INVESTIGATIONS OF ECOMORPHOLOGICAL FEATURES UNDER ARIDIFICATION: CRANIAL HEADGEAR AND CAROTID-RETE-MEDIATED SELECTIVE BRAIN COOLING

By

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Anthropogenic climate change presents one of the most pertinent risks to modern biodiversity. As the global climate becomes increasingly warmer and drier, it becomes equally as pertinent to understand how species respond to these shifts physiologically. To do so, we review environmental shifts throughout the Cenozoic (66 MY -present), specifically those relating to aridity – increasing environmental water scarcity – and commonly used climatic indicators for those environmental shifts, including hypsodonty and cursoriality. We then explore two additional, less-investigated potential ecomorphological traits that may correspond with environmental aridity: 1) elaborate cranial ornamentation (headgear) and 2) carotid-rete-mediated selective brain cooling. The aims of this thesis are: 1) to establish a foundational description of the osteohistology of a horncore of an arid-adapted species*, Antilocapra americana* and 2) investigate whether carotid-rete-mediated selective brain cooling is not only selectively advantageous but also provides a release from physiological constraint imposed by the environment, specifically aridity, in large mammals, using of $\delta^{18}O$ in tooth enamel as a proxy for water budget. I utilized standard osteohistological methods to examine the microanatomy of the horncores of both male and female *Antilocapra americana*, and found that these structures were composed of primarily trabecular bone tissue, supporting a role as a shock absorber in intraspecific combat. I also found evidence of reticular vascularization in the tissue surrounding the horncore, which may be indicative of a thermoregulatory function of *Antilocapra americana* headgear. To test for variance of $\delta^{18}O$ in the tooth enamel of large mammals, I completed both a non-parametric and comparative parametric analyses that compared both mean $\delta^{18}O$ values and $\delta^{18}O$ variance between species with and without carotid retia among three environmental categories: arid, dry subhumid, and humid. The results of this analysis found that, as aridity increased, the variance of $\delta^{18}O$ values of individuals possessing carotid retia exceeded that of those without. Concurrently, as water availability increased, variance equalized as the selective advantage of CR-SBC became less influential. Potential limitations to both of these studies are the low sample size of *Antilocapra americana* and the lack of $\delta^{18}O$ samples from carnivorans.

TABLE OF CONTENTS

Chapter **Page**

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

CHAPTER I

INTRODUCTION TO CLIMATIC INDICATORS OF ARIDIFICATION IN DEEP TIME

1. Introduction

Modern climate change poses one of the most pressing dangers to modern mammalian species diversity. In the next century, global temperatures are expected to rise at least 2.7 ºC (IPCC, 2013), and changes in rainfall patterns and snow melt are expected to make water availability less predictable and increase instances and severity of drought (IPCC, 2014; Cook et al., 2015; Putnam & Broecker, 2017). Within the past decade alone, up to 25% of mammalian species have been reclassified as threatened or endangered (Schipper et al., 2008), and some have even become extinct (Ceballos et al., 2017; Crooks et al., 2017). Huey et al. (2012) propose that the vulnerability of a species to climate change depends on the species' exposure and sensitivity to environmental change, and its potential to adapt to said change. Small-bodied mammals (<10kg) have been found to have high resilience to climatic and anthropogenic disturbance (Laliberte et al., 2004; Santini et al., 2019; Berdugo et al., 2020). In contrast, large-bodied (>50kg) mammals are at high risk (IUCN Red List, 2012; McCain & King, 2014; Urban, 2015) given their long generation time (Simpson, 1944), small population size (Stanley, 1979; Van Valkenburgh et al., 2004) and reliance on large range size (Webb, 1969; Brown & Maurer, 1989; Brown & Nicoletto, 1991; Diniz-Filho et al., 2005; Tucker et al., 2018). Human-induced range fragmentation is most deleterious for those mammals that rely on resources acquired across a large territory (Laliberte et al., 2004; McGuire & Davis, 2013; Lyons et al., 2016; Crooks et al., 2017), such as carnivorans and ungulate grazers (Laliberte et al., 2004; Crooks et al., 2017; Smith et al., 2019; Berdugo et al., 2020; Enquist et al., 2020). As of 2012, nearly 36% of global carnivoran and ungulate populations were threatened (IUCN, 2012). This is particularly problematic as carnivorans and ungulates serve key roles in facilitating ecological processes like predation (Soulé & Estes, 2003), herbivory (Pringle et al., 2007), and seed dispersal (Fragoso et al., 2003), and their absence within ecosystems may result in trophic cascades that could dramatically alter ecological structures (Estes et al., 2011).

In addition to reducing range size, human-induced range fragmentation affects the survivorship of large-bodied mammals by preventing access to preferred habitats (McGuire et al., 2016; Pineda-Munoz et al., 2021), as resource-rich temperate areas are frequently used for agriculture (Scherr & McNeely, 2008; Lambin & Meyfroidt, 2011; DiMarco et al., 2014; Kremen, 2015; Frison, 2016; Ceballos et al., 2017; Dinerstein et al., 2019). As a result, carnivorans and ungulates are often extirpated to arid, resource-poor areas that are among the most sensitive to modern climate change (Gerten et al., 2008; IPCC, 2014). Over the next century, these regions are expected to experience reductions in vegetation productivity and cover, and increased soil disruption and overall aridity (Huang et al., 2016; Berdugo et al., 2020). This is further exacerbated by increased variability of precipitation (Noy-Meir, 1973) due to climate change (IPCC, 2014). Precipitation is a limiting resource in arid, temperate, and dry sub-humid terrestrial ecosystems (Webb et al., 1983; Adler et al., 2006; Gerten et al., 2008; Deguines et al., 2016), and can directly impact vegetation productivity (Morris, 2000; Suttle, Thomsen, & Power, 2007) as well as influence animal species' osmoregulatory behavior and physiology (McCluney & Sabo, 2009; Takei et al., 2012).

This current and forecasted period of climate change is not the first time that a major shift in global climate has significantly affected large-bodied mammals and the ecological communities of which they are a part. In the past, increased aridification and habitat heterogeneity across continents contributed to a reduction of large mammal biodiversity (Tomiya, 2013), including at the Eocene-Oligocene boundary (Prothero, 1985; Hooker, 1992; Legendre & Hartenberger,1992; Goswami & Friscia, 2010), throughout the Miocene (Agustí & Moya-Sola, 1990; Janis et al., 2000, 2004; Fortelius et al., 2002; Barnosky et al., 2003), and at end of the Pleistocene (Koch & Barnosky, 2006; Barnosky et al., 2016). However, according to the fossil record, members of the mammalian taxonomic orders Artiodactyla and Carnivora proliferated during these periods, able to survive aridification and exploit the spread of grasslands (Vrba, 1995; Merceron et al., 2010; Cantalapiedra et al., 2011; Demiguel et al., 2014; Strauss et al., 2017). These deep-time dynamics, combined with their present species richness and global distribution (Goswami & Friscia, 2010; Groves & Grubb, 2011) makes these groups good model taxa for testing the selective advantage of adaptations to global climate change in the past, present, and future. As the world's climate becomes increasingly arid due to anthropogenic climate change, it becomes more pertinent to understand how large-bodied mammals, especially those at high risk, such as ungulates and carnivorans, have anatomically and physiologically adapted to climatic niche change through deep time to provide informed predictions for the conservation of current ecosystems and biodiversity (Martínez-Meyer et al., 2004; Terry & Rowe, 2015).

2. Climate Change Throughout the Cenozoic Era (66 MYA – Present)

At the onset of the Cenozoic, the global climate was extremely warm and humid (Buchardt, 1978; Wolfe, 1978; Wing, 1987; Huber & Sloan, 2001; Zachos, 2001; Janis, 2008; Zachos et al., 2008; Bowen & Zachos, 2010; Galeotti et al., 2010; Strömberg, 2011; Eronen et al., 2012) and extensive tropical and subtropical wetland environments spread across all continents (Jacobs et al., 1999; Strömberg, 2011; Saarinen, 2020). This climate continued throughout the Paleocene and early Eocene, peaking at the early Eocene climatic optimum (Zachos et al., 2001; Gutjahr et al., 2017). In the early to middle Eocene, forested systems remained dominant in North America and much of Eurasia (Leopold et al., 1992); however, there is some evidence of low biomass vegetation, such as sagebrush, savanna, or grassland, in South America and Africa (Jacobs et al., 1999), suggestive of the early origins of more open habitats in the form of "woody savannas" (Leopold et al., 1992). Coincident with this time, although not necessarily correlative, is the emergence of both artiodactyls ("even-toed") and perissodactyls ("odd-toed") ungulates in North America and Eurasia (Gentry, 1994; Janis et al., 1998; Métais & Vislobokova, 2007; Janis, 2008; Wang, 2021). There is also evidence of stem carnivorans emerging in North America and Eurasia at this time (Goswami & Friscia, 2010).

