AN ABSTRACT OF THE DISSERTATION OF

Brian P. Tanis for the degree of Doctor of Philosophy in Zoology presented on May 20, 2019.

Title: Dogs, Death, and Dietary Breadth: Insights into the Macroecology and Macroevolution of Canidae

Abstract approved: ____

Rebecca C. Terry

The size, shape, and stability of a species' dietary niche can both influence and reflect a variety of biological patterns, including species interactions, extinction risk, and ecosystem function. This is particularly apparent when dietary changes manifest at ecosystem and clade scales to profoundly affect macroecological and macroevolutionary trajectories. However, many studies exploring interactions, extinction, and ecosystem function rarely take into account dietary breadth across broad temporal and spatial scales, despite the fact that many ecological processes unfold over temporal and spatial scales that are beyond the scope of traditional ecology. This dissertation addresses this gap by testing the hypothesized drivers of two macroecological and macroevolutionary patterns using dietary niche breadth reconstructed from historical and paleontological canid specimens. Canid predators represent a model system for exploring broad patterns of ecology and evolution given their strong interspecific interactions coupled with a historical legacy of human-driven exterminations resulting in novel community dynamics. Additionally, North American canids offer a rich and diverse fossil history complete with iterative patterns of extinction and radiation used to describe macroevolutionary theory. I quantified dietary niche breadth for western North American canids via stable isotope analysis (SIA) and dental microwear texture analysis (DMTA) and applied these techniques across the spatial and temporal extent of canid distributions. Across space, I explored how mesopredator release has altered the dietary niche breadth of coyotes following the historical extirpation of gray wolves from the Pacific Northwest. Through time, I utilized the 33 million years of evolutionary history preserved in the North American canid fossil record to test the hypothesized link between dietary breadth and the ultimate extinction of canid lineages. In order to make more complete use of fossil, historical, and modern museum collections, which can contain fragmentary specimens, I also developed a novel approach to DMTA, devised to increase sample sizes while not biasing reconstructed dietary behaviors. I demonstrated that multiple facets along the cheek teeth in canids yield comparable microwear signals regardless of molar type or bite force (chapter 2). Thus scans from multiple molars can be combined to increase sample sizes among taxa with limited material. Looking across a latitudinal gradient along Western North America, I found that coyotes sympatric with wolves have reduced dietary niche breadth compared with coyotes sympatric with wolves. Furthermore, DMTA and SIA independently suggest released coyotes increased dietary plasticity following a reduction in scavenging behavior, previously facilitated by wolves (chapter 3). Extinction risk has been hypothesized to be positively correlated with dietary specialization, known as the macroevolutionary ratchet. The fossil record of canids has revealed iterative ratchets as multiple clades evolved towards hypercarnivory followed by rapid lineage extinctions. Morphological traits previously used to describe the macroevolutionary ratchet in canid evolution, however, are unable to capture the dietary breadth of a species. I found morphological traits were inferior to DMTA parameters at explaining extinction risk. Counter to expectations, I observed a positive correlation between specialization and lineage duration and that specialization was not correlated with traditionally-used dietary categories, suggesting that overspecialization in diet alone did not drive iterative extinctions in canids. Outcomes of this dissertation offer direct hypotheses for management officials dealing with proliferating mesopredators and trophic restructuring today. Additionally, my temporal analysis advances our fundamental understanding of macroevolutionary ratchets, and will enable future community-level studies of how species interactions influenced past evolutionary trajectories.

Dogs, Death, and Dietary Breadth: Insights into the Macroecology and Macroevolution of Canidae

by
Brian P. Tanis

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented May 20, 2019
Commencement June 2019

Doctor of Philosophy dissertation of Brian P. Tanis presented on May 20, 2019.

APPROVED:

Major Professor, representing Zoology

Chair of the Department of Integrative Biology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Brian P. Tanis, Author

ACKNOWLEDGEMENTS

This dissertation was only made possible with the support from a wide array of people. At the culmination of 13 years as a student of higher education, there are countless individuals across numerous institutions who have significantly influenced my personal trajectory. While there is not enough room to thank everyone by name, I am immensely appreciative of everyone who has been there for me along the way. First and foremost, I thank my advisor Rebecca Terry for being an outstanding mentor and an awe-inspiring scientist and person. I could not have possibly asked for a better advisor and I am deeply indebted to her amazing guidance, wisdom, and support over the years. Additionally, I thank my graduate committee: Larisa DeSantis, Taal Levi, Mark Novak, and Lisa Ganio. Through discussions individually, in group meetings, as well as in the classroom their insightful ideas, constructive comments, and welcoming hospitality have been instrumental to the following studies. I am grateful for members of the Terry and Novak labs, both past and present for sharing ideas and feedback. Specifically, I would like to thank, David Taylor, Jesse Laney, Mike Brawner, Tara Smiley, Rachel Reid-Brown, Bridget Reagan, Juniper Grimes, Elia DeJesus, and Morah West for assistance with specimen preparation and valuable assistance with data analyses. I also thank Jennifer McKay from the Oregon State University Stable Isotope Laboratory for performing isotope analysis and clarifying technical details. Additionally, I thank the DeSantis lab at Vanderbilt University for hosting and assisting me in scanning molds, specifically: Eva Biedron, Melissa Pardi, Greg Smith. I express my sincere gratitude to all the faculty and staff in the Integrative Biology Department for helping me navigate the bureaucracies of academia and making my time at OSU welcoming and supportive. I also thank the following curators and their institutions for their cooperation and assistance sampling from their respective collections: Jeff Bradley (University of Washington Burke Museum), Chris Stinson (University of British Columbia Beaty Museum of Biodiversity), Christopher Schierup and Nicholas Famoso (John Day Fossil Beds National Monument Collection), Peter Konstantinidis (Oregon State University Fisheries and Wildlife Collection), Pat Holroyd (University of California Museum of Paleontology), Christopher Conroy (Museum of Vertebrate Zoology), and Gary Shugart (Slater Museum of Natural

History). I thank my fellow graduate student colleagues, past and present, for providing stimulating discussion, helpful feedback, and the emotional maintenance necessary to undertake a doctoral degree. In particular I thank EBC, specifically Kyle Coblenz, Leah Segui, Trevor and Aurora Tivey, Jenna and Joe Sullivan-Stack, Katie Dziedzic, Danielle Tom, Syl Wyatt, Ian Morelan, Amy Jaron, Elise Heffernan, and Katie Wollstein for running with my delusions and enriching my life with laughter. I also thank my best friends from childhood whose unwavering camaraderie has provided a wonderful backdrop to my time in school. Finally, I thank my family, especially my parents Patricia and Leonard and my siblings Lauren and Kaitlyn, for their constant love and support while I pursued my dreams.

CONTRIBUTIONS OF AUTHORS

Chapter 2: Larisa R.G. DeSantis and Rebecca C. Terry helped design the study, contributed to data analysis, and provided critical revisions.

Chapter 3: Larisa R.G. DeSantis and Rebecca C. Terry helped design the study and contributed to data analysis. Rebecca C. Terry also provided valuable revisions.

Chapter 4: Larisa R.G. DeSantis facilitated data collection and provided valuable revisions. Rebecca C. Terry helped design the study and contributed to data analysis and provided valuable revisions.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX FIGURES

DEDICATION

I dedicate this thesis to Mira, for her camaraderie and emotional support. Thank you for telling me to stop working and play for a little.

Dogs, Death, and Dietary Breadth: Insights into the Macroecology and Macroevolution of Canidae

CHAPTER 1 - Introduction

Understanding the diet of individuals, populations, and species is a foundational component of ecology. Diet represents the way organisms meet their most basic needs surrounding the metabolic requirements necessary for maintaining homeostasis and increasing reproductive fitness. As such, the majority of an individual’s daily activity is allocated towards foraging (Rorberg 1977; Gilbert-Norton et al. 2009; Arias-Del Razo et al. 2011; Bonter et al. 2013; Chubaty et al. 2014). Given this central activity in life, it is unsurprising that diet can profoundly shape biological interactions, govern community processes, and influence evolutionary trajectories. Despite this, quantification of diet has historically been considered a “first-pass” question in ecology, a factor that while informative for natural history is a means to an end for higher-order questions of population dynamics, interaction networks, and ecosystem function. As such, a large amount of dietary information for species remains reduced into broad categories designated with little regard to biologically significant thresholds (e.g. hypocarnivore, mesocarnivore, hypercarnivore). Fortunately, the past two decades have seen a resurgence in the quantification of dietary ecology via the development of robust metrics which quantify diet along a continuous spectrum rather than categorical bins (Bearhop et al. 2004; Turner et al. 2010; Newsome et al. 2012; Yeakel et al. 2012; Murray et al. 2013; Syväranta et al. 2013; Cucherousset and Villéger 2015; Rossman et al. 2016). This endeavor, which has been partially spurred by a desire to document changes in species and population mean diet following contemporary perturbations and species extirpation, has been monumental in demonstrating dietary shifts following species invasions (Carreira et al. 2017; Terry 2017), climate change (Yeakel et al. 2013; Fairhurst et al.

2015; Beever et al. 2017; Carreira et al. 2017; DeSantis et al. 2017a), and landscape fragmentation (Quinn 1997; Riley et al. 2003; Sears et al. 2003).

Recently, new statistical approaches have been developed to better quantify the variability surrounding diets of individuals and populations (Bearhop et al. 2004; Jackson et al. 2011; Peterson 2011; Newsome et al. 2012; Syväranta et al. 2013; Rossman et al. 2016). Modern techniques, aimed at quantifying the core range of possible prey resources a species relies on (i.e. dietary breadth) have seen tremendous advancements, enabling robust quantification of dietary variability across multiple dietary axes (Bearhop et al. 2004; Syväranta et al. 2013; Swanson et al. 2015; Rossman et al. 2016). Variation is a foundational feature of ecology, enabling populations and species to adapt over time via selection. Recent work has reiterated the importance of variability within species, suggesting that the effects of reducing intraspecific variation can eclipse the effects of species removal on ecosystems (Bolnick et al. 2011; Violle et al. 2012; Des Roches et al. 2018). Furthermore, theoretical work has demonstrated the extent to which individual dietary specialization can dramatically alter trophic interactions and community stability (Yeakel et al. 2012; Rosenblatt et al. 2015). While many studies focusing on intraspecific variation have uncovered valuable insights into changes at local or community levels, extensions to how dietary breadth can manifest within individuals, populations, and species at broader temporal and spatial scales, and the extent to which dietary breadth shapes ecological and evolutionary patterns at these scales, are lacking.

In this dissertation, I provide evidence for the importance of quantifying dietary breadth in order to better understand macroecological and macroevolutionary processes. By focusing on North American canids (Mammalia: Carnivora: Canidae), I test the drivers of spatial and temporal hypotheses describing observed patterns at ecosystem and clade scales. Specifically, I provide evidence of previously undescribed continental-scale shifts in dietary breadth in coyotes (*Canis latrans*) from California to northern British Columbia following gray wolf *(Canis lupus*) extirpation at the turn of the last century. This work illuminates a cryptic and nuanced interaction between coyotes and gray wolves of the Pacific Northwest and can inform ongoing efforts to manage for the widespread phenomenon of mesopredator release. I also explore the hypothesized drivers of the macroevolutionary ratchet among extinct canids, where evolution towards hyperspecialization is thought to doom lineages to extinction, by explicitly testing the link between dietary breadth and extinction risk. I find that reduced dietary breadth, equivalent to more specialized foraging, has a strong negative relationship with extinction risk in fossil canids. These trends run counter to previous hypotheses, which my evidence attributes to the inability of morphological traits to accurately reflect dietary plasticity relative to dental microwear.

The importance of large-scale studies

As climate change and anthropogenic development continue to rapidly alter environmental conditions around the globe, there is a widespread effort among ecologists to document the biotic impacts of these accelerating changes and better understand the novel world of the Anthropocene (Ackerly et al. 2010; Rowe et al. 2011; Smith et al. 2019). Understanding the significance of these changes to ecosystem function is paramount for predicting the future and mitigating ecological collapse. Unfortunately, the majority of ecological studies aimed at documenting altered ecosystem processes focus on snapshot experiments of modern systems; and yet, most intense anthropogenic impacts to ecosystems have been ongoing for centuries, while pre-historic anthropogenic impacts date back to ~16,000 years in North America (Lyons et al. 2004a; Sandom et al. 2014; Tomašových and Kidwell 2017; Smith et al. 2019). Furthermore, many ecological and evolutionary patterns manifest at larger temporal and spatial scales than can typically be covered by ecological experimental design (Alroy 2006; Lyons and Smith 2010). This is particularly true for mammalian carnivores, which occupy diffuse and expansive home ranges and can cryptically persist in a locale without detection (Bekoff 1977; Gittleman and Harvey 1982; Beschta and Ripple 2009; Ripple et al. 2014). Snapshot studies, which are more tractable under current funding schemes, also typically only cover a narrow subset of conditions influencing a system. Thus many existing ecological and evolutionary hypotheses and theories lack complete testing of their proposed drivers, which is problematic for developing conservation practices. Over the past decade there has been a renaissance with respect to the importance of scale in ecology (Bell et al. 2003; Massol et al. 2011; Brewer et al. 2012; Peterson and Lieberman 2012; Chave 2013; Sutherland et al. 2013), led by historical re-surveys (Smol 2010; Miller 2011; Fritz et al. 2013; Yeakel et al. 2014) and widespread meta-analyses (Hooper et al. 2012); however, much work is still needed to understand the challenges of the Anthropocene. To more completely illuminate ecological and evolutionary processes, this dissertation uses the wealth of historic and prehistoric information contained in museum collections and the fossil record to reconstruct dietary dynamics at large spatial and temporal scales.

Quantification of Dietary Breadth

A multitude of methods exist for quantifying the diet of populations and species. Under ideal circumstances, diet can be directly quantified via observations of foraging activity (Novak 2010), or by analyzing the contents of digestive systems (Azevedo et al. 2006; Rosenblatt et al. 2015) and associated bi-products like scat (Rose and Polis 1998; Van Dijk et al. 2008; Murray et al. 2015) and pellets (Terry 2004, 2010). Unfortunately, these methods are often challenging to reproduce for retrospective studies (however see Terry 2010 and Wang et al. 2018 for exceptions), necessitating the use of dietary proxies to reconstruct dietary items.

One powerful tool for reconstructing diet in historical and paleontological species has been stable isotope analysis (SIA). SIA measures the ratios of different isotopes for specific elements within organic tissues in the context of ecological and environmental factors. This technique makes use of variation in the isotopic signal of the resources consumed (Koch et al. 2009; Newsome et al. 2012) as well as predicable patterns of fractionation of stable isotopes that occur within an animal's body as biochemical processes turn food into body tissue (Roth and Hobson 2011; Ben-David and Flaherty 2012). Thus SIA enables quantification of both the proportional contribution of various resources used by an animal to its diet (^{13}C), the trophic level at which it feeds (^{15}N), and the environment in which it lives (^{18}O)(Newsome et al. 2012). While SIA of modern and historical biological tissues provides valuable insights into trophic position and resource use, there are limitations to this technique within paleontological studies due to the diagenesis of biological tissues (specifically, the degradation and loss of protein and thus ^{15}N) during the process of fossilization, reducing the axes through which to view ancient resource use to ^{13}C and ^{18}O.

Fortunately, additional methods have been developed to infer diet within fossil taxa, including Dental Microwear Texture Analysis (DMTA)(Ungar et al. 2003; Scott et al. 2005, 2006; DeSantis et al. 2013; Calandra and Merceron 2016; DeSantis 2016). DMTA quantifies microscopic pitting and scratching etched into the surface of molars during mastication. Using three-dimensional scanning techniques paired with computerized quantification of the resulting tooth surface to quantify the geometric extent of wear features, it is possible to determine the physical attributes of dietary items and reconstruct forage selection and feeding behavior of the animal immediately prior to the death of the individual (Scott et al. 2005, 2006; Schubert et al. 2010; DeSantis et al. 2012a, 2015; Donohue et al. 2013; DeSantis 2016). Comparative work with known diets has shown that these microwear attributes correspond to contributions of meat, bone, vegetation and other broad categories (Scott et al. 2006; Schubert et al. 2010; Ungar et al. 2010; DeSantis et al. 2012a, 2015; DeSantis 2016).

Within this dissertation I primarily rely on DMTA to reconstruct the dietary niche breadth of canids across broad spatial and temporal scales, and bolster these inferences with additional independent analyses using stable isotopes. Specifically, in Chapter 2, I refine our understanding of variation in DMTA data, demonstrating that sampling an additional occlusal surface along the lower molar row of canids does not bias dietary reconstructions. Work from this chapter enabled me to confidently increase samples sizes of specimens for the remaining chapters, which use DMTA to test hypothesized drivers of ecological and evolutionary patterns (Chapters 3 and 4). Additionally, Chapter 3 makes use of SIA alongside DMTA, as an independent and complementary means of reconstructing dietary niche breadth.

Dietary niche breadth

The concept of a species' niche has served as a fundamental feature of ecology for a century (Grinnell 1917; Elton 1927; Leibold 1995; Soberón 2007; Sutherland et al. 2013). Defined by Hutchinson (1959) as an n-dimensional hypervolume encompassing the totality of an organism's interactions with both biotic and abiotic features of their environments, the niche provides a useful framework for identifying critical conditions and resources describing the fitness of a species. While this definition theoretically offers a quantifiable approach to a species' niche if one can measure per capita growth rates of populations across niche axes, in practice the niche has become fraught with difficulties stemming from challenges in defining and measuring an infinite set of interacting dimensions. Recently, ecologists have begun to narrowly define niche concepts to specifically relate to a few key aspects of a species ecology such as distribution and diet (Leibold 1995; Rotenberry et al. 2006; Adler et al. 2007; Carstens and Richards 2007; Raxworthy et al. 2007; Stynder 2009; Newsome et al. 2012; Winemiller et al. 2015). For example, the isotopic niche space has become a widely cited concept allowing for detailed studies comparing how populations and species interact with and persist in their environments (Newsome et al. 2012; Yeakel et al. 2013; Terry 2017). Although this and other similar modern niche concepts (e.g. trophic niche, trait niche, bioclimatic niche) no longer capture the spirit of Hutchinson's all-encompassing hypervolume, these niche measures offer a quantifiable reflection of one component of an organism's niche space and frequently serve as the only concrete metric with which to quantify the niche, especially at broad spatial scales. Despite suggestions that ecologists separate from the niche (Adler et al. 2007; Mcinerny and Etienne 2012a; b), the fundamental construct of niche concepts remains a vivid although vague explanatory factor for quantifying the dynamics of species and populations.

Throughout the chapters in this dissertation, I refer to the dietary niche breadth of populations or species. Technically, this language is a broad oversimplification, as dietary reconstructions using DMTA and SIA are representative of components of a textural and isotopic dietary niche space respectively, thus reflect only a small portion of a wholistic description of a niche. But this verbose description offers little additional insight. Thus a preponderance of recent papers describing niche dynamics over space or time have simplified the language to describe a dietary niche concept with respect to DMTA and SIA, such that the more detailed definition has become implied.

Why canids?

Carnivorans represent ecologically interesting taxa with an ability to control trophic networks and community stability through top-down effects (Estes et al. 1998; Beschta and Ripple 2009; Estes et al. 2011; Levi and Wilmers 2012; Miller et al. 2012; Pasanen-Mortensen et al. 2017; Wikenros et al. 2017). However, no other group of vertebrates has a more contentious history with humans, as carnivores have been highly persecuted due to real and perceived threats to safety and agricultural practices (Kellert 1985; Ripple et al. 2013, 2014; Prowse et al. 2014; DeCesare et al. 2018; Hody and Kays 2018; Moll et al. 2018; van Eeden et al. 2018). With the majority of all carnivores extant today at risk of extinction (Ripple et al. 2014), there is a concern that many ecosystem functions could be dramatically altered over the next century (Myers et al. 2007; Prugh et al. 2009; Estes et al. 2011; Ripple et al. 2013). Thus there has been a widespread focus on managing carnivores and studying their role in maintaining ecosystem function (Roemer et al. 2009; Letnic et al. 2011; Colman et al. 2014; Molsher et al. 2017; Suraci et al. 2017; Horne et al. 2019).

Within Carnivora, the canid family has served as a model system for studying ecological and evolutionary patterns. Canid species exhibit very strong, negative interspecific interactions with one another, coupled with renowned behavioral and dietary plasticity (Quinn 1997; Rose and Polis 1998; Van Valkenburgh 1999; Atwood and Gese 2008; Merkle et al. 2009). Together, these traits are hypothesized to influence an assortment of community and ecosystem dynamics (Paine 1969; Estes et al. 2011; Ikegawa et al. 2015). Canids have the additional benefit of being more conspicuous and abundant than feliform carnivorans, enabling sufficient sample sizes to test macroecological and macroevolutionary hypotheses. These factors not only apply to modern canid species but transcend deeper through their evolutionary history. Canids have a rich fossil record within North America, spanning from their earliest radiation during the Oligocene (34 Million years ago (Mya)) to the present (Van Valkenburgh 1991, 1999; Wang et al. 1999; Cope 2002; Roemer et al. 2009; Tedford et al. 2009). This enables the analysis of pervasive macroecological processes over an extended temporal axis, encapsulating a range of conditions that vary in terms of the potential strength of natural and anthropogenic environmental drivers.

Dissertation Work

In this dissertation, I used the lens of dietary niche breadth as viewed through DMTA and SIA in North American Canids to test underlying patterns and drivers of broad macroecological and macroevolutionary processes. Prior to delving into these processes, Chapter 2 addresses an important methodological issue in DMTA research:

broadening sampling approaches to include additional tooth surfaces along the tooth row of canids. Traditionally, DMTA for caniform carnivorans has focused on an occlusal surface of the lower second molar, which is an important location for food processing, particularly for hard textured foods such as bone (Van Valkenburgh 1989; Ungar et al. 2008, 2010; Schubert et al. 2010; DeSantis et al. 2012a). Despite being the hardest biological tissue, the enamel surface of molars can become cracked, worn away, or lost entirely during the organism’s lifespan or during taphonomic processes (Maas 1991; Rensberger 1999; Stefen 1999; Van Valkenburgh 2009), which can substantially reduce sample sizes of historical and fossil specimens enough to prohibit dietary inference about species. However, caniform carnivorans possess an additional occlusal surface, the talonid basin of the lower first molar, which is thought to be biomechanically analogous to the lower second molar (Van Valkenburgh 1989; Van Valkenburgh et al. 1990; Valkenburgh 2007; Asahara 2013, 2016; Severtsov et al. 2016). Chapter 2 provides evidence supporting that dental microwear textures were similar between the lower second molar and the talonid basin in two canids, the coyote (*Canis latrans*) and gray wolf (*Canis lupus*). As the lower first molars are more frequently recovered and more taxonomically identifiable than isolated second molars in the fossil record, chapter 2 demonstrates that regardless of molar type or bite force, sampling from multiple molars can be used to dramatically increase sample sizes from fossil and historical localities. Given the results of this chapter, all subsequent chapters use DMTA aggregated from both lower first and second molars to bolster sample sizes.

Chapter 3 of this dissertation reconstructs dietary niche breadth within modern and historical coyotes (*Canis latrans*) and wolves (*Canis lupus*) from California to British

Columbia to test for the effects of a pervasive trophic cascade unfolding at continental and century scales. Anthropogenic impacts over the last century have caused drastic changes in predator interactions and resulting trophic cascades. Among the most pervasive and damaging of these trophic cascades is mesopredator release, where extirpation of apex predators releases predators of intermediate trophic levels from competition, resulting in sudden and often unpredictable changes in their behavior and abundance. In North America, historical extirpation of the gray wolf has been linked to the release of coyotes, causing cascading effects to species interactions and ecosystem trophic dynamics. Typically, however, mesopredator release studies are limited in scale and focus only on changes in population abundance. I hypothesized that released mesopredators would also alter their foraging behaviors. To test this hypothesis, in the third chapter of my dissertation, I used historical museum specimens to quantify if mesopredator populations in the Pacific Northwest experienced any dietary change following release from apex predators over the last century. While the mean dietary position of coyotes did not shift following the loss of wolves, dietary variability decreased. This decrease corresponded with lower rates of bone consumption and scavenging, suggesting that although coyote abundances were suppressed by interactions with wolves, coyotes likely benefited from scavenging wolf kills. These results indicate that following apex predator extirpation, burgeoning coyote populations act as predators instead of scavengers, which suggests management officials could target and control select prey populations for mitigating coyote expansion.

Macroevolutionary ratchets, where successful morphotypes become increasingly specialized and eventually driven to extinction due to clade-level competition, are exemplified within the fossil record of carnivorans. However, specialization and its link to extinction has traditionally been inferred from morphological traits alone (e.g. body mass, molar surface area) rather than from direct dietary reconstruction. While a species' morphology reflects its overall dietary capability, individuals frequently forage in ways that morphology cannot predict. Thus it is the dietary plasticity of populations, which isn't captured by morphology, that truly defines a species' dietary specialization. In chapter 4, I address this gap by testing the association between dietary specialization and lineage extinction via analysis of the dietary niche of 9 extinct species, spanning all three Canidae subfamilies and 33.3 million years of their evolutionary history. I found dietary specialization as inferred from DMTA to be a better predictor of species duration than all considered measures of morphology, including the commonly used metric of body mass. Counter to expectations, I observed a positive correlation between specialization and lineage duration, that specialization was lowest for canids of intermediate body mass, and that specialization was not correlated with traditionally used dietary categories (i.e. hypo-, meso-, or hypercarnivory). My results therefore run counter to the macroevolutionary ratchet hypothesis, suggesting that overspecialization in diet was not enough to drive iterative extinctions in canids. Instead, I suggest that dietary specialization offers selective advantages during times of fluctuating prey abundance that facilitated the coexistence of a diverse canid assemblage in the Tertiary.

CHAPTER 2 - Dental microwear textures across cheek teeth in canids: implications for dietary studies of extant and extinct canids

Brian P. Tanis[a], Larisa R.G. DeSantis[b], and Rebecca C. Terry[a]

[a] Department of Integrative Biology, Oregon State University, Corvallis, OR 97331-8530, U.S.A.
[b] Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN 37235-1805, U.S.A.

Palaeogeography, Palaeoclimatology, Palaeoecology

(2018) 508:129-138

Abstract

Dental microwear texture analysis (DMTA) has been instrumental in reconstructing dietary ecology of extinct and extant carnivorans. Current sampling methods for canids focus on lower second molars (m2), where the grinding of flesh and bone captures dental microwear indicative of diet. However, dental microwear on other biomechanically analogous grinding facets (i.e. the talonid basin on the lower carnassial, m1) might be comparable and could help dramatically increase sample sizes of fossil specimens, as carnassials are more frequently recovered and identifiable than lower m2s. Here, we quantify the degree to which dental microwear textures between grinding facets on lower first and second molars are similar in two species of extant canids, coyotes (*Canis latrans*) and gray wolves (*Canis lupus*). Casts of paired m1s and m2s for each individual were sampled from museum collections and analyzed for three microwear parameters that correlate with diet in carnivorans: anisotropy, complexity, and textural fill volume. Within wolves, the m1 talonid and m2 are indistinguishable in all DMTA parameters. In coyotes, grinding facets of the m1 talonid and m2 are indistinguishable in complexity and textural fill volume, but anisotropy values of m1s are significantly lower than those of m2s. Differences in anisotropy between species were unlikely driven by biomechanical shifts in bite force between the m1 talonid and m2, but could stem from a combination of subtle morphological variation and intra-tooth variation. Overall, these data suggest that regions across molars with similar functions yield similar dental microwear textures. Finally, to demonstrate the effect of increased sample size, we show how the combination of DMTA data from lower m1 talonids and lower m2s of the hypocarnivorous Phlaocyonini canids from the John Day Formation of eastern Oregon,

USA, alters the size and shape, but not position, of their reconstructed dietary "niche" space and hence interpretations about dietary behavior.

Introduction

Quantifying the dietary behavior of a species is vital to understand its ecology and evolutionary history. This is especially true of extinct species, where dietary reconstructions often provide the strongest insights into behaviors, environmental pressures, and community structures of the past (e.g., (Cerling et al. 1997; Janis et al. 2002; Ungar et al. 2003; Scott et al. 2005; DeSantis et al. 2009, 2012a, 2015; Donohue et al. 2013; Calandra and Merceron 2016; Caporale and Ungar 2016; Jones and DeSantis 2017). Teeth record dietary information and are well represented within the fossil record due to the robustness of enamel relative to other biological tissues. Numerous methodologies have been developed to elucidate diet from fossil teeth, including morphology, biomechanics, stable isotope analysis, and dental microwear texture analysis (DMTA). Recently, dental microwear analyses have been bolstered by substantial technological advancements which reduce observer biases via the automated analysis of surface features in three dimensions (Scott et al. 2006; DeSantis et al. 2013). DMTA has been shown to be effective for reconstructing diets within a variety of mammalian taxa (e.g. carnivorans, artiodactyls, marsupials, xenarthrans, rodents, and primates) providing a direct window into how species acquired and processed their food in ancient and modern ecosystems (Scott et al. 2012, 2005; Prideaux et al. 2009; El-Zaatari 2010; El Zaatari et al. 2011; DeSantis et al. 2012a, 2017b; a; Donohue et al. 2013; Haupt et al. 2013; Caporale and Ungar 2016).

Early DMTA work focused on reconstructing diet in artiodactyls and primates, establishing standardized sampling locations along the dental arcade with respect to individual tooth facets (Ungar et al. 2008; Schulz et al. 2010) Pioneering work within Carnivora, focused on large feliform carnivorans, quantified microwear from the shearing surface of the lower carnassial (m1), which is biologically important for meat consumption (Van Valkenburgh et al. 1990; Goillot et al. 2009; Schubert et al. 2010; DeSantis et al. 2012a, 2017b; Haupt et al. 2013; DeSantis and Patterson 2017). Tests of the general utility of this surface among other carnivoran clades which retained multiple cheek teeth (e.g. Canidae), however, revealed that the hypoconid facet of the lower second molar (m2) is better able to discriminate diet (Ungar et al. 2010). This bunodont molar is primarily used for grinding and processing bone in Canidae, which is an important aspect of their diets which can be readily inferred from dental microwear. Subsequent work within Ursidae, another caniform carnivoran, has corroborated that microwear textures from the grinding facet of the m2 are more representative of diet than microwear textures etched into the shearing surface of the lower carnassial (Donohue et al. 2013). Thus, subsequent microwear studies have all followed the convention of reconstructing diet by using the shearing surface of the lower carnassial for feliform carnivorans (as subsequent cheek teeth including lower m2s are generally absent and thus bone processing occurs on the carnassial), in contrast to the grinding facet of lower m2s for canids and ursids (Stynder et al. 2011; DeSantis and Haupt 2014; DeSantis et al. 2015; DeSantis 2016; Jones and DeSantis 2016; DeSantis and Patterson 2017).

Although the lower m2 is considered the primary grinding surface for caniform carnivorans, many taxa also use the occlusal area on the talonid basin at the posterior end of the m1 for a similar purpose (Van Valkenburgh 1991). Specifically, most canid species possess two low cusps on the buccal (hypoconid) and lingual (entoconid) sides of the talonid basin (Fig. 1A). These cusps mirror those seen on the posterior of the m2, and the two regions are thought to be functionally analogous (Van Valkenburgh 1991). However, establishing the degree to which the m2 and the m1 talonid capture comparable information on feeding behavior has not been quantified. Additionally, compared to postcarnassial teeth (including lower m2s), carnassials are more diagnostic for taxonomic identification and are less prone to taphonomic alteration (Behrensmeyer et al. 1980; Dauphin and Williams 2007). As a result, m1s are more commonly preserved in modern and fossil death assemblages (Behrensmeyer et al. 1980). As carnivores are typically rarer than herbivorous taxa due to their lower abundance on the landscape, the rarity of carnivores (with the exception of tar seeps) combined with the rarity of m2s often limits the statistical power of dental microwear analysis due to low sample size. If dental microwear texture attribute values are similar across the cheek teeth of canids, aggregating data from the m2 and the m1 talonid basin could substantially increase sample sizes in paleontological studies and thus strengthen inferences about the dietary behavior of extinct species and the structure of their communities.

Here, we tested the hypothesis that DMTA attributes from the m1 talonid are equivalent to those measured from the m2 using paired samples from the same individual for two species of canids, coyotes (*Canis latrans*) and gray wolves (*Canis lupus*). Coyotes and wolves represent a noteworthy comparison as the two species are dominant among North America’s caniform meso- and apex predators, respectively. Interactions between these species are thought to increase dietary niche segregation (Newsome and

Ripple 2015; Benson et al. 2017; Otis et al. 2017), which has been detected via DMTA despite similar molar morphologies (Van Valkenburgh 1991; DeSantis et al. 2015). Furthermore, these species are notable for dietary plasticity which could skew dietary inference given DMTA only reflects the last several days to weeks of an individual's life, known as the Last Supper Effect (Grine 1986; Schubert et al. 2010; DeSantis 2016). Therefore, increasing sample sizes could overcome challenges pertaining to possible shifts in dietary behavior due to seasonality or senescence (Merceron et al. 2010; DeSantis et al. 2012a).

Location of the m1 and m2 within the toothrow (i.e. distance to the temporomandibular joint) makes them subject to subtle differences in forces during mastication (Turnbull 1970; Greaves 1985; Christiansen and Adolfssen 2005). Differences in bite force have been repeatedly shown to reflect feeding behaviors (Wroe et al. 2005; Therrien et al. 2016) and drive macroevolutionary patterns, particularly in carnivorous taxa (Christiansen and Wroe 2007; Valkenburgh 2007; Tseng and Flynn 2015). Furthermore, previous studies within a variety of mammalian taxa have shown a positive relationship between increased bite force and microwear width, but not microwear frequency (Gordon 1982; Teaford and Walker 1984; Teaford 1988; Van Valkenburgh et al. 1990; Grine et al. 2012; MacAfee and Green 2015) but see Jiang and DeSantis 2014). Therefore, we also quantified bite force at the m1 and m2 for a subset of specimens in order to assess the impact of this factor on dietary reconstructions from DMTA.

Finally, to illustrate the effect of combining first and second lower molars (and thus increasing sample sizes) on dietary inferences from fossils, we present a case study on the extinct borophagine canids from the John Day Formation of eastern Oregon. Specifically, we reconstruct the dietary behavior and quantify dietary breadth of the Phlaocyonini tribe using 39.7-18 Ma old specimens. This case study represents the geologically oldest fossil carnivorans to be quantified via DMTA to date, and reveals how improved dietary interpretations can be made via increasing sample sizes of fossil specimens.

Materials and Methods

Dental microwear texture analysis

Specimens of coyotes (n = 17) and wolves (n = 20) from the Pacific Northwest were sampled from three natural history collections: the University of British Columbia Beaty Museum of Biodiversity (UBCBBM), the University of Washington Burke Museum (UWBM), and the Oregon State University Fisheries and Wildlife Collection (FW) (Appendix A Table A.1). High-resolution molds of paired lower molars (m1 and m2) were made by cleaning the enamel surface with acetone and/or ethanol, then applying polyvinylsiloxane impression material (President Jet regular body, Coltène/Whaledent Inc.). Casts were made from a clear epoxy resin (EPO-TEK301, Epoxy Technology Inc.) and the resulting replicate molars were scanned via a Sensofar *PLu neox* optical profiler at Vanderbilt University. Scans were made on the hypoconid facet on both the m2 and m1 talonid for all specimens (Fig. 1A). Each scan consists of four adjacent quadrants of equal size (Fig. 1B; total size of 206 x 276 μm^2). Each quadrant was analyzed using scale-sensitive fractal analysis software (Sfrax and Toothfrax, Surfract Corp.) to compile microwear parameters (Fig. 2), with median values from the four scans used to represent a given specimen (per Scott et al. 2006).

We focused on three microwear parameters considered to be reflective of diet within carnivorans: anisotropy (*epLsar*), complexity (*Asfc*), and textural fill volume (*Tfv*). Anisotropy, the amount of alignment among wear features, is indicative of diet toughness (Scott et al. 2006; DeSantis 2016). Within carnivorans, higher anisotropy values (i.e. greater alignment) corresponds to texturally fibrous diets, such as greater flesh consumption (Schubert et al. 2010; DeSantis et al. 2012a). Complexity quantifies differences in wear feature relief across scales, and is used to differentiate consumption of hard and soft foods (Scott et al. 2005, 2006; DeSantis 2016). High complexity values have been particularly useful as indicators of increased bone consumption among scavenging predators (Schubert et al. 2010; DeSantis et al. 2012a, 2015, 2017b; Donohue et al. 2013; DeSantis and Haupt 2014; DeSantis and Patterson 2017; Stynder et al. 2018). Textural fill volume quantifies the size of wear features through differing volumetric cuboids (Scott et al. 2006; DeSantis 2016) and is greatest in animals that process bone (Schubert et al. 2010; DeSantis et al. 2012a, 2015, 2017b; Donohue et al. 2013; DeSantis and Haupt 2014; Stynder et al. 2018). Additional microwear parameters, such as scale of heterogeneity, have not been shown to correlate with aspects of extant carnivoran diets and thus were not included in this study (Schubert et al. 2010; DeSantis et al. 2012a).

