically and naturally modified by plants or animals becoming engineered to produce certain traits for survival. This raises the question of whether or not certain taxa can thrive in the face of these changes (Devictor et al., 2008). With previous studies that involve generalists and specialists, the relationship between mammalian specialization and extinction risk has been consistently supported, but the environment also plays a large role in whether or not a taxon survives. Paleontologists continue to research and study fossil mammals, the environmental fluctuations that surround those genera, and compare that information with extant taxa for reference (Colles et al., 2009). In doing so, the mammalian fossil record can be used to determine why certain species went extinct throughout time. Minor changes in the environment may have potentially significantly impacted their longevity in some way.

Conclusion

Dietary niche and standard deviation in relief index of small-bodied, arboreal mammals from the Bighorn Basin does not reflect longevity of the genera. This does not support the claim that genera with larger dietary niches (i.e., generalists) will have greater evolutionary “success” (measured by longevity) than genera with smaller dietary niches (i.e., specialists). Dental topography has historically been a sufficient tool in reconstructing dietary niche (Boyer, 2008). However, evolutionary longevity cannot be extrapolated from this concept.

Appendices

Appendix 1. ImageJ Protocol

1. Import image sequence.
2. Flip or rotate the image sequence using the “Transform” functions so that the occlusal surface is facing up.
3. Select the tooth of interest and then Image > Crop so that the tooth is isolated from the others on the disc.
4. Save the tooth as an image sequence for upload into Amira.

Appendix 2. Amira Protocol

1. Load set of .tif files for a given specimen into Amira.
2. Compute > LabelVoxel and uncheck “Bubbles.”
3. Click on Image Segmentation.
4. In the display and masking curve window, identify the lowest point of the curve. Apply that voxel size to LabelVoxel.
5. Go to Image Segmentation and verify that only the tooth is outlined.
6. Remove all islands for all slices.
7. Compute > SurfaceGen and change the Smoothing to “none.” Apply these settings.
8. Click SmoothSurface and change the iterations to 100. Apply these settings.
9. Select Surface Editor and change the Draw Style to “shaded” and the Colors to “boundary ids.”
10. Use the Draw contour option to highlight faces (D) with the interact tool. Remove faces with the buffer (D) tool. Remove all unnecessary objects or surfaces. Apply settings.
11. Highlight entire tooth and extra space. Select Buffer > Invert Highlights. Apply.

12. Select Buffer > Edit > Delete highlighted material. Save cropped specimen.

13. Choose the Simplifier icon and change the faces value to 10,000. Apply these settings.

14. Save the tooth image as a .ply to upload into MorphoTester.

Appendix 3. Raw Data for Specimen Sample

Family	**Genus**	**Specimen**	**Time Period**	**RFI**
Apatemyidae	*Apatemys*	USGS 26548	Wa0	2.960
		USGS 9614	Wa1-2	3.672
		USMN 527699	Wa3	3.401
		UM 67310	Wa4	2.999
		USNM 487861	Wa5	3.325
	Labidolemur	UM 71481	Cf2-3	2.951
		UM 81465	Wa1-2	3.053
		UM 68590	Wa3	3.904
Peradectidae	*Mimoperadectes*	UM 538314	Wa0	3.560
		UW 9826	Wa3	4.254
		YPM 35149	Wa5	4.082
	Peradectes	UM 109746	Cf2-3	4.095
		UW 9605	Wa0	3.487
		UM 68867	Wa1-2	4.165
		YPM 30594	Wa3	3.575
		USGS 17625	Wa4	4.028
Palaeoryctidae	*Didelphodus*	USNM 540166	Wa0	4.424
		USGS 9617	Wa1-2	4.131
		Uncat. (1)	Wa3	5.109
		USGS 9107	Wa5	3.767
	Eoryctes	UM 81555	Wa1-2	3.947
	Palaeoryctes	UM 82674	Cf2-3	3.861
		UM 79657	Wa1-2	5.417
Amphilemuridae	*Leipsanolestes*	UM 77572	Cf2-3	3.042
		UW 9672	Wa1-2	3.538
	Macrocranion	USGS 8098	Wa0	3.320
		UW 9640	Wa1-2	3.056
		USNM 542092	Wa3	3.086
		USNM 494902	Wa4	3.753
		USNM 495037	Wa5	2.847
	Scenopagus	UW 8998	Wa1-2	3.352
Adapidae	*Cantius*	US 25850	Wa0	3.087
		USGS 2558	Wa1-2	3.077
		USNM 522172	Wa3	3.130
		USGS 3670	Wa4	3.214
		USGS 28051	Wa5	3.027
	Copelemur	USGS 30189	Wa5	3.477
Omomyidae	*Absarokius*	UM 91756	Wa5	2.568
	Anemorhyis	UM 71288	Wa1-2	3.612
		UM 78965	Wa3	3.446
		USGS 27425	Wa4	3.121