In the late Eocene and across the Eocene-Oligocene boundary, the global climate became significantly cooler and drier (Prothero & Berggren, 1992; Diester-Haass & Zahn, 1996; Zachos et al. 2001; Lear et al., 2008). The tropical and paratropical forests that had characterized the Paleocene and Eocene were increasingly replaced by deciduous and temperate forests, although woodlands remained most dominant globally (Collinson & Hooker, 2003; Saarinen et al., 2020). Plant macrofossils (MacGinitie, 1969), paleosols (Sheldon & Hamer, 2010), and phytoliths (Strömberg, 2005) from the Eocene-Oligocene transition show evidence of the emergence of C4 grasses in North America and South America, likely in response to this global trend of cooling and aridification; however, grasslands were not yet particularly widespread (Jacobs et al., 1999; Strömberg, 2011; Saarinen et al., 2020). While new forms of vegetation began to emerge, many large mammals concurrently faced extinction (Prothero, 1985; Hooker, 1992; Legendre & Hartenberger,1992), including many early perissodactyls (Janis, 1976, 2008). In contrast, artiodactyls experienced a much higher degree of survivorship (Strauss et al., 2017) and even began to diversify into the modern lineages: suines (pig-related forms), tylopods (camel-related forms), and ruminants (Janis, 2008). Modern crown groups of carnivorans, such as Canidae, Mustelidae, and Ursidae, also proliferated, whereas stem carnivorans, like Viverravidae and Miacoidea, dramatically declined (Goswami & Friscia, 2010). Throughout the drier and more temperate Oligocene (Kennett, 1985; Ehrmann & Mackensen, 1992; Steinthorsdottir et al., 2021), the species richness of artiodactyls remained elevated (Strauss et al., 2017), and other crown carnivoran groups, namely Felidae, emerged (Goswami & Friscia, 2010). The landscape of this period was composed primarily of temperate woodlands (Janis, 1993, 2008; Jacobs et al., 1999; Janis et al., 2004; Strömberg, 2004, 2005, 2011; Eronen et al., 2012), although more open, arid habitats gradually continued their spread due to rising aridification (Janis, 2008).

Global aridification continued and temperatures began to rise again in the late Oligocene to early Miocene (Kennett, 1985; Zachos et al., 2001; Retallack, 2013). More open environments began to appear across all continents in response to changes from fairly humid conditions to more seasonally dry climates at various times throughout the Miocene. Paleosol data indicate the presence of expanding dry, open habitats at this time throughout North America (Janis, 1993; Jacobs et al., 1999; Janis et al., 2004; Strömberg, 2004, 2005, 2011; Eronen et al., 2012), South America (Kleinert & Strecker, 2001; Strömberg et al., 2013), western Eurasia (Saarinen et al., 2020), and West Africa (Morley & Richards, 1993; Jacobs et al., 2010). However, environments across most of Eurasia (Fortelius et al., 2002; Kovar-Eder, 2003; Eronen & Rössner, 2007; Eronen et al., 2010; Saarinen et al., 2020) and East Africa (Jacobs et al., 1999) remained predominantly humid forests. These increases in global temperature and aridification peaked during the early-middle Miocene at the Middle Miocene Climatic Optimum (Zachos et al., 2001; Steinthorsdottir et al., 2021). In North America, $\delta^{18}O$ precipitation data show a shift toward heightened aridification (Mix et al., 2013; Chamberlain et al., 2014) that, according to paleosol, phytolith, and fossil material analyses (Janis & Wilhelm, 1993; Jacobs et al., 1999; Retallack, 2004a, b; Solounias & Semprebon, 2002; Strömberg, 2004, 2005, 2006, 2011; Eronen et al., 2012) resulted in a broad expansion of grass ecosystems (Levering et al. 2016). This dramatic shift in habitat in North America coincided with the height of artiodactyl diversity (Janis et al., 2000, 2004; Barnosky et al., 2003), and the migration of carnivorans into Africa and South America (Goswami & Friscia, 2010). However, analyses indicate that a similar expansion of open habitats did not occur in the Old World until later (Eronen et al., 2012). Following this climatic optimum, temperatures gradually declined, but aridity continued to increase (Zachos et al., 2001; Ivanov et al., 2002).

The late Miocene is characterized primarily by the radiation of open woodlands and grass-dominated habitats, particularly those populated by C4 grasses (Cerling et al., 1993; Cerling et al., 1997; Pearson & Palmer, 2000; Retallack, 2001; Edwards et al., 2010;; Strömberg & McInerney et al., 2011; McInerney et al., 2011), in North America (Cerling et al., 1997; Retallack, 1997; Strömberg, 2011; Strömberg & McInerney, 2011; Eronen et al., 2012), Eurasia (Eronen et al., 2010; Eronen et al., 2012; Saarinen et al., 2020), and East Africa (Cerling et al., 1997; Saarinen et al., 2020). The increase of dry, highly seasonal conditions in North America during this time was most likely related to upwelling in the eastern Pacific, drying up rivers in the North American southwest (Jacobs et al., 2004), and resulting in the replacement of short-grass savannas with tall-grass prairie ecosystems (Retallack, 2001). In contrast, the increased aridification in Eurasia has been linked to changes in the magnitude of Atlantic oceanic heat transport via the development of the Panama seaway (Eronen et al., 2012). However, humid conditions returned to eastern Eurasia in the late Miocene (Eronen et al., 2012) due to the onset of the monsoon season (Fortelius et al., 2002). As habitats became increasingly arid, mammalian taxonomic diversity decreased (Fortelius et al., 2002). In western Eurasia, forest-adapted mammals, including perissodactyls and tragulid artiodactyls, became increasingly replaced by more open-habitat-adapted taxa, primarily ruminant artiodactyls (Agustí & Moya-Sola, 1990).

In contrast to the climatic fluctuations of the Miocene, the Pliocene was characterized by more stable conditions (Herbert el al., 2016; Saarinen et al., 2020), and open, dry grasslands continued to spread across Africa, Eurasia, and North America (Jacobs et al., 1999; Eronen et al., 2012; Saarinen et al., 2020). The formation of the land bridge between North and South America during this period, in addition to allowing transcontinental migration of fauna, disrupted circum-equatorial circulation of oceanic heat transport, resulting in the extreme aridification of East Africa (Janis, 2008). This aridification led to widespread C4-dominated grasslands (Cerling, 1992; Plummer et al., 1999; Levin et al., 2011) in the Pleistocene. The Pleistocene was characterized by strong climatic oscillations and recurrent glacial cycles in North America and Eurasia (Janis, 2008; Herbet et al., 2016; Saarinen et al., 2020) that are coincident with global, large-scale extinctions of large-bodied mammals (Koch & Barnosky, 2006; Barnosky et al., 2016).

The development of open, dry grassland ecosystems across the globe is a prominent feature of the Cenozoic, arising across a multistage process involving: the appearance of open-habitat grasses in the Paleogene, the spread of grass-dominated habitats in the Miocene, and, finally, the expansion of C4 grasses in tropical and subtropical regions in the late Miocene through to the Pliocene (Jacobs et al., 1999; Saarinen et al., 2020). The emergence of low biomass vegetation as a food source allowed for the radiation of ungulates (MacFadden, 1992) and their consumers, the carnivorans (Goswami & Friscia, 2010), closely linking the diversification of these groups with geographically widespread, long-term shifts in climate (Webb, 1969,1977; Vrba, 1992; Janis, 1993; Jernvall & Fortelius, 2004; Costeur & Legendre, 2008; Maridet & Costeur, 2010).

3. Climatic Indicators of Aridification

In addition to affecting biodiversity, studies have demonstrated that there is a close relationship between global climate change and functional anatomical and physiological traits through time (Fortelius et al., 2002; Eronen et al., 2010; Schap et al., 2021). Functional traits are measurable features that influence an organism's interaction with its environment (McGill et al., 2006; Violle et al., 2007), and, as a result, the morphological composition of a community can be a strong indicator of climate and environment (Valverde, 1964; Legendre, 1986; Brown & Nicoletto, 1991; Montuire, 1999; Millien et al., 2006; Violle et al., 2007; Saarinen et al., 2014; Enquist et al., 2015; Short & Lawing, 2021). Changes in food resources (Vrba, 1992; Janis et al., 2004; Strömberg, 2006) and habitat structure (Vrba, 1992; Janis, 1993; Jacobs et al., 1999; Janis et al., 2004; Retallack, 2004a,b) may influence taxon survivorship, driving these morphological shifts (Vrba, 1985, 1993). Webb (1977) proposed that changes in the morphology of ungulates throughout the Cenozoic were indicative of changing ecosystems, and further studies have found that these macroevolutionary patterns are consistent across continents (Saarinen et al., 2014). Two of the most frequently studied ecomorphological climate proxies include dietary characters, such as hypsodonty (high crowned molars; Webb, 1977; Janis, 1995; Spencer, 1995; Pérez-Barbería & Gordon, 2001; Mendoza et al., 2002; Solounias & Semprebon, 2002; Croft & Lorente, 2021), and locomotory characters, such as metapodial length (Webb, 1977; Scott, 1985; Kappelman, 1988; Mendoza & Palmqvist, 2006; Plummer et al., 2008; Croft & Lorente, 2021). These features are thought to provide information about the vegetation and climatic conditions of their paleoenvironment (Kappelman, 1991; Janis et al., 2002; Mihlbachler et al., 2011; Croft & Lorente, 2021). However, other functional traits, such as headgear (Morales et al., 1993), and vasculature, such as carotid retia, capable of facilitating conservation of body water (Fuller et al., 2007; Mitchell & Lust, 2008), have similarly been proposed as characters that emerged under the influence of global climate change, although they have received much less attention.