We tested whether dental microwear textures are systematically different between the lower m1 talonid and m2 grinding facets of the same individual within the genus (*Canis*), and within each species (*C. lupus* and *C. latrans*). We compared m1 talonids vs. m2s in DMTA metrics using either paired Student's t-tests or non-parametric Wilcoxon signed-rank tests (based on Shapiro-Wilk normality values, see Table 1; non-parametric tests were only performed when combining all *Canis* specimens for *Asfc* and *epLsar* comparisons). Within each species, we also assessed the strength and potential skew of the relationship between m1 and m2s via correlation (Pearson), as predictive information regarding m1 talonid DMTA values could be recorded on the m2 of an individual, and vice versa, even if there are significant differences between the m1 talonid and m2 DMTA median parameters across individuals. We also assessed the mean absolute value difference between microwear texture parameters from pairwise adjacent quadrants from a single m2 (i.e. intra-scan variation, differences between the four scanned regions), paired repeated scans of the same m2 (i.e. intra-tooth variation, differences between the median values resulting from four scans of two different scanned areas on the same m2), and paired samples of the m1 and m2 (i.e. inter-tooth variation). Pairwise adjacent quadrants and repeated scans of the same tooth were taken from a subset of individuals (*C. latrans*, n = 5; *C. lupus*, n = 4) including some specimens not used in testing the m1 talonid and m2 (see Appendix A Table A.1). Pairwise repeated scans did not overlap in area. For inter-tooth variation, we compared the mean absolute value of the difference between the m1 talonid and the m2 for both *C. latrans* and *C. lupus*, as well as the m1 shearing facet and the m2 for coyotes (using data from Ungar et al. 2010). Although this additional published dataset was derived from a different microscope (aka “Connie” at the University of Arkansas) as opposed to our de novo data (from “Dolly” at Vanderbilt University), these two systems specifically have been shown to give comparable results (Arman et al. 2016) and have been used for previous microwear comparison studies (e.g. Jones and DeSantis 2017). Given that microwear data from Ungar et al. (2010) were non-normally distributed and the low statistical power to detect normality among microwear parameter values from adjacent scans of a single m2 within our dataset, non-parametric

Kruskal-Wallis tests and Dunn’s procedure for multiple comparisons (Dunn 1964) were employed for intra-scan, intra-tooth, and inter-tooth variation in *C. latrans* and *C. lupus*. Šidák’s adjustment procedure (1967) was used to control for potential family-wise error rate inflation (i.e. alpha inflation) in repeated comparisons of tooth variation in both taxa. This adjustment procedure has higher power than a Bonferroni correction and therefore reduces type II error inflation.

Bite Force

To determine whether bite force influences DMTA metrics, a subset of the *C. latrans* (n = 11) and *C. lupus* (n = 3) specimens from the OSU FW collection were photographed and measured for maximum bite force estimation (see Appendix A Table A.1). Photographs were taken of the dorsal, ventral, and lateral views of the cranium and the lateral view of the dentary using a Nikon D3100 with a Nikon DX AF-S NIKKOR18-55mm 1:3.5-5.6G lens. Measurements for bite force estimation were taken from photographs using ImageJ (Schindelin et al. 2015). Bite force was calculated according to Thomason’s dry-skull procedure (Thomason 1991) using the cross-sectional area of jaw adductor muscles with lever moment arms to estimate force output.

$$F = \frac{(d_M \times \{M \times 300\} + d_T \times \{T \times 300\})}{d_o} \qquad (1)$$

Specifically, cross sectional areas were measured for the masseter group (M) and temporalis and pterygoideus groups (T) and multiplied by the estimated force for mammalian muscle, 300 kPa (Weijs and Hillen 1985; Thomason 1991). Inlever moment arms for each muscle group (d_M and d_T) were measured from the centroids of the cross-sectional area to the temporomandibular joint. The outlever moment arm (d_o) was measured from the distal tip of the mandibular condyle to both the grinding facets of the m2 and m1 to compare how bite force changes between those positions. Bite force estimates were not doubled as we were interested in the differences between bite forces at the grinding positions on one side of the dentary only (Christiansen and Adolfssen 2005). To correct for the underestimation of forces through dry-skull measurements and the influence of body mass on bite force, we used Thompson's correction method and skull length (L) as a proxy for mass (Van Valkenburgh et al. 1990) to calculate the bite force quotient (BFQ) for each individual at both the m1 and m2 positions (Sakamoto et al. 2010; Damasceno et al. 2013).

$$BFQ = \frac{F_{corr}}{F_L} = \frac{10^{(0.859 \times \log F + 0.559)}}{10^{(1.95 \times logL - 1.12)}} \tag{2}$$

Paired bite force quotients from the m2 and m1 talonid were tested for differences within both wolves and coyotes using a paired Student's t-test. The relationship between bite force quotient and dental microwear textures was compared for each molar individually. Furthermore, we compared how the change in BFQ values from paired molars related to the change in dental microwear textures between the same molars. Values from the m1 talonid for BFQ and microwear textures were always subtracted from the m2 as bite force will always increase with proximity to the posterior of the jaw (Turnbull 1970; Greaves 1985; Christiansen and Adolfssen 2005). All analyses were performed in program R version 3.4 (R Development Core Team 2008).

Phlaocyonini case study

To assess the influence of using DMTA data from both the talonids of lower m1s and lower m2s for dietary inferences, we examined specimens from the John Day

Formation in eastern Oregon (JODA) belonging to the tribe Phlaocyonini — an early radiation of canids within the subfamily Borophaginae. This world-renowned fossil collection includes the earliest and most diverse assemblage of extinct canids known from North America. The tribe Phlaocyonini consists of closely related taxa of small size and persisted from the early Arikareean to the early Barstovian North American land mammal ages (30 Ma – 15 Ma). On the basis of both dental and postcranial morphological characteristics, the group is thought to have a hypocarnivorous diet (Wang et al. 1999).

We sampled phlaocyonin specimens following the DMTA protocol described above (Appendix A Table A1). All fossil materials were examined for damage at a macro- and microscopic scale, with no evidence for consistent taphonomic degradation of enamel observed. Of the 13 available unique specimens, three were m2s and 10 were m1 talonids. This relative representation of m2:m1s is comparable to the ratio of all canid specimens containing m2s versus m1s within the John Day Collection. Using DMTA attribute space, defined by microwear parameters, we reconstructed the size, shape, and position of the phlaocyonin dietary niche for m2s alone, m1 talonids alone, and all specimens combined, using the sample size-corrected standard ellipse method of Jackson et al. (2011). Analyses were performed using the SIBER package in program R (Jackson et al. 2011).

Results

Dental Microwear Texture Analysis

Summaries of DMTA variables for each species and molar are reported in table 1. When comparing paired samples within the genus *Canis*, m1 talonid and m2 values are indistinguishable for complexity (Wilcoxon, $p = 0.068$), anisotropy (Wilcoxon, $p = 0.48$), and textural fill volume (t-test, $p = 0.74$). Within each species, paired samples of the m1 talonid and the m2 of *C. lupus* are indistinguishable for complexity ($p = 0.080$), anisotropy ($p = 0.092$), and textural fill volume ($p = 0.96$; Fig. 3A). In *C. latrans*, neither complexity nor textural fill volume are significantly different between paired tooth positions ($p = 0.358$, $p = 0.711$, respectively); however, anisotropy of m2s are significantly greater than that of m1 talonids ($p = 0.009$; Fig. 3B).

While the majority of DMTA parameters revealed no significant differences between paired m1 talonids and m2s (except for anisotropy of *C. latrans*), within each species, correlation between microwear textures on m1 talonids and m2s are mostly not significant. Within *C. lupus*, there are no observed correlations for anisotropy ($r = -0.06$, $p = 0.82$) or textural fill volume ($r = -0.26$, $p = 0.27$), although complexity of m1 talonids and m2s are significantly correlated ($r = 0.47$, $p = 0.04$). Within *C. latrans*, there are no significant correlations between teeth (anisotropy $r = 0.31$, $p = 0.23$, textural fill volume $r = -0.23$, $p = 0.37$, complexity: $r = 0.27$, $p = 0.29$).

For *C. lupus*, intra-tooth variation from repeated scans of the m2 is not significantly different from the inter-tooth variation observed between paired m1 talonids and m2s for anisotropy ($p = 0.623$), textural fill volume ($p = 0.464$), and complexity ($p = 0.568$; Fig. 4). Intra-scan variation from comparisons of the four adjacent quadrants of the m2 are not significantly different from either intra- and inter-tooth variation for anisotropy ($p > 0.470$ for both intra- and inter-tooth comparisons), textural fill volume ($p > 0.060$ for both intra- and inter-tooth comparisons), and complexity ($p > 0.496$ for both intra- and inter-tooth comparisons). In *C. latrans*, there are also no observed differences in intra-tooth variation from repeated scans of the m2 as compared to inter-tooth variation between the m1 talonid and m2 for anisotropy ($p = 0.563$), textural fill volume ($p = 0.222$), or complexity ($p = 0.813$). Intra-scan variation of adjacent quadrants on the m2 are not significantly different from observed intra- and inter-tooth variation for anisotropy ($p > 0.260$ for both intra- and inter-tooth comparisons) and complexity ($p > 0.881$ for both intra- and inter-tooth comparisons). Intra-scan variability for textural fill volume is not significantly different from the variation observed between paired m1 talonids and m2s ($p = 0.440$) but is significantly larger than variation in the same m2 ($p = 0.040$). The mean difference between the m1 shearing facet and m2 from *C. latrans* reported in Ungar et al. (2010) is significantly larger than the observed variation in the same tooth (m2) and between paired m1 talonids and m2s documented in this study for anisotropy ($p < 0.002$ for both intra- and inter-tooth comparisons), textural fill volume ($p < 0.06$ for both intra- and inter-tooth comparisons), and complexity ($p < 0.03$ for both intra- and inter-tooth comparisons; Fig. 4). Variation between adjacent quadrants of a single tooth (m2) and the variation between m1 shearing facets and m2s is significantly different for complexity ($p = 0.012$), but not for anisotropy ($p = 0.255$) or textural fill volume ($p = 0.935$).

Mean bite force quotients are higher at the m2 compared to the m1 talonid for *C. latrans* (m2 = 128.4, m1 = 106.1, $p < 0.001$), and for *C. lupus* (m2 = 134.6, m1 = 113.5, $p = 0.007$). Bite force quotients at the m1 talonid (Fig. 5A) have no relationship with coyote or wolf anisotropy (*C. latrans* $r = 0.11$, $p = 0.32$; *C. lupus* $r = 0.03$, $p = 0.89$), textural fill volume (*C. latrans* $r = 0.11$, $p = 0.75$; *C. lupus* $r = 0.80$, $p = 0.30$), or complexity (*C. latrans* $r < 0.01$, $p = 0.85$; *C. lupus* $r < 0.01$, $p = 0.94$) at the same tooth position. Similarly, at the m2 (Fig. 5B) bite force quotients had no relationship with either *C. latrans* or *C. lupus* dental microwear texture parameters of the m2 for anisotropy (*C. latrans* $r = 0.09$, $p = 0.36$; *C. lupus* $r = 0.36$, $p = 0.59$), textural fill volume (*C. latrans* $r < 0.01$, $p = 0.81$; *C. lupus* $r = 0.46$, $p = 0.53$), and complexity (*C. latrans* $r = 0.07$, $p = 0.44$; *C. lupus* $r = 0.8$, $p = 0.30$). Within *C. latrans*, the difference between m1 talonid and m2 bite force quotient and the differences observed in anisotropy ($r^2 = 0.11$, $p = 0.76$), textural fill volume ($r^2 = 0.05$, $p = 0.49$), or complexity ($r^2 = 0.03$, $p = 0.62$) are unrelated. Within *C. lupus* there are no obvious relationships between changes in bite force quotients and microwear attributes between the m1 talonid and the m2; however, our small sample size prohibits greater insight into this relationship including statistical analyses (Fig. 5C).

Phlaocyonini case study

Summaries of the DMTA parameters as well as standard ellipse areas (SEA_c) of the Phlaocyonini are reported in table 2. There were minimal differences between reconstructed mean DMTA metrics from the lower m1 talonids and lower m2s: anisotropy (m1 9.8% > m2), textural fill volume (m1 12.2% < m2), and complexity (m1 14.8% < m2). However, SEA_c based on m1 talonid data was ~35% greater than SEA_c based on m2 data, and the orientation of the axes of highest variation between m2 and m1 talonid ellipses in microwear bivariate space are approximately orthogonal and different in eccentricity (Fig. 6).

Discussion

Molar comparison

Given the morphological and functional similarities between lower m1 talonids and lower m2s, we expected that the microwear recorded by each molar within an individual would be comparable. Our results suggest that, as expected, mean dental microwear parameters are roughly equivalent, with the exception of anisotropy within *C. latrans*. However, we found that microwear texture parameters observed on the m1 talonid and m2 within the same dental arcade were not strongly correlated, indicating one cannot predict microwear across teeth within an individual.

Most microwear studies are interested in reconstructing the dietary ecology of populations and species; thus, it is encouraging that our results with respect to mean dental microwear parameters suggest that the m1 talonid and the m2 could be sampled together to bolster sample sizes of historical and paleontological specimens. Within species, however, anisotropy values did differ between molars within *C. latrans*, but not within *C. lupus*, suggesting that the equivalency of anisotropy along the dental arcade might not hold across all canid taxa.

One explanation for why values of anisotropy could differ between molars while complexity and textural fill volume do not, could stem from subtle differences in use between the m1 talonid and m2 grinding surfaces. Anisotropy measures the relative orientation of striations recorded in enamel, which is indicative of fibrous and ductile food consumption (Scott et al. 2006; Schubert et al. 2010). Foods with these textural properties tend to deform under pressure, rather than propagating cracks and cleaving, and thus are not optimally masticated on grinding surfaces but instead are better processed on shearing facets such as the carnassial blade. High complexity and textural fill volume, on the other hand, reflect durophagous diets, which are optimally processed on the grinding molars. While it is possible that measurements of anisotropy are more variable on different grinding surfaces, experimental manipulations of diet are needed to fully clarify reasons for these discrepancies.

Another factor which could influence the discrepancy in mean anisotropy values within *C. latrans* is the relative position of the talonid basin with respect to the carnassial blade. While our sample size for bite force estimation was small, in coyotes, the carnassial blade tended to be positioned farther away from the m2 than it was within wolves ($p = 0.07$), when accounting for differences in body size. As discussed above, fibrous foods are best fractured via the blade of the carnassial which is situated to the far buccal side of the molar row. It is possible that during carnassial slicing, the grinding surfaces posterior to the blade fall within a “carnassial shadow” which minimizes the overall amount and variability of fibrous microwear etched into the tooth enamel at this location. If the m2 of *C. latrans* lies outside a “carnassial shadow” while the m2 of wolves is subsumed within it, one would expect *C. latrans* m2s to display higher variability within anisotropy compared to relatively constant values at the m1 talonid (Fig. 3b). This could explain why differences between the two molars were only observed in *C. latrans*; however, this “carnassial shadow” hypothesis needs to be explicitly tested among a wider range of canid taxa.

The lack of any predictive relationship between microwear recorded by the m1 talonid and m2 within the dental arcade of the same individual (excepting complexity in wolves) is not surprising, given the notable intra-scan and intra-tooth variation in microwear textures (Figs. 3 and 4). While DMTA eliminates many of the subjective errors that plagued standard microwear studies in the past via repeatable quantification of microwear features with computer software, this technique is still subject to intra-tooth variation similar to all dental microwear methods; however, this is minimized by taking the median of four contiguous scans as is standard practice with DMTA analyses (Figs. 1 and 4).

Intra-tooth variation could also arise from the structure of the enamel surface and turnover of microwear features. The enamel layer capping mammalian teeth is comprised of numerous enamel rods oriented within Hunter-Schreger bands (HSBs). The orientation of rods within HSBs have a pronounced impact on the hardness and durability of the enamel layer. For example, hyaenids have teeth with highly complex banding patterns which help limit formation of cracks during bone consumption (Rensberger 1999). These banding patterns can differ within regions on a single tooth as well as across the dental arcade (Maas 1991; Stefen 1999; Tseng 2012). Furthermore, visually quantified microwear features such as pitting and scratching have been noted to be impacted by HSBs within bone consuming carnivorans (Tseng 2012).

An additional consideration is that the enamel surface on the teeth of living mammals is consistently turned over, with the deposition of new microscopic wear patterns erasing past dental microwear over the scale of months to weeks (Merceron et al. 2010). This window of microwear turnover is beneficial to studies exploring intraspecific variation across temporal gradients by minimizing the time-averaging recorded by DMTA signals (Merceron et al. 2010). But it is unclear whether rates of turnover ("overprinting" of wear features) are equivalent across all teeth and facets. It is therefore possible that the lack of a predictive relationship in microwear textures between the m1 talonid and the m2 of individuals is related to potential differences in the microstructural ability of the enamel to resist deformation.

Regardless of the causes of intra-tooth variability, there is no indication that variation obfuscates dietary inference at the species level from microwear textures either from the lower m2 or lower m1 talonid of canids. Furthermore, our measures of both intra-scan variation and intra-tooth variation within repeated scans of the m2 were minor, particularly when compared to differences between biologically non-analogous facets (Fig. 4). Finally, given that within a species there is no apparent difference between the interpretations from the mean attribute values for the m2 and the m1 talonid, grinding facets from these regions can both be directly used to reconstruct dietary behaviors without using a discrimination function.

Although bite force significantly increases with proximity to the temporomandibular joint, and therefore between the m1 talonid and the m2, change in bite force appears to have no impact on any dental microwear textures for both species, at either the m2 or m1 talonid (Fig. 5). Counter to expectation, there is also no relationship between the strength of the change in bite force between molars and the corresponding change in DMTA parameter values, suggesting that bite force is not a driving factor in the disparity observed between individual molars. These results are consistent with evidence from carnivorous Tasmanian devils (*Sarcophilus harrisii*) which demonstrate that position along the toothrow has no impact on dental microwear textures (Jiang and DeSantis 2014). However, it should be noted that Tasmanian devil molars consist of large shearing facets (the surfaces analyzed by Jiang and DeSantis 2014), and grinding facets in canids record greater variability in microwear indices than shearing facets (Ungar et al. 2010). Furthermore, studies in bovids and primates have noted that food becomes increasing processed as it is transferred from the front to the back of the mouth along the dental arcade, thereby changing its textural properties as it moves (Schulz et al. 2010). Other studies, including in vitro experimental approaches, found that bite force alone has a minimal impact to microwear textures, and is instead influenced by endogenous variables such as chewing angle and abrasive loads (Hua et al. 2015; MacAfee and Green 2015). Although our results suggest that changing bite force along the tooth row does not influence the dental microwear textures of *C. latrans*, we lack statistical power to make inferences, particularly for *C. lupus* (n = 3). Thus, the impacts of changing bite force with tooth position on DMTA parameters within Canidae needs more rigorous testing, particularly with both in vitro and in vivo experiments.

While our results suggest that there are minor variations in the dental microwear textures observed at the m1 talonid and the m2 in anisotropy in coyote mandibles, mean dietary information for a species should be able to be gleaned from both lower m1 talonids and lower m2s. Previous work by Ungar et al. (2010) and Donohue et al. (2013) showed that microwear textures from the shearing facet of the lower carnassial do not reflect similar microwear textures from the grinding facets of the m2. This work highlighted that differences in molar morphology will substantially impact interpretations and can lead to erroneous dietary inference if teeth with disparate functions are compared to one another. We found that differences between the shearing and grinding pairs reported from Ungar et al. (2010) were significantly greater than differences observed between the two grinding facets within our study, except for textural fill volume in *C.*

latrans (Fig. 3). This further validates the utility of DMTA microwear from the m1 talonid, suggesting that despite variation between molars, differences between m1 and m2 grinding facets are not large enough to be biologically significant, particularly among higher-order taxonomic levels of study. Further, in canids, the most telling DMTA attribute in terms of dietary behavior is complexity (DeSantis et al. 2015), where differences between the m1 talonid and m2 are not significant at the genus or species level.

Phlaocyonini case study

Motivation for assessing the comparability of DMTA from the m1 talonid and m2 stems from the practical need to increase sample sizes available for analysis of historical, archeological, and paleontological communities. Results from our case study on the extinct borophagine tribe Phlaocyonini using 39.7-18 Ma old specimens from the John Day Formation are consistent with our findings from modern *C. lupus* and *C. latrans* specimens: mean DMTA values of phlaocyonin lower m2s and lower m1 talonids were comparable. This suggests paleontological DMTA studies could benefit from the inclusion of added specimens (and thus increased sample sizes) by sampling facets from multiple teeth. This is important because sample sizes have a tremendous impact on quantification of the size, shape, and position of a taxon’s dietary behavior and/or "niche" (Qiao et al. 2017). Within the Phlaocyonini, the position of the "dietary space" occupied (as inferred from DMTA parameters) was relatively robust; however, the size and orientation of the "dietary space" differed greatly between reconstructions using only lower m2s versus lower m2s and lower m1 talonids together. Differences in sample size can be reduced when comparing variation via ellipse area analyses that corrects for small sample sizes (Jackson et al. 2011); however, very small sample sizes (n<5) such as those found within many paleontological systems, can lead to misleading interpretations. While analyzing both m1 talonids and m2s can increase sample sizes and bolster dietary reconstruction, we caution that care should be taken to minimize pseudoreplication by accounting for minimum number of individuals within an assemblage.

Dietary reconstruction of the phlaocyonin canids via DMTA provides evidence for this tribe exhibiting high variability in dietary behavior. Anisotropy values were moderate to low, indicating moderate consumption of tough or fibrous foods. While this metric typically is associated with meat consumption, high anisotropy could also reflect folivorous diets (Donohue et al. 2013). Folivory has been hypothesized to compose a portion of phlaocyonin diets based on tooth morphology (Wang et al. 1999). Based on our results from modern coyotes, however, anisotropy values from m1 talonids should be interpreted with caution, especially when coming from hypocarnivorous species. Complexity values ranged widely, yet compared with modern scavenging canids (DeSantis et al. 2015) there was little indication of extreme durophagy in phlaocyonin (only two individuals with *Asfc* values >4); although, due to differences in taxonomic scales these differences have not been statistically tested. Overall, our dietary reconstruction suggesting moderately hard and not particularly tough food consumption is consistent with morphological evidence for the tribe having general, hypocarnivorous to mesocarnivorous diets (Van Valkenburgh 1991; Tedford et al. 2009). However, detailed insights into the diets and ecology of phlaocyonin canids would benefit from increased sampling at the species level and additional comparison with more ecologically appropriate modern reference taxa (e.g. foxes and procyonids).

Conclusion

Our results show that the grinding facets of the m1 talonid and the m2 generally capture comparable microwear patterns in canids, with the exception of anisotropy in coyotes. Thus, sampling a combination of the two molars can increase sample sizes without skewing the reconstructed dietary behavior of target taxa. The caveat of anisotropy within coyotes may relate to differences in diet between coyotes and wolves, as well as other morphological factors that differ across these species such as the size of a “carnassial shadow.” Interestingly, while mean DMTA values are mostly indistinguishable across teeth, the consistent lack of correlation between m1 talonids and m2s within an individual suggest one tooth cannot be used to predict the DMTA parameters of the other. This lack of predictability is likely due to a combination of intra-tooth variability derived from subtle differences in scan location on the grinding facet, the structural property of enamel, enamel modeling rates across teeth, and subtle differences in gross-molar anatomy which would be absent in carnivorans with more uniform check teeth. This study offers insights into how dental microwear textural data from lower m1 talonids and lower m2s can be combined in canids (and likely extinct caniforms), and demonstrates the benefits of including multiple teeth in the analysis of extinct taxa.

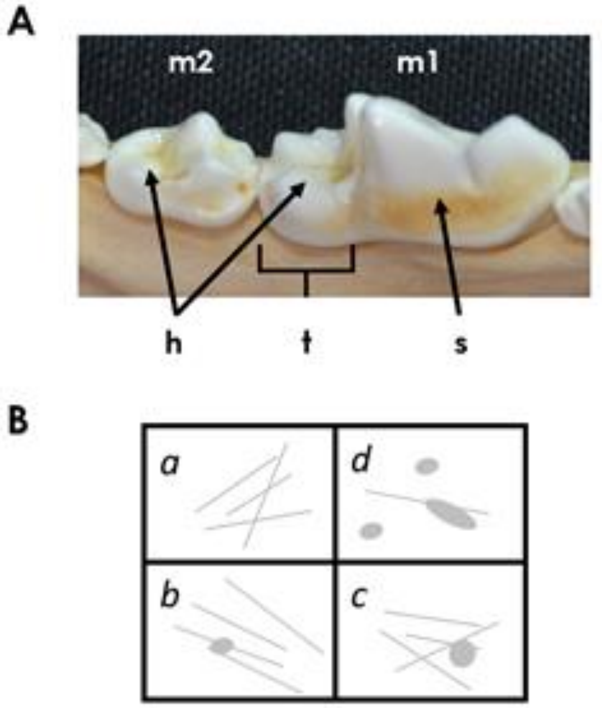


Figure 1. A) Dorso-lateral view of the lower right molars of a coyote (*Canis latrans*) with relevant morphological features labeled. DMTA studies within feliform carnivorans have focused on the shearing facet(s) of the lower first molar (m1); however, DMTA of caniform carnivorans has been performed on the hypoconid facet (h) of the second molar (m2). This crushing region is considered functionally analogous to the talonid basin (t) of the m1. We tested whether DMTA parameters from the hypoconid facet of the m1 and m2 are comparable in canids using paired samples from the same individual. Casts of molars were scanned in the designated regions (h) from both molars. B) Each scan consists of four adjacent quadrants which were analyzed via scale-sensitive fractal analysis. Median values from the four scans (*a*-*d*) were used to reconstruct dietary behavior via DMTA attributes including anisotropy, complexity, and textural fill volume.

Figure 2. A) Dorso-lateral view of the lower right molars of a coyote (*Canis latrans*) with relevant morphological features labeled. DMTA studies within feliform carnivorans have focused

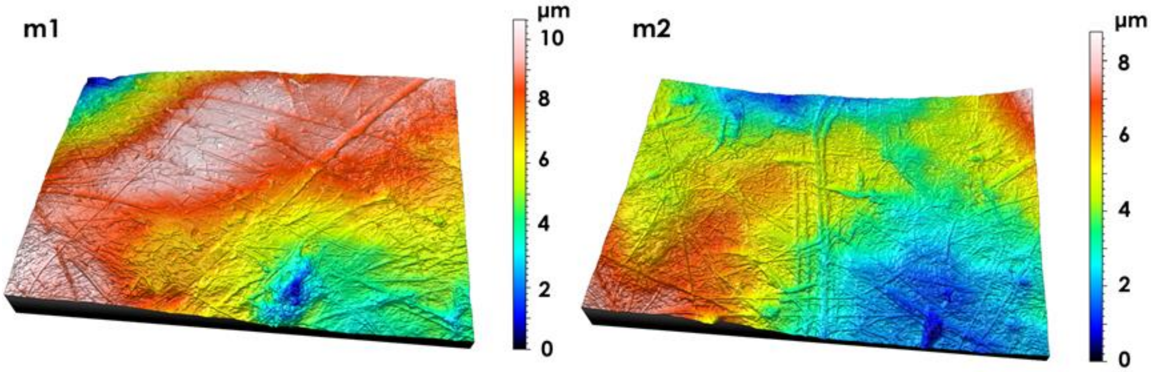


Figure 3: Example of paired 3D dental microwear surface scans of the hypoconid facet of both the talonid basin of the lower first molar (m1) and the lower second molar (m2) from *Canis lupus* (UBCBBM 17308).

Table 1: Summary of DMTA attribute values from the m1 talonid and m2 for 17 coyotes (*Canis latrans*) and 20 gray wolves (*Canis lupus*).

Species	**DMTA variable**	**Statistic**		
			m1 talonid	**m2**
Canis lupus	*Asfc*	Mean	2.455	2.071
		Min	1.198	0.794
		Max	4.146	3.989
		Standard Deviation	0.959	0.829
		Normality p-value	0.084	0.503
	epLsar	Mean	0.00321	0.00257
		Min	0.00088	0.00074
		Max	0.00403	0.00292
		Standard Deviation	0.00175	0.00105
		Normality p-value	0.996	0.212
	Tfv	Mean	11389	11435
		Min	7170	4356
		Max	16678	15958
		Standard Deviation	2300	2461
		Normality p-value	0.880	0.195
Canis latrans	*Asfc*	Mean	2.367	2.129
		Min	1.199	0.434
		Max	4.189	3.913
		Standard Deviation	0.965	0.981
		Normality p-value	0.081	0.453
	epLsar	Mean	0.00279	0.00460
		Min	0.00158	0.00125
		Max	0.00457	0.00959
		Standard Deviation	0.00676	0.00252
		Normality p-value	0.357	0.247
	Tfv	Mean	12159	12608
		Min	1638	8437
		Max	17908	17147
		Standard Deviation	4036	2281
		Normality p-value	0.118	0.937

Asfc (area-scale fractal complexity), *epLsar* (ansiotropy), *Tfv* (textural fill volume), Min (minimum value), Max (maximum value), Standard Deviation (n-1), Normality assessed via Shapiro-Wilk tests.

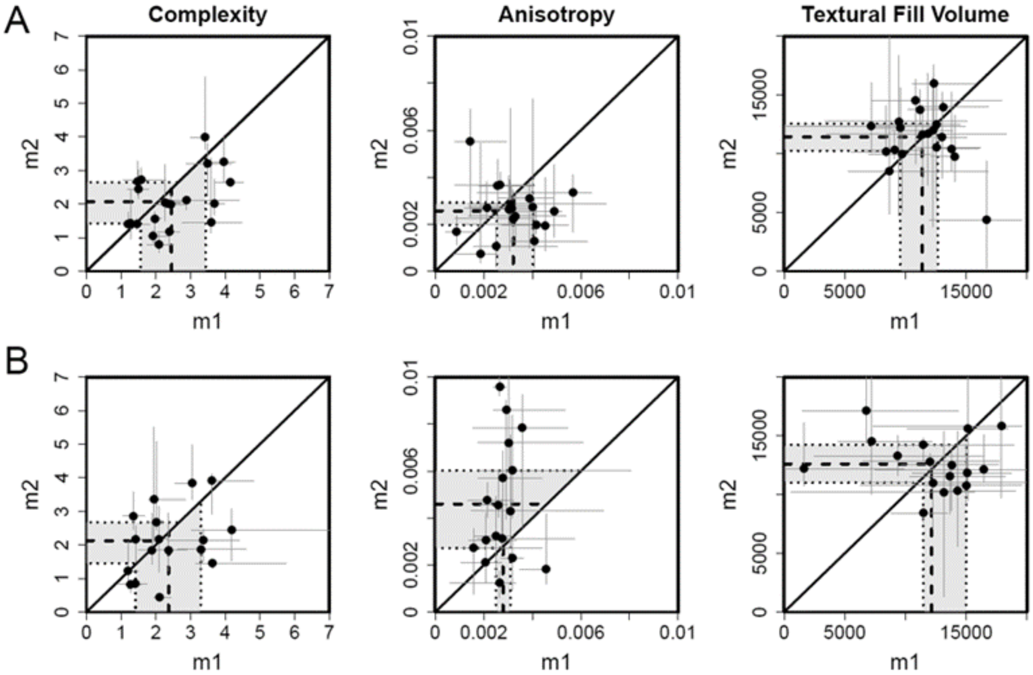


Figure 4: Median DMTA indices of paired lower m1 talonid and lower m2 samples for *Canis lupus* (A) and *Canis latrans* (B). Bars around points represent the range of microwear textures obtained from the four quadrants within each scan. Shaded regions represent means and quartiles, and were not significantly different for all metrics for both species (all p > 0.06), with the exception of anisotropy in *C. latrans* (p = 0.01). Diagonal 1:1 lines are presented to help visually assess skew within these data. There were no significant correlations between any of the microwear textures from the m1 talonid and m2 for either species (all p > 0.14), with the exception of complexity within *Canis lupus* (r = 0.46, p = 0.04). Ranges of microwear textures around each median frequently overlap the 1:1 line, suggesting that intra-tooth variation may be partially responsible for the lack of correlation.

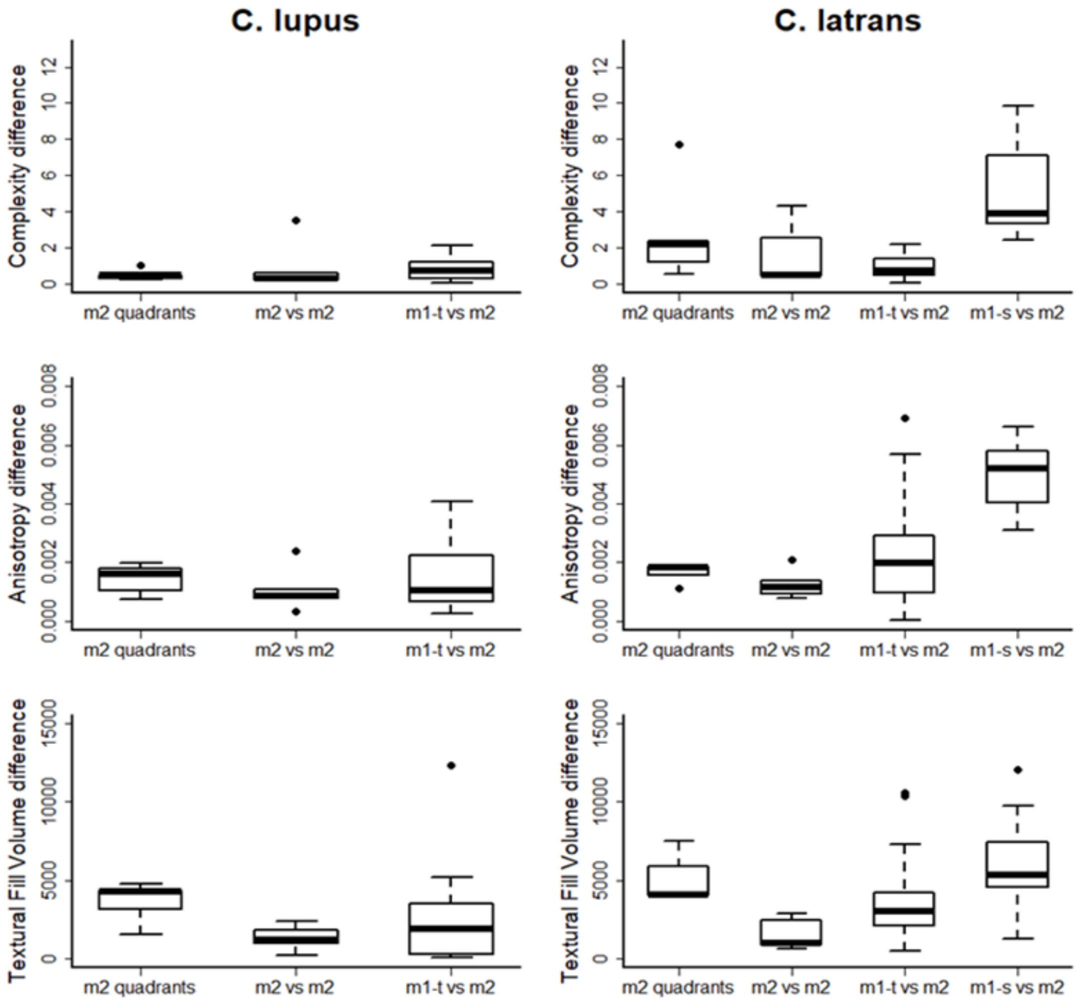


Figure 5: Comparison of the absolute value differences in dental microwear textures between pairwise comparisons of adjacent quadrants scanned from a single m2 (m2 quadrants) and sets of paired molars: the grinding surfaces of the m1 talonid and m2 from the same individual (m1-t vs m2), repeated scans within a single m2 (m2 vs m2), and between the shearing facet of the m1 carnassial and m2 from the same individual (m1-s vs m2; data for the m1 shearing facet vs m2 are taken from Ungar et al. (2010) and are available only for *C. latrans*). Sample sizes differed markedly between species and groups (see methods). There were no differences between mean variation from adjacent quadrants, lower m1 talonids, and repeated measures of a single lower m2 for all DMTA metrics in *C. lupus* ($p > 0.06$ for all). However, in *C. latrans* there were significant differences observed between adjacent quadrants, and repeated measures of a single lower m2 for textural fill volume ($p = 0.04$), yet no differences were observed between other comparisons or microwear parameters ($p > 0.22$ for all). The magnitude of differences observed between the lower m1 talonid and lower m2 were less than differences reported between the lower m1 shearing facet and the lower m2 ($p < 0.05$ for all DMTA metrics), which are not functionally analogous.