		USGS 15403	Wa5	3.001
	Arapahoivus	USNM 491904	Wa5	3.367
		USNM 491907	Wa5	3.379
	Pseudotetonius	USGS 5973	Wa4	2.891
	Teilhardina	USGS 12193	Wa0	3.246
		USGS 9156	Wa1-2	2.847
		YPM 30720	Wa3	2.671
	Tetonius	UM 76501	Wa1-2	3.225
		UM 69108	Wa3	3.063
		UM 73294	Wa4	3.034
	Tetonoids	UM 81485	Wa1-2	3.812
		UM 71513	Wa3	3.980
Leptictidae	*Palaeictops*	UM 80508	Wa1-2	4.227
		UM 73130	Wa4	3.935
		USNM 491876	Wa5	3.480
	Prodiacodon	USGS 6275	Wa0	3.871
		USGS 2566	Wa1-2	3.939
		USGS 9670	Wa3	3.637
Microsyopidae	*Arctodontomys*	UM 83015	Cf2-3	3.546
		UM 82279	Wa1-2	3.417
		UM 85689	Wa3	3.212
		UM 66780	Wa4	2.907
	Microsyops	USNM 54092	Wa0	3.096
		USNM 540227	Wa3	3.257
		UM 73099	Wa4	3.114
		UM 75637	Wa5	3.536
	Niptomomys	USGS 25496	Wa0	2.698
		UM 82190	Wa1-2	3.160
		USGS 23920	Wa3	2.635
		UM 74056	Wa4	3.452
		USGS 6703	Wa5	3.130
Paromomyidae	*Ignacius*	UM 69877	Cf2-3	2.806
		UW 7116	Wa0	2.519
		UM 86538	Wa1-2	2.581
		USNM 511224	Wa3	2.519
	Phenacolemur	USGS 27394	Wa0	2.543
		USGS 9606	Wa1-2	2.994
		USNM 488331	Wa3	2.944
		UMM 67333	Wa4	3.211
		USGS 2349	Wa5	2.851
Plesiadapidae	*Plesiadapis*	UM 98094	Cf2-3	2.688
Paramyidae	*Acritoparamys*	UM 71173	Cf2-3	2.820
		UM 82383	Wa0	2.722
		UM 77810	Wa1-2	2.801
		USGS 38256	Wa3	2.791
		UM 77816	Wa4	3.127
		USGS 9114	Wa5	3.003
	Leptotomus	USNM 4953	Wa4	2.687
		USNM 525128	Wa5	2.445
	Microparamys	UM 77719	Cf2-3	2.538
		USNM 488360	Wa0	2.577
		UM 85624	Wa1-2	2.665

		UM 85706	Wa3	2.236
		UM 81390	Wa4	2.513
		USGS 6740	Wa5	2.599
	Paramys	UM 65120	Cf2-3	2.859
		USNM 525634	Wa0	2.628
		UM 77823	Wa1-2	2.977
		UM 83031	Wa3	2.714
		UM 115376	Wa4	2.832
		UM 96619	Wa5	2.760
	Reithroparamys	UM 77742	Cf2-3	2.821
		UM 114570	Wa0	3.070
		UM 77853	Wa5	3.049
Sciuravidae	*Knightomys*	UM 78889	Wa1-2	2.992
		USNM 525109	Wa3	2.798
		USNM 495274	Wa4	2.484
Nesophontidae	*Leptacodon*	UM 68866	Cf2-3	3.915
		UM 98356	Wa1-2	3.266
	Plagioctenodon	UM 71689	Cf2-3	3.425
		USGS 17626	Wa1-2	3.804
		YPM 34257	Wa3	3.686
	Plagioctenoids	USGS 23805	Wa0	3.044
		USGS 2573	Wa1-2	3.354
	Wyonycteris	UM 68288	Cf2-3	3.622
		UM 95373	Wa1-2	2.920
		UM 83049	Wa3	3.556
Plagiomenidae	*Plagiomeme*	USNM 527689	Wa3	3.214
		UM 66800	Wa4	3.256
	Worlandia	UM 71042	Cf2-3	3.839
		UM 69601	Cf2--3	3.231