3.1 Hypsodonty

Although dental and locomotory characters have been frequently utilized as ecomorphological indicators, more recent evidence suggests that the signals they provide may not be reliably congruent with environmental shifts, specifically those resulting from aridification. For example, the overall increase of tooth crown height (hypsodonty) is often attributed to the shift toward C4-dominated open grasslands in the late Miocene (Cerling et al., 1997; Demiguel et al., 2014). Hypsodont, or high-crowned molar, teeth are well-suited to withstand the wear from grinding grit and phytolith-rich grasses (Van Valen, 1960; Fortelius, 1985; Janis, 1988; Janis & Fortelius, 1988; Williams & Kay, 2001; Janis, Damuth, & Theodor, 2002; Mendoza & Palmqvist, 2008; Eronen et al., 2010; Staver et al., 2011; Damuth & Janis, 2011; Jardine et al., 2012; Eronen et al., 2012; Lucas et al., 2014; Madden, 2015; Semprebon et al., 2019; Martin et al., 2020; Saarinen et al., 2020; Croft & Lorente, 2021). Communities within arid, open habitats are most often dominated by hypsodont taxa (Eronen et al., 2010; Fortelius et al., 2002; Janis et al., 2000; Damuth & Janis, 2011; Short & Lawing, 2021), resulting in hypsodonty indices for the presence of open, grass-dominated environments (MacFadden & Cerling, 1994; Jernvall et al., 1996; MacFadden, 2000; Janis et al., 2000; Solounias & Semprebon, 2002; Strömberg, 2006, 2011; Mihlbachler & Solounias, 2006; Janis 2007; Damuth & Janis, 2011; Jardine et al., 2012; Eronen et al., 2012; Morales-Garcia et al., 2020). However, several lines of evidence are not consistent with this traditional assumption. The earliest evidence of hypsodonty has been identified within exclusively South American ungulate lineages during the Eocene (Ortiz-Jaureguizar & Cladera, 2006; Janis, 2008; Strömberg et al., 2013; also see **Table 1.1**), predating the presence of open environments in South America (Fortelius et al. 2002; Eronen et al. 2010; Strömberg, 2011; Strömberg et al., 2013; Madden, 2015). Additionally, tooth wear in hypsodont notoungulates has been found to be indicative of browsing and mixed feeding as opposed to grazing, which is typical of ungulates inhabiting open grasslands (MacFadden, 2005; Townsend & Croft, 2005, 2008; Croft & Weinstein, 2008). Thus, this dental character may not have evolved in South American ungulates as a dietary adaptation for consuming grasses, but rather an adaptation to an accumulation of highly abrasive material in the diet, namely volcanic ash (Billet et al., 2009; Strömberg et al., 2013; Saarinen et al., 2020). In contrast, increased hypsodonty in many North American ungulates around the early-middle Miocene transition (Janis et al., 2002; see also **Table 1.1**) slightly post-dates the appearance of grass-dominated open habitats (Strömberg, 2002, 2006). Tooth wear in hypsodont North American ungulates suggest that they were primarily browsers and mixed feeders (Hayek et al. 1992; MacFadden et al. 1999; Janis, 2008) and the emergence of true, specialized grazers is not evident until the Plio-Pleistocene transition (Spencer, 1997; Janis., 2008). Given these lines of evidence, there is no simple correlation between the presence of hypsodonty and arid, open habitats (Janis, 2008; Strömberg et al., 2013). Rather, hypsodonty is an indicator of the presence abrasive material in diet, which, in contrast to previous assumptions, may be independent of an open environment (Jardine et al., 2012; Strömberg et al., 2013). Hypsodonty is, therefore, not the most accurate potential indicator of environmental aridity (Janis, 2008).

3.2 Cursoriality

Previous research has also correlated locomotory-related characters with habitat, including calcaneal morphology, limb elongation, and lateral digit reduction (all of which result in cursoriality), as a marker for habitat openness (Kowalevsky, 1873; Lull, 1904; Gregory, 1912; Howell, 1944; Coombs, 1978; Sinclair, 1983; Hildebrand, 1985; Scott, 1985; Garland et al., 1988; Kappelman, 1988; Garland & Janis, 1993; Hildebrand et al., 1995; Polly & MacLeod, 2008; Plummer et al., 2008; Bormet, 2010; Clifford, 2010; Levering et al., 2016; Panciroli et al., 2017; Morales-Garcia et al., 2020; Croft & Lorente, 2021; Short & Lawing, 2021). The elongation of the autopod (distal limb segment) has been found to be biomechanically advantageous in open habitats by increasing stride length (Lull, 1904; Hildebrand et al., 1995; Levering et al., 2016) in North America (Janis & Wilhelm, 1993) and Eurasia (Agustí & Anton, 2002; Janis, 2008). As a result, the presence of cursorial limb morphologies has been proposed as sufficient support for the presence of open, savanna-like habitats in the mid-to-late Miocene in North America (Webb, 1977; Janis, 1993; Janis et al., 2004; Levering et al., 2016), Eurasia (Eronen et al., 2009), and South America (Webb, 1978) – see also **Table 1.1**. However, this trend is not consistent across continents. Highly cursorial South American ungulates have been found exclusively in closed, forested habitats during the Oligocene (Janis & Wilhelm, 1993;

Soria, 2001; Cassini et al., 2012; Corona et al., 2019; Morosi & Ubilla, 2019). This directly contrasts with observations within the North American fossil record, which find cursoriality increases with habitat openness characteristic of the Miocene (Fedak et al., 1982; Kram & Taylor, 1990; Alexander, 2002; Hoyt et al., 2006; Levering et al., 2016). Additionally, strong relationships between calcaneal morphology, vegetation cover, and precipitation have been proposed in artiodactyls (Clifford, 2010; Short & Lawing, 2021) and carnivorans (Polly, 2010; Short & Lawing, 2021), where communities with low calcaneal gear ratios inhabit areas with low vegetation cover and precipitation, and communities with high calcaneal gear ratios reside in areas with high vegetation cover and precipitation (Short & Lawing, 2021). However, Polly (2010) found the distribution of mean calcaneal gear ratio is not directly affected by precipitation, and its observed influence is likely indirectly imposed via the density of vegetation cover (Polly, 2010; Barr, 2017, 2020). Given this, cursoriality is not a consistent reliable indicator for habitat openness (Croft & Lorente, 2021) or aridity (i.e. precipitation; Polly, 2010).

3.3 Headgear

For my thesis, I will explore two additional, less-investigated potential ecomorphological traits that may correspond with environmental aridity: elaborate cranial ornamentation (headgear) and carotid-rete-mediated selective brain cooling. Cranial headgear, such as horns and antlers, may indicate adaptation to global climate change response (Morales et al., 1993). Horned ruminants – pecorans (*sensu* Hassannin et al., 2012) – diverged from more ancestral artiodactyls at the Oligocene-Miocene transition (Foss & Prothero, 2007). According to the fossil record, the emergence of headgear occurred concurrently in the early-mid Miocene in North America (Morales et al., 1993; Janis, 2008; Demiguel et al. 2014), Eurasia (Morales et al., 1993; Gentry, 2000; Janis, 2008; Demiguel et al. 2014), and Africa (Morales et al., 1993; Demiguel et al. 2014; see also **Table 1.1**) during a period of heightened global aridification (Kennett, 1985; Zachos et al., 2001; Retallack, 2013; Steinthorsdottir et al., 2021). Given the near simultaneous emergence of this feature, it has been hypothesized that the presence of pecoran headgear is correlated with large-scale climate change (Geist, 1971; Morales et al., 1993). Patterns of cooling and drying that increased global seasonality (described by Zachos et al., 2001), have been proposed as the driving factor for the presence of these appendages (Janis 1982, 1990; Morales et al. 1993; Demiguel et al. 2014). This hypothesis is supported by the functionality of headgear as thermoregulatory structures. In large-bodied mammals especially, highly vascular extremities can serve as conduits for releasing heat load (Scholander et al., 1950). The internal horncores in bovids (Taylor, 1962, 1966; Picard et al., 1994; Picard et al., 1999; Hoefs, 2000; Parés-Casanova & Kucherova, 2014) and giraffids (Ganey, 1990; O'Brien et al., 2016) are highly vascularized, and have been found to provide significant contributions to heat dissipation (Taylor, 1966; Picard et al., 1994; Picard et al., 1999; Hoefs, 2000). This is further corroborated as horned ruminants in more arid, open environments tend to have larger headgear, increasing surface area for heat loss (Wehausen & Ramey, 1993; Picard et al., 1996; Picard et al., 1999; Hoefs, 2000), and appendages are typically present in both sexes (Jarman, 1974; Hoefs, 2000); whereas, in more humid, closed conditions, headgear tends to be smaller (Wehausen & Ramey, 1993; Picard et al., 1996; Picard et al., 1999; Hoefs, 2000) and only present in males (Jarman, 1974). The convergent evolution of headgear across continents during a period of high global aridification, as well as its proposed function as a thermoregulatory structure and correlation to habitat dryness and openness, make pecoran cranial appendages good potential indicators of environmental shifts, especially those resulting from aridification. In Chapter II, I will investigate the thermoregulatory potential of cranial appendages using headgear of pronghorn antelope (*A. americana*), an arid-adapted species, as a model specimen. This requires the establishment of a foundational description of the osteohistology of *A. americana* horncores given the dearth of current literature.