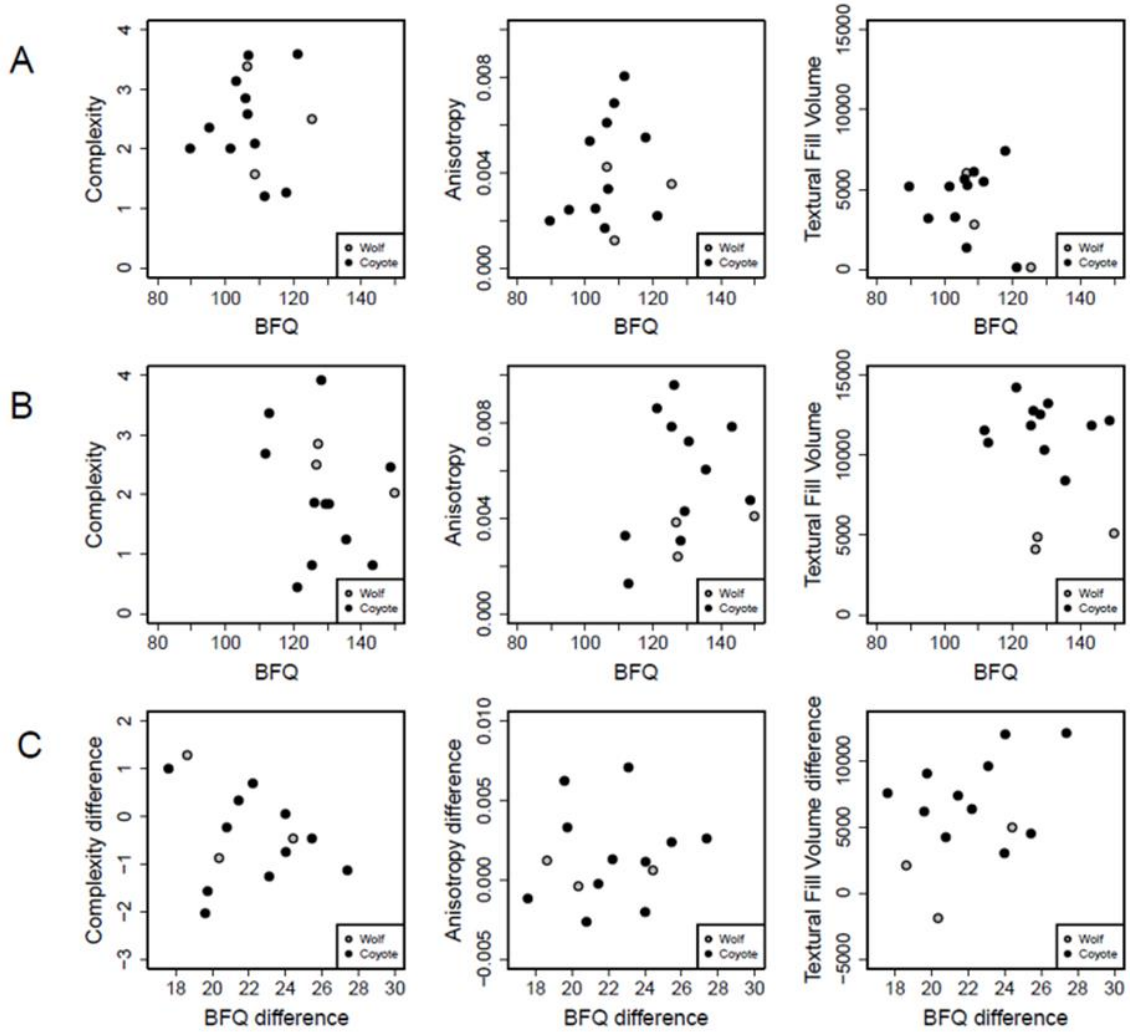
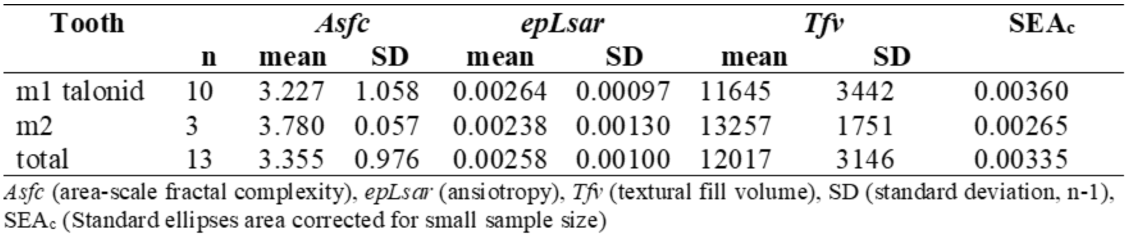


Figure 6: Relationships between the bite force quotient adjusted for body mass (BFQ) and paired dental microwear textures from the same tooth, at the lower m1 talonid (A), and the lower m2 (B) among *C. lupus* (gray) and *C. latrans* (black). There were no observed correlations between BFQ and dental microwear textures recorded at either molar for both species. C) The difference in BFQ between the two molars (m2-m1 talonid) also demonstrated no correlations with the difference in any of the DMTA indices between the molars (m2-m1 talonid).

Table 2: Summary of DMTA attribute values and corrected Standard Ellipse Areas (SEA_c) from lower m1 talonids and lower m2s for Phlaocyonini from the John Day Formation.



Tooth		***Asfc***		***epLsar***		***Tfv***		**SEA_c**
	n	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	
m1 talonid	10	3.227	1.058	0.00264	0.00097	11645	3442	0.00360
m2	3	3.780	0.057	0.00238	0.00130	13257	1751	0.00265
total	13	3.355	0.976	0.00258	0.00100	12017	3146	0.00335

Asfc (area-scale fractal complexity), *epLsar* (ansiotropy), *Tfv* (textural fill volume), SD (standard deviation, n-1), SEA_c (Standard ellipses area corrected for small sample size)

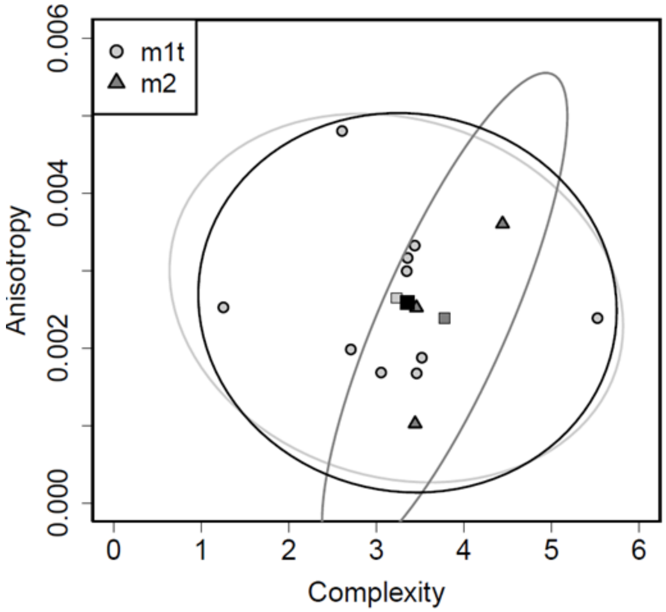


Figure 7: Bivariate plot of DMTA indices for the Phlaocyonini derived from samples of m1 talonids (circles) and m2s (triangles). Group means are represented by squares for lower m2 samples only (light gray), lower m1 talonid samples only (dark gray), and all data together (black). Standard ellipses surround the 95% confidence regions for each tooth group, colored accordingly. Means for all three groups are relatively comparable: complexity (m1 14.8% < m2), anisotropy (m1 9.8% > m2), and textural fill volume (m1 12.2% < m2), suggesting that like contemporary canids, microwear from m1 talonids are comparable to microwear from m2s in the extinct Phlaocycnini canids. Sample-size standardized ellipses are similar in area, yet are orthogonally oriented and differ in eccentricity (ellipse width) and thus give different interpretations to the degree of dietary specialization of the phlaocyonin.

CHAPTER 3 - Dietary breadth contraction in coyotes: an unexpected legacy of mesopredator release at a continental scale

Brian P. Tanis[a], Larisa R.G. DeSantis[b], and Rebecca C. Terry[a]

[a] Department of Integrative Biology, Oregon State University, Corvallis, OR 97331-8530, U.S.A.
[b] Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN 37235-1805, U.S.A.

Abstract

Loss of apex predators frequently releases medium-sized mesopredators from competition, resulting in trophic cascades with widespread ecological impacts. For example, within the Pacific Northwest, historical extirpation of the gray wolf (*Canis lupus*) has been linked to the release of coyotes (*Canis latrans*), causing cascading effects impacting prey populations and ecosystem stability. Typically, mesopredator release studies focus on changes in population abundance; however, this data is challenging to collect over the broad spatial and temporal scales of wolf extirpation and coyote release. As such there is uncertainty in the degree to which released coyotes have shifted their ecologies over the historical loss of wolves from the landscape. Here, we test if mesopredator release resulted in cascading dietary niche shifts using museum specimens of coyotes and wolves. We quantified dietary niche using two separate indices: Dental Microwear Texture Analysis and analysis of stable isotopes from hair. Coyotes were categorized as released from wolves by spatial and temporal proximity along a transect of Western North America. Mean dietary position did not change for coyotes that underwent competitive release; however, dietary breadth decreased and shifted away from dietary parameters indicative of scavenging. This suggests that historical coyote diets were subsidized by an abundance of wolf-killed carcasses. These findings point to a more nuanced interaction between wolves and coyotes than purely antagonistic and that the rewilding of apex predators could permit the restoration of energy flow in communities.

Introduction

The loss of strong top-down forces by apex consumers often results in widespread impacts to ecosystems via trophic cascades (Estes et al. 1998, 2011; Halaj and Wise 2017). One type of trophic cascade that has become a major focal point for ecological research is mesopredator release (Crooks and Soulé 1999; Prugh et al. 2009; Estes et al. 2011). Mesopredators, defined here as 1-15kg predators from intermediate trophic levels, frequently experience antagonistic interactions from apex predators (Roemer et al. 2009). These interactions, which can be either direct or behaviorally mediated, are important for regulating mesopredator abundances (Gehrt and Prange 2007; Roemer et al. 2009; Levi and Wilmers 2012; Miller et al. 2012). Studies have shown that when these antagonistic consequences are removed due to the extirpation or functional loss of apex predators, mesopredator populations can dramatically increase in abundance, with negative implications for prey species and changes to community structure (Prugh 2005; Prugh et al. 2009; Letnic et al. 2011; Colman et al. 2014). Furthermore, such trophic cascades have been shown to irreparably disrupt energy flow and community composition (Estes et al. 2011; Molsher et al. 2017). Unfortunately, these cascades are becoming ever more common, as over the last two centuries apex predators across the globe have become reduced at an astonishingly high rate due to human activities (Ripple et al. 2014).

While mesopredator release has become a globally pervasive phenomenon garnering major conservation concern in recent decades (Prugh et al. 2009; Letnic et al. 2012; Molsher et al. 2017), it is not a new phenomenon. In many terrestrial ecosystems, mesopredators were released a century or more ago, following human-aided removal of apex predators (Pasanen-Mortensen et al. 2017). This presents a key challenge to our understanding of how mesopredator release alters ecosystems, as the communities we observe today have already been highly altered. For example, the strong and well-documented antagonistic interactions within North American canids, specifically the gray wolf (*Canis lupus*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*), have inspired ecologists to use them as a model system for making predictions regarding mesopredator release (Beschta and Ripple 2009; Levi and Wilmers 2012; Miller et al. 2012; Newsome and Ripple 2015). However, much of our current understanding of trophic cascades in these taxa come from case studies where coyotes have been released from wolves for over a century. Furthermore, like most terrestrial carnivores, canids are elusive and have large home ranges. Therefore, documenting the numerical effects of mesopredator release on local predator and prey populations is often logistically unfeasible. Finally, while excellent work has been carried out demonstrating mesopredator release at local (Crooks and Soulé 1999; Cove et al. 2012; Molsher et al. 2017), regional (Levi and Wilmers 2012; Khalil et al. 2014), and continental scales (Newsome and Ripple 2015; Newsome et al. 2017), these studies have relied on pre-defined geographic regions of total apex predator loss. In reality, the loss of apex predators unfolds in a patchwork mosaic that is asynchronous in both space and time.

Here we address these challenges by testing if released populations of mesopredators (coyotes) retain similar ecologies and behaviors following apex predator (wolf) removal across a north-south transect spanning the west coast of North America over the last century. To do this, we take a novel approach and view mesopredator release through a lens of dietary niche space as opposed to tracking shifts in abundance. Dietary niche space is one aspect of mesopredator ecology and behavior which is expected to shift following release from apex predators, yet has remained largely unstudied to date. While not focused on mesopredators, previous work has demonstrated that chronic perturbations (e.g. species extinctions and climate change), including those involving trophic cascades, can force species to alter their foraging strategies as access to resources shift (Carreira et al. 2017).

Given the loss of strong antagonistic top-down interactions in the case of mesporedator release, it is likely that released mesopredators alter their foraging strategies in several ways. First, it is possible that the dietary niche space of mesopredators is constrained in the presence of apex predators but would expand via competitive release, enabling use of previously excluded food resources (Moreno et al. 2006). Alternatively, as many mesopredators are opportunistic generalists, greater competition among conspecifics due to increases in population size could trigger an increase in dietary plasticity (Prugh 2005; Dupuy et al. 2009). An increase in mesopredator dietary plasticity following release could theoretically put increased pressure on less abundant prey typically stabilized/sheltered via prey-switching behavior of their predators (Murdoch 1969; Prugh 2005; Bolnick et al. 2007; Peers et al. 2014). This would increase the susceptibility of prey populations to crashes, destabilizing the system. Alternatively, released mesopredators might completely or partially fill ecological roles once filled by extirpated apex predators, thereby restoring lost aspects of ecological function and promoting overall stability in ecosystems (Arjo et al. 2002; Letnic et al. 2012). Further insight concerning how mesopredator dietary behavior changes during mesopredator release is thus key to understanding broader-scale ecological consequences with respect to ecosystem stability and the retention of ecosystem services, the success of conservation efforts, curtailing expanding mesopredator distributions, and initiatives to re-wild apex predators in their former ranges (Colman et al. 2014; Molsher et al. 2017).

Fortunately, an ecological memory of Canid communities from prior to apex predator (wolf) extirpation, as well as the historical legacy of anthropogenic persecution of wolves and other predators, have been preserved in museum collections. It is thus possible to reconstruct the resource use of mesopredators (coyotes) and the ecological context of Canid communities from places and times prior to their release (i.e. when coyotes were sympatric with wolves) and after their release (i.e. after wolf extirpation). Furthermore, museum specimens enables sampling across a range of temporal and spatial scales that can help account for otherwise confounding variables (e.g. patchwork and asynchronous loss of apex predators, climate change, and geographic environmental gradients), allowing broad-scale ecological trends in dietary shifts to emerge.

To test the hypothesis that mesopredator release triggers a shift in mesopredator dietary ecology and behavior, we evaluated museum specimens of coyotes and wolves spanning a transect along the western margin of North America that captures the historical extirpation of wolves by humans throughout the 1900s and the subsequent release of coyotes. Specifically, we quantified dietary niche space across spatial and temporal scales within these two species using two dietary indices: Dental Microwear Texture Analysis (DMTA) and Stable Isotope Analysis (SIA). DMTA and SIA reflect different yet complementary aspects of the dietary composition and foraging behavior of species and are readily obtainable from museum study specimens. Specifically, DMTA quantifies three-dimensional abrasions etched into the enamel surface of molars by food, providing insight into the textural properties of foods recently consumed prior to the death of an individual (i.e. the last supper effect) (Scott et al. 2005; DeSantis et al. 2012a; DeSantis 2016). In contrast, SIA uses isotopic ratios preserved within biological tissues to assess the contribution of different resources to an individual's diet (^{13}C) and the trophic position of an individual (^{15}N) (Koch et al. 2009; Ben-David and Flaherty 2012; Newsome et al. 2012). When each of these multidimensional dietary indices are aggregated across individuals, derived parameters reflect aspects of the dietary niche space of a population, enabling robust quantification of variation within the dietary niche of species across space and time.

Counter to our expectations, we found that coyotes from western North America that have been released from competition with gray wolves exhibit less variability in dietary niche space than prior to their release. This reduction in dietary niche breadth appears to coincide with a reduction in scavenging behaviors (i.e. reduced bone consumption) which would have been historically available prior to wolf extirpation due to wolf-killed carcasses on the landscape. This suggests that historical interactions between coyotes and wolves were highly nuanced, including well-documented antagonistic exclusion among individuals while at the same time facilitation of coyotes via a carcass subsidy. Thus restoration of apex predators could restore both negative and positive interactions, altering ecosystem services and trophic networks in previously unrecognized ways.

Materials and Methods

Historical Background of Study System

Targeted wolf persecution (e.g. governmental removal programs and bounties) in western North America began in earnest during the mid-1800s resulting in the southern range of gray wolves retreating northward. By the early 1940s, a century of institutionalized eradication programs and bounties led to the total extirpation of wolves from northern California (circa 1924) and Oregon (circa 1935, Appendix Figure B1), with only isolated dispersing individuals left throughout Washington (ODFW, 2005; Wiles, Allen, & Hayes, 2011). In Canada, similar wolf reduction programs were implemented in the early 1920s and succeeded in eliminating wolves from the southern portions of British Columbia. Sparse populations of wolves persisted in northern British Columbia and what is today the Yukon Territories until a ban on wilderness poisoning campaigns went into effect in 1961 (B.C. Ministry of Forests, Lands and Natural Resource Operations, 2014). During this century of intensive predator control measures, coyotes proved to be more resistant to human eradication programs due to pack structure and other behaviors (Bekoff 1977; Séquin et al. 2003; Ripple et al. 2013). As wolves were extirpated, coyotes were released from top-down pressure and were able to expand their range through habitats that previously hosted high wolf densities, including northward to interior Alaska and, perhaps more notably, eastward leading to coyote-wolf-dog hybridizations in New England (Sears et al. 2003; Kays et al. 2008; Levy 2012; Hody and Kays 2018). Currently, legal protection of wolves has allowed for population recovery in the northern parts of their historical range, as well as permitting the natural re-wilding of portions of the western United States.

Specimen Sampling

Specimens of coyotes and wolves from Western North America were sampled for dental microwear texture analysis and/or stable isotope analysis from five natural history collections: the University of British Columbia Beaty Museum of Biodiversity (UBCBBM), the University of Washington Burke Museum (UWBM), the Museum of Vertebrate Zoology (MVZ), the Oregon State University Fisheries and Wildlife Collection (FW), and the Slater Museum of Natural History (PSM). Additionally, to increase sample sizes of target populations, DMTA and isotopic data from previously published studies (Reid 2014; DeSantis et al. 2015) were added to our dataset (Appendix B Tables A2-3). Coyote specimens covered a geographic extent from Northern California to British Columbia (59.6 to 35.0°N latitude), and the Pacific coastline to the Western Cordillera of Canada (-117.6 to -133.4°W longitude) (Figure 7). Temporally, coyote specimens span from the early 1900s to 2000s (Figure 7 inserts). Wolf specimens, which serve as a biological reference within our study, cover a similar temporal extent; however, spatially sampled specimens range farther north and west than coyotes (Appendix B Figure B2).

Defining released versus sympatric coyotes

To assess diet changes in coyotes following wolf extirpation we binned coyote specimens into two treatment groups: released and sympatric. Rather than use bins defined on geopolitical boundaries, which have little biological significance, or from broad, estimated species range maps, we binned coyotes based on their known spatio-temporal proximity to wolves. Specifically, sampled coyotes were compared to a database of all western North American wolf occurrences from natural history collections with both temporal data (i.e. month and year) and georeferenced localities (n = 2230, queried and merged from GBIF and VertNet 2018, Appendix B Figure B3). Individual coyotes were considered released if they occurred both > 200 km and more than 24 months apart from a known wolf specimen occurrence. These cutoffs were determined based on previous studies that have investigated the spatial (Newsome et al., 2017; Newsome & Ripple, 2015) and temporal (Catling and Burt 1995; Arjo and Pletscher 2011) scales associated with mesopredator release in canids and other terrestrial carnivores. We took this approach to more accurately capture the spatially and temporally asynchronous patchwork of removal of wolves from western North America.

Dental Microwear Texture Analysis

High-resolution molds were created of either the lower second molar or the talonid basin of the lower first molar, depending on which enamel surface was the least degraded by microwear (i.e. cracks and chips). Previous work has shown dental microwear textures from these two surfaces to be equivlent (Tanis et al. 2018). Molds were made by cleaning the enamel surface with acetone and ethanol, then applying polyvinylsiloxane impression material (President Jet regular body, Coltène/Whaledent Inc.). Molds were later filled with a clear epoxy resin (EPO-TEK301, Epoxy Technology Inc.) and the resulting casts were scanned via a Sensofar PLu neox optical profiler at Vanderbilt University. Scans were made on the hypoconid facet, regardless of molar type. Digital surface scans were analyzed using scale-sensitive fractal analysis software (Sfrax and Toothfrax, Surfract Corp.) to compile microwear parameters (per Scott et al. 2006).

We focused our analysis on three microwear parameters with known dietary correlations within canids: anisotropy (*epLsar*), complexity (*Asfc*), and textural fill volume (*Tfv*). Anisotropy, the amount of alignment among wear features caused by mastication of tough dietary items (Scott et al. 2006; Ungar et al. 2010; DeSantis et al. 2012a; DeSantis 2016), is indicative of flesh consumption (Schubert et al. 2010; DeSantis et al. 2012a). Complexity quantifies differences in wear feature relief across magnification scales and discriminates between hard and soft foods (Scott et al. 2005, 2006; DeSantis 2016). High complexity values are particularly useful as indicators of increased bone consumption among scavenging predators (Schubert et al. 2010; DeSantis et al. 2012a, 2015; Donohue et al. 2013; DeSantis and Haupt 2014; Stynder et al. 2018). Textural fill volume quantifies the size of wear features through differing volumetric cuboids (Scott et al. 2006; Calandra and Merceron 2016; DeSantis 2016) and also increases with highly durophagous diets (Peigne et al. 2009; DeSantis et al. 2012a, 2013; Donohue et al. 2013; DeSantis and Haupt 2014; DeSantis and Patterson 2017). Additional microwear parameters, such as scale of heterogeneity, have not been shown to correlate with aspects of extant carnivoran diets (Schubert et al. 2010; Ungar et al. 2010; DeSantis et al. 2012a) and thus were not included in this study.

Dental microwear textures are continuously eroded and replaced by more recent meals, therefore dietary reconstruction is limited to the last days to weeks of an individual’s life, known as the “Last Supper Effect”. Given this tight window of inference, it is possible to use DMTA to elucidate seasonal changes in diet (Merceron et al. 2010; Calandra and Merceron 2016; DeSantis 2016). As highly opportunistic predators, both coyotes and wolves will make use of seasonally abundant food resources, such as neonatal ungulates in the spring and increased carrion consumption in the winter (Fox-Dobbs et al. 2007; Arjo and Pletscher 2011). However, it is unclear to what degree ephemeral resource pulses swamp overall dietary signals from microwear. Given the potential for seasonal impacts on diet, we tested if microwear parameters differ according to season of specimen collection via a Kruskal-Wallis test. Due to unequal sampling across months that is likely the result of seasonally biased trapping effort, we pooled data from months into three seasonal bins, winter (Nov-Feb), spring (Mar-Jun), and summer/fall (Jul-Oct), delineated based on biological significance (Appendix B Table 4). Additional assessment for the possibility of our DMTA dietary reconstructions to be biased by confounding variables (i.e. climate, annual, and spatial) was conducted using Pearson correlation and linear regression both before and after binning into treatments (Appendix B figures 4-5).

DMTA statistical analysis

DMTA dietary space was reconstructed for coyotes by treatment group (released and sympatric) and gray wolves, treating each as independent populations. DMTA parameters were modeled using a Bayesian framework to reconstruct three-dimensional ellipsoids following Rossman et al. (2016). Models were run with non-informative priors using Markov-Chain Monte Carlo sampling via programs R and JAGS (citations). We ran the models in three chains of 100,000 iterations with the first 50,000 as burn in and thinning by 15, producing a posterior distribution of 63,334 draws. Models were assessed for convergence and posterior distributions were used to calculate and compare differences in median standard ellipsoid volume (SEV) and centroid location between treatment groups.

Stable Isotope Analysis

Isotope analysis was performed on hair samples taken from museum study skins of coyotes and wolves, and aggregated by the same treatment groups described above (Appendix B Tables B2-3). Guard hairs were removed by hand from the dorsal surface of the skin along the pelvic girdle, about 10cm to the right of the sagittal plane. Given our interest in large spatial and temporal averages, we did not discriminate between molting and non-molting individuals. Hairs were cleaned following established protocols (Ben-David and Flaherty 2012; Terry 2017) and analyzed for carbon isotopes (^{13}C) and nitrogen isotopes (^{15}N) using a Carlo Erba NA1500 elemental analyzer coupled with a DeltaPlus isotope ratio mass spectrometer at the Oregon State University Stable Isotope Laboratory. We focused on these commonly used isotopes as they reflect variation in the isotopic value of the baseline resources consumed as well as predictable patterns of fractionation of stable isotopes that occur within an animal's body as biochemical processes turn food into body tissue (Urton and Hobson 2005; Fox-Dobbs et al. 2007; Roth and Hobson 2011). Specifically, $\delta^{13}C$ values are well known to reflect the photosynthetic pathways of the primary producers at the base of food webs (C3, C4, CAM), and $\delta^{15}N$ values have been shown to become enriched by ~3.5‰ with each increase in dietary trophic level (Kelly 2000; Fox-Dobbs et al. 2007; Roth and Hobson 2011; Craine et al. 2015).

Isotopic values for carbon were corrected for the atmospheric shift in $\delta^{13}C$ values that has been caused by fossil fuel burning (i.e. the Suess Effect, Tans, De Jong, & Mook, 1972). All $\delta^{13}C$ values were standardized to the year 1900 C.E. following Terry (2017). Finally, carbon and nitrogen isotopic values have also been shown to vary across an array of environmental factors, such as gradients in temperature and aridity (Kelly 2000; Pardo and Nadelhoffer 2010). Thus the relationships between δ^{13}C and δ^{15}N values and temperature and precipitation were assessed via linear regression. Climate data were obtained for all specimens with GPS data via two online repositories, the PRISM Climate Group (Daly et al. 2008) for specimens within the continental United States, and Climate WNA (Wang et al. 2012, 2016) for specimens from Alaska and Canada. Both datasets use normalized historical weather station data to model climatic variables with reference to elevation (Daly et al. 2008; Wang et al. 2012). Climate variables of interest were mean temperature and precipitation for the 12 months preceding specimen collection. Ultimately, no relationship was observed between temperature and either δ^{13}C or δ^{15}N ($p > 0.15$ for both). A weak relationship was observed between precipitation and δ^{13}C ($p = 0.03$, ${}_{adj}R^2 = 0.1$). However, both treatments groups equally span the climatic gradients, supporting our interpretation that observed isotopic differences reflect patterns driven by biotic factors (Appendix B figures 6-7).

SIA Statistical Analysis:

Isotopic values for the two coyote groups and gray wolves were plotted in a bivariate δ-space, with the reconstructed niche space calculated using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.4 (Jackson et al. 2011). This procedure, which calculates Bayesian standard ellipse areas (SEA_b), is computationally analogous to a two-dimensional version of the Rossman et al. (2016) method used for comparisons of DMTA described above. Finally, pairwise differences among centroid positions of the three groups were calculated and tested for significant divergence via a residual permutation procedure (Turner et al. 2010).

Results

DMTA results

Our binning procedure resulted in 81 released and 36 sympatric coyotes which we compared with 60 gray wolves (Appendix B Table B2). Within wolves, there was no indication that dental microwear parameters differed by season ($p \geq 0.13$ for all microwear parameters). For coyotes, complexity and textural fill volume showed no differences across seasons ($p > 0.26$ for both); however, there was a significant shift in anisotropy towards lower values during the summer ($p= 0.01$), indicative of less tough food (i.e. flesh) consumption. However, when we accounted for whether coyotes were released versus sympatric in our assessment of seasonal differences, we recovered no differences across seasons for any microwear parameters when coyotes were sympatric with wolves ($p > 0.27$ for all). When coyotes were released from wolves, complexity and textural fill volume also showed no differences across seasons ($p > 0.40$ for both); but we still recovered the significant difference in anisotropy during the summer ($p= 0.02$). While our dataset contains noise from variation in phenology across large spatial and temporal scales, the difference between seasonal means to the total mean for each microwear parameter predominantly falls within 1 standard deviation of the global mean (Figure 8). This suggests that while seasonal dietary fluctuations are being recorded by DMTA, they are not large enough in magnitude to deviate substantially from typical annual diets in coyotes and impact our results with respect to shifts in dietary niche space within our groups (wolves, released coyotes, sympatric coyotes). Therefore, we did not factor seasons into our Bayesian dietary niche space models.

Investigation of confounding variables ultimately revealed no indication that dental microwear for coyotes was correlated with sex, climate, latitude, or longitude. While some abiotic factors (climate, year, and latitude) initially appeared to weakly correlate with microwear values, a post hoc assessment showed these relationships were driven by coyotes becoming released in a semi-predictable pattern of historical wolf extirpation from south to north over a span of several decades (Appendix B Figures 4-5).

The Bayesian model for DMTA suggests that released coyotes experienced a contraction in overall dietary breadth. Specifically, standard ellipsoid volume of released coyotes was nearly half the volume of coyotes sympatric with gray wolves (Figure 9). Reduction in niche space volume for released coyotes was primarily driven by lower variation in textural fill volume; however, released coyotes did show increased variation in anisotropy values, specifically only extending to larger values (Figure 10). Overall this is indicative of an increase in hypercarnivory and a decrease in durophagous behaviors such as scavenging among coyotes that have undergone mesopredator release. Centroid location did not significantly differ between coyote groups, although pairwise distances between textural fill volume was trending towards significance. Comparisons with gray wolves showed highly similar dietary niche space to sympatric coyotes (Figure 9). Overall there was no difference in niche position (centroid length) between wolves and either coyote group. However, there were significant differences between individual mean microwear parameters.

SIA results

Treatment groups assigned by our binning procedure consisted of 16 released and 26 sympatric coyotes, along with 18 gray wolves. There was no indication that either $\delta^{13}C$ or $\delta^{15}N$ values between groups were biased by abiotic factors (e.g. aridity, temperature, longitude, or latitude), therefore no correction factors were implemented prior to analysis other than for the Seuss effect (Appendix B Figures B6-7). Bayesian dietary space showed that released coyotes had significantly reduced isotopic dietary niche breadth compared with coyotes sympatric to gray wolves (Figure 9). This change included a ~1‰ reduction along the $\delta^{15}N$ axis, and a roughly 3‰ decrease along the $\delta^{13}C$ axis (Figure 11). These shifts suggest that following mesopredator release, the core dietary niche space of coyotes became more constrained, and suggests increased reliance on animal protein and prey resources consuming vegetation that contains a higher proportion of plants utilizing the C4 photosynthetic pathway.

Discussion

The results from both DMTA and SIA derived reconstructions of dietary niche space indicate that despite no changes to core niche space values (i.e. centroids), coyotes that have undergone mesopredator release due to the extirpation of apex gray wolves from western North America experienced a contraction in their dietary niche space. Furthermore, this contraction was mirrored across two independent assessments of the dietary niche: DMTA and SIA. Although we are unable to equate this dietary niche space reduction to a numerical change in prey diversity, the contraction in dietary space still represents behavioral shifts towards less heterogeneous resource use following mesopredator release. Given what is known about how DMTA and SIA parameters correlate with diet (Scott et al. 2006; Koch 2007; Schubert et al. 2010; Newsome et al. 2012; DeSantis et al. 2015; DeSantis 2016), our results suggest that the reduction in dietary niche breadth within released coyotes is primarily categorized by a decreased reliance on hypocarnivory and durophagy.

While our evidence supports overall dietary niche breadth reductions in western North American coyotes following mesopredator release, the precise drivers of this change are not certain. Changes in dietary space could result from removal of interspecific interactions with apex predators (i.e. opening of niche space), or as a result of changes to intraspecific interactions as population growth occurs in the absence of apex predator suppression. However, current theory suggests that as populations expand, so should the overall dietary breadth of a population, as competition for resources increases and individuals resort to less quality foraging opportunities (Bolnick et al. 2007; Newsome et al. 2015; Sivy et al. 2018). Alternatively, under a competitive exclusion model, theory predicts that released coyotes would either shift their overall dietary niche position and compensate for or fill the vacated apex predator’s dietary niche space (Paquet 2006; Cupples et al. 2011; Benson et al. 2017; Suraci et al. 2017), or utilize previously restricted foraging opportunities (Azevedo et al. 2006). While these are not necessarily mutually exclusive scenarios, both theories are inconsistent with the results of our study showing no significant shift of the position of the dietary niche and contraction of niche breadth. Instead, our data supports a third possible driver of dietary niche breadth reduction in coyotes: that coyotes sympatric with gray wolves experienced facilitation in the form of scavenging wolf-killed carcasses. Thus, we hypothesize that following wolf extirpation, there were less carcasses available to coyotes, prompting the reduction in durophagy and increased reliance on hypercarnivory observed in our data (Figures 10 and 11).

Often interspecific interactions are thought of as clearly defined, and uniform. As such, the historic extirpation of gray wolves has typically been described as a benefit for coyotes, permitting range expansion and increases in abundance (Ripple et al. 2013; Meachen et al. 2014; Newsome and Ripple 2015; Newsome et al. 2017; Hody and Kays 2018). This stems from a preponderance of studies showing that wolves will actively suppress coyote activity within their ranges (Merkle et al. 2009; Arjo and Pletscher 2011; Ripple et al. 2013) and numerical increases in coyote populations following wolf extirpation (Levi and Wilmers 2012; Newsome and Ripple 2015). However, as often the case for ecological phenomenon, this view is likely overly simplistic. Regional evidence from wolf relocations suggests that coyotes are able to effectively coexist with wolves along the edges of pack territories (Merkle et al. 2009). Additionally, coyotes sympatric with wolf populations have larger social groups and diets that contain a higher percentage of ungulates (Arjo et al. 2002; Merkle et al. 2009; Arjo and Pletscher 2011). Typically, coyotes are unable to successfully hunt large ungulates unless aided by large social groups (Sanabria et al. 1996; Quinn 1997; Lukasik and Alexander 2012; Benson et al. 2017). As such, increases in ungulate material observed within coyote scat is often attributed to scavenging opportunities. While wolves will guard kills against scavengers, they frequently will leave some portion of a carcass behind that can later be used by mesopredators (Wikenros et al. 2017). These resources could supplement coyote diets in ways that make them less reliant on smaller game, particularly when seasonally less abundant. Observational studies of coyotes within wolf territories confirm that coyotes make use of carcass subsidies (Paquet 2006; Merkle et al. 2009). Our data suggests that this was an important and widespread phenomenon across western North America prior to the extirpation of wolves.

Our outcomes have several implications for conservation and management of canids and their ecosystems in western North America. Currently, wolf populations are recovering in Pacific states and territories, with natural re-wilding occurring in the southern extent of their former range (Atwood and Gese 2008; Marshall et al. 2013; Bradley et al. 2015; Horne et al. 2019). As this occurs, coyote populations will begin to experience interspecific interactions that in some cases have been missing for over a century. Our evidence suggests that this will lead to an increase in coyote dietary niche breadth, which could cause substantial impacts to larger-scale community and ecosystem dynamics. Increasing the variation in dietary niche space among coyotes could permit prey-switching behavior (Murdoch 1969; Peers et al. 2014; Newsome et al. 2015). This density-dependent selection of prey items has been shown to have dramatic impacts on ecosystem stability by reducing pressure on less abundant prey populations. For example, it has been hypothesized that a long-term decline in lagomorph abundances are attributed to continuous levels of high predation by coyotes following mesopredator release (Ripple et al. 2013). If coyotes can subsidize protein requirements via increased carrion scavenging, it might actually result in reduced predation pressure on threatened and endangered lagomorphs (e.g. pygmy rabbits (Green and Flinders 1981; Crawford 2008)). Additionally, given that low-protein diets are thought to increase coyote conflicts with humans in both urban and rural environments (Murray et al. 2015), the added carrion resources from reintroduced wolves could naturally attenuate nuisance coyotes and possibly lessen livestock depredation (Conover 1999). However, additional studies are needed to understand to what degree the increased dietary breadth of sympatric coyotes is due to more generalized foraging at the individual level or is a population-level manifestation of more tightly constrained individuals, and how those different scenarios will impact ecosystem-scale trophic networks (Bolnick et al. 2007; Wilson and Wolkovich 2011).

Conclusions

Understanding how mesopredator release can change the ecologies of species is of vital importance for conservation and management. This is particularly critical for North American carnivores, in which historically altered ecosystems have been the prevailing baseline of reference for over a century. We demonstrated using DMTA and SIA reconstructions that dietary niche space of coyotes has been significantly reduced following the extirpation of wolves from western North America, counter to the expectations of mesopredator release theory. Specifically, coyotes which are sympatric with gray wolves utilized a greater variety of durophagous and hypocarnivorous resources, a pattern that is consistent with the hypothesis of facilitation via wolf-killed carcasses on the landscape. These changes in dietary niche breadth have important implications for community stability and trophic networks following the natural re-wilding of apex predators into western North America.