References

Allen, K. L., Cooke, S. B., Gonzales, L. A., & Kay, R. F. (2015). Dietary inference from upper and lower molar morphology in platyrrhine primates: E0118732. *PLoS One*, *10*(3).

Angermeier, P. (1995). Ecological Attributes of Extinction-Prone Species: Loss of Freshwater Fishes of Virginia. *Conservation Biology,9*(1), 143-158.

Behrensmeyer, A. K., and A. Turner. (2013). Taxonomic occurances of Suidae recorded in the Paleobiology Database. *Fossilworks.*

Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(24), 10075–10079.

Bolnick, D., Svanbäck, R., Fordyce, J., Yang, L., Davis, J., Hulsey, C., . . . Associate Editor: MarkA. McPeek. (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist*, *161*(1), 1-28.

Bonsall, M. B., & Mangel, M. (2009). Density dependence, lifespan and the evolutionary dynamics of longevity. *Theoretical Population Biology*, *75*(1), 46-55.

Boyer, D. M. (2008). Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. *Journal of Human Evolution, 55*(6), 1118-1137.

Boyer, D. M., Evans, A. R., & Jernvall, J. (2010). Evidence of dietary differentiation among late Paleocene-early Eocene plesiadapids (mammalia, primates). *American Journal of Physical Anthropology, 14(2),* 194-NA.

Bown, T. M., & Rose, K. D. (1987). Patterns of dental evolution in early eocene anaptomorphine primates (omomyidae) from the bighorn basin, wyoming. *Memoir (the Paleontological Society), 23,* 1-162.

Breed, G., Bowen, W., McMillan, J., & Leonard, M. (2006). Sexual Segregation of Seasonal Foraging Habitats in a Non-Migratory Marine Mammal. *Proceedings: Biological Sciences, 273*(1599), 2319-2326.

Bunn, J. M., Boyer, D. M., Lipman, Y., St. Clair, E. M., Jernvall, J., & Daubechies, I. (2011). Comparing dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. *American Journal of Physical Anthropology, 145*(2), 247-261.

Chew, A. (2005). Biostratigraphy, paleoecology and synchronized evolution in the early Eocene mammalian fauna of the central Bighorn Basin, Wyoming.

Christensen, H. B. (2014). Similar associations of tooth microwear and morphology indicate similar diet across marsupial and placental mammals: E102789. *PLoS One, 9*(8)

Colles, A., Liow, L. H., & Prinzing, A. (2009). Are specialists at risk under environmental change? neoecological, paleoecological and phylogenetic approaches. *Ecology Letters, 12*(8), 849-863.

Cooke, S. B. (2011). Paleodiet of extinct platyrrhines with emphasis on the caribbean forms: Three-Dimensional geometric morphometrics of mandibular second molars. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology, 294*(12), 2073-2091.

Crowley, P. H., Ehlman, S. M., Korn, E., & Sih, A. (2016). Dealing with stochastic environmental variation in space and time: Bet hedging by generalist, specialist, and diversified strategies. *Theoretical Ecology*, 9(2), 149-161.

Cuozzo, F. P. (2008). Using extant patterns of dental variation to identify species in the primate fossil record: A case study of middle eocene omomys from the bridger basin, southwestern wyoming. *Primates, 49*(2), 101-15.

Devictor, V., Julliard, R., & Jiguet F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos, 117(4),* 507-514.

Evans, Alistair R. and Gordon D. Sanson. (2005). Correspondence between tooth shape and dietary biomechanical properties in insectivorous microchiropterans. Evolutionary Ecology Research. 7(453-478).

Evans, A., Hunter, J., Fortelius, M., & Sanson, G. (2005). The scaling of tooth sharpness in mammals. Annales Zoologici Fennici, 42(6), 603-613.

Evans, A. (2013). Shape descriptors as ecometrics in dental ecology. *Hystrix, the Italian Journal of Mammalogy, 24*(1), 133-140.