3.4 Selective Brain Cooling

Carotid-rete-mediated selective brain cooling is another potentially good metric to indicate environmental aridity, as it is known to result in conservation of body water (Taylor, 1970a,b; Baker, 1989; Kuhnen & Jessen, 1991; Jessen et al., 1998), and is found in taxa, namely artiodactyls and feliform carnivorans (Baker & Hayward, 1968a,b; Baker, 1972; Baker & Doris, 1982; Mitchell et al., 1987; Caputa, 2004; Fuller at al., 2007; Mitchell & Lust, 2008; O'Brien & Bourke, 2015; O'Brien, 2016, 2018, 2020; Strauss et al., 2017) that proliferated during periods of past aridification (Mitchell & Lust, 2008; Strauss et al., 2017; O'Brien, 2018), such as at the Oligocene-Miocene transition (Kennett, 1985; Retallack, 2013; see also **Table 1.1**). Carotid-rete-mediated selective brain cooling attenuates evaporative cooling by indirectly reducing the temperature of the hypothalamus (Strauss et al., 2017), the temperature response center of the brain (Benzmger, 1973; Smiles et al., 1976; Mitchell et al., 1987; McKinley et al., 2008). Within arid environments, water scarcity exerts a selective pressure in which utilizing body water for evaporative cooling may be more disadvantageous than developing hyperthermia (Schmidt-Nielsen et al., 1956; Taylor, 1970a,b; Baker, 1989; Baker & Turlejska, 1989; Jessen et al., 1998; McKinley et al., 2008; Hetem et al., 2016). Therefore, the conservation of body provided by the reduction of evaporative cooling via carotid-rete-mediated selective brain cooling has been proposed as a key adaptation to combating the selective constraints imposed by environmental aridity (Fuller et al., 2007; Mitchell & Lust, 2008). The selectively advantageous water-conserving physiology produced by carotid-rete-mediated selective brain cooling and its presence in taxa with pronounced periods of diversification under increasing global aridity indicate that carotid retia may be a provide a reliable marker of environmental shifts toward aridification. In Chapter III, I will investigate the variation of water economies across several mammalian taxa to determine the relationship between environmental constraint (i.e. aridity) and conservation of body water through carotid-rete-mediated selective brain cooling using $\delta^{18}O$ values derived from tooth enamel as a proxy for water metabolism and presence of the carotid rete as a metric for aridity resistance.

	Africa	**Eurasia**	**North America**	**South America**
Holocene (12k – now)	**Hypsodonty**			
Pleistocene (2.58mya – 12k)	**Cursoriality**			
Pliocene (5.3mya-2.58mya)				
Miocene (23mya-5.3mya)	**Headgear** **Carotid retia**	**Cursoriality** **Headgear** **Carotid retia**	**Hypsodonty** **Cursoriality** **Headgear** **Carotid retia**	
Oligocene (33.9mya-23mya)				**Cursoriality**
Eocene (56mya – 33.9mya)		**Hypsodonty**		**Hypsodonty**
Paleocene (66mya – 56mya)				

Table 1.1. *Timeline of evidence for climatic indicators to environmental aridity across continents and through geological time.*

4. Conclusion

Global climate change throughout the Cenozoic, especially that resulting in aridification, has driven a myriad of adaptations in Ferungulata (artiodactyls, perissodactyls, and carnivorans), including characters such as hypsodont dentition, cursorial metapodial traits, cranial appendages, and carotid retia. These ecomorphological traits have previously been used as potential indicators of factors of environmental aridity, including habitat openness; however, hypsodonty indices and anatomical features of cursoriality have been found to provide inconsistent determinations across continents. While addressing all of these characters is beyond the scope of this thesis, features that influence thermoregulatory physiologies and body water conservation, such as cranial appendages and carotid retia, are integral to understanding species’ responses under increasing modern global aridification.

A FOUNDATIONAL DESCRIPTION OF *ANTILOCAPRA AMERICANA* HORNCORE OSTEOHISTOLOGY

1. Introduction

Cranial bony projections, otherwise known as "headgear" (Gadow, 1902), have a diversity of forms and functions in mammals (Hopkins, 2005; Mihlbachler, 2008; Davis, Brakora & Lee, 2011; Nasoori, 2020). Most often, headgear is associated with even-toed ungulates, specifically the artiodactyl infraorder Pecora, which includes ruminants such as cervids, bovids, giraffids, moschids, and antilocaprids (*sensu* Hassanin et al., 2012; **Fig. 2.1**). All pecorans – or "horn bearers" – are characterized by headgear that are integument-covered osseous protrusions of the frontal or parietal bone (Davis, Brakora & Lee, 2011), with the exception of moschids, wherein headgear has been secondarily lost (Chen et al., 2019). These cranial appendages serve important functions both behaviorally; such as defense, species recognition, mate selection (Bruhin, 1953; Kitchen, 1974), and physiologically; such as thermoregulation (Taylor, 1966; Stonehouse, 1968; Picard et al., 1996; Picard et al., 1999; Hoefs, 2000). Pecoran headgear is categorized into four unique types based on composition and phylogeny, including: 1) bovid "true" horns, or permanent bony projections of the frontal bones overlain by a permanent keratinous sheath that can be found in both sexes (Janis & Scott, 1987; Davis, Brakora & Lee, 2011); 2) cervid antlers, or periodic, branched bony projections from permanent outgrowths of the lateral crest of the frontal bones that are typically only observed in males (Davis, Brakora & Lee, 2011; Landete-Castelljos et al., 2019); 3) giraffid ossicones, or permanent bony projections of dermal bones covered by integument that can be found in both sexes (although only in males in *Okapia*) (Spinage, 1968; Churcher, 1990; Ganey, 1990); and 4) antilocaprid pronghorns, or permanent bony projections of the frontal bones overlain by a deciduous keratinous sheath that can be found in both sexes (O'Gara, 1990; Davis, Brakora & Lee, 2011).

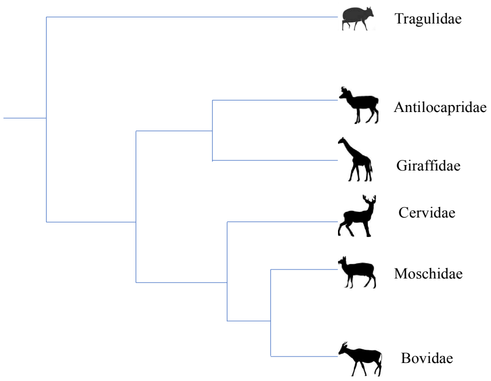

Figure 1. *Phylogeny of Pecora* (*sensu* Hassanin et al. 2012). The artiodactyl supraorder Pecora includes the taxonomic families Antilocapridae (image credit: Roberto Díaz Sibaja), Giraffidae (image credit: Public Domain 1.0), Cervidae (image credit: image credit: Public Domain 1.0), Moschidae (image credit: Public Domain 1.0), and Bovidae (image credit: Public Domain 1.0). Tragulidae (Ruminantia) (image credit: StockImages), serves as the outgroup.

Interests in hunting and animal husbandry have propelled previous studies investigating the development, evolutionary and ecological histories, compositions, and functions of headgear in cervids (Banks & Newbrey, 1983; Caro et al., 2003; Skedros et al., 2014; Akhtar et al., 2019; Wang et al., 2019; Landete-Castelljos et al., 2019; Rössner et al., 2021), bovids (Geist, 1966; Jarman, 1974; O'Gara & Matson, 1975; Caro et al., 2003; Davis, Brakora & Stilson, 2014; Zhang et al., 2018; Wang et al., 2019), and giraffids (Spinage, 1968; Ganey, 1990; Churcher, 1990; Badlangana et al., 2011; O'Brien et al., 2016). In contrast, there is a paucity of literature on the headgear of antilocaprids, with currently available studies mostly restricted to keratin sheath growth (O'Gara, 1990) and macroscopic male headgear growth (Brown, Gonzalsez-Suarez & Hankda, 2006; Mitchell & Maher, 2006) in *Antilocapra americana* (*A. americana*) (Ord, 1815). Additionally, conflicting descriptions aligning *A. americana* (or pronghorn) headgear growth and hormonal development with the disparate patterns of other pecorans (O'Gara & Matson, 1975; Janis & Scott, 1987; Solounias, 1988), have left an understanding of pronghorn headgear growth, development, composition, and function unresolved, especially in females. Further studies of headgear in *A. americana* are therefore important with respect to understanding how this feature is impacted by its function in the contexts of behavior and ecology.

The microanatomy of bone tissue has been found to be influenced by four internal and external signals: phylogeny, biomechanical function, ontogeny, and environment (Horner et al., 1999, 2000; de Ricqlès et al., 2001; Padian et al., 2001; Padian & Lamm, 2013). *A. americana* are phylogenetically isolated as the sole extant lineage of Antilocapridae; however, investigations of the osteohistology of the their horncores may aid in resolving lingering questions about their function, growth and development, and interactions with the environment.