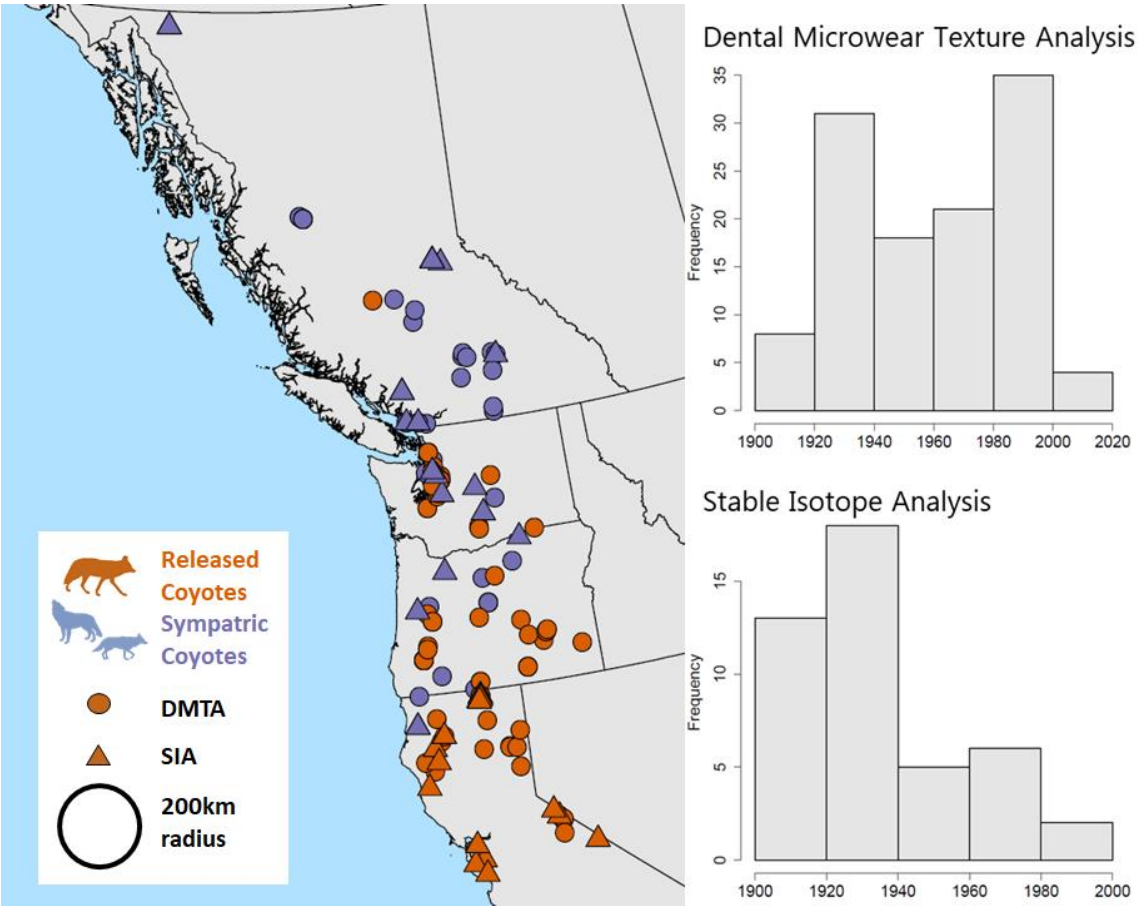


Figure 8: Location of sampled coyote specimens across western North America. Coyotes were binned according to their spatio-temporal proximity (≤ 200km and 24 months) to known wolf localities as either sympatric (blue) with wolves or released (orange). Specimens were sampled for dental microwear texture analysis (circles) or stable isotope analysis (triangles), representing two independent measures of dietary niche space. Temporal extent of sampled specimens for each analysis is shown via histograms.

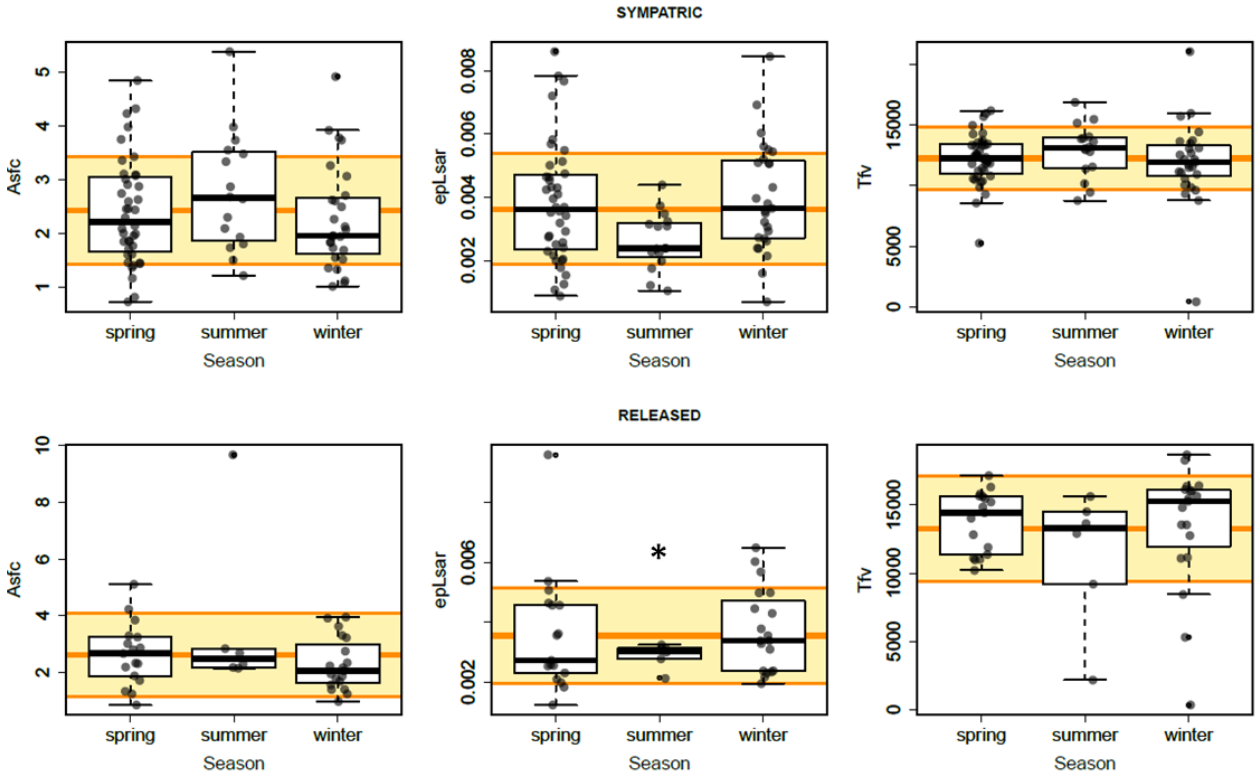


Figure 9: Coyote microwear data for populations sympatric with gray wolves (top) and released (bottom) summarized by season for each DMTA parameter. Seasons; winter (Nov-Feb), spring (Mar-Jun), and summer (Jul-Oct), were clustered based off biological significance. Sample sizes within each month are not uniform, instead reflecting skewed collection efforts. The only significant difference between seasonal microwear signals was observed within anisotropy values of released coyotes (Fig. 2E), where summer values were significantly lower than other seasons (denoted with asterisk). Shaded regions behind boxplots depict one standard deviation from the global mean (thick orange line). All seasonal means fall within one standard deviation of the global mean suggesting that any seasonal changes to dietary microwear, such as that observed in the late summer months for anisotropy, do not deviate substantially from typical annual diets.

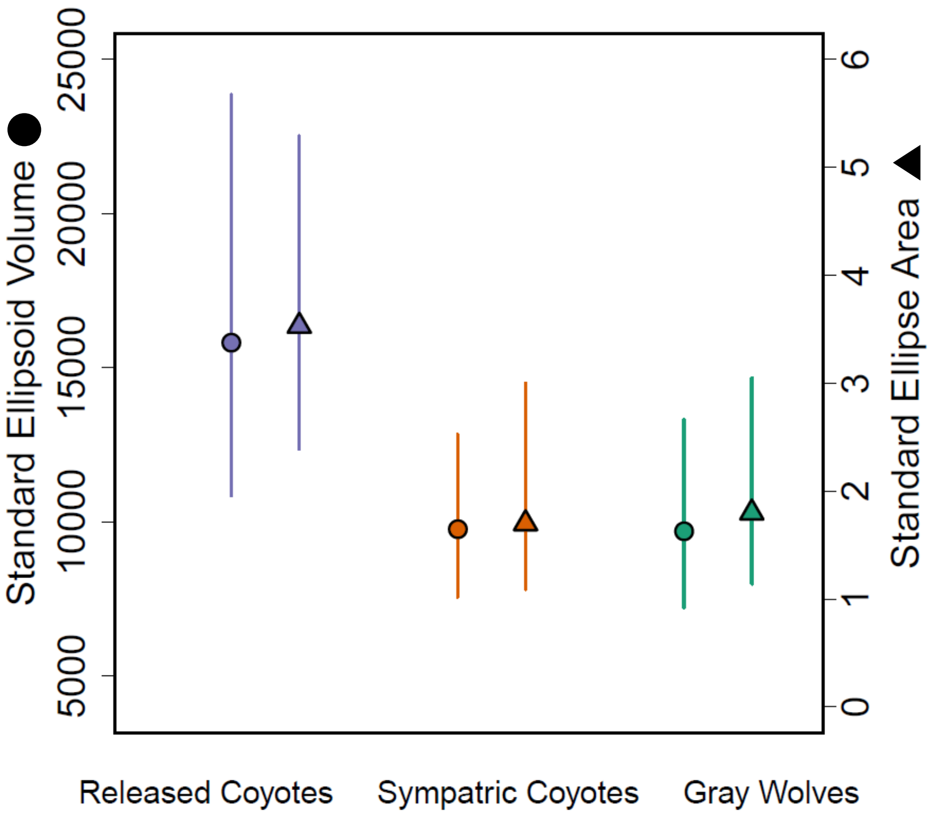


Figure 10: Summary of the posterior distributions for Bayesian reconstructions of dietary niche space, along with 95% credible intervals. Reconstructions from both DMTA (circles, Standard Ellipsoid Volume) and SIA (triangles, Standard Ellipse Area) show that coyotes occurring sympatrically with gray wolves have larger dietary niche space than coyotes following mesopredator release.

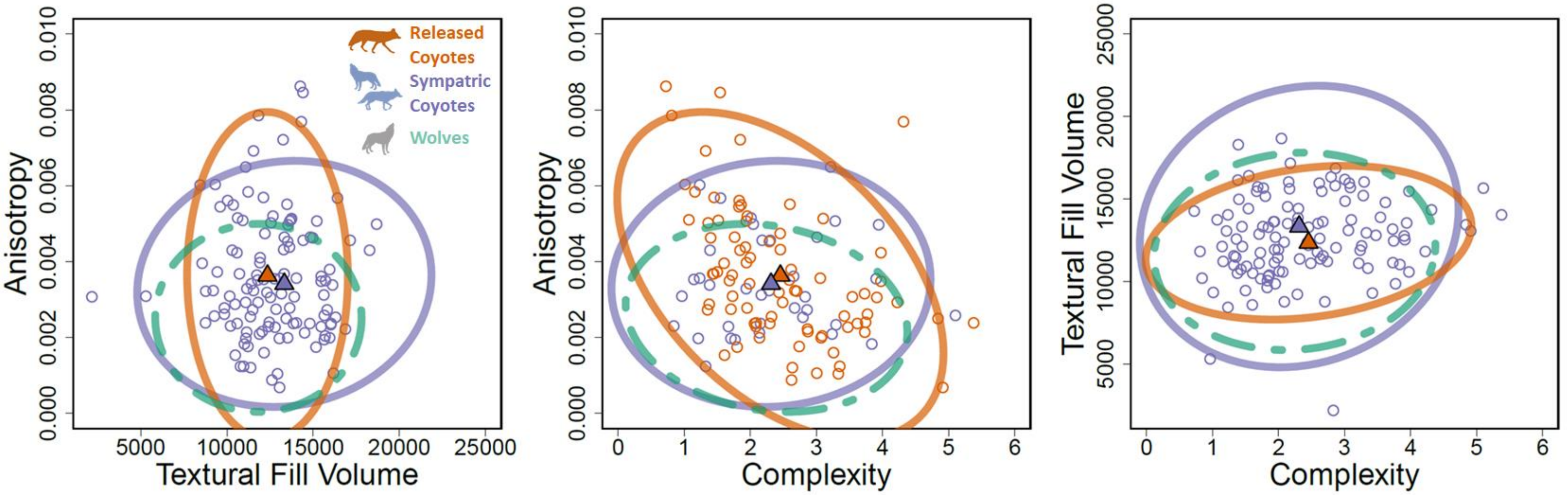


Figure 11: Bivariate representations of three-dimensional Bayesian ellipsoids modeled from dental microwear parameters for coyotes sympatric with gray wolves (blue), coyotes released from wolves (orange) and gray wolves (green). For clarity, individual points are shown only for coyotes of each treatment group (circles) along with their corresponding centroids (triangles). Standard Ellipsoid Volume was larger for sympatric coyotes, primarily due to increased variation among textural fill volumes, and a decrease in anisotropy. These microwear signals are indicative of a dietary shift towards increased carnivory and reduced durophagy in coyotes following mesopredator release.

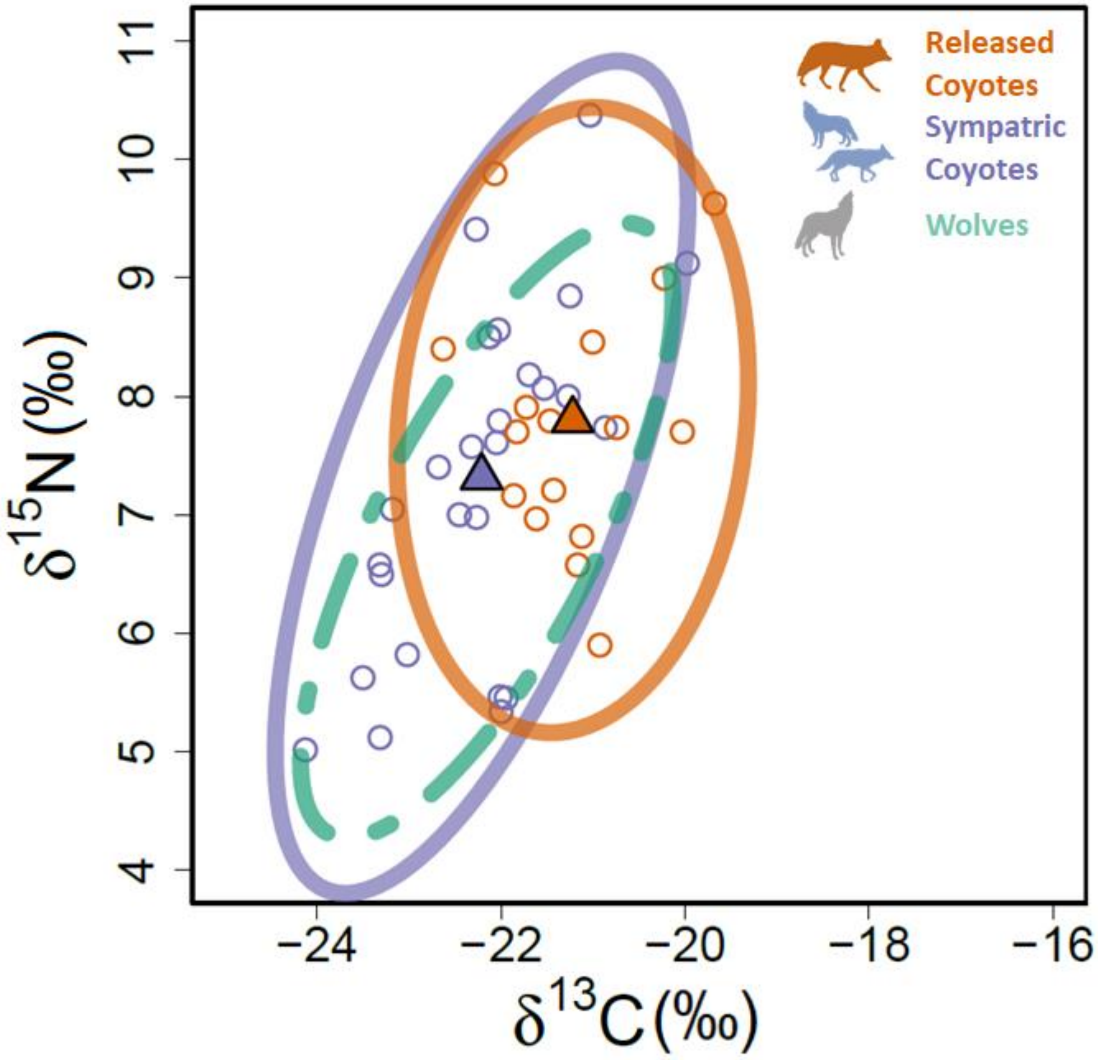


Figure 12: Isotopic niche space reconstructions depicted by 95% Bayesian standard ellipse space for coyotes sympatric with gray wolves (blue), coyotes released from wolves (orange) and gray wolves (green). For clarity, individual points are shown only for coyotes of each treatment group (circles) along with their corresponding centroids (triangles). Standard ellipse area is significantly reduced among released coyotes, due to less variability in both δ^{15}N and δ^{13}C.

CHAPTER 4 – Loosening the macroevolutionary ratchet: Does dietary plasticity alter morphological insights into Canidae extinction?

Brian P. Tanis[a], Larisa R.G. DeSantis[b], and Rebecca C. Terry[a]

[a] Department of Integrative Biology, Oregon State University, Corvallis, OR 97331-8530, U.S.A.
[b] Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN 37235-1805, U.S.A.

Abstract

The canid family (Mammalia: Carnivora) has an exceptional fossil history reflecting dynamic macroevolutionary patterns. One prevalent pattern is the macroevolutionary ratchet, where convergent evolution of successful morphotypes leads to increasingly specialized species that are eventually driven to extinction. While this iterative process is well recognized in the fossil record, dietary specialization and its link to extinction risk has previously been inferred only indirectly from morphological traits such as body mass and molar surface area, rather than directly via dietary reconstructions. While morphology reflects overall dietary behavior and metabolic constraints, individuals (and species) frequently forage opportunistically in ways morphology does not always reflect. We investigated if direct reconstructions of canid dietary niche space align with macroevolutionary trends inferred from species-level morphologies. Specifically, we tested for the hypothesized association between dietary specialization and the ultimate extinction of canid lineages. We quantified dietary niche space of 10 extinct species spanning the past 33.3 million years of Canidae evolution, representing the Hespercyoninae, Borophaginae, and Caninae subfamilies, via Dental Microwear Texture Analysis (DMTA). DMTA quantifies microscopic wear patterns created on tooth enamel as food is masticated, reflecting the types of foods consumed, thus capturing a comprehensive picture of resource use including behavioral specialization and plasticity. Standard ellipsoid volumes of DMTA parameter space were calculated for each species as a measure of dietary breadth and tested for correlation with species durations. We found that dietary behaviors inferred from DMTA parameters better explain species durations than morphological traits, including the widely-used metric of body mass.

Counter to expectation, a positive correlation emerged between increased specialization (smaller niche breadth) and lineage duration. Dietary generalization was greatest for canids of intermediate body mass and was not correlated with foraging strategies (i.e. hypo- or hypercarnivory). Our results disrupt the prevailing macroevolutionary ratchet hypothesis, suggesting that overspecialization in diet alone did not drive iterative extinctions of fossil canid clades. Additionally, dietary specialization was not restricted to more derived species. Prevailing wisdom suggests specialization is linked to increased extinction risk, causing an inability to adapt to sudden fluctuations in prey availability. However, dietary specialization potentially offers additional benefits, such as reduced handling times and lower rates of competition with congeners.

Introduction:

Understanding broad patterns of mammalian macroevolution are important for advancing fundamental understanding and informing conservation and management of species amid global change. In particular, studies disentangling natural and anthropogenic drivers of extinction are critical when 16% of all species are at risk of extinction (Urban 2015). One hypothesized process which has considerable support for explaining patterns of natural extinction within mammalian carnivores is the macroevolutionary ratchet (Van Valkenburgh et al. 2004; Silvestro et al. 2015; Slater 2015). Ratchets here refers to a broad type of evolutionary “toy model” in which lineages over time become reduced in some measure of variation, primarily due to trade-offs of evolutionary history or physiology (Alicea and Gordon 2014; DiMartino 2017).

Much of our understanding of the macroevolutionary ratchet and other patterns of evolution and extinction stems from the mammalian fossil record, which provides a natural laboratory for studying ratchet-induced extinctions over million-year time-scales. For instance, the fossil history of the dog family Canidae captures repeated ratchets, in which convergent morphological adaptations for increasing hypercarnivory leads to extinction and replacement by sister clades of radiating generalist mesocarnivores, which themselves then evolve towards hypercarnivory, resetting an iterative process (Van Valkenburgh 1991; Van Valkenburgh et al. 2004; Valkenburgh 2007; Colles et al. 2009; Silvestro et al. 2015; Slater 2015; Balisi et al. 2018). These ratchet-like patterns have been well recognized in the fossil record and manifest at multiple taxonomic levels, including among tribes, subfamilies, and suborders (Wang et al. 1999; Cope 2002; Van Valkenburgh et al. 2004; Tedford et al. 2009; Tseng and Wang 2011; Slater 2015).

Early research identifying the macroevolutionary ratchet in canids attributes this pattern to metabolic constraints of larger bodied carnivores requiring higher levels of protein consumption (Van Valkenburgh et al. 2004). Canids generally follow Cope's rule of steadily increasing body mass over evolutionary trajectories (Alroy 1998; Van Valkenburgh et al. 2004). Furthermore, there is a well-established allometric link between energetic requirements of mammals at either tail of the distribution of body mass (Alroy 1998; Carbone et al. 1999, 2007; Carbone and Gittleman 2002; Christiansen and Wroe 2007; Hatton et al. 2015), where tradeoffs between prey size and prey availability theoretically constrain optimal foraging strategies and favor dietary specialization (Chubaty et al. 2014). Therefore, it has been hypothesized that overspecialization in hypercarnivorous foraging ultimately limits species temporal durations within the canid family (Van Valkenburgh et al. 2004). Subsequent research has demonstrated that extinction rates in fossil canids are not due to climate alterations and appear to be linked with overspecialized hypercarnivores being outcompeted by sister-clades, comprised of generalist foragers independently radiating into specialized hypercarnivorous morphologies (Figueirido et al. 2015; Silvestro et al. 2015; Slater 2015). Furthermore, recent research suggests that overspecialization in hypocarnivorous diets is also correlated with limited species durations in fossil canids (Balisi et al. 2018), thus reinforcing the hypothesis that dietary specialization increases extinction risk within canids.

While numerous studies have linked specialized diet as a major driver of extinction risk in the macroevolutionary ratchet of canids, these patterns have previously been indirectly inferred from morphological traits, not dietary reconstructions, despite assumptions about clade-level foraging strategies transitioning from hypo- to hypercarnivory over time. There is an ongoing effort in ecology to link quantifiable species traits with macroecological and macroevolutionary patterns (McKinney 1997; Alroy 2006; Winemiller et al. 2015; Cantalapiedra et al. 2017). Such trait-based approaches have become nearly ubiquitous in an effort to focus on functional roles rather than species identities (Aguilera and Navarrete 2012; Zakharova et al. 2019). Dietary categorization via quantifiable traits within canids has focused largely on tooth morphology, such as grinding surface area and carnassial blade length (Van Valkenburgh 1989; Stefen 1999; Valkenburgh et al. 2003; Valkenburgh 2007; Anderson and LaBarbera 2008; Tedford et al. 2009; Tseng et al. 2010; Tseng and Wang 2011; Meloro et al. 2015). It has been well established that these traits correspond with differential mastication efficiencies for ranges of food types and serve as robust ecomorphological indicators in the fossil record (Valkenburgh 2007; Anderson and LaBarbera 2008;

Stynder 2009; Tseng and Wang 2011; Drake et al. 2015; Meloro et al. 2015; Tseng and Flynn 2015). Furthermore, dental cusps or entire teeth that are lost over time with increased specialization rarely re-evolve (Gould 1970; Anderson and LaBarbera 2008; Jernvall and Thesleff 2012), thus supporting the macroevolutionary ratchet (Valkenburgh 2007; Tseng and Wang 2011; Balisi et al. 2018).

While morphology provides insight into broad physical capabilities of species, inferences can differ according to the traits analyzed (Matheus 1995; Wesley-Hunt 2005; Meloro 2011; Donohue et al. 2013; Jones and DeSantis 2016; Stynder et al. 2018). Furthermore, despite categorization of specialized foragers by morphology, non-morphological dietary reconstructions can show pronounced dietary plasticity (Terry et al. 2017). Modern canids are renowned for their high degree of dietary plasticity (Sanabria et al. 1996; Quinn 1997; Rose and Polis 1998; Benson et al. 2017). For example, gray wolves (*Canis lupus*) have strong hypercarnivorous dentition and yet studies have confirmed a non-trivial component of their diet can include vegetative and non-vertebrate prey items (Van Valkenburgh 1989, 1991; Urton and Hobson 2005; Watts and Newsome 2016). It is this dietary plasticity of populations, which is not captured by morphology, that truly defines a multidimensional dietary niche space. Yet it is unclear the degree to which dietary plasticity could effectively enable morphologically specialized species to stall or escape from the macroevolutionary ratchet.

To fill these gaps, we investigated if direct reconstructions of canid dietary niche dynamics through time align with macroevolutionary trends inferred from species-level morphologies. Specifically, we used the exceptional fossil record and well-studied evolutionary history of canids to test the hypothesized link between increased dietary specialization through time and the ultimate extinction of canid lineages. Additionally, we compared how reconstructed dietary variability corresponds with morphological categorizations of diet, and interpret the potential for dietary analyses as predictors of extinction risk.

Methods:

We quantified dietary specialization in fossil canids using Dental Microwear Texture Analysis (DMTA). This technique quantifies microscopic wear patterns created on tooth enamel as food is masticated, reflecting the textural types of foods consumed (Egan and Funk 2006; DeSantis et al. 2013; Calandra and Merceron 2016; DeSantis 2016). DMTA thus captures the foraging activity of an individual, which can be aggregated across populations and at a species level to reconstruct a comprehensive picture of diet that can be used to make comparisons between species and across time periods (Schubert et al. 2010; Stynder et al. 2011; DeSantis et al. 2012a, 2015; DeSantis and Haupt 2014; DeSantis and Patterson 2017). This differs from previous studies using mean morphological traits to broadly categorize species into the extremes of hypo- and hypercarnivory; variation in DMTA parameters occurs at the level of the individual, while variation in morphology is primarily captured at the level of populations or species. While DMTA parameters cannot at this time be correlated with the identity of prey items, so as to measure specialization in prey diversity, they have been shown to correlate strongly with textural types of foods. Thus, in addition to capturing individual-level variation, they also capture much more nuanced signals of resource consumption within species (e.g., durophagy, carnivory, frugivory, browsing, grazing, etc.) and thus reflect axes of resource-use specialization and plasticity (Peigne et al. 2009; Merceron et al. 2010; Jones and DeSantis 2016, 2017).

DMTA analysis was conducted by casting molars of fossil canids spanning the past 33.3 million years from the John Day Fossil Beds National Monument (JODA), University of California Museum of Paleontology (UCMP), and the University of Washington Burke Museum (UWBM). Specifically, we cast 77 specimens representing 8 species, distributed across the subfamilies Hespercyoninae, Borophaginae, and Caninae (Table 3). To this dataset we added published values from one additional fossil species, *Canis dirus* (DeSantis et al. 2015) and four modern taxa (Tanis et al. 2018). These previously published datasets were collected under identical protocols and scanned with the same optical profiler, therefore eliminating inter-microscope variability (Arman et al. 2016). Additionally, the taxa included in this study represent all dietary categorizations (i.e. hypo-, meso-, and hypercarnivory) as determined in the published literature on the basis of morphological features (Van Valkenburgh et al. 1990; Silvestro et al. 2015; Slater 2015; Balisi et al. 2018).

Following Tanis et al. (2018), high resolution molds were created from either the lower second molar or talonid basin of the lower first molar using polyvinylsiloxane impression material (President Jet regular body, Coltène/Whaledent Inc.). Molds were filled with a clear epoxy resin (EPO-TEK301, Epoxy Technology Inc.) and the resulting casts scanned via a Sensofar PLu neox optical profiler at Vanderbilt University. Each scan comprised four adjacent quadrants totaling 206×276 μm^2 which were analyzed via scale-sensitive fractal analysis software (Sfrax and Toothfrax, Surfract Corp.) to compile microwear parameters. Median values from the four scans were used to represent a given specimen (per Scott et al. 2006)).

We focused our analysis on three microwear parameters with known dietary correlations within canids: anisotropy (*epLsar*), complexity (*Asfc*), and textural fill volume (*Tfv*). The mathematical derivations of these parameters have been established by Scott et al. (2006), here we will focus on the biological interpretations of each parameter in relation to diet in carnivorans (Schubert et al. 2010; Ungar et al. 2010; DeSantis et al. 2012a; DeSantis 2016). Anisotropy represents wear feature alignment as caused by mastication of tough dietary items such as high flesh consumption (Schubert et al. 2010; DeSantis et al. 2012b; DeSantis and Patterson 2017). Complexity is an index of scale-corrected wear feature relief which increases with predominantly hard and brittle foods. Thus complexity values are chiefly used to identify bone consumption within scavengers and omnivores (Schubert et al. 2010; Ungar et al. 2010; Stynder et al. 2011, 2018; Donohue et al. 2013; DeSantis et al. 2015). Textural fill volume is used to discriminate relative depth of wear features and also increases with highly durophagous diets in carnivores. Additional microwear parameters, such as scale of heterogeneity, have not been shown to correlate with aspects of extant carnivoran diets (Schubert et al. 2010; DeSantis et al. 2012a; Calandra and Merceron 2016) and thus were not included in this study.

Quantification of dietary specialization was performed for each species by aggregating all three DMTA parameters together into a three-dimensional dietary texture niche space. We then used a Bayesian framework to reconstruct 95% probability ellipsoids reflecting dietary niche space for each species (Rossman et al. 2016). Bayesian models were run with non-informative priors using Markov-Chain Monte Carlo sampling via programs R and JAGS (R Development Core Team 2008; Denwood 2016). We ran the models using the default priors (Rossman et al. 2016) in three chains of 100,000 iterations with the first 50,000 as burn in and thinning by 15, producing a posterior distribution of 63,334 draws. Models were assessed for convergence and posterior distributions were used to calculate median standard ellipsoid volume (SEV) for each species, which was used as a relative measure of dietary specialization. Additionally, four morphological features commonly derived from skeletal elements to categorize dietary specialization in canids were also compiled for each species from the literature and are summarized in table 3 (Wang et al. 1999; Valkenburgh et al. 2003; Tedford et al. 2009; Meloro et al. 2015; Silvestro et al. 2015; Balisi et al. 2018). These values were compared with individual DMTA parameters via Pearson correlation to assess the degree to which dietary reconstructions of species align with morphological categorization of hypercarnivory and durophagy.

As any single fossil specimen is unlikely to represent the extremes of a species stratigraphic range, first and last appearance dates were estimated from known occurrences to calculate species duration (Foote and Raup 1996; Alroy 2006). Species occurrence data was downloaded from the Paleobiology Database (last accessed 8 February 2019). First and last appearance dates were calculated following established Birth-Death Markov chain Monte Carlo procedures via the *PyRate* package of program Python (Silvestro et al. 2014). Specifically, we ran 10 million iterations with the first 200,000 as burn in, thinning by 1,000. Median first and last appearance times were used from the resulting posterior distributions to calculate species duration times. Species durations were used to create a series of multiple linear regressions for correlation with the morphological traits and standard ellipsoid volumes previously mentioned, as well as qualitative measures of phylogenetic positions (Table 4). We assessed correlations using Akaike's information criterion adjusted for small sample sizes, selecting the top ranked model for further comparisons (Anderson et al. 1998; Anderson and Burnham 2002; Grueber et al. 2011). Modern taxa, which have censored duration times, were modeled separately from fossil taxa to avoid right skew (Rich et al. 2010). Outlier analysis suggested that the species duration of *Canis dirus* was inconsistent with fossil canids. As current evidence suggests that *C. dirus* extinction was linked to the human-induced end-Pleistocene megafaunal extinctions (Lyons et al. 2004a; b; Tedford et al. 2009; Pardi and Smith 2016), we grouped it with modern taxa with censored extinction times for further analysis.

Results:

The link between DMTA variables and hypercarnivorous vs durophagous diets has been well established (Ungar et al. 2010; Schubert et al. 2010; DeSantis et al. 2012a, 2015, 2017b; Donohue et al. 2013; DeSantis and Haupt 2014; DeSantis 2016; Jones and DeSantis 2016; DeSantis and Patterson 2017; Stynder et al. 2018). As such, morphological predictors of these dietary categories would be expected to mirror DMTA parameters. We found that DMTA parameters do not correlate with the morphological traits frequently used to categorize diet in canids (Appendix C Figure C8). Correlation coefficients were non-significant ($p > 0.05$) and less than 0.38 for all pairwise combinations of DMTA parameters and morphological traits.

Model ranking for fossil canids shows higher support for correlation between DMTA derived dietary niche breadth and species durations than between morphological traits and species durations (ΔAICc >3), including the widely-used metric of body mass (Table 4). Furthermore, there was no indication that categorial dietary values from literature accounts correlated with dietary breadth (Appendix C Figure C9). We did recover a qualitative trend that species falling within the tails of the canid body mass distribution had narrower (i.e. more specialized) dietary breadths than canids of intermediate body mass, although we did not have large enough sample sizes to model each tail of the body mass distribution separately (Appendix C Figure C10). Counter to expectation, we recovered a positive correlation within fossil taxa between increased specialization (smaller dietary breadth) and species duration ($p=0.02$; $R^2_{adj} = 0.54$ Figure 12).

Model ranking for modern canids similarly showed higher support for correlation between DMTA derived dietary niche breadth and species durations than morphological traits and species durations (ΔAICc >12), however caution should be used interpreting these findings given majority of these taxa are censored (Table 4). The top model for the modern mirrored the correlation observed in the fossil taxa, where species with increased specialization have persisted longer ($p=0.008$; ${}_{adj}R^2 = 0.91$), although the slope of the correlation was not as steep (Figure 12).

Discussion:

Our results disrupt the prevailing macroevolutionary ratchet hypothesis for the iterative pattern of canid evolution, suggesting that specialization in diet was not associated with extinction risk in canids. While morphology reflects overall dietary capabilities and metabolic constraints of species, individuals will forage opportunistically in ways morphology alone cannot predict, because of species being more or less plastic in diet. Optimal foraging theory suggests that dietary choices typically follow energy or time maximization strategies (Rorberg 1977; Carbone et al. 1999; Jørkov et al. 2007). Trends over time in Canid dental morphology towards hypercarnivory (i.e. increasing the ratio of shearing to grinding facets along the molar tooth row) have primarily decreased processing times (i.e. mastication) and digestibility of flesh taken from already killed prey items, thus increasing overall efficiency (Van Valkenburgh 1991, 1999; Carbone et al. 1999, 2007). However, these morphological changes do not necessarily limit what prey can be consumed. This is because even the most “hypercarnivorous” canids retain some form of a talonid basin on the carnassial and at least one post-carnassial molar, unlike other predator clades which have lost all post carnassial molars (e.g. feliform carnivores). Thus, regardless of molar cusp shape, it is possible that retention of this talonid basin and post-carnassial molar enables greater plasticity.

The observed mismatch between DMTA dietary reconstructions and morphology suggests that behavioral plasticity in diet has been widespread within canids throughout their evolutionary history. DMTA parameters have been well documented to discriminate between hypercarnivory and durophagy in modern and fossil carnivores (Ungar et al. 2010; Schubert et al. 2010; DeSantis et al. 2012a, 2015, 2017b; Donohue et al. 2013; DeSantis and Haupt 2014; DeSantis 2016; Jones and DeSantis 2016; DeSantis and Patterson 2017; Stynder et al. 2018). Although morphological traits have also been used as predictors of hypercarnivorous and durophagus dietary strategies in canids, majority of categorization has been done within aggregated principle component space (Raia 2004;

Van Valkenburgh et al. 2004; Tseng et al. 2011; Silvestro et al. 2015; Balisi et al. 2018). While multidimensional combinations morphological features have been shown to represent a morphological dietary continuum, the morphological features are highly correlated. Thus it is likely that the inability of these combined features to discriminate within PCA space, as well as the scale of variability inherent in behavioral versus morphological features, accounts for the mismatch between DMTA and morphology.

Counter to expectation, species longevity was greatest in species with higher dietary specialization. Prevailing wisdom suggests specialization is linked to increased extinction risk, as a reliance on limited prey diversity increases susceptibility of predators to extirpation during high intensity perturbations or extreme fluctuations in prey availability (Balmford 1996; Boyles and Storm 2007; Tinker et al. 2008; Colles et al. 2009; Rosenblatt et al. 2015). However, when environmental conditions are stable, dietary specialization is associated with numerous fitness advantages which could explain why increased dietary breadth (i.e. generalization) is correlated with decreased duration times for fossil canids. One example of the potential advantages of dietary specialization is reduced interspecific competition. Previous work has demonstrated that extinctions in fossil canids tended to coincide with radiations of sister clades and were not tied to climatic events (Silvestro et al. 2015; Slater 2015; de Moura Bubadué et al. 2016; Pardi and Smith 2016). Dietary specialization could help buffer against clade competition from radiating generalists given that specialists frequently develop behavioral adaptations which can lower handling times and increase net energy gain (Carbone et al. 1999, 2007; Egan and Funk 2006; Devictor et al. 2010; Hartstone-Rose and Stynder 2013; Chubaty et al. 2014). Increasing efficiency of energy gain in this manner can also permit exploitation of novel resources otherwise too costly to peruse (Carbone et al. 1999; Rosenblatt et al. 2015). Additionally, competition between species will often result in resource partitioning, which could manifest as reduced dietary breadth within two competing species if the resource pool is unchanged and niche overlap decreases (Polis 1984; Azevedo et al. 2006; Casula et al. 2006; Pardi and Smith 2016; Otis et al. 2017; Sivy et al. 2018). Alternatively, interspecific competition might manifest in utilization of a novel set of resources to reduce niche overlap without concomitant changes in overall niche breadth.

Our evidence does not provide support for specialist taxa utilizing a novel set of resources to persist, as would be expected under the hypothesis of intense clade-competition within canids. Importantly though, our data does not reject the hypothesis that specialization provides a mechanism to mitigate interspecific competition (Appendix C Figure C11). DMTA parameters quantify textural properties of foods, therefore we are unable to discern species using different yet similarly textured resources. Previous evidence also suggests that changes or loss to interspecific interactions can alter dietary plasticity in unforeseen ways. For example, evidence demonstrates that following the extirpation of gray wolfs from western North America, coyotes dramatically reduced their dietary breath despite being freed from intense top-down competition from an apex predator (Tanis et al. *in prep*).