Friscia, Anthony R. and Blaire Van Valkenburgh. (2010). "Ecomorphology of North American Eocene carnivores: evidence for competition between Carnivorans and Creodonts." 311-341.

Gingerich, Philip D. (1980). Early Cenozoic Palenotology and Stratigraphy of the Bighorn Basin, Wyoming. University of Michigan Papers on Palentology, 24(1-156).

Gingerich, P. D., Smith, B. H., & Rosenberg, K. (1982). Allometric scaling in the dendition of primates and prediction of body weight from tooth size in fossils. *America Journal of Physical Anthropology, 58*(1), 81-100.

Griffith, T., & Sultan, S. E. (2012). Field-based insights to the evolution of specialization: Plasticity and fitness across habitats in a specialist/generalist species pair. *Ecology and Evolution, 2*(4), 778.

Janis, C. M. Gunnell, Gregg E., & Uhen, Mark D. (2008). *Evolution of Tertiary Mammals of North America.* Cambridge: Cambridge: University Press.

Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology, 15*(2), 173-190.

Kostikova, A., Litsios, G., Salamin, N., & Pearman, P. B. (2012). Linking life-history traits, ecology, and niche breadth evolution in north American eriogonoids (polygonaceae). *The American Naturalist, 182*(6), 760-774.

Kubo, M. O., & Yamada, E. (2014). The inter-relationship between dietary and environmental properties and tooth wear: Comparisons of mesowear, molar wear rate, and hypsodonty index of extant sika deer populations: E90745. *PLoS One, 9*(6), e90745.

Lahdenperä, M., Mar, K. U., & Lummaa, V. (2014) Reproductive cessation and post-reproductive lifespan in asian elephants and pre-industrial humans. *Frontiers in Zoology, 11,* 54.

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

Lehmann, D., John Kazgeba Elijah Mfune, Gewers, E., Cloete, J., Brain, C., & Voigt, C. C. (2013). Dietary plasticity of generalist and specialist ungulates in the Namibian desert: A stable isotypes approach: E72190. *PLoS One, 8*(8).

Li, S., Jovelin, R., Yoshiga, T., Tanaka, R., & Cutter, A. D. (2014). Specialist versus generalist life histories and nucleotide diversity in caenorhabditis nematodes. *Proceedings. Biological Sciences / the Royal Society, 281*(1777), 20132858.

Loxdale, H. D., & Harvey, J. A. (2016). The 'generalism' debate: Misinterpreting the term in the empirical literature focusing on dietary breadth in insects. *Biological Journal of the Linnean Society, 119*(2), 265-282.

Machovsky-Capuska, G. E., Senior, A. M., Simpson, S. J., & Raubenheimer, D. (2016). The multidimensional nutritional niche. *Trends in Ecology & Evolution, 31*(5), 355-365.

M'kiera, F., & Ungar, P. S. (2003). Occlusal Relief Changes With Molar Wear in Pan troglodytes troglodytes and Gorilla gorilla gorilla. *American Journal of Primatology, 60*(2), 31.

Navarro-López, J., Vergara, P., & Fargallo, J. A. (2014). Trophic niche width, offspring condition and immunity in a raptor species. *Oecologia, 174*(4), 1215-1224.

Pampush, J. D., Winchester, J. M., Moorse, P. E., Vining, A. Q., Boyer, D. M., & Kay, R. F. (2016). Introducing molaR: a new R package for quantitative topographic analysis of teeth (and other topographic structures). *Journal of Mammalian Evolution, 23*(4), 397-412.

Peers, M. J. L., Thornton, D. H., & Murray, D. L. (2012). Reconsidering the specialist-generalist paradigm in niche breadth dynamics: Resource gradient selection by canada lynx and bobcat. *PloS One, 7*(12), e51488.

Perry, J. M. G., St Clair, E. M., & Hartstone-Rose, A. (2015). Craniomandibular signals of diet in adapids, *American Journal of Physical Anthropology, 158*(4), 646-662.

Plyusnin, I., Evans, A. R., Karme, A., Gionis, A., & Jernvall, J. (2008). Automated 3D phenotype analysis using data mining. *PloS One*, *3*(3), e1742.