A. americana are particularly gregarious (White et al., 2012) and have been observed using their headgear for intraspecific social communication (Kitchen, 1974) as well as combat between males to gain access to females (Bromley, 1969; Kitchen, 1974). Studies investigating the effects of intraspecific male combat in bovids (Snively & Theodor, 2011; Drake et al., 2016; Zhu, Zhang & Zhao, 2016; Zhang et al., 2018) found that this behavior was facilitated by the microanatomy of the horncores, specifically an increased portion of the cortical area composed of remodeled trabecular bone. The functional properties of trabecular bone as a shock absorber reduces the load of biomechanical stress that would otherwise be imposed on tissues of the cranial vault by engaging headgear in combat (Romanovskaya et al., 1986; Farke, 2008; Snively & Theodor, 2011; Drake, 2016). Given similar behavior in male pronghorns, we predict the extensive presence of trabecular bone within the horncore.

Other studies of pecoran headgear have found that cranial appendages are also sites of physiological processes, such as thermoregulation (Taylor, 1966; Stonehouse, 1968; Picard et al. 1996; Picard et al., 1999; Hoefs, 2000; Mitchell & Skinner, 2004; Parés-Casanova & Kucherova, 2014), although similar investigations have not yet been made of *A. americana* headgear. In bovids, the bony horncore is well-vascularized and is surrounded by a permanent keratinous sheath. Unlike the horncore, the keratinous sheath is a nonliving tissue, and has been found to be a poor insulator of heat radiating from the core surface (Taylor, 1966; Picard et al., 1996). The vascularized horncores therefore provide an enlarged surface area through which heat may be dissipated, with little insulatory resistance from the keratinous sheath (Taylor, 1966; Picard et al., 1996). However, while the composition of *A. americana* headgear is similar to that of bovids, the keratinous sheath is cast annually. Furthermore, female *A. americana* headgear is smaller relative to males or even absent (O'Gara, 1969). Therefore, further investigation of the vascularity density of the tissue surrounding the horncore is needed to determine its potential as a thermoregulatory structure. The present dearth of literature on *A. americana* headgear hinders a greater understanding of structures that may record important functional and environmental factors affecting *A. americana.*

This study aims to examine microanatomical features of *A. americana* horncores, including cortical density, cortical porosity, secondary remodeling, cortical drift, and vascular density, then correlating them with biomechanical and growth selective pressures of known *A. americana* behavior and ecology. Notably, this study is a foundational work that aims to provide baseline descriptions of adult *A. americana* horncores to promote further inquiry into other relevant realms of investigation, including ontogenetic patterning of the horncore, female headgear function, fossil antilocaprid headgear development, and association of *A. americana* headgear with both internal (i.e. thermoregulation) and external (i.e. social displays) characters.

2. Methods

2.1 Specimen Acquisition

We prepared histological slides from one male specimen (WY-DNR Interstate Tag 02005) (F**ig. 2.2-2.3**) and one female specimen (WY-DNR Interstate Tag 02004) (**Fig. 2.4-2.5**) that were obtained in 2013 as salvage from game processing centers in Casper, Wyoming, USA, with the approval of the Wyoming Department of Natural Resources. No animals were killed for the purpose of this study. Specimens were stored frozen until the time of this study. Given the lack of deciduous dentition, both specimens are mature individuals (Lubinski, 2001). Additionally, both specimens come from wild populations and would have been subject to natural conditions affecting skeletal growth of the horncores, including environmental, behavioral, and biomechanical stresses. Access to specimens was limited to on-hand individuals at the research center due to chronic wasting disease in pronghorn populations (Cullingham et al., 2020).

2.2 Tissue processing and osteohistological slide preparation

We removed headgear from the head using a water-cooled band saw (JET Tools, Tennessee) to section the horncore and sheath as close to the frontal bone as possible. Following removal, each specimen was sectioned into approximately 2.5-5 cm fragments that included a transverse section of the base of the horncore (**Figs. 2.2, 2.4**) and a longitudinal section of the shaft (**Figs.**

2.3, 2.5) leading up to the bifurcation of the prongs using a water-cooled tile saw fitted with a continuous rim diamond blade (Tilematic TS250X3, Husqvarna, Sweden). To remove integument and hair remaining on the horncore, samples were dehydrated in a 10% diluted Tergazyme™ (Alconox Inc., New York) solution for 72 hours, then fixed in 10% neutral buffered formalin for 48 hours, before being subjected to increasing levels of ethanol (70%, 85%, 100%) in 24 hour blocks. Finally, samples were cleared in Clear Advantage xylene substitute (Polysciences Inc., Pennsylvania) for 6 hours and embedded in an epoxy-based resin Epothin2 (Buehler, Illinois Toolworks, Illinois). Samples were sectioned into one mm thin sections using an Isomet 1000 diamond-embedded precision saw blade (Buehler, Illinois Toolworks, Illinois) and then mounted on plastic slides, allowing 48 hours for specimens to adhere to the slide with Starbond cyanoacrylate instant adhesive (Starbond Premium, California). Samples were ground into approximately 100-400 µm thin sections with a Buehler Ecomet4 grinder wheel (Buehler, Illinois Toolworks), and liquid coverslips were applied with Polymount (Polysciences Inc., Pennsylvania). Slides were visualized and examined using a Nikon digital sight camera and petrographic microscope (DS-U3 and DS-Fi2; Nikon Instruments, New York) and photographed using NIS-Elements: Documentation software (F4.00.00; Nikon Instruments, New York) under three light regimes: 1) plain, 2) full wavelength cross-polarized, and 3) circularly-polarized light.

For this study, we quantified aspects of the horncore, like cortical density and porosity, using IMAGEJ (1.53v; Schneider et al., 2012). Other features of the horncore, such as those resulting from bone growth and vascular density, were examined, compared, and categorized based on observation of each respective specimen. We specifically categorized types of bone present based on porosity (compact vs cancellous/trabecular cortex), the organization of the bony matrix (i.e. lamellar, woven-fibered, parallel-fibered, fibrolamellar, or Haversian), the presence of immature, woven (primary) or mature, lamellar (secondary) bone, and the pattern of vascular orientation (longitudinal, laminar, plexiform, reticular, or radial) where applicable. Terminology was derived from Francillon-Vieillot et al. (1990) and Padian and Lamm (2013).

3. Results

3.1 Male Pronghorn

3.1.1 Base of Horncore (transverse section)

The medullary region of the bone in this transverse section (**Fig. 2.2A-C**) (total cortical area = 671 mm^2) is composed of remodeled trabecular cortex (337 mm^2 or 50.2% porosity). The outer region of the bone (334 mm^2) is composed of compact cortex. Compact cortical density is between 2521 μm posteromedially and 4080 μm posterolaterally. There is no evidence of annuli representative of lines of arrested growth or an external fundamental system (EFS). However, this may be due to active remodeling, resulting in the infilling of inner trabecular tissue with lamellar tissue, forming compacted coarse cancellous bone (CCCB) (**Fig. 2.2D-F**), that is characterized by erosional tide lines or scalloping throughout the bone (Heck et al., 2019). CCCB infill is most prominent posteromedially, where it continues to the periosteal surface, but also composed 77% (2095 μm^2) and 83% (3387 μm^2) of the compact cortical area of the posterior and posterolateral aspects of the base of the horncore respectively. Measurements from the anterior side of the bone were difficult to calculate as the boundaries between periosteal-derived and CCCB tissue were obscured by secondary osteons. The majority of compact cortex is composed of CCCB, except for approximately 613-693 μm (in posterior and posterolateral aspects respectively) of primary tissue at the periosteal surface. The thin outer cortex of compact tissue at the periosteal surface is classified as fibrolamellar bone due to its high vascular density, lamellar primary osteons, and woven-fibered matrix (Padian & Lamm, 2013).

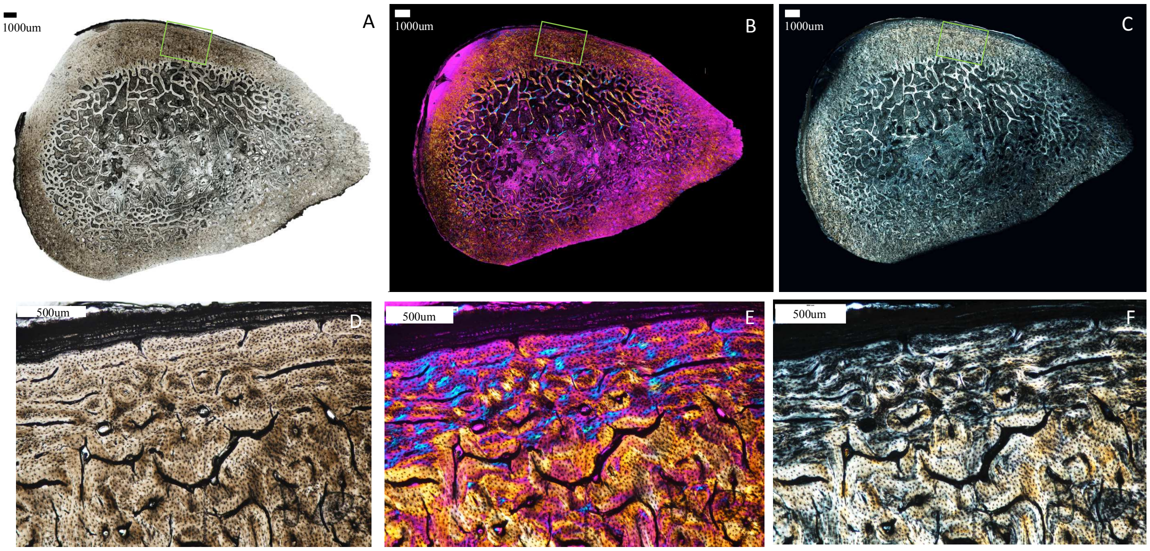

Figure. 2 *Osteohistological features of WY-DNR Interstate Tag 02005 (Male) Horncore Base/Transverse Section.* Transverse section of base of horncore under plain (A,D), full wavelength cross-polarized (B,E), and circularly polarized (C,F) light. The inner medullary region is composed of remodeled trabecular cortex, and the outer, compact cortical area is composed of compacted coarse cancellous bone (CCCB) proximally and fibrolamellar bone (FLB) distally. A dashed line indicates the line of resorption delineating the transition from CCCB to FLB within the compact cortex of the lateral side of the base of the horncore (D-F). The layer of t was not maintained in the male specimen.