Although the macroevolutionary ratchet in canids has been previously linked to the metabolic costs of increased body mass (Gittleman and Harvey 1982; Van Valkenburgh 1989; Alroy 1998; Carbone et al. 1999, 2007; Palmqvist et al. 2002; Van Valkenburgh et al. 2004), recent work has shown that increased body mass has not been a leading factor in extinction risk among mammals throughout the past 65 million years of mammalian evolutionary history (Tomiya 2013; Smith et al. 2019). Large body mass tends to lower metabolic costs associated with maintaining homeostasis (Gittleman and Harvey 1982; Alroy 1998; Hatton et al. 2015). While large predators receive diminishing returns hunting smaller bodied prey (Carbone et al. 1999, 2007), bigger bodies can also buoy fat reserves allowing for increased time between meals (Millar and Hickling 1990). Recent paleoecological studies have calculated that higher rates of diversity coupled with larger mean body mass of herbivores throughout the Tertiary would create higher rates of carrion as a resource subsidy to fossil carnivores (Blumenschine 1989; Wilson and Wolkovich 2011; McHorse et al. 2012; Kane et al. 2017), thus further reducing the metabolic demands of larger body mass. Finally, body mass in modern canids is also partially correlated with social group hunting behavior. Pack dynamics enable canids to successfully hunt substantially larger prey and results in an overall net increase in energy gain (Atwood and Gese 2008; Arjo and Pletscher 2011; Zimmermann et al. 2015; Benson et al. 2017; Horne et al. 2019). Despite numerous but poorly supported hypotheses, social systems in extinct canid species have not been rigorously identified (Van Valkenburgh 1999; Valkenburgh et al. 2003; Andersson 2005; McHorse et al. 2012; Damasceno et al. 2013; Martín-Serra et al. 2016). However, given that pack hunting has evolved independently multiple times across the vertebrates (Packer and Ruttan 1988), it is highly likely that some large-bodied fossil canids were social hunters and thereby able to readily offset the metabolic costs of large size.

Comparing these findings to modern taxa suggests that extant North American canids have relatively specialized diets compared to their fossil ancestors. This would indicate a low natural extinction risk in modern canids. However, it is likely that human impacts have dramatically altered the ecological and evolutionary trajectory of canids, with effects escalating since the end of the Pleistocene. Specifically, we find additional support for the significant role of humans in driving the megafaunal extinctions at the end Pleistocene in the dramatic reduction of dire wolf duration compared with this species' level of dietary specialization. Since then, the evolution of the Canine subfamily through Holocene has primarily occurred amid the impoverished faunal diversity more characteristic of the Anthropocene. Although modern canid durations are censored (i.e. species are not yet extinct), our data show evidence that while the direction of the relationship between dietary specialization and duration is the same as recovered in the fossil record, the strength of this relationship is weaker (slope of the regression is less). This is possibly a manifestation of the diversity of modern canids being nearly 4x lower today than during the Oligocene.

Conclusion:

Despite the prevailing hypothesis that increased dietary specialization through time has driven the macroevolutionary ratchet in canids, we observed a positive correlation between specialization and lineage duration. Furthermore, specialization does not correlate with traditionally-used dietary categories inferred from morphology. Thus we propose that specialization in diet alone did not drive iterative extinctions in canids. Instead, we hypothesize that dietary specialization offers selective advantages during times of fluctuating prey abundance that facilitated the coexistence of a diverse canid assemblage in the Tertiary.

Table 3: Summary of sampled Canidae dietary reconstructions quantified via dental microwear texture analysis compared with traditional morphological traits and classifications from the literature.

Subfamily	**Species**	**n**	**Dental Microwear Attributes**				**Morphological Traits**				
			Asfc	***epLsar***	***Tfv***	**SEV**	**RBL**	**RUGA**	**JDJL**	**Log Mass**	**Dietary classification**
Hespercyoninae	*Philotrox condoni†*	4	3.61	0.00372	11670.33	37419.73	0.719	0.814	0.202	1.058	hyper
	Mesocyon coryphaeus†	6	3.01	0.00288	9878.56	39843.74	0.711	0.892	0.175	0.989	hyper
	Paraenhydrocyon josephi†	5	2.34	0.00224	9608.91	23434.47	0.708	0.905	0.158	0.892	hyper
Borophaginae	*Rhizocyon oregonensis†*	11	2.57	0.00285	12619.87	19393.55	0.658	1.033	0.16	0.519	hypo
	Phlaocyon latidens†	23	2.84	0.00242	13130.28	20086.84	0.652	1.081	0.164	0.446	hypo
	Cynarctodies lemur†	14	3.16	0.00252	12097.93	28241.96	0.639	1.063	0.167	0.36	hypo
	Paratomarctus temerarius	4	4.81	0.00167	12865.09	43914.51	0.704	0.957	0.172	1.097	meso
	Borophagous littoralis	10	2.40	0.00209	8323.92	16118.88	0.67	0.863	0.195	1.37	hyper
Caninae	*Canis dirus¿*	18	3.46	0.00234	14352.39	26381.18	0.69	0.772	0.18	1.553	hyper
	*Canis latrans**	123	2.42	0.00362	12758.09	8213.78	0.643	0.847	0.14	1.146	meso
	*Canis lupus**	62	2.47	0.002502	11977.08	15779.01	0.646	0.862	0.166	1.712	hyper
	*Urocyon cinereoargenteus**	18	2.71	0.00246	12043.23	20513.25	0.613	1.119	0.121	0.653	hypo
	*Vulpes vulpes**	40	3.35	0.00322	12385.93	18236.95	0.629	0.883	0.133	0.778	meso

† (occurs within John Day National Fossil Beds assemblage), ¿ (DMTA data taken from DeSantis et al. 2015), *(extant species), n (number of specimens sampled for DMTA), *Asfc* (area-scale fractal complexity), *epLsar* (anisotropy), *Tfv* (textural fill volume), SEV (standard ellipsoid volume), RBL (relative blade length), RUGA (relative upper grinding area), JDJL (jaw depth to jaw length ratio).

Table 4: Results of linear models testing the relationship between species duration and parameters related to dietary breadth reconstruction. Model performance was assessed via differences in Akaike's Information criterion corrected for small sample sizes (ΔAICc) and adjusted R^2 (R^2_{Adj}).

Model Covariates	**ΔAICc**	**R^2_{Adj}**
SEV	0.00	0.539
RBL	5.26	0.110
RUGA	7.16	-0.129
JDJL	7.33	-0.153
Log Body Mass	7.38	-0.161
SEV and JDJL	8.24	0.517
SEV and Log Body Mass	8.47	0.503
SEV and RUGA	9.27	0.451
SEV and RBL	9.30	0.449
RBL and RUGA	13.03	0.122
RBL and JDJL	13.34	0.087
RUGA and JDL	15.10	-0.138

SEV (standard ellipsoid volume), RBL (relative blade length), RUGA (relative upper grinding area), JDJL (jaw depth to jaw length ratio)

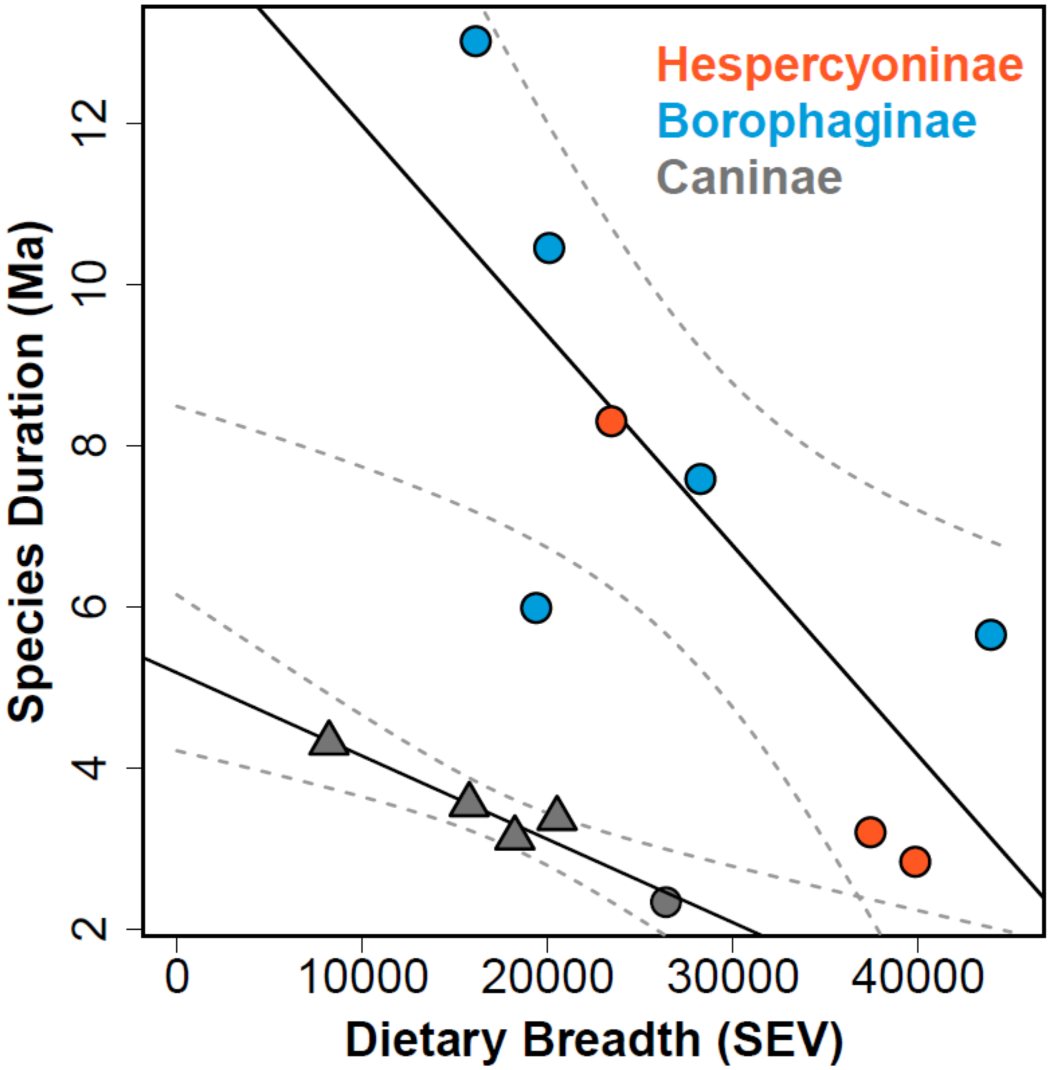


Figure 13: Negative relationship between lineage duration (millions of years) and increasing dietary breadth (Standard Ellipsoid Volume) for fossil Canidae (circles). Gray lines depict 10,000 bootstrapped regressions. Color of points corresponds with subfamily designation. Extant canids (triangles), shown for comparison, cluster together as species are relatively nascent compared with average full linage durations. Regardless of their truncated durations, however, they too show the negative relationship between lineage duration and increasing dietary niche breadth.

Chapter 5 - Directions of Future Research

Introduction

In the preceding chapters, I have shown that reconstruction and quantification of dietary breadth is a highly informative lens for understanding broad ecological and evolutionary patterns and processes. Studies which span modern, historical, and paleontological time scales are essential to better comprehend shifting baselines and mitigate perturbations to biological systems. These themes are evident as I demonstrated how dietary breadth responded to changes in historical community composition and influenced patterns of extinction within North American Canids. These studies offer insight relevant for both fundamental and applied objectives, particularly as the accelerating changes of the Anthropocene create novel systems. However, descriptions of dietary breadth are inherently relative terms, dependent on comparisons to other populations and species. Therefore, continued work needs to be done to understand dietary breadth as it relates to aggregate ecosystem properties such as community stability and ecosystem functionality. This final chapter will detail several avenues of future research stemming from concepts and systems highlighted throughout my dissertation. While some of these hypotheses have been addressed briefly in their respective chapters, here I provide more detail along with speculative projections for the types of study systems and datasets necessary for forthcoming projects.

Continuing down the trophic cascade of North American Canids

In chapter 3 of this dissertation, I demonstrated that the extirpation of an apex predator can modify the dietary niche breadth of released mesopredators. However, the true concern over trophic cascades like mesopredator release is that unanticipated shifts in interaction strengths chain occur that could potentially result in ecological hysteresis (Estes et al. 1998; Allesina and Pascual 2008; Aguilera and Navarrete 2012; Yeakel et al. 2013; Toscano and Griffen 2014; Yeakel et al. 2014). For the model system of mesopredator release in canids, this is often measured as a multiple trophic level cascade from wolves through coyotes, foxes, and small vertebrate prey (Levi and Wilmers 2012; Newsome and Ripple 2015). In this dissertation, I quantified only the first link in the cascade, measuring changes to coyote dietary breadth following wolf extirpation. While this study serves as proof of concept and offers insight into the modified ecologies of coyotes, the de facto apex predator remaining in the system, it is unclear the degree of alterations to foraging behavior in the remainder of the trophic network. In subsequent studies I plan to address dietary changes within foxes including red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) via dental microwear and stable isotope analysis. Following extirpation of wolves and increases in coyotes, fox populations decline precipitously (Levi and Wilmers 2012; Kays et al. 2015; Newsome and Ripple 2015; Rota et al. 2016; Molsher et al. 2017). Thus I hypothesize that changes to fox dietary breadth would be opposite that of coyotes and expand in regions where wolves are absent.

Quantification of species interactions via dietary breadth

Many of the chapters in this dissertation elude to how dietary breadth alters the interactions between species. Both interspecific and intraspecific interactions constitute the theoretical foundation for quantifying ecological networks, modeling rules of community assembly, and predicting responses to future perturbations (Wootton and Emmerson 2005; Bolnick et al. 2007; Ives and Carpenter 2007; Allesina and Pascual

2008; Allesina and Tang 2012; Mougi and Kondoh 2012; Yeakel et al. 2014). Although calculating trophic interaction strengths is paramount for quantitative ecology, methods to derive these parameters are often challenging or hinge upon untested assumptions (e.g. population abundances near equilibrium). These problems can be insurmountable when dealing with historical or paleontological systems in which evidence such as per capita attack rate is not attainable. However, robust measures of dietary plasticity have been used to derive consumer-resource interaction matrices, necessary for calculating a trophic link-strength between and within species (Novak 2010; Novak and Wootton 2010; Yeakel et al. 2012, 2013). Specifically, measures of isotopic breadth and morphological characters have been combined with principles of allometric scaling and metabolic theory to calculate distributions of potential interaction strengths within historical and paleontological systems (Yodzis and Innes 1992; Woodward et al. 2005; Morales-Castilla et al. 2015). Given the possibilities to leverage quantitative measures of species interactions into models of aggregate ecosystem properties such as community stability and ecosystem functionality, a logical extension of the work within this dissertation is to derive and interpret interaction strengths.

Interaction strengths and ecosystem function following species invasion

One system for which modeled interaction strengths derived from dietary niche breadth would produce significant understanding is alteration to ecosystem functions alongside faunal turnover from biological invasions. Given the unprecedented rates of faunal extinctions and introductions of non-native species throughout the globe, many ecosystems are facing restructuring of community composition (De Vos et al. 2015; Alstad et al. 2016; Lewthwaite et al. 2017; Seebens et al. 2017). Understanding the significance of these changes to ecosystem function is paramount for predicting and mitigating ecological collapse. Invasion often triggers cascading extinctions, ecological hysteresis, or total collapse, particularly if invaders exhibit ecologically novel behaviors (Duffy 2003; Gurevitch and Padilla 2004; Estes et al. 2011). However, when introduced species can partially replicate native species interactions within a community, it is possible that ecosystem functions remain relatively stable (Drenovsky et al. 2012; Huijbers et al. 2016). Understanding the threshold of niche differentiation that leads to ecological tipping points or stasis is critical both for protecting core habitats and planning for species re-introductions.

As established in my dissertation, leveraging historical and modern museum specimens of mammalian mesopredators to reconstruct dietary breadth can enable deeper insight into the macroecology of species invasion and ecosystem function. Small bodied mesopredators are among the most globally destructive invasive species (Lariviere and Pasitschniak-Arts 1996; Lowe et al. 2000; Doherty et al. 2015). Additionally, small mesopredators offer ecosystem services highly beneficial to humans, such as impacting tick-borne diseases via control of small mammal host vectors (Levi et al. 2012). Thus a future direction of my research will be to leverage dietary breadth to model interaction strengths in mammalian mesocarnivores experiencing species turnover due to invasions. Specifically, modeling mesopredator networks under viable alternative foraging strategies (i.e. generalist vs specialist and hyper- vs hypocarnivory) can be used to assess correlations between foraging behavior, interaction strengths, and community stability dynamics. These data can then be fed into ecological network analysis to model changes in community structure and function that have unfolded as non-native mesopredators have encroached on and replaced native species.

Dental microwear and interaction strengths

Dental microwear has become a highly used technique for classifying diets within extinct and extant species, lending to tremendous gains in reconstructing paleoenvironments and behaviors. However, this technique has thus far not been extrapolated to quantify the relationship of interactions between populations or species. In chapter 3 of this dissertation, I focused on the well-studied interspecific interactions of the mesopredator release hypothesis. This chapter used a 'before-and-after removal' style approach to demonstrate that extirpation of wolves from the northwestern North America resulted in changes to coyote dietary breadth, with microwear evidence suggesting a loss of scavenged resources hypothesized to historically come from wolf kills. However, while this hypothesis is supported by observational data from small-scale case studies, currently it is not possible to completely ascertain the identity of released coyote prey items or quantify a true link strength between coyotes and wolves.

While dental microwear accurately reflects the textural properties of food items, a variety of dietary items possess similar textural properties. For example, dental microwear indicative of a highly durophagous diet could be reflecting bone consumption via scavenging, bone consumption during a predation event, or consumption of hard seed cases within fruits. Understanding the biology of species and their modern analogs can help account for some of this ambiguity but ideally modeling of interaction strengths should be derived from more detailed categorization of prey identities. Experimental validation of specific prey items and greater accounting of sources of error within microwear data could enable more finely-binned dental microwear categorization. Fractal properties of dietary items have previously been assessed via machines simulating mastication (e.g. BITE Master)(Meullenet and Gandhapuneni 2006; Hua et al. 2015). Comprehensive tests with machines and with captive organisms could be used to discriminate categories of prey items, such as insects versus vertebrate flesh consumption. Similar studies have already been conducted on primates with success (Scott et al. 2012; Hua et al. 2015). Results from this line of work in carnivores could result in some form of a textural mixing-model for dental microwear, which could enable robust measures of interaction strength and enable the quantification and inference of larger ecological processes.

Experimental studies with highly controlled settings remain an ambitious and long-term goal. However similar to studies deriving link strength from isotopic analyses, combing microwear attributes with morphology and metabolic theory could permit quantification of competition and other trophic interactions. For example, in the paleocommunity of canids in the John Day Basin multiple canid species coexisted, with highly overlapping dietary niche breadths (Appendix C Figure C11). Competition between sister taxa has been hypothesized to have driven extinctions within fossil Canidae and other carnivorans (Silvestro et al. 2015). Unfortunately, due to the challenges highlighted above, is not possible to parse out the use of specific dietary items to quantify competition coefficients. Although, by combining measures of dietary breadth with biological expectations founded in metabolic theory it might be possible to tease apart a probability of textural diet space that is unique to a species (see Appendix C). Body mass can undoubtably be used to help infer competition coefficients between fossil canids of the John Day Basin. Extinct canid body masses span several orders of magnitude (Alroy 1998; Palmqvist et al. 2002; Carbone et al. 2007). Thus metabolic needs of some species will markedly differ (Carbone et al. 1999; Carbone and Gittleman 2002). Capitalizing upon this data would enable identification of unique combinations of textural dietary niche space scaled according to trophic positions and modeled prey use to derive link strength distributions. Another possible trait which could be highly informative for discriminating more nuanced dietary reconstructions is bite force. Evidence from chapter 2 demonstrated that changes in bite force along the tooth row of canids does not account for any variation in dental microwear textures (Tanis et al. 2018). This reinforces that prey items leave comparable microwear regardless of force applied during mastication. As such, it can be postulated that maximum bite forces for species could be used as a threshold for teasing apart unique dietary composition of dental microwear indicative of high durophagy. Bite force and body mass are just two functional traits founded in metabolic theory which could be incorporated into dietary reconstructions from dental microwear. Finding appropriate combinations of traits should provide an appropriate scaling factor to constrain areas of true dietary overlap, yielding more accurate estimations of competition coefficients.

Dietary breadth and diversity

The paleocommunity of the John Day Basin in central Oregon, introduced in chapter 4, is a fascinating case study for testing a wide variety of macroevolutionary and macroecological patterns. One lingering question from this system stems from the staggering diversity of canids which co-occur in the fossil assemblages. During the Arikareean (39.7 to 13.6 Mya), over 10 species of canids were present in the ecosystem, more than double the highest diversity of canids observed in any ecosystem today (Wang et al. 1999; Tedford et al. 2009; Orcutt and Hopkins 2011; McHorse et al. 2012; Liow and Finarelli 2014). This mirrors the high canid diversity across all of North America, which peaked at 25 species during the late Oligocene (~30 to 28Mya). Understanding patterns of species diversity has been a critical theme of ecological research and considered one of the most fundamental questions in biology (Pennisi 2005; Sutherland et al. 2013). However, the drivers of global patterns of biodiversity remain highly controversial with a vast array of proposed hypotheses (Gaston 2000; Willis and Whittaker 2002; Adler et al. 2007; Fritz et al. 2013; Zuloaga and Kerr 2017). One hypothesis for the establishment of high species diversity is that increased resource partitioning and specialization enables greater numbers of species within a community. Preliminary data from chapter 4 contradicts that hypotheses in that modern canids have similarly generalized diets to fossil canids in more diverse communities. An alternative explanation for the high diversity of canids observed during the Arikareean is that a lack of other carnivore taxa (e.g. Procyonidae, Mustelidae, Herpestidae) enabled similar ecological roles to be filled by canids.

In subsequent studies, I plan to explore the relationship between biodiversity and dietary specialization by quantifying the dietary breadth from entire modern predator communities spanning a gradient of high to low alpha diversity. Given my current datasets from this dissertation and those available from published studies, it would be logical to focus on predator communities in the arctic of North America, the Pacific Northwest, and southern Africa. Each of these systems has similar canid diversity (2-4 species) but varies greatly in the number of additional carnivorous taxa. Additionally, many of the large carnivores have previously been the focus of stable isotope and dental microwear studies (Schubert et al. 2010; Stynder et al. 2011; DeSantis et al. 2012a, 2015, 2017b; Donohue et al. 2013; DeSantis and Patterson 2017). Thus I would prioritize small and medium sized taxa, particularly from families outside of Canidae, Felidae, Hyaenidae, and Ursidae. This project would tease apart how dietary niche packing versus partitioning alters with the diversity of the predator community. For instance, the frequency and relative importance of scavenging is hypothesized to increase with the prevalence of large bodied predators abandoning kills (Blumenschine 1989; DeVault et al. 2003; Wilson and Wolkovich 2011; Huijbers et al. 2016; Kane et al. 2017). Results from this line of research should provide clarity on how community diversity is established and maintained. Additionally, comparing modern and deep-time communities can offer additional insight into how human-induced megafaunal extinctions of the end Pleistocene have shifted aggregate community properties.

Conclusion

Quantification of dietary niche breadth can enable informative insight into fundamental and applied questions of macroecology and macroevolution. This dissertation made strides demonstrating that dental microwear texture analysis and stable isotope analysis are viable methods for answering these questions in the dynamic and tractable system of canids. The future research directions highlighted above outline a wide-ranging research agenda delving into the nuances of mammalian mesopredator macroecology and evolution via dietary breadth quantification. I have already begun developing aspects of each of these projects, which will likely form the framework of my career as a scientist. However, like the museum specimens from where the data originated, much of the value of this dissertation will stem from concepts and theories yet to be identified. This dissertation provides a foundation on which future researchers can build to advance understanding of biological systems in the past and into the future.

Bibliography

ACKERLY, D. D. ET AL. 2010. The geography of climate change: Implications for conservation biogeography. Diversity and Distributions 16:476–487.

ADLER, P. B., J. HILLERISLAMBERS, AND J. M. LEVINE. 2007. A niche for neutrality. Ecology Letters 10:95–104.

AGUILERA, M. A., AND S. A. NAVARRETE. 2012. Functional identity and functional structure change through succession in a rocky intertidal marine herbivore assemblage. Ecology 93:75–89.

ALICEA, B., AND R. GORDON. 2014. Toy models for macroevolutionary patterns and trends. BioSystems 122:25–37.

ALLESINA, S., AND M. PASCUAL. 2008. Network structure, predator - Prey modules, and stability in large food webs. Theoretical Ecology 1:44–64.

ALLESINA, S., AND S. TANG. 2012. Stability criteria for complex ecosystems. Nature.

ALROY, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280:731–734.

ALROY, J. 2006. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26:707–733.

ALSTAD, A. O. ET AL. 2016. The pace of plant community change is accelerating in remnant prairies. Science Advances 2:e1500975.

ANDERSON, D. R., AND K. P. BURNHAM. 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. The Journal of Wildlife Management 66:912–918.

ANDERSON, D. R., K. P. BURNHAM, AND G. C. WHITE. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. Journal of Applied Statistics 25:263–282.

ANDERSON, P. S. L., AND M. LABARBERA. 2008. Functional consequences of tooth design: effects of blade shape on energetics of cutting. Journal of Experimental Biology 211:3619–3626.

ANDERSSON, K. 2005. Were There Pack-Hunting Canids in the Tertiary, and How Can We Know? Paleobiology 31:56–72.

ARIAS-DEL RAZO, I., L. HERNÁNDEZ, J. W. LAUNDRÉ, AND O. MYERS. 2011. Do predator and prey foraging activity patterns match? A study of coyotes (Canis latrans), and lagomorphs (Lepus californicus and Sylvilagus audobonii). Journal of Arid Environments 75:112–118.

ARJO, W. M. ;, D. H. PLETSCHER, AND R. R. REAM. 2002. Dietrary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy 83:754–766.

ARJO, W. M., AND D. H. PLETSCHER. 2011. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Canadian Journal of Zoology 77:1919–1927.

ARMAN, S. D., P. S. UNGAR, C. A. BROWN, L. R. G. DESANTIS, C. SCHMIDT, AND G. J. PRIDEAUX. 2016. Minimizing inter-microscope variability in dental microwear texture analysis. Surface Topography: Metrology and Properties.

ASAHARA, M. 2013. Unique inhibitory cascade pattern of molars in canids contributing to their potential to evolutionary plasticity of diet. Ecology and Evolution 3:278–285.

ASAHARA, M. 2016. The origin of the lower fourth molar in canids, inferred by individual variation. PeerJ 4:e2689.

ATWOOD, T. C., AND E. M. GESE. 2008. Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. Animal Behaviour 75:753–762.

AZEVEDO, F. C. C., V. LESTER, W. GORSUCH, S. LARIVIÈRE, A. J. WIRSING, AND D. L. MURRAY. 2006. Dietary breadth and overlap among five sympatric prairie carnivores. Journal of Zoology 269:127–135.

BALISI, M., C. CASEY, AND B. VAN VALKENBURGH. 2018. Dietary specialization is linked to reduced species durations in North American fossil canids. Royal Society Open Science 5:171861.

BALMFORD, A. 1996. Extinction filters and current resilience: The significance of past selection pressures for conservation biology. Trends in Ecology and Evolution 11:193–196.

BEARHOP, S., C. E. ADAMS, S. WALDRON, R. A. FULLER, AND H. MACLEOD. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007–1012.

BEEVER, E. A. ET AL. 2017. Behavioral flexibility as a mechanism for coping with climate change. Frontiers in Ecology and the Environment 15:299–308.

BEHRENSMEYER, A. K., D. E. DECHANT BOAZ, AND A. P. HILL. 1980. The recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. Pp. 72–92 in Fossils in the making: Vertebrate taphonomy and paleoecology. The University of Chicago Press.

BEKOFF, M. 1977. Canis latrans. Mammalian Species 79:1–9.

BELL, T., W. E. NEILL, AND D. SCHLUTER. 2003. The effect of temporal scale on the outcome of trophic cascade experiments. Oecologia 134:578–586.

BEN-DAVID, M., AND E. A. FLAHERTY. 2012. Stable isotopes in mammalian research: a beginner's guide. Journal of Mammalogy 32:312–328.

BENSON, J. F., K. M. LOVELESS, L. Y. RUTLEDGE, AND B. R. PATTERSON. 2017. Ungulate predation and ecological roles of wolves and coyotes in eastern North America. Ecological Applications 27:718–733.

BESCHTA, R. L., AND W. J. RIPPLE. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

BLUMENSCHINE, R. J. 1989. A landscape taphonomic model of the scale of prehistoric scavenging opportunities. Journal of Human Evolution 18:345–371.

BOLNICK, D. I. ET AL. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

BOLNICK, D. I., R. SVANBACK, M. S. ARAUJO, AND L. PERSSON. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences 104:10075–10079.

BONTER, D. N., B. ZUCKERBERG, C. W. SEDGWICK, AND W. M. HOCHACHKA. 2013. Daily foraging patterns in free-living birds: Exploring the predation-starvation trade-off. Proceedings of the Royal Society B: Biological Sciences 280:20123087.

BOYLES, J. G., AND J. J. STORM. 2007. The perils of picky eating: Dietary breadth is related to extinction risk in insectivorous bats. PLoS ONE 2:e672.

BRADLEY, E. H. ET AL. 2015. Effects of Wolf removal on livestock depredation recurrence and Wolf recovery in Montana, Idaho, and Wyoming. Journal of Wildlife Management 79:1337–1346.

BREWER, S., S. T. JACKSON, AND J. W. WILLIAMS. 2012. Paleoecoinformatics: Applying geohistorical data to ecological questions. Trends in Ecology and Evolution 27:104–112.

CALANDRA, I., AND G. MERCERON. 2016. Dental microwear texture analysis in mammalian ecology. Mammal Review 46:215–228.

CANTALAPIEDRA, J. L., J. L. PRADO, M. HERNÁNDEZ FERNÁNDEZ, AND M. T. ALBERDI. 2017. Decoupled ecomorphological evolution and diversification in Neogene-Quaternary horses. Science.

CAPORALE, S. S., AND P. S. UNGAR. 2016. Rodent incisor microwear as a proxy for ecological reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 446:225–233.

CARBONE, C., AND J. L. GITTLEMAN. 2002. A common rule for the scaling of carnivore density. Science.

CARBONE, C., G. M. MACE, S. C. ROBERTS, AND D. W. MACDONALD. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature.

CARBONE, C., A. TEACHER, AND J. M. ROWCLIFFE. 2007. The costs of carnivory. PLoS Biology.

CARREIRA, B. M., P. SEGURADO, A. LAURILA, AND R. REBELO. 2017. Can heat waves change the trophic role of the world’s most invasive crayfish? Diet shifts in Procambarus clarkii. PLoS ONE 12:1–15.

CARSTENS, B. C., AND C. L. RICHARDS. 2007. Integrating Coalescent and Ecological Niche Modeling in Comparative Phylogeography.

CASULA, P., A. WILBY, AND M. B. THOMAS. 2006. Understanding biodiversity effects on prey in multi-enemy systems. *Ecology Letters*. .

CATLING, P. C., AND R. J. BURT. 1995. Why are red foxes absent from some eucalypt forests in eastern New South Wales? Wildlife Research 22:535–546.

CERLING, T. E. ET AL. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158.

CHAVE, J. 2013. The problem of pattern and scale in ecology: What have we learned in 20 years? Ecology Letters 16:4–16.

CHRISTIANSEN, P., AND J. S. ADOLFSSEN. 2005. Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora). Journal of Zoology.

CHRISTIANSEN, P., AND S. WROE. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. Ecology 88:347–58.

CHUBATY, A. M. ET AL. 2014. On the evolution of omnivory in a community context. Ecology and Evolution.

COLLES, A., L. H. LIOW, AND A. PRINZING. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. Ecology Letters 12:849–863.

COLMAN, N. J., C. E. GORDON, M. S. CROWTHER, AND M. LETNIC. 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. Proceedings of the Royal Society B: Biological Sciences 281.

CONOVER, M. R. 1999. Effect of Preventive Coyote Hunting on Sheep Losses to Coyote Predation. The Journal of Wildlife Management 63:606–612.

COPE, E. D. 2002. On the Extinct Dogs of North America. The American Naturalist 17:235–249.

COVE, M. V. ET AL. 2012. Use of Camera Traps to Examine the Mesopredator Release Hypothesis in a Fragmented Midwestern Landscape. The American Midland Naturalist.

CRAINE, J. M. ET AL. 2015. Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. Springer International Publishing. *Plant and Soil*. .

CRAWFORD, J. A. 2008. Survival, Movements and Habitat Selection of Pygmy Rabbits on the Great Basin of Southeastern Oregon and Northwestern Nevada.

CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

CUCHEROUSSET, J., AND S. VILLÉGER. 2015. Quantifying the multiple facets of isotopic diversity: New metrics for stable isotope ecology. Ecological Indicators.

CUPPLES, J. B., M. S. CROWTHER, G. STORY, AND M. LETNIC. 2011. Dietary overlap and prey selectivity among sympatric carnivores: Could dingoes suppress foxes through competition for prey? Journal of Mammalogy 92:590–600.

DALY, C. ET AL. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology.

DAMASCENO, E. M., E. HINGST-ZAHER, AND D. ASTÚA. 2013. Bite force and encephalization in the Canidae (Mammalia: Carnivora). Journal of Zoology.

DAUPHIN, Y., AND T. C. WILLIAMS. 2007. The chemical compositions of dentine and enamel from recent reptile and mammal teeth—variability in the diagenetic changes of fossil teeth. CrystEngComm 9:1252–1261.

DECESARE, N. J. ET AL. 2018. Wolf-livestock conflict and the effects of wolf management. Journal of Wildlife Management 82:711–722.

DENWOOD, M. J. 2016. runjags: An R Package Providing Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS. Journal of Statistical Software 71:1–25.

DESANTIS, L. R. G. ET AL. 2013. Direct Comparisons of 2D and 3D Dental Microwear Proxies in Extant Herbivorous and Carnivorous Mammals. PLoS ONE.

DESANTIS, L. R. G. 2016. Dental microwear textures: Reconstructing diets of fossil mammals. Surface Topography: Metrology and Properties 4:023002.

DESANTIS, L. R. G., R. S. FERANEC, AND B. J. MACFADDEN. 2009. Effects of Global Warming on Ancient Mammalian Communities and Their Environments. PLoS ONE 4:e5750.

DESANTIS, L. R. G., J. H. FIELD, S. WROE, AND J. R. DODSON. 2017a. Dietary responses of Sahul (Pleistocene Australia-New Guinea) megafauna to climate and environmental change. Paleobiology 43:181–195.

DESANTIS, L. R. G., AND R. J. HAUPT. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. Biology

Letters 10:20140203.

DeSantis, L. R. G., and B. D. Patterson. 2017. Dietary behaviour of man-eating lions as revealed by dental microwear textures. Scientific Reports 7.

DeSantis, L. R. G., B. W. Schubert, E. Schmitt-Linville, P. S. Ungar, S. L. Donohue, and R. J. Haupt. 2015. Dental Microwear Textures of Carnivorans from the La Brea Tar Pits, California, and Potential Extinction Implications. Science Series 42:37–52.

DeSantis, L. R. G., B. W. Schubert, J. R. Scott, and P. S. Ungar. 2012a. Implications of Diet for the Extinction of Saber-Toothed Cats and American Lions. PLoS ONE.

DeSantis, L. R. G., R. A. Tracy, C. S. Koontz, J. C. Roseberry, and M. C. Velasco. 2012b. Mammalian niche conservation through deep time. PLoS ONE.

DeSantis, L. R. G., Z. J. Tseng, J. Liu, A. Hurst, B. W. Schubert, and Q. Jiangzuo. 2017b. Assessing niche conservatism using a multiproxy approach: Dietary ecology of extinct and extant spotted hyenas. Paleobiology 43:286–303.

DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. OIKOS 102:225–234.

Devictor, V. et al. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology*. .

Van Dijk, J. et al. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. Journal of Animal Ecology.

DiMartino, T. J. 2017. Ratchet Mechanisms in Macroevolutionary Processes. University of Colorado, Boulder.

Doherty, T. S., C. R. Dickman, D. G. Nimmo, and E. G. Ritchie. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biological Conservation 190:60–68.

Donohue, S. L., L. R. G. DeSantis, B. W. Schubert, and P. S. Ungar. 2013. Was the giant short-faced bear a hyper-scavenger? A new approach to the dietary study of ursids using dental microwear textures. PloS one.

Drake, A. G., M. Coquerelle, and G. Colombeau. 2015. 3D morphometric analysis of fossil canid skulls contradicts the suggested domestication of dogs during the late Paleolithic. Scientific Reports.

Drenovsky, R. E. et al. 2012. A functional trait perspective on plant invasion. Annals of Botany 110:141–153.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Dunn, O. J. 1964. Multiple Comparisons Using Rank Sums. Technometrics 63:241–252.

Dupuy, G., P. Giraudoux, and P. Delattre. 2009. Numerical and dietary responses of a predator community in a temperate zone of Europe. Ecography.

van Eeden, L. M. et al. 2018. Carnivore conservation needs evidence-based livestock protection. PLoS Biology 16:1–8.

Egan, S. P., and D. J. Funk. 2006. Individual advantages to ecological specialization: Insights on cognitive constraints from three conspecific taxa. Proceedings of the Royal Society B: Biological Sciences 273:843–848.

El-Zaatari, S. 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. International Journal of Osteoarchaeology 20:67–87.