Price, S. A., Samantha S. B. Hopkins, Smith, K. K., & Roth, V. L. (2012). Tempo of trophic evolution and its impct on mammalian diversification. *Proceedings of the National Academy of Sciences of the United States of America, 109*(18), 7008-7012.

Prufrock, Kristen A., Lopez-Torres, Sergi, Silcox, Mary T., and Boyer, Doug M. (2016). Surfaces and Spaces: troubleshooting the study of dietary niche space overlap between North American stem primates and rodents. *Journal of Surface Topography:* Metrol Prop. 4.

Qiao, H., Saupe, E. E., Soberon, J., Peterson, A. T., & Myers, C. E. (2016). Impacts of niche breadth and dispersal ability on macroevolutionary patterns. *The American Naturalist, 188*(2), 149-162.

Ramdarshan, A., Merceron, G. and Marivaux, L. (2012), Spatial and temporal ecological diversity amongst eocene primates of france: Evidence from teeth. Am. J. Phys. Anthropol., 147: 201–216.

Safi, K., & Kerth, G. (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology*, 18(5), 1293-1303.

Skinner, M. M., Wood, B. A., Boesch, C., Olejniczak, A. J., Rosas, A., Smith, T. M., & Hublin, J. (2008). Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. *Journal of Human Evolution, 52*(2), 173-186.

Smith, T. (1990). Resource Use by Bill Morphs of An African Finch: Evidence for Intraspecific Competition. *Ecology, 71*(4), 1246-1257.

Staudinger, M. D., McAlarney, R. J., McLellen, W. A., & Ann Pabst, D. (2014). Foraging ecology and niche overlap in pygmy (kogia breviceps) and dwarf (kogia sima) sperm whales fromo waters of the U.S. mid-Atlantic coast. *Marine Mammal Science, 30*(2), 626-655.

Strait, S. G. (2001). Dietary reconstruction of small-bodied omomyoid primates. *Journal of Vertebrate Paleontology, 21*(2), 322-334.

Terraube, J., Arroyo, B., Madders, M., & Mougeot, F. (2011). Diet specialisation and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators. *Oikos, 120*(2), 234-244.

Ungar, P. (1998). Dental allometry, morphology, and wear as evidence for diet in fossil primates. *Evolutionary Anthropology: Issues, News, and Reviews, 6*(6), 205-217.

Ungar, P. (2004). Dental topography and diets of australopithecus afarensis and early homo. *Journal of Human Evolution, 46*(5), 605-622.

Ungar, Peter S. *Mammal Teeth: Origin, Evolution, and Diversity*. Johns Hopkins University Press, Baltimore, 2010.

Vamosi, J. C., Armbruster, W. S., & Renner, S. S. (2014). Evolutionary ecology of specialization: Insights from phylogenetic analysis. *Proceedings. Biological Sciences / the Royal Society, 281*(1795)

Vera, E., Bernardes de Jesus, B., Foronda, M., Flores, J. M., & Blasco, M. A. (2012) The rate of increase in short telomeres predicts longevity in mammals. *Cell Reports, 2*(4), 732-737.

Wilder, S. M., Le Couteur, D. G., & Simpson, S. J. (2013). Diet mediates the relationship between longevity and reproduction in mammals. *Age, 35*(3), 921-927.

Wilf, P. (2000). Late Paleocene-early eocene climate changes in southwestern wyoming: Paleobotanical analysis. *Geological Society of American Bulletin*, *112*(2), 292-307.

Wilson, B., & Hayek, L. C. (2015). Distinguishing relative specialist and generalist species in the fossil record. *Marine Micropaleontology*, *119*, 7-16.

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

Winchester, J. M., Boyer, D. M., St. Clair, E. M., Gosselin-Ildari, A. D., Cooke, S. B. and Ledogar, J. A. (2014), Dental topography of platyrrhines and prosimians: Convergence and contrasts. *Am. J. Phys. Anthropol*., 153: 29–44.

Winchester, J. M. (2016). MorphoTester: An Open Source Application for Morphological Topographic Analysis. *PLoS ONE*, *11*(2), e0147649.

Xu, J., Wen, Z., Gong, Z., Zhang, M., Xie, P., Hansson, L., . . . Faculty of Science. (2012). Seansonal trophic niche shift and cascading effect of a generalist predator fish. *PloS One*, *7*(12), e49691.