3.1.2 Shaft of horncore (longitudinal section)

The bone of the longitudinal section of the shaft of the horncore (**Fig. 2.3**) is similar to that of the base. The cortical area is primarily remodeled trabecular cortex, and, deep to the periosteal surface, the presence of a woven-tissue scaffold with lamellar infill forming primary osteons and a high vascular density is indicative of fibrolamellar bone. Notably, scalloping that demarcates the transition from CCCB to fibrolamellar bone is less clear than in the transverse section, especially more proximally.

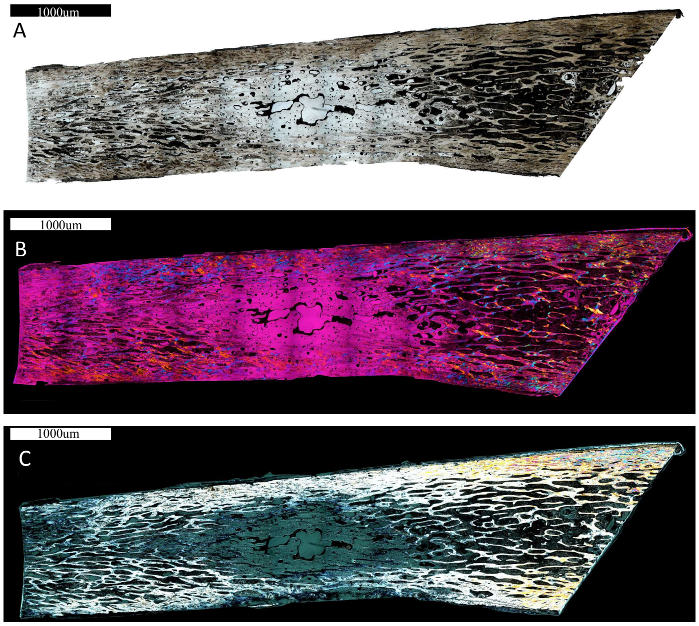

Figure 2.3. *Osteohistological features of WY-DNR Interstate Tag 02005 (Male) Horncore Shaft/Longitudinal Section.* Longitudinal section of the shaft of the horncore under plain (A), full wavelength cross-polarized (B), and circularly polarized (C) light. The composition of the shaft is similar to the base (**Figure 2.2**) in that it is composed of remodeled trabecular cortex, and the compact cortical area is composed of CCCB deep to FLB, which rests at the periosteal surface. It is notable that the tide lines demarcating the transition from CCCB to FLB is less clear than in the transverse section, especially more proximally.

3.2 Female

3.2.1 Base of Horncore (transverse section)

The medullary region of the bone in this transverse section (**Fig. 2.4**) (total cortical area = 545 mm^2) is composed of remodeled trabecular cortex (202 mm^2 or 37% porosity). The outer region of the bone is composed of compact cortex (343 mm^2). Compact cortical density is between 2091 µm posterolaterally and 2815 µm posteromedially. In contrast to the male specimen, CCCB made up only 42% (1172 µm^2) of the compact cortical area posteromedially, although it made up 77% (1617 µm^2) of the posterolateral compact cortical area. The outer layer of compact cortex, near the periosteal border, is composed of primary bone classified as fibrolamellar bone due to its woven-fibered matrix, lamellar primary osteons, and high vascular density (**Fig. 2.4B,E,H**), although it should also be noted there is also a high density of secondary osteons. The tissue between the horncore and the keratinous sheath was maintained in the female specimen (**Fig. 2.4C,F,I**), and shows evidence of reticular vascularization (Padian & Lamm, 2013) near the periosteal surface.

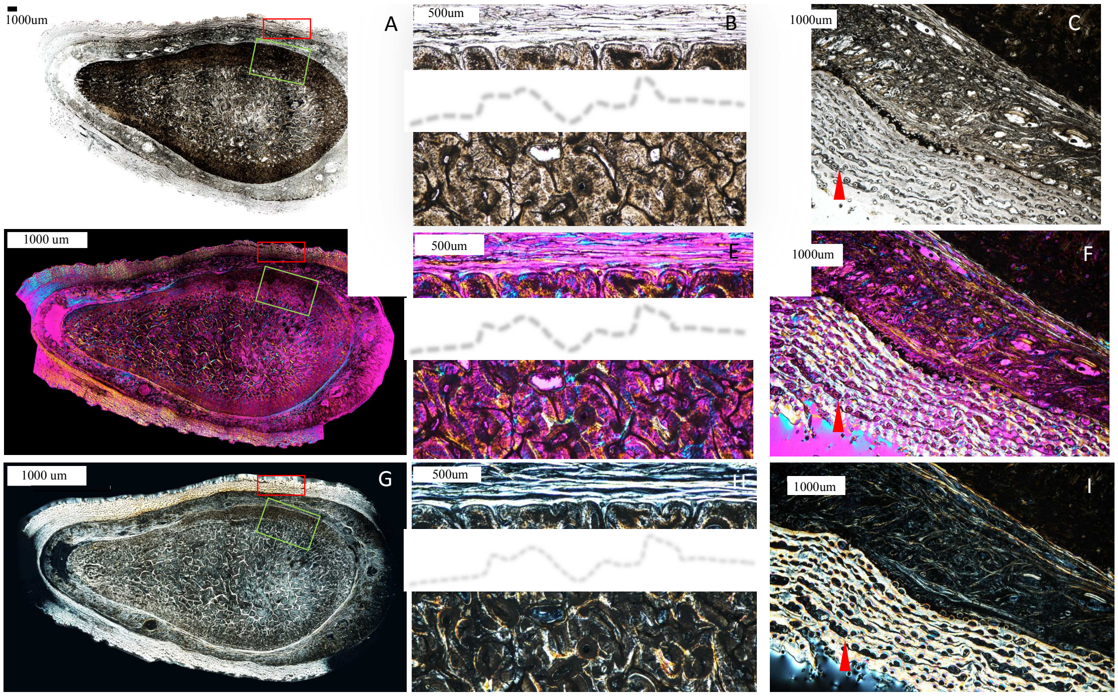

Figure 2.4. *Osteohistological features of WY-DNR Interstate Tag 02004 (Female) Horncore Base/Transverse Section.* Transverse section of base of horncore under plain (A-C), full wavelength cross-polarized (D-F), and circularly polarized (G-I) light. The inner medullary region is composed of remodeled trabecular cortex, and the outer, compact cortical area is composed of CCCB proximally and FLB distally. A dashed line indicates where CCCB has been resorbed and has since been overlain by the primary bone of FLB, delineating the transition from CCCB to FLB within the compact cortex of the posterolateral side of the base of the horncore (B,E,H). Integument was maintained in the female specimen. Images of the posterolateral side of the base of the horncore (C,F,I) show blood vessels (arrow) run throughout the integument covering the horncore, beneath the deciduous keratin sheath. The vascular pattern is characterized as reticular, given that the vessels are oblique in section (Padian & Lamm, 2013).

3.2.2 Shaft of horncore (longitudinal section)

The bone of the longitudinal section of the shaft of the horncore (**Fig. 2.5**) is similar to that of the base. The medullary cortical area is primarily remodeled trabecular cortex. Notably, there is no clear evidence of CCCB in the longitudinal section of the female specimen; however, at the periosteal surface, the presence of primary bone with a woven-fibered matrix, lamellar-oriented primary osteons, and high vascular density is indicative of fibrolamellar bone. In the layer of tissue between the horncore and the keratin sheath, reticular vasculature continues along the shaft of the horncore, beyond its attachment to the frontal bone.