ELTON, C. S. 1927. Animal Ecology. Sidgwick & Jackson, London.

ESTES, J. A. ET AL. 2011. Trophic Downgrading of Planet Earth. Science 333:301–306.

ESTES, J. A., M. T. TINKER, T. M. WILLIAMS, AND D. F. DOAK. 1998. Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems. Science 282:473–476.

FAIRHURST, G. D., A. L. BOND, K. A. HOBSON, AND R. A. RONCONI. 2015. Feather-based measures of stable isotopes and corticosterone reveal a relationship between trophic position and physiology in a pelagic seabird over a 153-year period. Ibis.

FIGUEIRIDO, B., A. MARTÍN-SERRA, Z. J. TSENG, AND C. M. JANIS. 2015. Habitat changes and changing predatory habits in North American fossil canids. Nature Communications.

FOOTE, M., AND D. M. RAUP. 1996. Fossil preservation and the stratigraphic ranges of taxa. Paleobiology 22:121–140.

FOX-DOBBS, K., J. K. BUMP, R. O. PETERSON, D. L. FOX, AND P. L. KOCH. 2007. Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. Canadian Journal of Zoology.

FRITZ, S. A., J. SCHNITZLER, J. T. ERONEN, C. HOF, K. BÖHNING-GAESE, AND C. H. GRAHAM. 2013. Diversity in time and space: Wanted dead and alive. *Trends in Ecology and Evolution*. .

GASTON, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

GEHRT, S. D., AND S. PRANGE. 2007. Interference competition between coyotes and raccoons: A test of the mesopredator release hypothesis. Behavioral Ecology 18:204–214.

GILBERT-NORTON, L. B., T. A. SHAHAN, AND J. A. SHIVIK. 2009. Coyotes (Canis latrans) and the matching law. Behavioural Processes 82:178–183.

GITTLEMAN, J. L., AND P. H. HARVEY. 1982. Carnivore Home-Range Size, Metabolic Needs and Ecology.

GOILLOT, C., C. BLONDEL, AND S. PEIGNÉ. 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) - Implications for the reconstruction of the diet of extinct taxa. Palaeogeography, Palaeoclimatology, Palaeoecology.

GORDON, K. D. 1982. A study of microwear on chimpanzee molars: Implications for dental microwear analysis. Am. J. Phys. Anthropol. 59:195–215.

GOULD, S. J. 1970. Dollo on Dollo's law: Irreversibility and the status of evolutionary laws. Journal of the History of Biology 3:189–212.

GREAVES, W. S. 1985. The generalized carnivore jaw. Zoological Journal of the Linnean Society 85:267–274.

GREEN, J. S., AND J. T. FLINDERS. 1981. Diets of sympatric red foxes and coyotes in southeastern Idaho. Great Basin Naturalist 41:251–254.

GRINE, F. E. 1986. Dental evidence for dietary differences in Australopithecus and Paranthropus: a quantitative analysis of permanent molar microwear. Journal of Human Evolution 15:783–822.

GRINE, F. E., M. SPONHEIMER, P. S. UNGAR, J. LEE-THORP, AND M. F. TEAFORD. 2012.

Dental microwear and stable isotopes inform the paleoecology of extinct hominins. American Journal of Physical Anthropology.

GRINNELL, J. 1917. Field tests and theories concerning distributional control. American Naturalist 51:115–128.

GRUEBER, C. E., S. NAKAGAWA, R. J. LAWS, AND I. G. JAMIESON. 2011. Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*. .

GUREVITCH, J., AND D. K. PADILLA. 2004. Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19:470–474.

HALAJ, AND WISE. 2017. Terrestrial Trophic Cascades: How Much Do They Trickle? The American Naturalist 157:262.

HARTSTONE-ROSE, A., AND D. D. STYNDER. 2013. Hypercarnivory, durophagy or generalised carnivory in the mio-pliocene hyaenids of South Africa? South African Journal of Science.

HATTON, I. A. ET AL. 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. Science.

HAUPT, R. J., L. R. G. DESANTIS, J. L. GREEN, AND P. S. UNGAR. 2013. Dental microwear texture as a proxy for diet in xenarthrans. Journal of Mammalogy 94:856–866.

HODY, J. W., AND R. KAYS. 2018. Mapping the expansion of coyotes (Canis latrans) across North and Central America. ZooKeys 759:81–97.

HOOPER, D. U. ET AL. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature.

HORNE, J. S., D. E. AUSBAND, M. A. HURLEY, J. STRUTHERS, J. E. BERG, AND K. GROTH. 2019. Integrated population model to improve knowledge and management of Idaho wolves. Journal of Wildlife Management 83:32–42.

HUA, L. C., E. T. BRANDT, J. F. MEULLENET, Z. R. ZHOU, AND P. S. UNGAR. 2015. Technical note: An in vitro study of dental microwear formation using the BITE Master II chewing machine. American Journal of Physical Anthropology 158:769–775.

HUIJBERS, C. M. ET AL. 2016. Functional replacement across species pools of vertebrate scavengers separated at a continental scale maintains an ecosystem function. Functional Ecology 30:998–1005.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. American Naturalist 870:145–159.

IKEGAWA, Y., H. EZOE, AND T. NAMBA. 2015. Effects of generalized and specialized adaptive defense by shared prey on intra-guild predation. Journal of Theoretical Biology.

IVES, A. R., AND S. R. CARPENTER. 2007. Stability and diversity of ecosystems. *Science*. .

JACKSON, A. L., R. INGER, A. C. PARNELL, AND S. BEARHOP. 2011. Comparing isotopic nice widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

JANIS, C. M., J. DAMUTH, AND J. M. THEODOR. 2002. Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? Proceedings of the National Academy of Sciences 97:7899–7904.

JERNVALL, J., AND I. THESLEFF. 2012. Tooth shape formation and tooth renewal: evolving with the same signals. Development.

JIANG, T., AND L. R. G. DESANTIS. 2014. Dental microwear texture analysis of the tasmanian devil: assessing variability among teeth. Young Sci. 4:30–32.

JONES, D. B., AND L. R. G. DESANTIS. 2017. Dietary ecology of ungulates from the La Brea tar pits in southern California: A multi-proxy approach. Palaeogeography, Palaeoclimatology, Palaeoecology 466:110–127.

JONES, D., AND L. R. G. DESANTIS. 2016. Dietary ecology of the extinct cave bear: evidence of omnivory as inferred from dental microwear textures. Acta Palaeontol. Pol. 61:735–741.

JØRKOV, M. L. S., J. HEINEMEIER, AND N. LYNNERUP. 2007. Evaluating bone collagen extraction methods for stable isotope analysis in dietary studies. Journal of Archaeological Science.

KANE, A., K. HEALY, T. GUILLERME, G. D. RUXTON, AND A. L. JACKSON. 2017. A recipe for scavenging in vertebrates – the natural history of a behaviour. Ecography.

KAYS, R. ET AL. 2015. Cats are Rare Where Coyotes Roam. Journal of Mammalogy.

KAYS, R. W., M. E. GOMPPER, AND J. C. RAY. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications.

KELLERT, S. R. 1985. Public perceptions of predators, particularly the wolf and coyote. Biological Conservation 31:167–189.

KELLY, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

KHALIL, H., M. PASANEN-MORTENSEN, AND B. ELMHAGEN. 2014. The relationship between wolverine and larger predators, lynx and wolf, in a historical ecosystem context. Oecologia.

KOCH, P. L. 2007. Isotopic studies of the biology of modern and fossil vertebrates. Pp. 99–154 in Stable isotopes in ecology and environmental science.

KOCH, P. L., K. FOX-DOBBS, AND S. D. NEWSOME. 2009. The isotopic ecology of vertebrates and conservation biology. Conservation paleobiology: using the past to manage the future 15:95–112.

LARIVIERE, S., AND M. PASITSCHNIAK-ARTS. 1996. Vulpes vulpes. Mammalian Species 537:1–11.

LEIBOLD, M. A. 1995. The Niche Concept Revisited: Mechanistic Models and Community Context.

LETNIC, M. ET AL. 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? Global Ecology and Biogeography.

LETNIC, M., E. G. RITCHIE, AND C. R. DICKMAN. 2012. Top predators as biodiversity regulators: The dingo Canis lupus dingo as a case study. Biological Reviews.

LEVI, T., A. M. KILPATRICK, M. MANGEL, AND C. C. WILMERS. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences 109:10942–10947.

LEVI, T., AND C. C. WILMERS. 2012. Wolves-coyotes-foxes: a cascade among carnivores. Ecology 93:921–929.

LEVY, S. 2012. Rise of the coyote: The new top dog. Nature.

LEWTHWAITE, J. M. M., D. M. DEBINSKI, AND J. T. KERR. 2017. High community turnover and dispersal limitation relative to rapid climate change. Global Ecology and

Biogeography 26:459–471.

LIOW, L. H., AND J. A. FINARELLI. 2014. A dynamic global equilibrium in carnivoran diversification over 20 million years. Proceedings of the Royal Society B: Biological Sciences.

LOWE, S., M. BROWNE, S. BOUDJELAS, AND M. DE POORTER. 2000. 100 of the World'S Worst Invasive Species. Aliens 12:s1–s12.

LUKASIK, V. M., AND S. M. ALEXANDER. 2012. Spatial and Temporal Variation of Coyote (Canis latrans) Diet in Calgary, Alberta.

LYONS, S. K., AND F. A. SMITH. 2010. Using a macroecological approach to study geographic range, abundance and body size in the fossil record. The Paleontological Society Papers 16:117–141.

LYONS, S. K., F. A. SMITH, AND J. H. BROWN. 2004a. Of mice, mastodons and men: Human-mediated extinctions on four continents. Evolutionary Ecology Research.

LYONS, S. K., F. A. SMITH, P. J. WAGNER, E. P. WHITE, AND J. H. BROWN. 2004b. Was a "hyperdisease" responsible for the late Pleistocene megafaunal extinction? Ecology Letters.

MAAS, M. C. 1991. Enamel structure and microwear: An experimental study of the response of enamel to shearing force. American Journal of Physical Anthropology.

MACAFEE, R. K., AND J. L. GREEN. 2015. The role of bite force in the formation of orthodentine microwear in tree sloths (Mammalia: Xenarthra: Folivora): implications for feeding ecology. Arch. Oral Biol. 60:181–192.

MARSHALL, K. N., N. THOMPSON HOBBS, AND D. J. COOPER. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proceedings of the Royal Society B: Biological Sciences.

MARTÍN-SERRA, A., B. FIGUEIRIDO, AND P. PALMQVIST. 2016. In the Pursuit of the Predatory Behavior of Borophagines (Mammalia, Carnivora, Canidae): Inferences from Forelimb Morphology. Journal of Mammalian Evolution.

MASSOL, F., D. GRAVEL, N. MOUQUET, M. W. CADOTTE, T. FUKAMI, AND M. A. LEIBOLD. 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*. .

MATHEUS, P. E. 1995. Diet and Co-ecology of Pleistocene Short-Faced Bears and Brown Bears in Eastern Beringia. Quaternary Research 44:447–453.

MCHORSE, B. K., J. D. ORCUTT, AND E. B. DAVIS. 2012. The carnivoran fauna of Rancho La Brea: Average or aberrant? Palaeogeography, Palaeoclimatology, Palaeoecology.

MCINERNY, G. J., AND R. S. ETIENNE. 2012a. Pitch the niche - taking responsibility for the concepts we use in ecology and species distribution modelling. Journal of Biogeography 39:2112–2118.

MCINERNY, G. J., AND R. S. ETIENNE. 2012b. Ditch the niche - is the niche a useful concept in ecology or species distribution modelling? Journal of Biogeography 39:2096–2102.

MCKINNEY, M. L. 1997. Extinction vulnerability abd selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics:495–516.

MEACHEN, J. A., A. C. JANOWICZ, J. E. AVERY, AND R. W. SADLEIR. 2014. Ecological changes in coyotes (canis latrans) in response to the ice age megafaunal extinctions. PLoS ONE.

MELORO, C. 2011. Feeding habits of Plio-Pleistocene large carnivore as revealed by the mandibular geometry. Journal of Ve 31:428–446.

MELORO, C., A. HUDSON, AND L. ROOK. 2015. Feeding habits of extant and fossil canids as determined by their skull geometry. Journal of Zoology.

MERCERON, G., G. ESCARGUEL, J. M. ANGIBAULT, AND H. VERHEYDEN-TIXIER. 2010. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5:e9542.

MERKLE, J. A., D. R. STAHLER, AND D. W. SMITH. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56–63.

MEULLENET, J.-F., AND R. K. GANDHAPUNENI. 2006. Development of the BITE Master II and its application to the study of cheese hardness. Physiology & Behavior 89:39–43.

MILLAR, J. S., AND G. J. HICKLING. 1990. Fasting Endurance and the Evolution of Mammalian Body Size. Functional Ecology 4:5–12.

MILLER, B. J., H. J. HARLOW, T. S. HARLOW, D. BIGGINS, AND W. J. RIPPLE. 2012. Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals. Canadian Journal of Zoology 90:70–78.

MILLER, J. H. 2011. Ghosts of Yellowstone: Multi-decadal histories of wildlife populations captured by bones on a modern landscape. PLoS ONE.

MINISTRY, B. C. 2014. Management Plan for the Grey Wolf (Canis lupus) in British Columbia. B.C. Ministry of Forests, Lands and Natural Resource Operations.

MOLL, R. J. ET AL. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems.

MOLSHER, R., A. E. NEWSOME, T. M. NEWSOME, AND C. R. DICKMAN. 2017. Mesopredator management: Effects of red fox control on the abundance, diet and use of space by feral cats. PLoS ONE 12:e0168460.

MORALES-CASTILLA, I., M. G. MATIAS, D. GRAVEL, AND M. B. ARAÚJO. 2015. Inferring biotic interactions from proxies. Trends in Ecology and Evolution 30:347–356.

MORENO, R. S., R. W. KAYS, AND R. SAMUDO JR. 2006. Competitie release in diets of ocelot (Leopardus pardalis) and puma (Puma concolor) after jaguar (Panthera onca) decline. Journal of Mammalogy 87:808–816.

MOUGI, A., AND M. KONDOH. 2012. Diversity of interaction types and ecological community stability. Science.

DE MOURA BUBADUÉ, J., N. CÁCERES, R. DOS SANTOS CARVALHO, AND C. MELORO. 2016. Ecogeographical Variation in Skull Shape of South-American Canids: Abiotic or Biotic Processes? Evolutionary Biology.

MURDOCH, W. W. 1969. Switching in General Predators : Experiments on Predator Specificity and Stability of Prey Populations. Ecological Monographs 39:335–354.

MURRAY, M., A. CEMBROWSKI, A. D. M. LATHAM, V. M. LUKASIK, S. PRUSS, AND C. C. ST CLAIR. 2015. Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. Ecography.

MURRAY, M. J., R. BOWDEN, L. P. TYRRELL, M. L. FOGEL, S. D. NEWSOME, AND M. VIENS. 2013. Vibrissae growth rates and trophic discrimination factors in captive southern sea otters (Enhydra lutris nereis) . Journal of Mammalogy 94:331–338.

MYERS, R. A., J. K. BAUM, T. D. SHEPHERD, S. P. POWERS, AND C. H. PETERSON. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science.

NEWSOME, S. D., H. M. GARBE, E. C. WILSON, AND S. D. GEHRT. 2015. Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115–128.

NEWSOME, S. D., J. D. YEAKEL, P. V. WHEATLEY, AND M. T. TINKER. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. Journal of Mammalogy.

NEWSOME, T. M. ET AL. 2017. Top predators constrain mesopredator distributions. Nature Communications.

NEWSOME, T. M., AND W. J. RIPPLE. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. Journal of Animal Ecology.

NOVAK, M. 2010. Estimating interaction strengths in nature: experimental support for an observational approach.

NOVAK, M., AND J. T. WOOTTON. 2010. Using experimental indices to quantify the strength of species interactions. Oikos.

ORCUTT, J. D., AND S. S. B. HOPKINS. 2011. The canid fauna of the Juntura Formation (late Clarendonian), Oregon. Journal of Vertebrate Paleontology.

OTIS, J. A., D. THORNTON, L. RUTLEDGE, AND D. L. MURRAY. 2017. Ecological niche differentiation across a wolf-coyote hybrid zone in eastern North America. Diversity and Distributions 23:529–539.

PACKER, C., AND L. RUTTAN. 1988. The evolution of cooperative hunting. The American Naturalist 132:159–198.

PAINE, R. T. 1969. A Note on Trophic Complexity and Community Stability. The American Naturalist.

PALMQVIST, P., M. MENDOZA, A. ARRIBAS, AND D. R. GRÖCKE. 2002. Estimating the body mass of Pleistocene canids: discussion of some methodological problems and a new “taxon free” approach. Lethaia.

PAQUET, P. C. 2006. Prey Use Strategies of Sympatric Wolves and Coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 73:337–343.

PARDI, M. I., AND F. A. SMITH. 2016. Biotic responses of canids to the terminal Pleistocene megafauna extinction. Ecography 39:141–151.

PARDO, L. H., AND K. J. NADELHOFFER. 2010. Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. Pp. 221–250 in Isoscapes Understanding movement, pattern, and process on Earth through isotope mapping (J. B. West, G. J. Bowen, T. E. Dawson & K. P. Tu, eds.). Springer.

PASANEN-MORTENSEN, M. ET AL. 2017. The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. Journal of Animal Ecology 86:566–576.

PEERS, M. J. L., M. WEHTJE, D. H. THORNTON, AND D. L. MURRAY. 2014. Prey switching as a means of enhancing persistence in predators at the trailing southern edge. Global Change Biology 20:1126–1135.

PEIGNE, S., C. GOILLOT, M. GERMONPRE, C. BLONDEL, O. BIGNON, AND G. MERCERON. 2009. Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of Ursus spelaeus from Goyet, Belgium. Proceedings of the National Academy of Sciences.

PENNISI, E. 2005. What determines species diversity. Science 309:90.

PETERSON, A. T. 2011. Ecological niche conservatism: A time-structured review of evidence. Journal of Biogeography.

PETERSON, A. T., AND B. S. LIEBERMAN. 2012. Species' Geographic Distributions Through Time: Playing Catch-up with Changing Climates. Evolution: Education and Outreach.

POLIS, G. A. 1984. Age Structure Component of Niche Width and Intraspecific Resource Partitioning: Can Age Groups Function as Ecological Species?

PRIDEAUX, G. J. ET AL. 2009. Extinction implications of a chenopod browse diet for a giant Pleistocene kangaroo. Proceedings of the National Academy of Sciences 106:11646.

PROWSE, T. A. A., C. N. JOHNSON, C. J. A. BRADSHAW, AND B. W. BROOK. 2014. An ecological regime shift resulting from disrupted predator-prey interactions in Holocene Australia. Ecology.

PRUGH, L. R. 2005. Coyote Prey Selection and Community Stability during a Decline in Food Supply. Oikos 110:253–264.

PRUGH, L. R. ET AL. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

QIAO, H., L. E. ESCOBAR, E. E. SAUPE, L. JI, AND J. SOBERÓN. 2017. A cautionary note on the use of hypervolume kernel density estimators in ecological niche modelling. Global Ecology and Biogeography 26:1066–1070.

QUINN, T. 1997. Coyote (Canis latrans) Food Habits in Three Urban Habitat Types of Western Washington. Northwest Science 71:1–5.

R DEVELOPMENT CORE TEAM. 2008. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAIA, P. 2004. Morphological correlates of tough food consumption in large land carnivores. Italian Journal of Zoology.

RAXWORTHY, C. J., C. M. INGRAM, N. RABIBISOA, AND R. G. PEARSON. 2007. Applications of ecological niche modeling for species delimitation: A review and empirical evaluation using day geckos (Phelsuma) from Madagascar. Systematic Biology 56:907–923.

REID, R. E. B. 2014. Dietary Ecology of Coastal Coyotes (Canis latrans): Marine-Terrestrial Linkages from the Holocene to Present. University of California Santa Cruz.

RENSBERGER, J. M. 1999. Enamel microstructural specalization in the canine of the spotted hyena, Crocuta crocuta. Scanning Microscopy 13:343–361.

RICH, J. T., J. G. NEELY, R. C. PANIELLO, C. C. J. VOELKER, B. NUSSENBAUM, AND E. W. WANG. 2010. A practical guide to understanding Kaplan-Meier curves. *Otolaryngology - Head and Neck Surgery*. .

RILEY, S. P. D. ET AL. 2003. Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California.

RIPPLE, W. J. ET AL. 2014. Status and ecological effects of the world's largest carnivores. *Science*. .

RIPPLE, W. J., A. J. WIRSING, C. C. WILMERS, AND M. LETNIC. 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160:70–73.

DES ROCHES, S. ET AL. 2018. The ecological importance of intraspecific variation. Nature Ecology and Evolution 2:57–64.

ROEMER, G. W., M. E. GOMPPER, AND B. VAN VALKENBURGH. 2009. The Ecological Role of the Mammalian Mesocarnivore. BioScience 59:165–173.

RORBERG, R. A. 1977. An Ecological Theory on Foraging Time and Energetics and Choice of Optimal Food- Searching Method. Journal of Animal Ecology 46:511–529.

ROSE, M. D., AND G. A. POLIS. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea.

ROSENBLATT, A. E. ET AL. 2015. Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator. Oecologia 178:5–16.

ROSSMAN, S., P. H. OSTROM, F. GORDON, AND E. F. ZIPKIN. 2016. Beyond carbon and nitrogen: Guidelines for estimating three-dimensional isotopic niche space. Ecology and Evolution 6:2405–2413.

ROTA, C. T. ET AL. 2016. A two-species occupancy model accommodating simultaneous spatial and interspecific dependence.

ROTENBERRY, J. T., K. L. PRESTON, AND S. T. KNICK. 2006. GIS-based niche modeling for mapping species’ habitat. Ecology 87:1458–1464.

ROTH, J. D., AND K. A. HOBSON. 2011. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. Canadian Journal of Zoology 78:848–852.

ROWE, R. J., R. C. TERRY, AND E. A. RICKART. 2011. Environmental change and decliing resource availability for small-mammal communities in the Great Basin. Ecology 92:1366–1375.

SAKAMOTO, M., G. T. LLOYD, AND M. J. BENTON. 2010. Phylogenetically structured variance in felid bite force: The role of phylogeny in the evolution of biting performance. Journal of Evolutionary Biology.

SANABRIA, B., C. ARGUELLES-MENDEZ, AND A. ORTEGA-RUBIO. 1996. Occurrence of the endeangered pronghorn Antilocapra americana penisularis in coyote diets from northwestern Mexico. Texas Journal of Science 48:159–162.

SANDOM, C., S. FAURBY, B. SANDEL, AND J. C. SVENNING. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. Proceedings of the Royal Society B: Biological Sciences.

SCHINDELIN, J., C. T. RUEDEN, M. C. HINER, AND K. W. ELICEIRI. 2015. The ImageJ ecosystem: An open platform for biomedical image analysis. Molecular Reproduction and Development 82:518–529.

SCHUBERT, B. W., P. S. UNGAR, AND L. R. G. DESANTIS. 2010. Carnassial microwear and dietary behaviour in large carnivorans. Journal of Zoology.

SCHULZ, E., I. CALANDRA, AND T. M. KAISER. 2010. Applying tribology to teeth of hoofed mammals. Scanning.

SCOTT, R. S. ET AL. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature.

SCOTT, R. S. ET AL. 2006. Dental microwear texture analysis: technical considerations.

Journal of Human Evolution.

SCOTT, R. S., M. F. TEAFORD, AND P. S. UNGAR. 2012. Dental microwear texture and anthropoid diets. American Journal of Physical Anthropology 147:551–579.

SEARS, H. J., J. B. THEBERGE, M. T. THEBERGE, I. THORNTON, AND G. D. CAMPBELL. 2003. Landscape influence on Canis morphological and ecological variation in a Coyote-Wolf C. lupus x latrans hybrid zone, southeastern Ontario. Canadian Field-Naturalist.

SEEBENS, H. ET AL. 2017. No saturation in the accumulation of alien species worldwide. Nature Communications 8:1–9.

SÉQUIN, E. S., M. M. JAEGER, P. F. BRUSSARD, AND R. H. BARRETT. 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. Canadian Journal of Zoology.

SEVERTSOV, A. S., A. A. KORMYLITSIN, E. A. SEVERTSOVA, AND I. A. YATSUK. 2016. Functional differentiation of teeth in the wolf (Canis lupus, Canidae, Carnivora). Biology Bulletin.

ŠIDÁK, Z. 1967. Rectangular Confidence Regions for the Means of Multivariate Normal Distributions. Journal of the American Statistical Association 62:626–633.

SILVESTRO, D., A. ANTONELLI, N. SALAMIN, AND T. B. QUENTAL. 2015. The role of clade competition in the diversification of North American canids. Proceedings of the National Academy of Sciences 112:8684–8689.

SILVESTRO, D., N. SALAMIN, AND J. SCHNITZLER. 2014. PyRate: A new program to estimate speciation and extinction rates from incomplete fossil data. Methods in Ecology and Evolution 5:1126–1131.

SIVY, K. J., C. B. POZZANGHERA, K. E. COLSON, M. A. MUMMA, AND L. R. PRUGH. 2018. Apex predators and the facilitation of resource partitioning among mesopredators. Oikos 127:607–621.

SLATER, G. J. 2015. Iterative adaptive radiations of fossil canids show no evidence for diversity-dependent trait evolution. Proceedings of the National Academy of Sciences.

SMITH, F. A., R. E. ELLIOTT SMITH, S. K. LYONS, J. L. PAYNE, AND A. VILLASEÑOR. 2019. The accelerating influence of humans on mammalian macroecological patterns over the late Quaternary. Quaternary Science Reviews 211:1–16.

SMOL, J. P. 2010. The power of the past: Using sediments to track the effects of multiple stressors on lake ecosystems. Freshwater Biology 55:43–59.

SOBERÓN, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

STEFEN, C. 1999. Enamel Microstructure of Recent and Fossil Canidae (Carnivora: Mammalia).

STYNDER, D. D. 2009. Tooth crown form as an indicator of niche partitioning among Late Miocene/Early Pliocene hyenas from “E” Quarry, Langebaanweg, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology.

STYNDER, D. D., L. R. G. DESANTIS, S. L. DONOHUE, B. W. SCHUBERT, AND P. S. UNGAR. 2018. A Dental Microwear Texture Analysis of the Early Pliocene African Ursid Agriotherium africanum (Mammalia, Carnivora, Ursidae). Journal of Mammalian Evolution.

STYNDER, D. D., P. S. UNGAR, J. R. SCOTT, AND B. W. SCHUBERT. 2011. A Dental Microwear Texture Analysis of the Mio-Pliocene Hyaenids from Langebaanweg, South Africa. Acta Palaeontologica Polonica 57:485–496.

SURACI, J. P., M. CLINCHY, AND L. Y. ZANETTE. 2017. Do large carnivores and mesocarnivores have redundant impacts on intertidal prey? PLoS ONE.

SUTHERLAND, W. J. ET AL. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

SWANSON, H. K., M. LYSY, M. POWER, A. D. STASKO, J. D. JOHNSON, AND J. D. REIST. 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap.

SYVÄRANTA, J., A. LENSU, T. J. MARJOMÄKI, S. OKSANEN, AND R. I. JONES. 2013. An Empirical Evaluation of the Utility of Convex Hull and Standard Ellipse Areas for Assessing Population Niche Widths from Stable Isotope Data. PLoS ONE.

TANIS, B. P., L. R. G. DESANTIS, AND R. C. TERRY. 2018. Dental microwear textures across cheek teeth in canids: Implications for dietary studies of extant and extinct canids. Palaeogeography, Palaeoclimatology, Palaeoecology 508:129–138.

TANS, P. P., A. F. . DE JONG, AND W. G. MOOK. 1972. Natural atmospheric 14 C variation and the Suess effect. Nature 280:826–828.

TEAFORD, M. F. 1988. A review of dental microwear and diet in modern mammals. Scanning microscopy 2:1149–1166.

TEAFORD, M. F., AND A. WALKER. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of Sivapithecus. American Journal of Physical Anthropology 64:191–200.

TEDFORD, R. H., X. WANG, AND B. E. TAYLOR. 2009. Phylogenetic Systematics of the North American Fossil Caninae (Carnivora: Canidae). Bulletin of the American Museum of Natural History.

TERRY, R. C. 2004. Owl pellet taphonomy: a preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest. PALAIOS 19:497–506.

TERRY, R. C. 2010. On raptors and rodents: testing the ecological fidelity and spatiotemporal resolution of cave death assemblages. Paleobiology 36:137–160.

TERRY, R. C. 2017. Isotopic niche variation from the Holocene to today reveals minimal partitioning and individualistic dynamics among four sympatric desert mice. Journal of Animal Ecology 87:173–186.

TERRY, R. C., M. E. GUERRE, AND D. S. TAYLOR. 2017. How specialized is a diet specialist? Niche flexibility and local persistence through time of the Chisel-toothed kangaroo rat. Functional Ecology 31:1921–1932.

THERRIEN, F., A. QUINNEY, K. TANAKA, AND D. K. ZELENITSKY. 2016. Accuracy of mandibular force profiles for bite force estimation and feeding behavior reconstruction in extant and extinct carnivorans. The Journal of Experimental Biology 219:3738–3749.

THOMASON, J. J. 1991. Cranial strength in relation to estimated biting forces in some mammals. Canadian Journal of Zoology 69:2326–2333.

TINKER, M. T., G. BENTALL, AND J. A. ESTES. 2008. Food limitation leads to behavioral diversification and dietary specalization in sea otters. Proceedings of the National Academy of Sciences 105:560–565.

TOMAŠOVÝCH, A., AND S. M. KIDWELL. 2017. Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. Proceedings of the Royal Society B: Biological Sciences.

TOMIYA, S. 2013. Body Size and Extinction Risk in Terrestrial Mammals Above the Species Level. The American Naturalist.

TOSCANO, B. J., AND B. D. GRIFFEN. 2014. Trait-mediated functional responses: Predator behavioural type mediates prey consumption. Journal of Animal Ecology.

TSENG, Z. J. 2012. Connecting Hunter-Schreger Band Microstructure to Enamel Microwear Features: New Insights from Durophagous Carnivores. Acta Palaeontologica Polonica.

TSENG, Z. J., M. ANTÓN, AND M. J. SALESA. 2010. The evolution of the bone-cracking model in carnivorans: cranial functional morphology of the Plio-Pleistocene cursorial hyaenid Chasmaporthetes lunensis (Mammalia: Carnivora). Paleobiology 37:140–156.

TSENG, Z. J., AND J. J. FLYNN. 2015. Are cranial biomechanical simulation data linked to known diets in extant taxa? A method for applying diet-biomechanics linkage models to infer feeding capability of extinct species. PLoS ONE.

TSENG, Z. J., J. L. MCNITT-GRAY, H. FLASHNER, X. WANG, AND R. ENCISO. 2011. Model sensitivity and use of the comparative finite element method in mammalian jaw mechanics: Mandible performance in the Gray Wolf. PLoS ONE.

TSENG, Z. J., AND X. WANG. 2011. Do convergent ecomorphs evolve through convergent morphological pathways? Cranial shape evolution in fossil hyaenids and borophagine canids (Carnivora, Mammalia). Paleobiology.

TURNBULL, W. D. 1970. The mammalian masticatory apparatus. Fieldiana Geol. 18:149–356.

TURNER, T. F., M. L. COLLYER, AND T. J. KRABBENHOFT. 2010. A general hypothesis testing framework for stable isotope ratios in ecological studies. Ecology 91:2227–2233.

UNGAR, P. S., C. A. BROWN, T. S. BERGSTROM, AND A. WALKER. 2003. Quantification of Dental Microwear by Tandem Scanning Confocal Microscopy and Scale-Sensitive Fractal Analyses. Scanning 25:185–193.

UNGAR, P. S., F. E. GRINE, AND M. F. TEAFORD. 2008. Dental Microwear and Diet of the Plio-Pleistocene Hominin Paranthropus boisei. PLOS ONE 3:e2044.

UNGAR, P. S., J. R. SCOTT, B. W. SCHUBERT, AND D. D. STYNDER. 2010. Carnivoran dental microwear textures: Comparability of carnassial facets and functional differentiation of postcanine teeth. Mammalia.

URBAN, M. C. 2015. Accelerating extinction risk from climate change. Science 348.

URTON, E. J. M., AND K. A. HOBSON. 2005. Intrapopulation variation in gray wolf isotope (δ15N and δ13C) profiles: Implications for the ecology of individuals. Oecologia.

VAN VALKENBURGH, B. 1989. Carnivore Dental Adaptations and Diet: A Study of Trophic Diversity within Guilds. Carnivore Behavior, Ecology, and Evolution.

VAN VALKENBURGH, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17:340–362.

VAN VALKENBURGH, B. 1999. Major patterns in the history of carnivorus mammals.

Annual Review of Earth and Planetary Sciences 27:463–493.

VALKENBURGH, B. VAN. 2007. Déjà Vu: The Evolution of Feeding Morphologies in the Carnivora. Integrative and Comparative BiologyComparative Biology 47:147–163.

VAN VALKENBURGH, B. 2009. Costs of carnivory: Tooth fracture in Pleistocene and recent carnivorans. Biological Journal of the Linnean Society.

VALKENBURGH, B. VAN, S. PROFILE, AND X. WANG. 2003. Pack hunting in Miocene borophagine dogs: Evidence from craniodental morphology and body size Paleobiology Database View project.

VAN VALKENBURGH, B., M. F. TEAFORD, AND A. WALKER. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, Smilodon fatalis. The Zoological Society of London 222:319–340.

VAN VALKENBURGH, B., X. WANG, AND J. DAMUTH. 2004. Cope’s rule, hypercarnivory, and extinction in North American canids. Science 306:101–104.

VIOLLE, C. ET AL. 2012. The return of the variance: Intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

DE VOS, J. M., L. N. JOPPA, J. L. GITTLEMAN, P. R. STEPHENS, AND S. L. PIMM. 2015. Estimating the normal background rate of species extinction. Conservation Biology 29:452–462.

WANG, T., A. HAMANN, D. SPITTLEHOUSE, AND C. CARROLL. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:1–17.

WANG, T., A. HAMANN, D. L. SPITTLEHOUSE, AND T. Q. MURDOCK. 2012. ClimateWNA-high-resolution spatial climate data for western North America. Journal of Applied Meteorology and Climatology 51:16–29.

WANG, X. ET AL. 2018. First bone-cracking dog coprolites provide new insight into bone consumption in Borophagus and their unique ecological niche. eLife 7:1–28.

WANG, X., M. F. TEAFORD, AND B. E. TAYLOR. 1999. Systematics of Borophaginae. Bulletin of the American Museum of Natural History 243:1–391.

WATTS, D. E., AND S. D. NEWSOME. 2016. Exploitation of marine resources by wolves in southwestern Alaska. Journal of Mammalogy.

WEIJS, W. A., AND B. HILLEN. 1985. Cross-sectional areas and estimated intrinsic strength of the human jaw muscles. Acta Morphol Neerl Scand. 23:267–274.

WESLEY-HUNT, G. D. 2005. The morophological diversification of carnivores in North America. Paleo 31:35–55.

WIKENROS, C. ET AL. 2017. Fear or food - Abundance of red fox in relation to occurrence of lynx and Wolf. Scientific Reports.

WILDLIFE, O. D. OF F. AND. 2005. Oregon Wolf Conservation and Management Plan.

WILES, G. J., H. L. ALLEN, AND G. E. HAYES. 2011. Washington Department of Fish and Wildlife Wildlife Program Wolf Conservation and Management Plan.

WILLIS, K. J., AND R. J. WHITTAKER. 2002. Species diversity - Scale matters. Science 295:1245–1248.

WILSON, E. E., AND E. M. WOLKOVICH. 2011. Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution*. .

WINEMILLER, K. O., D. B. FITZGERALD, L. M. BOWER, AND E. R. PIANKA. 2015. Functional traits, convergent evolution, and periodic tables of niches. Ecology

Letters.

WOODWARD, G. ET AL. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20:402–409.

WOOTTON, J. T., AND M. EMMERSON. 2005. Measurement of Interaction Strength in Nature. Annual Review of Ecology, Evolution, and Systematics.

WROE, S., C. MCHENRY, AND J. THOMASON. 2005. Bite club: Comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. Proceedings of the Royal Society B: Biological Sciences 272:619–625.

YEAKEL, J. D. ET AL. 2014. Collapse of an ecological network in Ancient Egypt.

YEAKEL, J. D., P. R. GUIMARÃES, H. BOCHERENS, AND P. L. KOCH. 2013. The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. Proceedings of the Royal Society B: Biological Sciences.

YEAKEL, J. D., P. R. GUIMARÃES, M. NOVAK, K. FOX-DOBBS, AND P. L. KOCH. 2012. Probabilistic patterns of interaction: The effects of link-strength variability on food web structure. Journal of the Royal Society Interface.

YODZIS, P., AND S. INNES. 1992. Body size and consumer-resource dynamics. The American Naturalist 139:1151–1175.

EL ZAATARI, S., F. E. GRINE, P. S. UNGAR, AND J.-J. HUBLIN. 2011. Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. Journal of Human Evolution 61:411–424.

ZAKHAROVA, L., K. M. MEYER, AND M. SEIFAN. 2019. Trait-based modelling in ecology: lessons from two decades of research. PeerJ Preprints.

ZIMMERMANN, B., H. SAND, P. WABAKKEN, O. LIBERG, AND H. P. ANDREASSEN. 2015. Predator-dependent functional response in wolves: From food limitation to surplus killing. Journal of Animal Ecology 84:102–112.

ZULOAGA, J., AND J. T. KERR. 2017. Over the top: do thermal barriers along elevation gradients limit biotic similarity? Ecography.

APPENDICES

Appendix A: Supplementary materials for Chapter 2

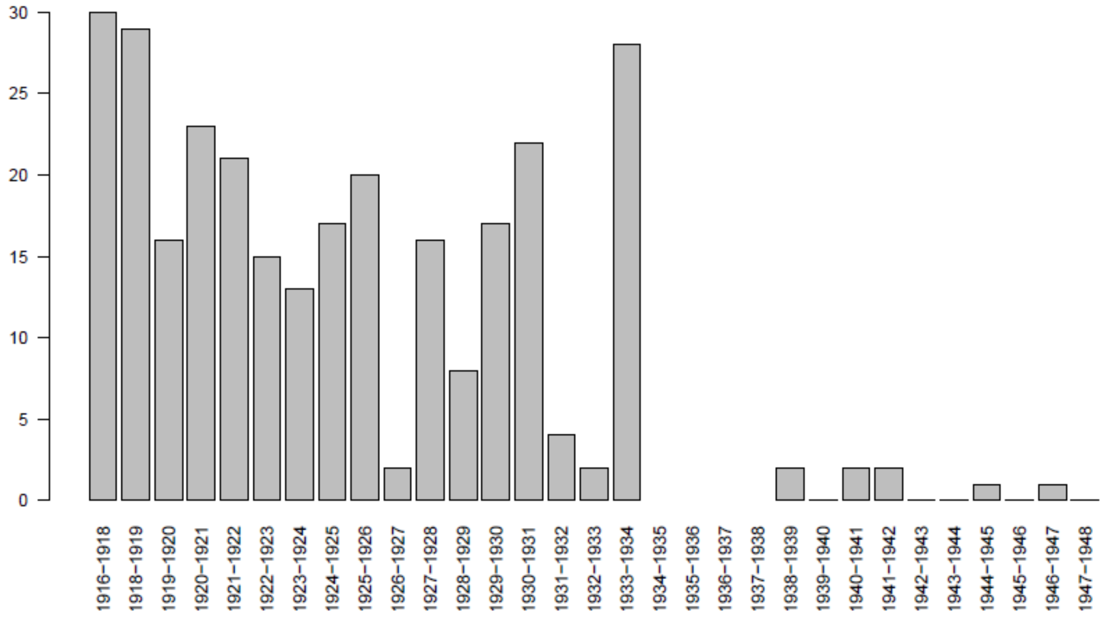
Appendix Table A1: Complete list of all specimens analyzed during this project, DMTA attribute values for each specimen, and the specific analysis in which each specimen was used: paired lower m1 talonid and lower m2 (Pairs), Intra-tooth variation (Var.), bite force calculation (BF), and standard ellipse area corrected for small sample size (SEA_c). Specimens were sampled from the University of British Columbia Beaty Museum of Biodiversity (UBCBBM), the University of Washington Burke Museum (UWBM), the Oregon State University Fisheries and Wildlife Collection (FW), and the John Day National Monument Collection (JODA).

Species	Catalogue Number	Tooth	*Asfc*	*epLsar*	*Tfv*	Pairs	Var.	BF	SEA_c
Canis latrans	FW 1184	m1	2.021612	0.0025045	13652	X		X	
		m2	2.674176	0.003236	11538	X		X	
	FW 1185	m1	3.303629	0.0026595	12021	X		X	
		m2	1.868551	0.0095915	12817	X		X	
	FW 1511	m2	2.038399	0.0031545	12396		X		
		m2	2.453892	0.0043185	13292		X		
	FW 1517	m1	2.107164	0.002937	11457	X		X	
		m2	0.434306	0.008613	14247	X		X	
	FW 1519	m1	1.949076	0.0026515	15012	X		X	
		m2	3.353805	0.001246	10787	X		X	
	FW 1521	m1	3.632978	0.002786	16447	X		X	
		m2	1.452614	0.0056875	12116	X		X	
	FW 1522	m1	1.270588	0.0035735	15094	X		X	
		m2	0.809437	0.007842	11822	X		X	
	FW 1523	m1	3.614771	0.00209	13812	X		X	
		m2	3.913677	0.0030585	12527	X		X	
	FW 1525	m1	1.883978	0.0030935	14291	X		X	
		m2	1.843823	0.004302	10302	X		X	
	FW 1532	m1	2.371637	0.003023	9343	X		X	
		m2	1.846652	0.0072095	13262	X		X	
	FW 1537	m2	4.839092	0.002505	13434		X		
		m2	7.3996355	0.0046075	12806		X		
	FW 1539	m1	4.188517	0.0021335	1638	X		X	
		m2	2.449742	0.004745	12194	X		X	
	FW 3092	m1	1.198893	0.003184	11472	X		X	
		m2	1.232127	0.006022	8437	X		X	
	UBCBBM 33	m1	3.36784	0.0020675	7218	X			
		m2	2.139117	0.002119	14504	X			
	UBCBBM 34	m1	3.051728	0.0045665	12274	X			
		m2	3.837123	0.001827	11008	X			
	UBCBBM 88	m1	1.415947	0.002764	15132	X			
		m2	2.167173	0.003126	15620	X			
	UBCBBM 3437	m1	1.355951	0.001577	17908	X			
		m2	2.857725	0.00272	15812	X			
	UBCBBM 3438	m1	1.40992	0.0031835	13164	X			
		m2	0.8403885	0.0023025	10203	X			
	UBCBBM 38312	m2	6.278778	0.0042885	13619		X		
		m2	1.9543055	0.0052055	12673		X		
	UBCBBM 38315	m2	1.8610035	0.006014	12124		X		
		m2	1.399196	0.0046325	14966		X		
	UBCBBM 9293	m1	2.094167	0.002592	6773	X			
		m2	2.1782605	0.004562	17147	X	X		
		m2	1.6878565	0.003766	19630		X		

Appendix Table A1: Continued

Canis lupus	FW 1510	m1	2.3356665	0.003045	7170	X		X	
		m2	2.0216045	0.0026345	12327	X		X	
	FW 2415	m1	3.596735	0.003885	16678	X		X	
		m2	1.4598945	0.0031095	4356	X		X	
	FW 3161	m1	1.4728125	0.0008765	8405	X		X	
		m2	2.6836545	0.001678	10158	X		X	
	UBCBBM 92	m1	1.2713955	0.002556	9717	X			
		m2	1.4292415	0.0036305	9941	X			
	UBCBBM 249	m1	3.9631935	0.0026625	11193	X			
		m2	3.2559245	0.0036655	13766	X			
	UBCBBM 872	m1	3.48928	0.001868	11863	X			
		m2	3.2013475	0.0007415	11713	X			
	UBCBBM 873	m1	1.9174365	0.0014405	10814	X			
		m2	1.040616	0.005526	14514	X			
	UBCBBM 874	m1	1.58282	0.0032145	12283	X			
		m2	2.7276215	0.00224	11997	X			
	UBCBBM 2203	m1	1.1982725	0.0030655	9474	X			
		m2	1.403638	0.002688	12753	X	X		
		m2	0.7978935	0.0023655	11551		X		
	UBCBBM 2432	m1	1.5042955	0.0045325	12347	X			
		m2	2.443603	0.001947	15959	X	X		
		m2	2.284553	0.0043295	13575		X		
	UBCBBM 2435	m1	4.145652	0.0040795	9584	X			
		m2	2.637205	0.001269	12191	X			
	UBCBBM 2454	m1	1.4582895	0.005674	8670	X			
		m2	1.404517	0.0033325	8482	X			
	UBCBBM 3080	m1	1.972966	0.00416	13795	X			
		m2	1.567397	0.0019855	10428	X			
	UBCBBM 3418	m1	2.2703495	0.002133	11401	X			
		m2	2.0506555	0.002679	11652	X	X		
		m2	2.2740625	0.0034615	11823		X		
	UBCBBM 6151	m1	3.6923975	0.0032985	13125	X			
		m2	2.0182755	0.0023475	13977	X	X		
		m2	1.7001685	0.003419	12135		X		
	UBCBBM 17306	m1	2.3985685	0.00311	14064	X			
		m2	1.1779605	0.002859	9762	X			
	UBCBBM 17308	m1	2.889192	0.0025145	12546	X			
		m2	2.117181	0.0010615	12494	X			
	UWBM 58801	m1	3.4165425	0.00315	12999	X			
		m2	3.988874	0.0026475	11378	X			
	UWBM 58815	m1	2.4341865	0.0049005	9109	X			
		m2	1.9924255	0.00255	10293	X			
	UWBM 81860	m1	2.089727	0.004009	12546	X			
		m2	0.793975	0.0027455	10552	X			
Cynarctoides lemur	JODA 790	m1	3.461432	0.0016755	16436				X
	JODA 1243	m1	2.708176	0.001981	11565				X
	JODA 1373	m1	5.5259165	0.002389	11431				X
	JODA 4858	m1	1.252925	0.0025305	10140				X
	JODA 5775	m2	3.4575505	0.0025205	15204				X
	JODA 10260	m1	2.6089655	0.004806	5329				X
Phlaocyon latidens	JODA 747	m1	3.5192585	0.001874	12321				X
	JODA 4861	m1	3.3550115	0.0031685	13430				X
	JODA 4920	m1	3.437278	0.003328	9976				X
	JODA 5785	m1	3.348068	0.002999	16901				X
	JODA 8579	m2	4.4407945	0.003601	11812				X
	JODA 10271	m2	3.441978	0.001022	12755				X
	JODA 14545	m1	3.055058	0.001686	8919				X

Appendix B: Supplementary materials for Chapter 3



Appendix Figure B1: Wolf bounty returns across Oregon as reported from the Oregon State Game Commission (precursor to Oregon Department of Fish and Wildlife) biannual reports spanning 1916 until 1948. Price of wolf bounties were not constant through time, with marginal increases in 1925 and 1933. Not all Oregon counties paid bounties set by the commission. The four reports associated with the years 1934 through 1938 lacked any published record of bounties paid and do not necessarily correspond with zero returns.

Appendix Table B2: Complete list of all coyote specimens analyzed in this study. Specimen metadata includes collection locality: latitude (Lat) and longitude (Long); collection year (Year); and mean climatic variables preceding collection (24 months for DMTA and 12 months for SIA): temperature (temp) and precipitation (ppt). Individual specimen values are given for DMTA attributes (*Asfc*, *epLsar*, *Tfv*) and stable isotope values (δ^{13}C, δ^{15}N) respectively. Treatment indicates if coyotes were sympatric with gray wolves or released as derived from our binning procedure. Specimens were sampled from the University of British Columbia Beaty Museum of Biodiversity (UBCBBM), the University of Washington Burke Museum (UWBM), the Oregon State University Fisheries and Wildlife Collection (FW), and from literature datasets of specimens from the California Academy of Science (CAS).

Catalogue Number	**Lat**	**Long**	**Year**	**temp**	**ppt**	**Asfc**	**epLsar**	**Tfv**	**d13C**	**d15N**	**Treatment**
FW1184	43.67	-119.667	1913	5.77	25.48	2.67	0.00324	11538.1	NA	NA	released
FW1187	43.06504	-118.967	1913	7.11	25.41	3.73	0.00315	13164.6	NA	NA	released
FW1188	43.27	-119.467	1913	6.54	22.72	1.73	0.00309	10156.4	NA	NA	released
FW1511v2	42.93	-123.283	1964	11.55	84.86	2.45	0.00432	13291.9	NA	NA	released
FW1517	42.42	-119.667	1964	6.07	31.72	0.72	0.00861	14247.5	NA	NA	released
FW1519	42.2	-121.383	1964	7.47	29.21	3.35	0.00125	10786.6	NA	NA	released
FW1520	42.93	-123.283	1964	11.55	84.86	3.10	0.00513	13747.7	NA	NA	released
FW1521	44.12	-123	1964	10.49	122.97	1.45	0.00569	12116.5	NA	NA	released
FW1522	43.9336	-122.837	1964	11.38	90.92	0.81	0.00784	11821.6	NA	NA	released
FW1523	43.3	-123.083	1964	11.22	90.63	3.91	0.00306	12527.1	NA	NA	released
FW1525	42.2	-121.383	1964	7.47	29.21	1.84	0.00430	10301.9	NA	NA	released
FW1526	42.93	-123.283	1964	11.55	84.86	2.62	0.00087	12606.4	NA	NA	released
FW1532	42.93	-123.283	1964	11.55	86.60	1.85	0.00721	13261.7	NA	NA	released
FW1534	42.42	-119.667	1964	6.07	31.72	4.22	0.00292	11797.9	NA	NA	released
FW1535v2	42.42	-119.667	1964	6.07	31.72	1.61	0.00153	10479.3	NA	NA	released
FW1536	42.93	-123.283	1964	11.55	86.60	4.32	0.00768	14317.2	NA	NA	released
FW1537	42.93	-123.283	1964	11.55	86.60	4.84	0.00251	13433.8	NA	NA	released
FW1539	42.93	-123.283	1964	11.55	86.60	2.45	0.00475	12193.9	NA	NA	released
FW1540	43.2	-123.117	1964	10.77	117.43	1.45	0.00368	13321.8	NA	NA	released
FW1541	43.9336	-122.837	1964	11.38	90.92	3.98	0.00424	10577.3	NA	NA	released
FW3092	44.33	-122.9	1976	10.57	132.23	1.23	0.00602	8437.0	-16.95	7.34	sympatric
MVZ107247	38.37705	-119.343	1947	4.14	41.00	3.48	0.00227	12790.8	-21.01	8.46	released
MVZ107709	38.26492	-119.221	1947	6.80	19.99	3.98	0.00347	15462.6	NA	NA	released
MVZ107710	38.27192	-119.219	1947	6.79	19.48	1.80	0.00175	15161.9	NA	NA	released
MVZ126949	39.8465	-120.371	1961	7.79	30.60	1.71	0.00274	12849.1	NA	NA	released
MVZ13504	43.8953	-121.144	1966	5.98	27.68	3.77	0.00261	9841.6	NA	NA	released
MVZ19706	39.96697	-123.251	1913	12.02	84.35	2.64	0.00121	11371.8	NA	NA	released
MVZ20965	42.0253	-121.599	1914	7.22	29.72	2.66	0.00361	15462.6	NA	NA	sympatric
MVZ23701	40.41788	-120.651	1916	9.15	29.06	2.62	0.00380	15955.2	NA	NA	released

Appendix Table B2: Continued

MVZ23701	40.41788	-120.651	1916	9.15	29.06	2.62	0.00380	15955.2	NA	NA	released
MVZ23723	40.38659	-120.648	1916	9.00	29.87	1.68	0.00349	15718.1	NA	NA	released
MVZ23864	40.3651	-120.422	1916	9.78	18.07	1.43	0.00368	10728.0	NA	NA	released
MVZ33423	40.73111	-122.941	1923	10.98	67.47	3.62	0.00237	14802.2	NA	NA	released
MVZ34307	37.92462	-119.252	1925	0.77	61.66	3.06	0.00356	13099.9	NA	NA	released
MVZ34755	40.4147	-121.532	1924	5.85	111.02	3.33	0.00104	12937.1	NA	NA	released
MVZ34989	40.22517	-123.543	1925	11.99	109.59	2.14	0.00200	13522.3	NA	NA	released
MVZ36364v2	40.79823	-120.232	1926	6.53	18.58	1.72	0.00365	11737.0	NA	NA	released
MVZ51978	40.87667	-122.831	1932	10.69	66.63	2.32	0.00255	11359.7	-21.62	6.96	released
MVZ59748	41.15783	-121.313	1933	8.14	34.34	5.38	0.00238	14026.1	NA	NA	released
MVZ70352	41.99978	-123.564	1935	9.97	139.94	3.30	0.00233	16018.8	NA	NA	sympatric
MVZ70469	41.77689	-121.45	1936	8.29	22.54	3.07	0.00199	15960.3	-21.86	7.16	released
MVZ70499	41.83283	-121.441	1936	8.24	22.31	3.42	0.00257	9276.6	-21.25	8.85	released
MVZ70500	41.83283	-121.441	1936	8.24	22.31	3.09	0.00204	15689.1	-21.04	10.38	released
MVZ70501	41.83338	-121.45	1936	8.24	22.31	3.00	0.00107	16177.2	-21.27	8.00	released
MVZ72098	42.4728	-122.704	1934	11.77	42.10	3.01	0.00464	14845.2	NA	NA	sympatric
MVZ78396	42.8392	-117.627	1937	9.44	15.92	3.54	0.00307	13898.8	NA	NA	released
MVZ81405	41.3481	-123.032	1937	10.01	100.05	3.26	0.00159	12146.1	NA	NA	released
MVZ86908	45.2597	-119.675	1927	10.50	25.08	2.83	0.00307	2163.6	NA	NA	sympatric
MVZ87046	44.2386	-120.748	1939	8.60	26.44	3.24	0.00210	11890.3	NA	NA	sympatric
MVZ87047	44.2386	-120.748	1939	8.60	26.44	5.10	0.00258	15649.0	NA	NA	sympatric
MVZ87405	44.2386	-120.748	1939	8.60	26.44	2.80	0.00253	16309.4	NA	NA	sympatric
UBCBBM118	54.617	-126.9	1938	2.77	32.64	1.94	0.00328	11151.2	NA	NA	sympatric
UBCBBM119x	54.695	-127.048	1935	2.80	40.88	1.39	0.00429	18273.2	NA	NA	sympatric
UBCBBM120	54.617	-126.9	1938	2.48	32.32	2.04	0.00498	18675.5	NA	NA	sympatric
UBCBBM121v2	54.695	-127.048	1935	2.80	40.88	1.55	0.00568	16407.7	NA	NA	sympatric
UBCBBM1467x	54.617	-126.9	1945	3.37	30.76	0.96	0.00309	5300.9	NA	NA	sympatric
UBCBBM193	52.4	-124.033	1940	NA	NA	1.38	0.00287	10474.6	NA	NA	released
UBCBBM232	50.16667	-120.667	1933	NA	NA	1.14	0.00353	12129.2	NA	NA	sympatric
UBCBBM252	49.1	-122.3	1941	11.10	112.48	1.70	0.00198	11095.9	NA	NA	sympatric
UBCBBM293v2	54.617	-126.9	1944	3.74	29.76	1.23	0.00356	14021.7	NA	NA	sympatric
UBCBBM3081v2	54.617	-126.9	1950	1.58	34.00	1.77	0.00195	15650.4	NA	NA	sympatric
UBCBBM33	50.7	-120.52	1935	8.00	24.72	2.14	0.00212	14503.9	NA	NA	sympatric
UBCBBM34	50.799	-120.458	1937	4.73	31.56	3.84	0.00183	11008.1	NA	NA	sympatric
UBCBBM3437	49.161	-123.091	1951	9.21	108.64	2.86	0.00272	15811.6	NA	NA	sympatric
UBCBBM3438	49.161	-123.091	1951	9.21	108.64	0.84	0.00230	10202.5	NA	NA	sympatric
UBCBBM41	50.675	-120.327	1935	NA	NA	2.01	0.00515	10616.4	NA	NA	sympatric
UBCBBM508v2	49.1825	-119.551	1941	11.31	23.68	2.30	0.00457	14418.9	NA	NA	sympatric
UBCBBM6156	51.73972	-122.401	1931	7.18	16.96	2.67	0.00277	13636.2	NA	NA	sympatric
UBCBBM6161	49.29	-119.531	1931	9.90	14.48	2.29	0.00324	9196.6	NA	NA	sympatric
UBCBBM6162	50.7	-119.28	1948	7.04	43.28	2.15	0.00237	16044.4	NA	NA	sympatric

Appendix Table B2: Continued

UBCBBM88	52.39	-123.1	1940	2.63	41.88	2.17	0.00313	15620.0	-22.68	7.40	sympatric
UBCBBM884	52.06	-122.27	1943	5.72	28.56	3.90	0.00355	12753.9	NA	NA	sympatric
UBCBBM9064	50.629	-119.124	1947	7.23	34.92	1.32	0.00123	10965.1	-22.03	8.56	sympatric
UBCBBM924	50.233	-119.35	1943	7.67	33.48	1.67	0.00229	15459.7	NA	NA	sympatric
UBCBBM9293	49.13333	-122.617	1966	9.32	121.16	2.18	0.00456	17147.2	-23.32	5.12	sympatric
UWBM20183	44.917	-120.853	1958	9.14	30.16	1.21	0.00198	13042.9	NA	NA	sympatric
UWBM20186	44.9353	-120.391	1959	10.40	32.65	2.49	0.00293	11079.8	NA	NA	released
UWBM32821	48.1242	-122.185	1982	10.09	108.07	1.38	0.00338	16128.0	-23.50	5.62	sympatric
UWBM33347	47.83217	-122.263	1983	10.37	97.23	3.21	0.00649	11086.7	-22.27	9.41	sympatric
UWBM33373	46.26728	-120.73	1984	6.32	73.02	1.83	0.00561	10041.1	NA	NA	released
UWBM33374	46.20937	-120.73	1984	6.57	72.48	1.07	0.00510	13717.4	NA	NA	released
UWBM35534	48.3406	-122.342	1988	10.58	60.09	2.29	0.00237	13856.2	NA	NA	released
UWBM38287	47.70937	-122.134	1989	11.21	73.57	2.87	0.00215	12044.8	NA	NA	released
UWBM38288v3	47.96632	-122.199	1989	10.48	69.96	1.76	0.00465	13333.4	NA	NA	released
UWBM38291	47.70937	-122.134	1989	11.04	77.23	3.74	0.00240	12453.1	NA	NA	released
UWBM38292	47.56771	-121.994	1989	10.68	92.31	2.43	0.00319	12323.8	NA	NA	released
UWBM38293	47.56771	-121.994	1989	10.68	92.31	1.16	0.00583	11223.5	NA	NA	released
UWBM38294v3	47.75578	-122.237	1988	11.37	71.63	2.70	0.00322	8765.8	NA	NA	released
UWBM38296v2	47.70937	-122.134	1990	10.85	84.84	1.54	0.00846	14414.1	NA	NA	released
UWBM38297	47.56771	-121.994	1989	10.82	90.83	2.09	0.00239	8754.2	NA	NA	released
UWBM38298	46.8999	-122.606	1989	10.33	80.18	1.50	0.00373	9440.6	NA	NA	released
UWBM38302	47.83224	-122.263	1990	10.30	79.92	1.83	0.00544	9609.7	NA	NA	released
UWBM38304	47.70937	-122.134	1989	10.92	81.44	2.60	0.00550	13488.7	NA	NA	released
UWBM38305	47.7	-121.96	1989	10.37	103.08	1.32	0.00692	11538.4	NA	NA	released
UWBM38306	47.70937	-122.134	1989	11.22	76.60	1.01	0.00604	9318.5	NA	NA	released
UWBM38307	47.70937	-122.134	1989	10.92	81.44	2.06	0.00237	10586.7	NA	NA	released
UWBM38308	46.8999	-122.606	1989	10.33	80.18	1.93	0.00439	13626.0	NA	NA	released
UWBM38310	47.56771	-121.994	1990	10.34	106.42	1.94	0.00396	11914.7	NA	NA	released
UWBM38311	47.70937	-122.134	1989	10.78	82.82	1.35	0.00272	11486.3	NA	NA	released
UWBM38312v2	47.56771	-121.994	1989	10.29	102.71	1.95	0.00521	12672.6	NA	NA	released
UWBM38313	47.56771	-121.994	1990	10.42	108.71	2.59	0.00352	11791.0	NA	NA	released
UWBM38315v2	47.70937	-122.134	1990	10.90	87.63	1.40	0.00463	14966.4	NA	NA	released
UWBM38316	47.56771	-121.994	1990	10.42	108.71	2.00	0.00410	11929.6	NA	NA	released
UWBM38317	47.56771	-121.994	1990	10.42	108.71	1.86	0.00549	10364.6	NA	NA	released
UWBM38318	47.56771	-121.994	1990	10.42	108.71	1.99	0.00342	11423.6	NA	NA	released
UWBM38324	47.70937	-122.134	1990	11.23	83.36	2.29	0.00453	13523.8	NA	NA	released
UWBM38325	47.56771	-121.994	1990	10.76	104.20	1.36	0.00501	12551.8	NA	NA	released
UWBM38626	43.2658	-118.843	1991	8.12	15.13	2.86	0.00222	16868.1	NA	NA	released
UWBM38627	43.2658	-118.843	1992	7.98	16.08	4.91	0.00069	13056.1	NA	NA	released
UWBM39393	47.54588	-120.027	1990	7.11	24.95	3.73	0.00214	11137.5	NA	NA	released
UWBM39395	48.3472	-122.347	1987	10.20	70.06	1.95	0.00278	9845.6	NA	NA	released

Appendix Table B2: Continued

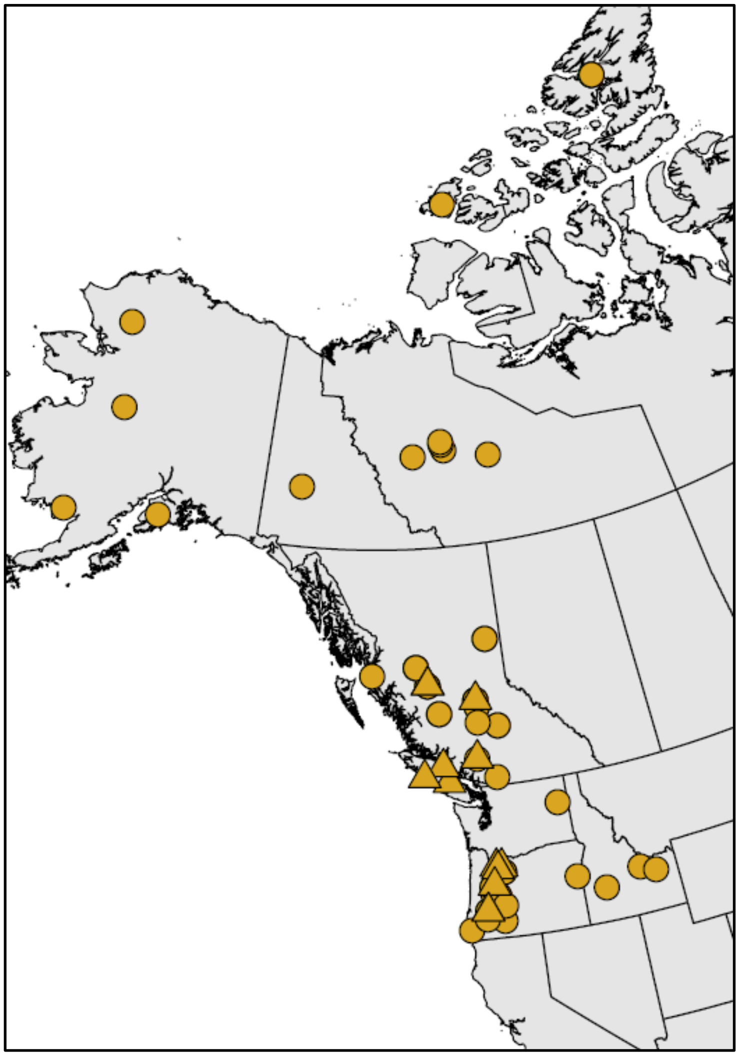
UWBM58823v2	46.0192	-118.674	1947	12.12	26.75	2.74	0.00177	11210.5	NA	NA	released
UWBM60985v2	47.1772	-122.185	1983	11.60	34.02	1.94	0.00506	13635.2	NA	NA	released
UWBM73091	43.3117	-118.794	1957	7.89	22.96	1.60	0.00395	8558.9	NA	NA	released
UWBM81801	47.8095	-122.531	2007	10.97	88.88	3.94	0.00498	13538.5	NA	NA	sympatric
UWBM81986	47.245	-122.113	2011	10.74	109.06	2.08	0.00229	12390.6	NA	NA	released
UWBM82021	47.4509	-122.313	2011	11.17	88.68	1.51	0.00508	10919.5	NA	NA	released
UWBM82438v2	46.9415	-119.986	2009	10.40	11.85	3.28	0.00507	15212.4	NA	NA	sympatric
CAS1128	37.48688	-121.921	1916	15.11	41.82	NA	NA	NA	-21.73	7.90	released
CAS120	35.08311	-120.032	1909	14.14	63.66	NA	NA	NA	-20.23	9.00	released
CAS1328	41.18762	-123.704	1916	13.04	151.59	NA	NA	NA	-22.13	8.50	sympatric
CAS1329	41.18762	-123.704	1916	13.04	151.59	NA	NA	NA	-22.13	8.50	sympatric
CAS165	39.54139	-123.489	1910	12.10	123.32	NA	NA	NA	-20.93	5.90	released
CAS263	37.3836	-122.232	1908	14.10	48.53	NA	NA	NA	-22.63	8.40	released
CAS92	35.08311	-120.032	1909	14.14	63.66	NA	NA	NA	-20.03	7.70	released
CAS928	37.09257	-121.887	1913	13.27	103.27	NA	NA	NA	-21.43	7.20	released
CAS955	37.88555	-122.114	1914	14.75	72.57	NA	NA	NA	-21.83	7.70	released
FW3091	44.22	-123.35	1974	11.32	136.00	NA	NA	NA	-23.30	6.49	sympatric
FW3642	45.17759	-122.211	1914	10.98	105.52	NA	NA	NA	-24.13	5.02	sympatric
MVZ12876	40.55444	-123.182	1911	11.57	70.86	NA	NA	NA	-21.17	6.57	released
MVZ25900	37.59175	-118.222	1917	-1.36	45.12	NA	NA	NA	-19.68	9.63	released
MVZ34397	59.6	-133.433	1924	-1.78	43.46	NA	NA	NA	-21.95	5.45	sympatric
MVZ34398	59.6	-133.433	1924	-1.78	43.46	NA	NA	NA	-22.00	5.33	sympatric
MVZ40172	53.2667	-121.267	1928	3.02	70.00	NA	NA	NA	-22.27	6.98	sympatric
MVZ40173	53.1833	-120.917	1928	2.25	82.08	NA	NA	NA	-22.01	5.46	sympatric
MVZ40174	53.2667	-121.267	1928	1.78	73.08	NA	NA	NA	-23.32	6.57	sympatric
MVZ41066	53.2667	-121.267	1928	1.78	73.08	NA	NA	NA	-23.02	5.82	sympatric
MVZ43897	53.2667	-121.267	1928	1.78	73.08	NA	NA	NA	-22.45	7.00	sympatric
MVZ51979	40.19919	-123.096	1932	9.52	107.51	NA	NA	NA	-21.12	6.82	released
MVZ70470	41.7626	-121.45	1936	8.22	25.72	NA	NA	NA	-22.07	9.87	released
MVZ70471	41.71879	-121.517	1936	8.91	27.75	NA	NA	NA	-20.87	7.73	sympatric
MVZ70472	41.70003	-121.497	1936	8.47	30.82	NA	NA	NA	-20.75	7.74	released
UBCBBM9461	49.96667	-123.15	1970	7.11	130.15	NA	NA	NA	-21.53	8.07	sympatric
UBCBBM9462	49.96667	-123.15	1970	6.23	139.62	NA	NA	NA	-22.32	7.57	sympatric
UWBM14999	47.2044	-121.99	1937	9.84	91.20	NA	NA	NA	-19.97	9.12	sympatric
UWBM30199	47.2843	-120.698	1966	6.99	44.55	NA	NA	NA	-21.70	8.18	sympatric
UWBM41663	45.8406	-119.288	1958	13.15	25.47	NA	NA	NA	-22.02	7.79	sympatric
UWBM6795	46.6	-120.5	1916	9.68	21.98	NA	NA	NA	-22.05	7.60	sympatric
UWBM76188	38.56	-119.5	1953	8.35	19.61	NA	NA	NA	-21.47	7.79	released

Appendix Table B3: Complete list of all wolf specimens analyzed for dietary breadth during this project with DMTA attributes (*Asfc*, *epLsar*, *Tfv*) and stable isotope values (δ^{13}C, δ^{15}N) respectively. Metadata for locality of collection: latitude (Lat) and longitude (Long) and year (Year) are provided. Specimens were sampled from the University of British Columbia Beaty Museum of Biodiversity (UBCBBM), the University of Washington Burke Museum (UWBM), the Oregon State University Fisheries and Wildlife Collection (FW), and from literature datasets of specimens from the Smithsonian National Museum of Natural History (USNM).