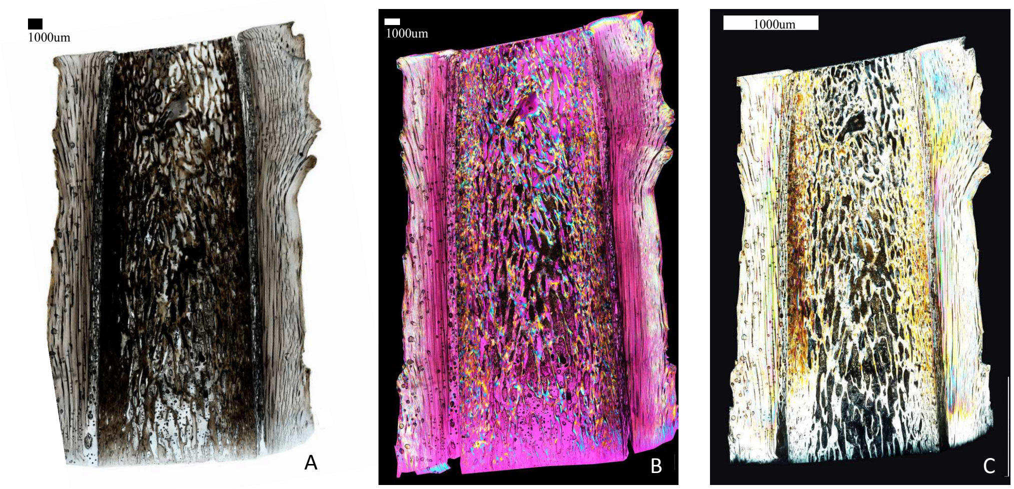

Figure 2.5. *Osteohistological features of WY-DNR Interstate Tag 02004 (Female) Horncore Shaft/Longitudinal Section***.** Longitudinal section of the shaft of the horncore under plain (A), full wavelength cross-polarized (B), and circularly polarized (C) light. The composition of the shaft is similar to the base (**Figure 2.4**) in that the inner, medullary region is composed of remodeled trabecular cortex, and the outer, compact cortical area is composed of FLB. There is no clear evidence of CCCB in the longitudinal section of the female specimen. In the integument, reticular vasculature continues along the shaft of the horncore.

4. Discussion

This study provides the first evidence that the microanatomy of the *A. americana* horncore is likely related to its function in behavior and environmental interaction. The inner medullary region of the base of the male *A. americana* horncore (**Fig. 2.2**) is composed primarily of remodeled trabecular cortex (50.2% pore space). This microanatomy may play a role in shock absorption during intraspecific combat. Previous studies investigating the effects of combat on headgear microanatomy in bovids (Snively & Theodor, 2011; Drake et al., 2016; Zhu, Zhang & Zhao, 2016; Zhang et al., 2018), have found the horn absorbs and transfers the force of impact from the keratinous sheath to a layer of fluid between the sheath and the horncore, then to the horncore and the frontal sinus -- which pneumatizes in the horncores of bovids – and, finally, to the muscles of neck and shoulder girdle. The bovid horncore itself is composed mostly of trabecular cortex (Li et al., 2011; Cappelli et al., 2017) that serves to absorb and dissipate impact energy and protect the brain cavity (Currey, 1988; Drake et al., 2016; Zhu, Zhang & Zhao, 2016; Cappelli et al., 2017) as males engage in ramming, stabbing, fencing, and wrestling with their headgear (Vander & Dumont, 2019). In wild populations of *A. americana*, males interlock their pronged horns, and push and twist against their opponent (Zhang et al., 2018) in order to compete for access and control of females and territory (Bromley, 1969; Kitchen, 1974; O'Gara, 1990). Given the function of the trabecular cortex as a microanatomical shock absorber in bovids, it likely serves a similar purpose in *A. americana* horncores.

Perhaps the most surprising result of this study was the presence of CCCB in the compact cortical area (**Fig. 2.2D-F**). CCCB refers to lamellar bone tissue that infills trabecular cortex, thereby compacting it (Heck et al., 2019). Its presence was unexpected as CCCB is most typically found in the metaphyseal region of long bones (Enlow, 1963), which develop through endochondral ossification rather than the intramembranous ossification that is characteristic of the bones of the cranial vault, including the frontal bones of which *A. americana* horncores are processes. Under this assumption, the presence of CCCB indicates that, similar to long bones, the horncore is load-bearing. This is further corroborated by the extensive presence of trabecular cortex, which likely reduces biomechanical stresses incurred by male-male combat. While it is not possible within the context of the present study to determine if *A. americana* horncores exhibit endochondral growth, there is some precedent for the presence of endochondral bone in pecoran headgear, namely in cervid pedicles (Li ,2013; Landete-Castelljos et al., 2019). Further studies investigating the ontogenetic patterning of *A. americana* headgear should therefore test for the presence of endochondral ossification. Alternatively, evidence of CCCB within *A. americana* horncores may indicate that intramembranous bones may also be able to produce CCCB, rather than being restricted to endochondral processes as previously assumed (Enlow, 1963). To further investigate this, future studies of other pecoran headgear should be especially diligent to check for the presence of CCCB. The ongoing internal compaction of trabeculae by CCCB in the mature male specimen also suggests that the compaction rate of the horncore is superseded by its rate of elongation. This is supported by the presence of fibrolamellar bone at the periosteal surface, indicating that male *A. americana* horncores are growing rapidly, and then compacting later in development.

At the edges of the compact cortical area, the presence of fibrolamellar bone at the periosteal surface (**Fig. 2.2D-F**) is indicative of a high growth rate (de Margerie et al., 2002). This is further corroborated by studies that have found male *A. americana* possess precocial headgear growth, displaying mature, functional headgear in only 2-3 years (O'Gara & Janis, 2004; Mitchell & Maher, 2006). Comparatively, other pecorans achieve full-size headgear in 6-8 years (Mattioli et al., 2021). Given that sexually selective pressures have often been attributed to the evolution of headgear in other male pecorans (Geist, 1966; Bro-Jørgensen, 2007), it is possible that osteohistological signals of rapid growth in *A. americana* headgear, notably fibrolamellar bone at the periosteal surface, could indicate similar sexually selective pressures driving precocial growth in *A. americana*. Additionally, the presence of fibrolamellar bone at the periosteal surface implies that the horncores were still growing at the time of death. Fibrolamellar bone is typically found in juvenile individuals undergoing rapid growth and is remodeled into secondary Haversian bone upon skeletal maturation (de Margerie et al., 2002; Mori et al., 2005). Therefore, the presence of osteohistologically immature bone in the horncores of sexually mature *A.americana* may indicate that skeletal maturity of the horncores is achieved after sexual maturity of the individual. Alternatively, it could indicate that horncore growth may be indeterminate, growing continuously throughout the individual's life. However, further studies investigating the growth of the horncore throughout ontogeny are needed.

The female specimen differs from the male in several notable ways. Most basically, female *A. americana* possess smaller headgear than males or even lack it altogether (O'Gara, 1969, 1990). Microanatomically, the majority of the cortical area in the inner medullary region of the female specimen (**Fig. 2.4**) is more compact (less pore space) than the male. This may be an indication of lower or less frequent biomechanical stress loads (Zhang et al., 2018), as females do not engage in the same intraspecific combat as males (Bromley, 1969; Kitchen, 1974; O'Gara, 1990). Interestingly, female *A. americana* retain their keratin sheaths after the rut and cast them at irregular intervals throughout the year in comparison to the immediate post-rut casting of the sheath in males (O'Gara, 1969). Currently, there is no literature investigating the function of headgear in female *A. americana*; however, studies of female reindeer, which also possess cycles of headgear growth and casting asynchronous with that of males (Loe et al., 2019), have observed that females use their headgear to aid in browsing, and in competition with other females and antlerless males for food acquisition during gestation (Lincoln & Tyler, 1999; Nasoori, 2020 and references therein). Behavioral studies are needed to illuminate if similar mechanical and/or ecological stresses are present in *A. americana* females.

There is also evidence of less CCCB in the female horncore (**Fig. 2.4B,E,H**) compared to the male (**Fig. 2.2D-F**) -- an average of 59.2% of the compact cortical area in the female compared to an average of 91.5% in the male. As female *A. americana* do not use their headgear for mate competition as observed in males, there is likely less selective pressure to develop functional headgear, and, therefore, compaction rate exceeds rate of elongation. Similarly to the male, the presence of fibrolamellar bone at the periosteal surface in a mature specimen implies that the female *A. americana* horncore may have a delayed offset of growth or possibly indeterminate growth.