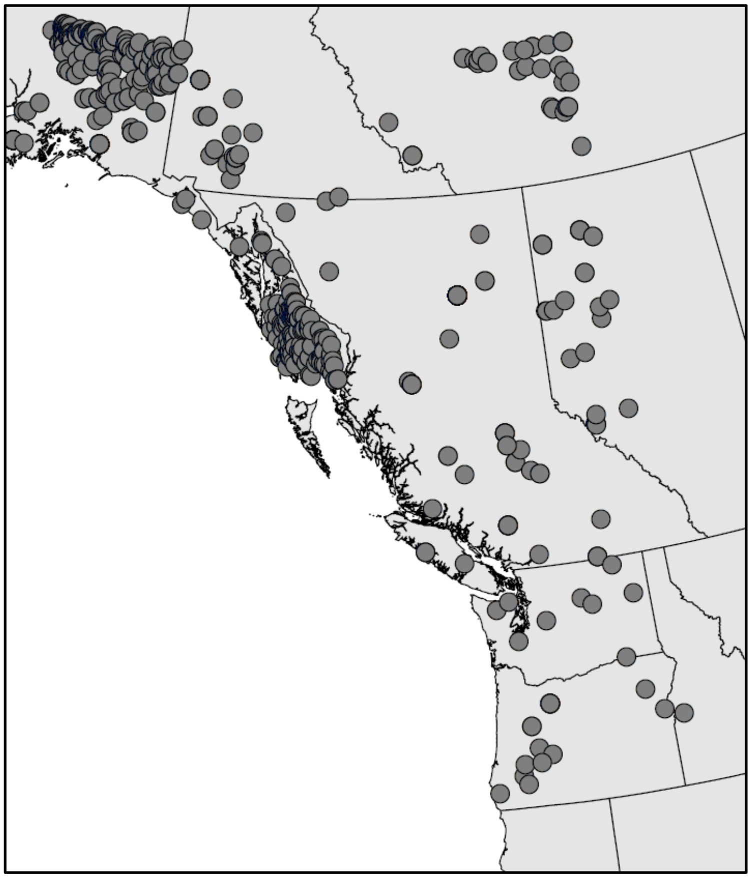
Catalogue Number	**Lat**	**Long**	**Year**	**Asfc**	**epLsar**	**Tfv**	**d13C**
UBCBBM3420	51.69972	-121.071	1951	0.613138	0.001239	12235.45	NA
UWBM81860	43.6	-115.6	2008	0.793975	0.002746	10551.82	NA
UBCBBM873	52.467	-125.317	1944	1.040616	0.005526	14514.36	NA
UBCBBM17306	55.72	-121.22	1940	1.177961	0.002859	9762.499	NA
USNM283586	80	-86	1948	1.181	0.003	15248	NA
MVZ59681	45.0142	-121.835	1933	1.222312	0.001503	8178.607	NA
MVZ29771	42.5083	-124.178	1918	1.292056	0.004578	8938.699	NA
UBCBBM6926	64.217	-126.267	1954	1.294873	0.002095	9110.664	NA
UBCBBM2203v2	54.617	-126.9	1946	1.403638	0.002688	12753.08	NA
UBCBBM2454	52.633	-122.45	1948	1.404517	0.003333	8481.904	NA
UBCBBM92	54.31278	-130.325	1941	1.429242	0.003631	9940.972	NA
UBCBBM3080	53.807	-126.043	1945	1.567397	0.001986	10428.23	NA
USNM290428	NA	NA	1949	1.651	0.0019	10855	NA
MVZ86873	42.8	-122.1	1934	1.683614	0.001875	13090.57	NA
MVZ29772	44.1075	-122.676	1919	1.683725	0.001794	12275.18	NA
USNM507338	79.98	-85.94	1949	1.72	0.0036	7063	NA
UWBM81792	47.86	-117.71	2008	1.768778	0.001873	16043.66	NA
UBCBBM2453	52.633	-122.45	1948	1.794243	0.001651	11383.88	-19.6922
UBCBBM3078	53.807	-126.043	1945	1.805843	0.002015	13380.72	NA
MVZ30515v2	44.4106	-122.671	1919	1.818084	0.001377	18016.45	NA
UBCBBM2434	52.982	-122.495	1948	1.865658	0.001968	10324.39	NA
UBCBBM6917	64.817	-123.317	1954	1.882483	0.002532	12498.93	NA
MVZ86872	43.7467	-122.461	1934	1.923734	0.004466	15568.8	NA
UBCBBM3074	53.807	-126.043	1945	1.985981	0.002709	10274.93	NA
UWBM58815	59.041	-158.458	1956	1.992426	0.00255	10293.36	NA
UWBM81857	43.88	-112.39	2008	2.013769	0.002053	13915.46	NA
UBCBBM6151c	50.322	-122.805	1945	2.018276	0.002348	13976.68	NA
FW1510	43.3	-123.083	1914	2.021605	0.002635	12326.62	NA
MVZ30514	44.4106	-122.671	1919	2.038087	0.004723	9643.227	NA
UBCBBM3418	51.69972	-121.071	1951	2.050656	0.002679	11651.64	NA
USNM291008	76.248	-119.35	1949	2.078	0.0038	10936	NA
UCBBBM17308	55.72	-121.22	1940	2.117181	0.001062	12493.9	NA
UBCBBM871	54.617	-126.9	1943	2.177706	0.002147	10815.91	NA
MVZ28001	43.99	-122.33	1918	2.197024	0.002422	12270.16	NA

Appendix Table B3: Continued

MVZ59682	45.0142	-121.835	1933	2.24083	0.0046	12503.1	NA
UWBM58814	62.766	-137.383	1956	2.322412	0.00241	6673.566	NA
USNM282819	80	-86	1947	2.358	0.0026	15019	NA
USNM290425	68.1	-159.6	1949	2.398	0.0014	9603	NA
MVZ28004	43.99	-122.33	1918	2.43859	0.002276	13881.04	NA
UBCBBM2432	52.982	-122.495	1948	2.443603	0.001947	15959	NA
MVZ4776	60.16667	-150.25	1906	2.468955	0.001954	6833.747	NA
MVZ86912	43.5094	-121.968	1930	2.553145	0.001487	11969.2	NA
MVZ86910	42.9714	-123.168	1929	2.569586	0.001718	14403.77	NA
UBCBBM6916	64.717	-123.267	1954	2.632355	0.003135	9534.049	NA
UBCBBM2435	52.982	-122.495	1948	2.637205	0.001269	12191.4	NA
FW3161	43.3	-123.083	NA	2.683655	0.001678	10158.28	NA
MVZ28002	43.99	-122.33	1918	2.717202	0.003178	12375.45	-22.5633
UBCBBM874	52.467	-125.317	1943	2.727622	0.00224	11997.09	NA
FW2932	44.35	-117.283	1974	2.814174	0.003999	13984.43	NA
UBCBBM7162	63.967	-118.55	1956	2.869038	0.002009	9037.082	NA
UBCBBM3234	NA	NA	NA	3.006093	0.003679	16651.53	NA
UWBM81855	44.2	-113.3	2008	3.162114	0.003464	10877.81	NA
UBCBBM872	54.617	-126.9	1943	3.201348	0.000742	11713.22	NA
UBCBBM249x	49.36667	-121.55	1941	3.255925	0.003666	13765.86	NA
FW8727	43.31	-122.41	1978	3.512205	0.001088	12115.58	NA
UBCBBM6913	64.417	-123.067	1954	3.655311	0.001685	13690.51	NA
MVZ28003	43.99	-122.33	1918	3.720589	0.002414	13520.13	NA
UWBM58801	51.9667	-122.517	NA	3.988874	0.002648	11377.91	NA
UWBM33494v2	64.33333	-156.75	1985	4.212011	0.002255	8913.415	NA
USNM291012	80	-86	1949	5.398	0.0022	11491	NA
UBCBBM17450	49.3166	-124.9	1932	NA	NA	NA	-23.316
FW2797	45.28	-121.967	1915	NA	NA	NA	-23.2826
UBCBBM2459	53.80672	-126.043	1946	NA	NA	NA	-22.8735
UBCBBM2457	53.80672	-126.043	1946	NA	NA	NA	-22.827
UBCBBM2458	53.80672	-126.043	1946	NA	NA	NA	-22.6275
UWBM82296	48.99	-188.22	2012	NA	NA	NA	-22.5201
FW3158	45.3	-122.3	1914	NA	NA	NA	-22.1912
MVZ13005	49.6	-126.617	1909	NA	NA	NA	-22.1504
UBCBBM3728	50.04861	-125.258	1950	NA	NA	NA	-22.0852
UBCBBM17452	50.32202	-122.805	1936	NA	NA	NA	-22.0749
FW3656	45.17759	-122.211	1913	NA	NA	NA	-22.0018
OSC1611	NA	NA	1915	NA	NA	NA	-21.762
FW3659	43.3	-123.083	1913	NA	NA	NA	-21.584
FW3657	44.45	-122.533	1913	NA	NA	NA	-21.5825
FW3658	43.3	-123.083	1913	NA	NA	NA	-21.3867



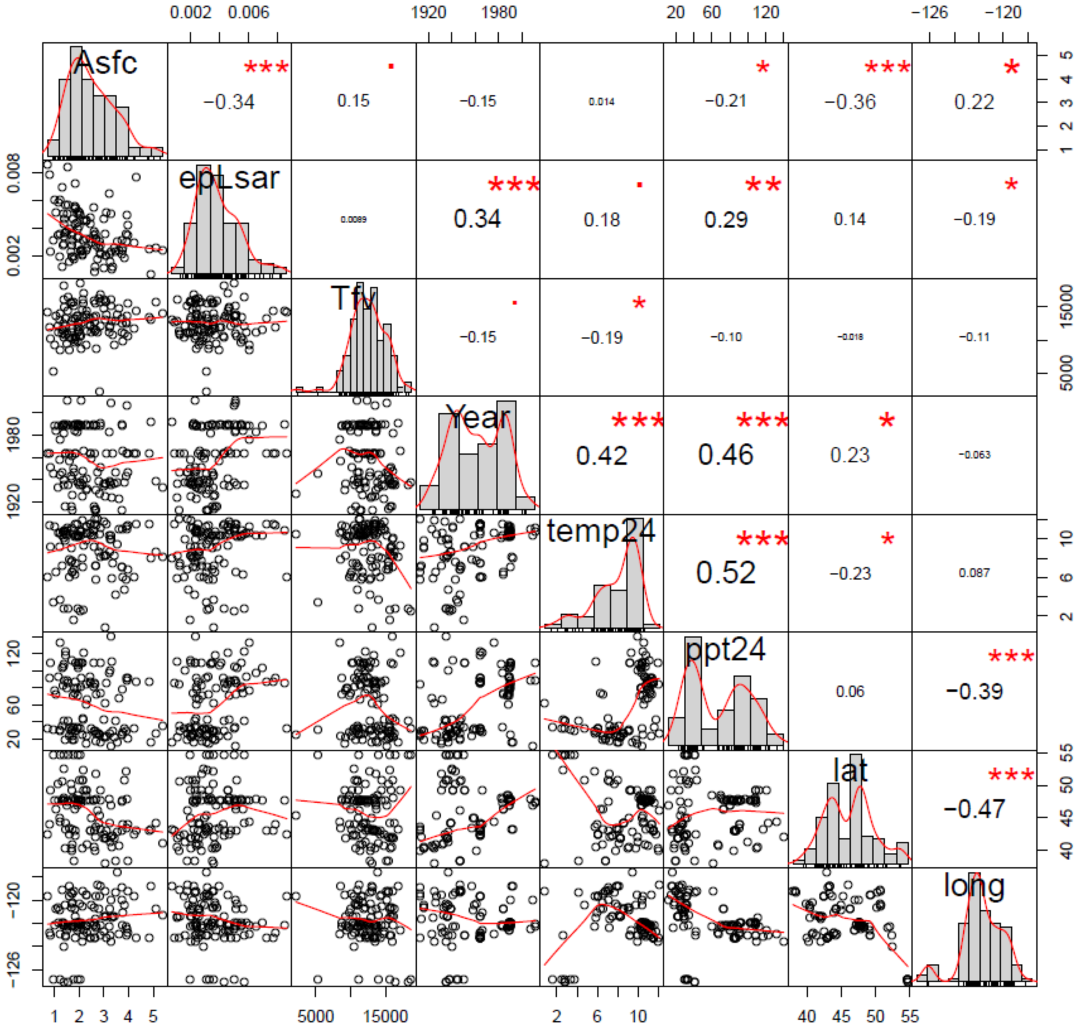
Appendix Figure B2: Spatial distribution of gray wolf museum specimens sampled for dental microwear texture analysis (circles) and stable isotope analysis (triangles).



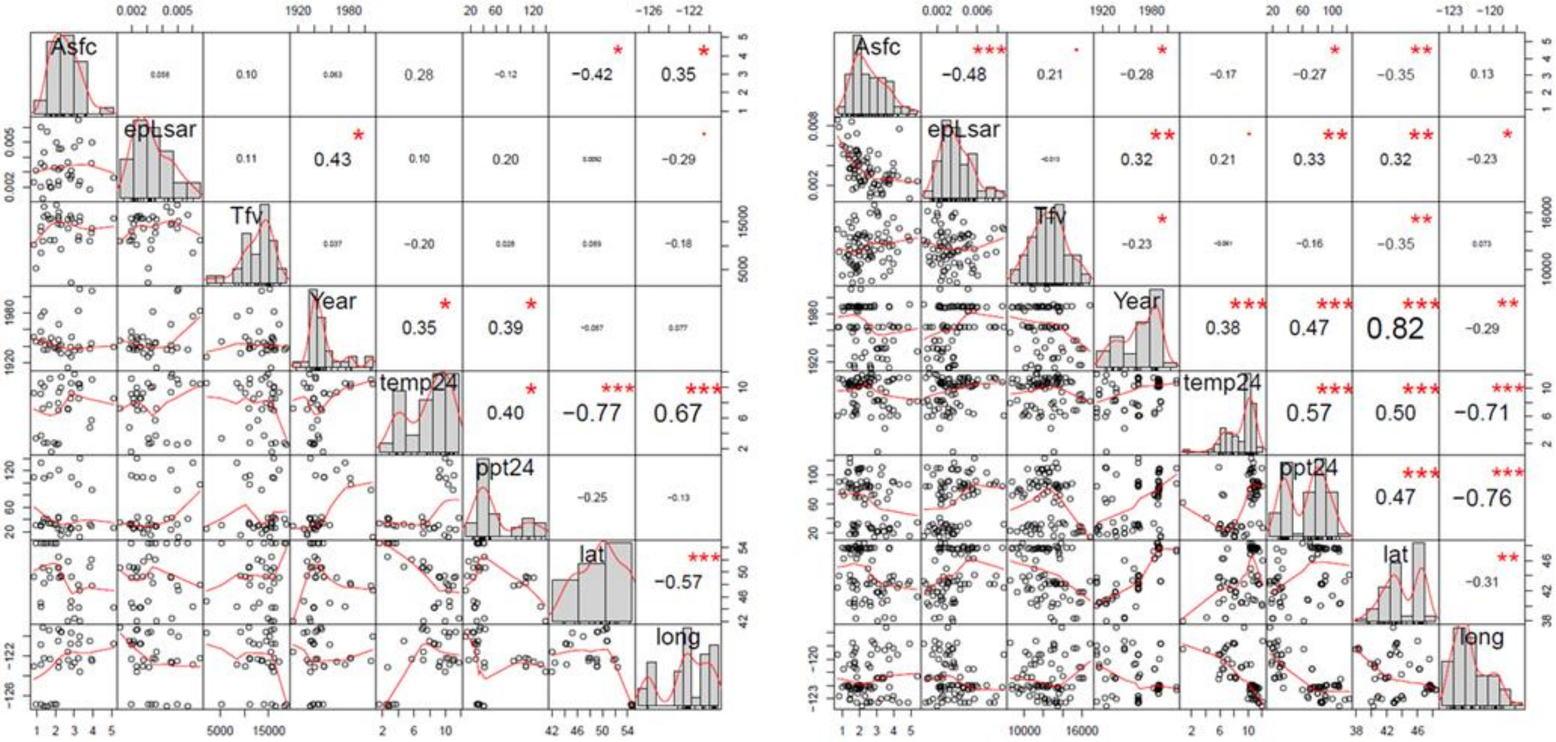
Appendix Figure B3: Spatial distribution of historical gray wolf museum specimens used for quantifying coyote specimens as sympatric or released. Occurrence points represent known wolf museum specimens for which there is both spatial and temporal data. Data was downloaded and aggregated from VertNet (last accessed March 2018) and the Global Biodiversity Information Facility (last accessed on March 2018).

Appendix Table B4: Seasonal distribution of coyote specimens according to treatment, sympatric with wolves or released.

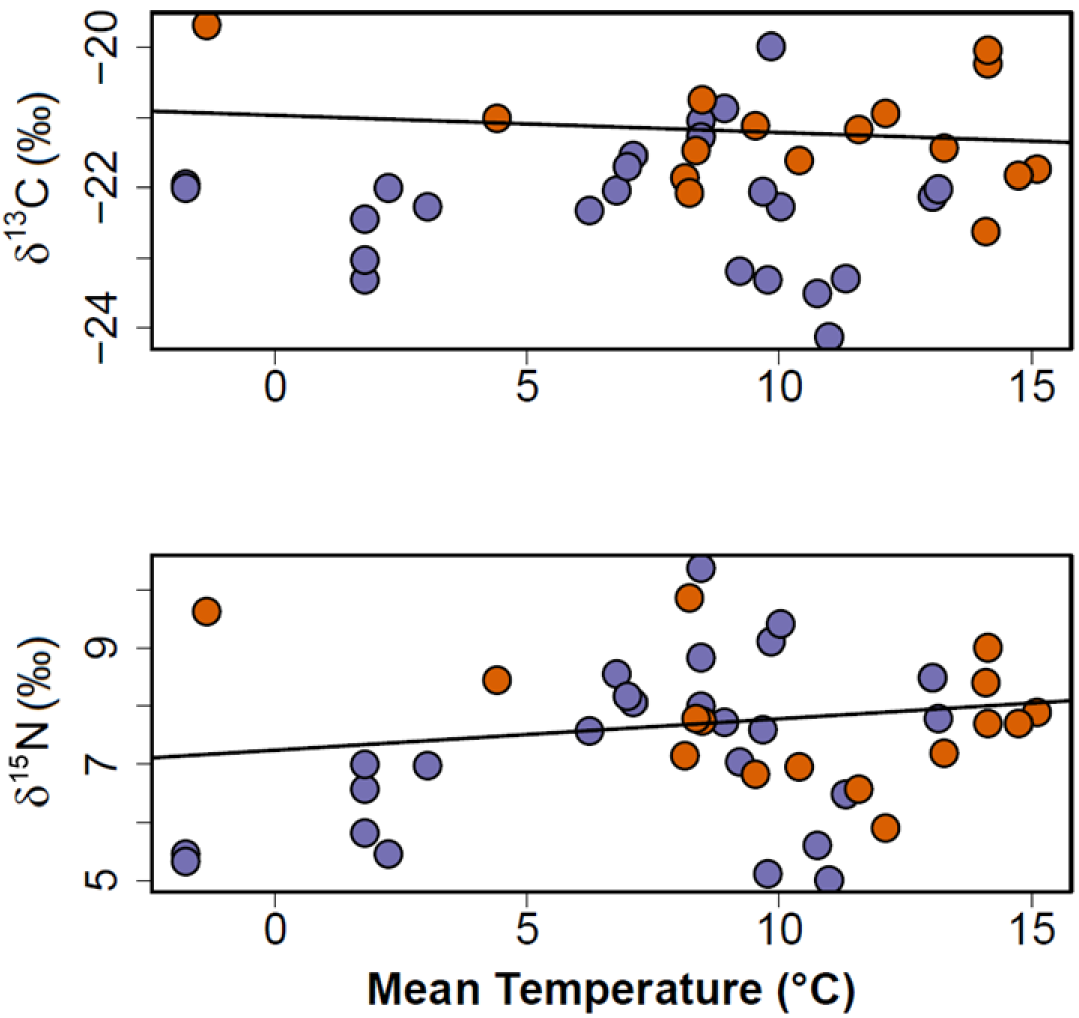
Treatment	**Spring**	**Summer**	**Winter**
Sympatric	14	5	14
Released	40	16	25



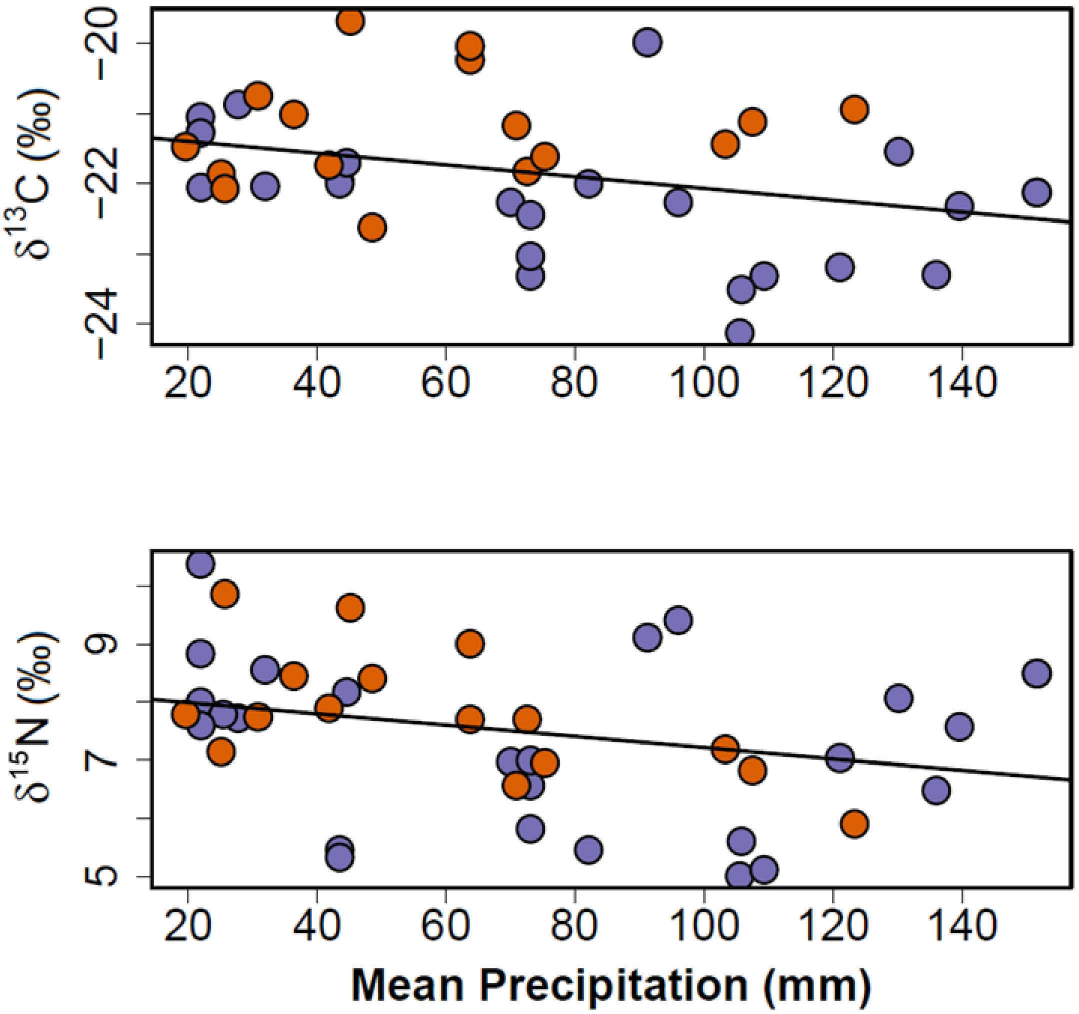
Appendix Figure B4: Pearson correlations between DMTA attributes (*Asfc*, *epLsar*, and *Tfv*), year of specimen collection (Year), mean climatic variables over the 24 months prior to specimen collection - temperature (temp24) and precipitation (ppt24), and specimen occurrence - latitude (lat) and longitude (long) for all coyotes regardless of treatment type (n = 117). Stars are indicative of p-values: *** = p<0.001, ** = p<0.01, * = p<0.05, ˙= p<0.1.



Appendix Figure B5: Pearson correlations between DMTA attributes (*Asfc*, *epLsar*, and *Tfv*), year of specimen collection (Year), mean climatic variables over the 24 months prior to specimen collection - temperature (temp24) and precipitation (ppt24), and specimen occurrence - latitude (lat) and longitude (long). Analyses were run separately for coyotes sympatric with gray wolves (left) and released from gray wolves (right). Stars are indicative of p-values: *** = p<0.001, ** = p<0.01, * = p<0.05, ˙= p<0.1. Significant correlations between DMTA attributes and spatial and temporal covariates were compared with an added variables assessment with results indicative of being driven by the historical trend in wolf extirpation.

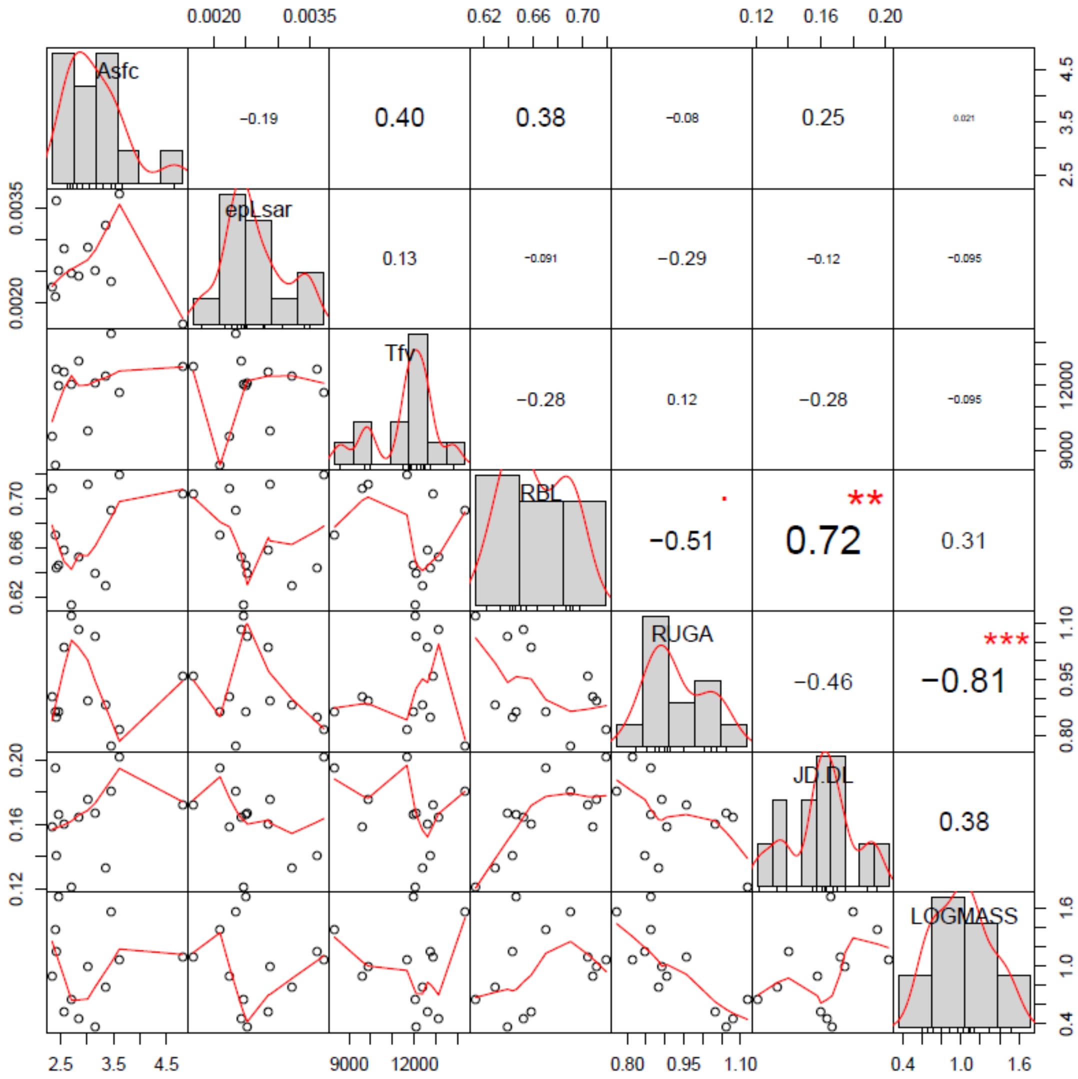


Appendix Figure B6: Relationship between coyote isotopic values and mean temperature over the 12 months prior to specimen collection. Points are colored by treatment group: sympatric with gray wolves (blue) and released (orange). Lines represent regressions of the entire data set. No relationship was observed between isotope values and mean temperature for either $\delta^{13}C$ ($p = 0.72$, $R^2_{adj} = 0.02$) or $\delta^{15}N$ ($p = 0.015$, $R^2_{adj} = 0.03$).

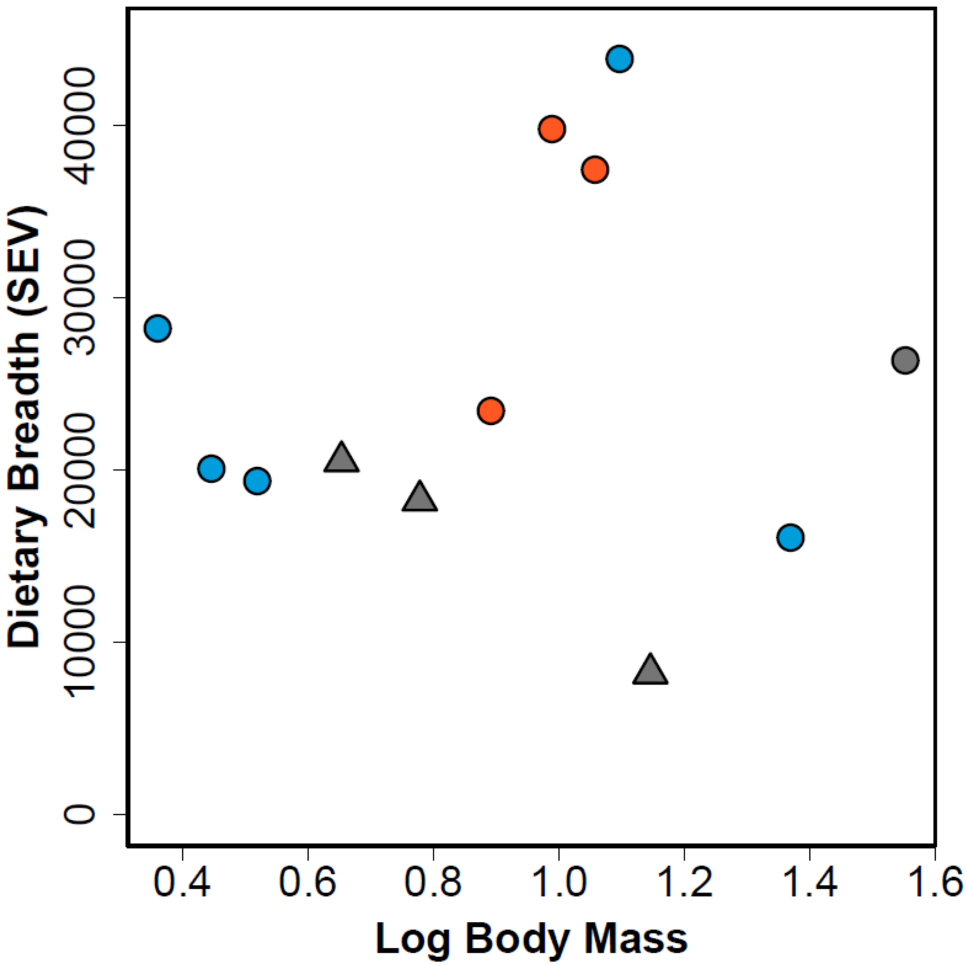


Appendix Figure B7: Relationship between coyote isotopic values and mean precipitation over the 12 months prior to specimen collection. Points are colored by treatment group: sympatric with gray wolves (blue) and released (orange). Lines represent regressions of the entire data set. The relationship between isotope values and mean precipitation was negative for both $\delta^{13}C$ ($p = 0.03$, $R^2_{adj} = 0.10$) and $\delta^{15}N$ ($p = 0.06$, $R^2_{adj} = 0.06$). Given the poor fitting residuals and an overall interest in variation over means, no correction factor for precipitation was applied to the data prior to final analyses. Furthermore, as data from both treatments relatively equally spans the precipitation gradient the relationship between isotope values and precipitation, patterns observed between treatments accurately reflect biological differences not climatic patterns.

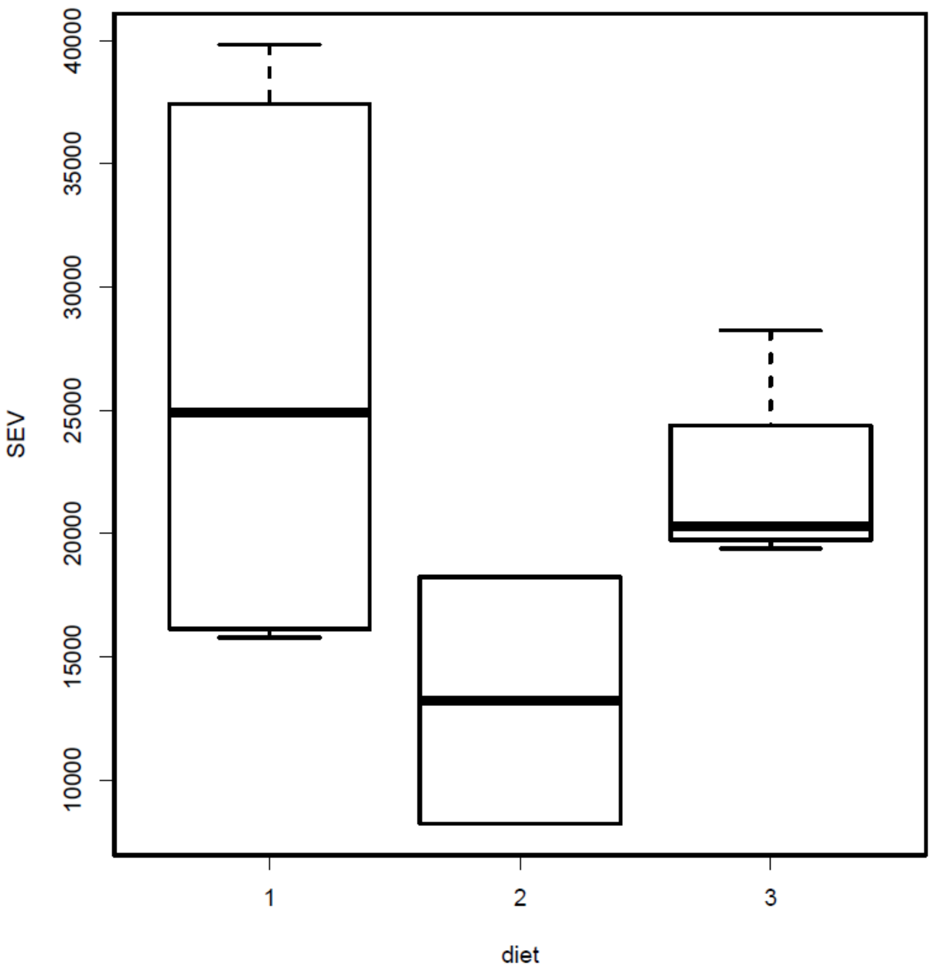
Appendix C: Supplementary materials for Chapter 4



Appendix Figure C8: Pairwise Pearson correlations between DMTA attributes (*Asfc*, *epLsar*, and *Tfv*), morphological traits commonly used to categorize diet in canids (RBL, RUGA, JD:JL), and log body mass (LOGMASS). Stars are indicative of p-values: *** = p<0.001, ** = p<0.01, * = p<0.05, ˙= p<0.1. There were no correlations between DMTA attributes and morphological traits, suggesting a mismatch between adaptive traits and behavioral foraging plasticity.



Appendix Figure C9: Relationship between dietary breadth and body mass for canids. Color of points corresponds with subfamily designation: Hespercyoninae (orange), Borophaginae (blue), and Caninae (gray). Triangles denote extant taxa. General trends suggest that intermediate sized canids had the more generalist diets compared with species at the higher or lower ends of the distribution of body mass, however, we lack power to statistically analyze those trends.



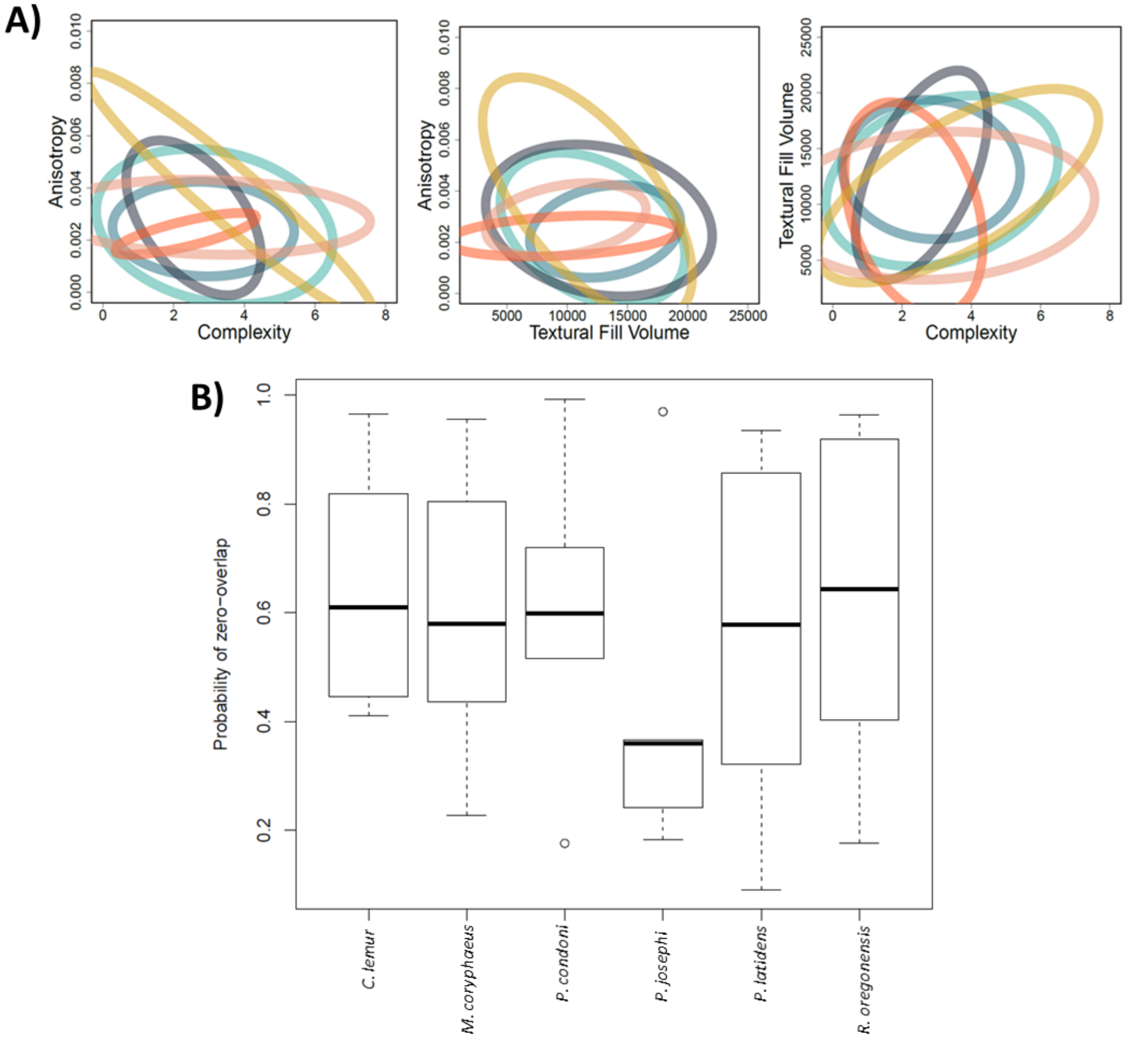
Appendix Figure C10: Comparison of dietary breadth from standard ellipsoid volume (SEV) and dietary categories (hypercarnivore: 1, mesocarnivore: 2, and hypocarnivore: 3) defined in the literature from morphological traits.

A theoretical framework for quantifying competition via DMTA

One of the main hypothesized benefits for species to evolve dietary specialization is to escape from competition over resources. Additionally, evolutionary rate models suggest that fossil canids were frequently driven to extinction by competition with radiating sister clades (Van Valkenburgh 1999; Silvestro et al. 2015). As such, we might hypothesize that extinction risk would be highly correlated with a competition coefficient between taxa. A trophic link-strength between taxa, related to interaction strengths, could be quantified as the area of overlap between the entirety of a species dietary breadth. However, given the variety of food items with similar textural properties and the absence of additional biological data necessary for quantifying interspecific interactions, area of overlap of dental microwear niche space is not equivalent to competition for similar resources.

However, it is theoretically possible to quantify the contribution of unique prey items to each species diet by measuring zero-overlapping areas in DMTA parameter space among a population of sympatric species. Zero-overlapping regions are areas within a species' niche space that are entirely unique to that species, thus zero-overlap regions are a reflection of the minimum value of competition-free resources. If the entirety of sympatric species are sampled, zero-overlap could indicate which species are more specialized and free of trophic competition. Unfortunately, calculating the probability of an individual from a species falling within the zero-overlapping region of all sympatric species is computationally expensive. Currently, this can only be achieved for individual species pairs. Although, this cannot yield enough resolution to reliably make inference to the ecology of the community, here we detail this method for reference until such time that it can be performed in greater detail.

To derive the zero-overlap index, our dataset was first subset to just species known from the Turtle Cove assemblage of the John Day Formation (roughly 30.6-28.1 Ma) of eastern Oregon. This resulted in 6 species of canids with intermixed fossil occurrences within this singular assemblage (Table 3). We calculated the cumulative posterior probability that individuals of each species would not fall within the three-dimensional dietary niche space of each sympatric species (Swanson et al. 2015). These values were used to qualitatively assess level of unique resource use (i.e. specialization). Outcomes suggested that the probability of an individual from any species of extinct canid at the John Day being within a zero-overlapping region of dietary niche space was very small (Appendix C Figure C11). However, this is conflated by the inability to tease apart conditional probabilities of multiple species dietary niche overlap.



Appendix Figure C11: A) Dietary niche space of six sympatric fossil canids from the John Day Formation of eastern Oregon. Panels show bivariate representations of three-dimensional Bayesian Ellipsoids built from DMTA parameters. Regions of zero-overlap in dietary space between species is very low, suggestive of the possibility that species were not specializing on unique combinations of prey items. B) Distribution of probabilities that an individual of that taxa does not occur within the dietary niche space of another taxa. Variation within a single species probability of zero-overlap of sympatric species pairs is high.