The tissue between the keratin sheath and the horncore was preserved in the female (**Fig. 2.4C,F,I**) and shows evidence of reticular vascularization (vessels oblique in section; Padian & Lamm, 2013), which, similar to the presence of fibrolamellar bone, is indicative of a high growth rate (Padian & Lamm, 2013). This vascularization may serve as a potential source for the diffusion of nutrients that contribute to the annual growth of a deciduous keratin sheath, or, as established in previous literature on other pecorans, as a site of heat load diffusion (Taylor, 1966; Stonehouse, 1968; Ganey, 1990; Picard et al., 1996; Picard et al., 1999; Hoefs, 2000). In bovids, the bony horncore provides an increased vascular surface and the overlaying keratinous sheath has little resistance to heat flow (Taylor, 1966; Picard et al., 1996; Picard et al., 1999). Arterial blood from the central arteries circulates through capillaries in two layers of tissue: the periosteum, adjacent to the horncore, and the corium, adjacent to the keratinous sheath (Taylor, 1962, 1966; Picard et al., 1999; Hoefs, 2000). If arterial blood temperature at the base of the horncore exceeds ambient temperature, excess heat will be transferred across the blood-keratin boundary by forced convection, then through the poorly-insulated keratinous sheath via conduction, and, finally dissipated into the environment by either free or forced convection (Picard et al.,1999). The relationship between climatic temperature and headgear is strong enough that variation in the former affects both the core-to-sheath ratio and the thickness of the keratinous sheath (Picard et al., 1996). In previous studies, bovids in hotter climates tended to possess larger horncores and thinner sheaths, whereas those inhabiting more temperate climates possessed smaller horncores and thicker sheaths (Picard et al., 1996; Picard et al.,1999; Hoefs 2000). The reduction in the size of the horncore and the increased thickness of the sheath in more temperate bovids serves to decrease the vascular surface area and increase resistance to heat flow respectively; thereby attenuating overall heat loss (Picard et al., 1996; Picard et al., 1999). Giraffid ossicones are also highly vascularized (Ganey, 1990; O'Brien et al., 2016) and, as a result, have been suggested as also having thermoregulatory properties (Mitchell & Skinner, 2004). Given the presence of reticular vascularization of the tissue surrounding the *A. americana* horncore, it is likely that pronghorn headgear similarly plays a role in thermoregulation. However, due to the deciduous nature of the keratin sheath in *A. americana*, this function requires further inquiry.

Overall, *A. americana* horncores tend to be composed mostly of remodeled, porous trabecular cortex, and are fast-growing. They also possess evidence of CCCB, which implies potential endochondral ossification or that CCCB may not be restricted to endochondral processes as previously believed. These features allow for the rapid development of mature headgear with microanatomy that facilitates intraspecific combat in males, although their current function in females is unknown and requires further investigation. The overlaying reticular vasculature may contribute to physiological processes, such as nutrient diffusion or thermoregulation; however, additional studies on the arterial network around the horncore are needed.

Conclusion

Despite their accessibility, the headgear of *A. americana* have been significantly understudied in comparison to other pecorans. Therefore, the aim of this study was to provide a foundational knowledge of the osteohistology of *A. americana* headgear. Slides of two adult specimens (one male and one female) were prepared under standard osteohistological conditions. Although a larger dataset with better-known life histories is preferable, the specimens used in this study were utilized due to their accessibility. The results of this study found that *A. americana* horncores were composed mostly of remodeled, porous trabecular cortex, were fast-growing, and exhibited some potential features of bone undergoing endochondral ossification, namely the presence of CCCB tissue -- although alternative hypotheses, such as the presence of CCCB in non-endochondral bone, are also viable. The male horncore was considerably more porous than the female and also contained a greater quantity of CCCB, indicative of a higher rate of elongation than compaction. Both of these features are mechanically beneficial in promoting the rapid growth of strong, shock-absorbent headgear for male-specific behaviors, such as intraspecific combat. In contrast, the female horncore tended to be more compact, with less compact cortical area composed of CCCB, indicating potential lower biomechanical stress loads to the female horncore and greater rates of compaction than elongation respectively. This is further corroborated as female *A. americana* headgear tends to be smaller or even absent. Slides from the female specimen also included preserved tissue between the horncore and the keratinous sheath, which showed a reticular vascular pattern that was further indicative of rapid growth, and a potential source of nutrient circulation and heat dispersal.

Future studies should address the ontogenetic patterning of *A. americana* horncores comparable to similar studies performed in other pecoran taxa (Dove, 1935; Janis & Scott, 1987; Goss, 1983; Ganey, 1990; Li & Suttie, 1994; Solounias, 2007); headgear function, especially of female *A. americana*; and osteohistology of fossil antilocaprids, which are currently diagnosed primarily by their headgear (Davis, 2007).

CHAPTER III

VARIANCE OF CAROTID-RETE-MEDIATED SELECTIVE BRAIN COOLING ACROSS ARIDITY INDICES

1. Introduction

Species-environment interactions are integral to survivorship, even more so when those environments test the extremes of organismal physiology. Hot and arid environments exemplify this relationship as the environment imparts direct effects on individuals through greater heat gain via high solar radiation and ambient temperatures, as well as imposing increased rates of evaporative water loss to dissipate heat load in spite of minimal access to water and food resources (Feldhamer et al., 1999; Fuller et al., 2014). Species have developed myriad morphological, behavioral, and physiological strategies to contend with these harsh environmental conditions. Morphological adaptations that may reduce heat load and minimize water loss include body size and shape, pelage characteristics, and patterns of fat deposition (Louw & Seely, 1982; Cain et al., 2006). Behavioral strategies, such as shade-seeking (Cain et al., 2006; Fuller et al., 2016), diet selection (Taylor, 1968, 1969; Schmidt-Nielsen, 1979; Jhala et al., 1992), use of microhabitats (i.e. burrowing) (Taylor and Lyman, 1967; Bigalke, 1972; Sowls, 1997; Tull et al., 2001), temporal niche switching (i.e. nocturnality) (Zervanos & Hadley, 1973; Belovsky & Jordan, 1978; Grenot, 1992; Hayes & Krausman, 1993; Sargeant et al., 1994; Berger, 1999; Dussault et al., 2004; Maloney et al., 2005a), and postural changes (Berry et al., 1984; Fryxell & Sinclair, 1988; Maloney et al., 2005b) can also reduce heat stress, but may come at the cost of energy and water acquisition (Fuller et al., 2016). Physiological strategies, including thermal windows and peripheral vasodilation (Tattersall et al., 2012), reduction of water loss in feces and urine (Maloiy et al., 1979; Cain et al., 2006), and utilization of evaporative cooling, such as panting, sweating, and cutaneous evaporation (Robertshaw & Taylor, 1969; Bligh, 1972; Jenkinson et al., 1972; Sokolov, 1982; Simon et al., 1986; Jessen, 2001; Robertshaw, 2006), are also efficient, but similarly incur a high amount of evaporative water loss (Fuller et al., 2016). Mechanisms that enable thermoregulation at the cost of body water may lead to physiological dysfunctions such as dehydration (Kuhnen, 1997; McKinley et al., 2008), heat stress (Laburn et al., 1988; Kuhnen, 1997), or even fatality (Shibolet et al., 1976). Thus, competing homeostatic demands arise between the maintenance of body temperature and body water conservation (McKinley et al., 2008).

Large-bodied mammals (>50 kg) possess a lower surface area-to-volume ratio than small-bodied mammals, resulting in higher thermal inertia (Fuller et al., 2016; Hetem et al., 2016). This means that their body temperatures are comparatively slower to change in response to changes in ambient temperature. A relatively high thermal inertia insulates large-bodied mammals from the thermal consequences of radiant heat loads and aids in the conservation of body water by allowing body temperature to rise during the day, thereby increasing the gradient for dry heat loss to the environment (Mitchell et al., 1987; Mitchell et al., 2002; Fuller et al., 2016). Stored heat load is then dissipated via non-evaporative cooling, such as convection and radiation, when ambient temperatures have significantly decreased (Mitchell et al., 2002). However, large body size prevents the utilization of some behavioral and evaporative thermoregulatory strategies. The variety of microhabitats available to an individual is inversely related to body size (Fuller et al., 2016); therefore, behavioral strategies, such as shade-seeking and burrowing, which are widely used by small-bodied mammals (Walsberg, 2000), may become less efficient or inaccessible to large-bodied mammals. Other competitive stressors, like predation, may also prevent large-bodied mammals from temporal niche switching (Fuller et al., 2014).

Additionally, large-bodied mammals have considerably higher energetic demands (Calder, 1996); as a result, they are more likely to expend a relatively greater proportion of their water budget on thermoregulatory behaviors (Kuhnen, 1997; Hetem et al., 2016). Notably, large body size is associated with increased use of cutaneous evaporative cooling, as a low surface area-to-volume ratio results in lower rates of non-evaporative heat loss (Cain et al., 2006; Hetem et al., 2016). Compared to other forms of evaporative cooling, such as panting, which is typically employed by small-bodied mammals (Robertshaw, 2006), cutaneous evaporation has a higher rate of evaporative water loss (Jessen, 2001). Therefore, despite the benefits toward body water conservation provided by large body size, risk of dehydration remains prevalent as a result of reduced access to thermoregulatory strategies, higher energetic demands, and lower rates of non-evaporative heat loss. Without a physiological mechanism for conserving water, large mammals may be more challenged in arid environments than small mammals.

In arid ecosystems, artiodactyls – the “even-toed” ungulates – (Yousef, 1976; Jones et al., 2009) and carnivorans (Wagner, 1980; Cloudsley-Thompson, 1993,1996) comprise the majority of large-bodied mammals capable of living in high aridity environments due to physiological mechanisms that combat heat stress and water loss. Artiodactyls and feliform carnivores in particular possess specialized physiology that increases the conservation of body water by reducing brain temperature below core body temperature known as carotid-rete-mediated selective brain cooling (CR-SBC) (Baker & Hayward, 1968a,b; Baker, 1972; Baker & Doris, 1982; Mitchell et al., 1987; Caputa, 2004; Fuller at al., 2007; Mitchell & Lust, 2008; O'Brien & Bourke, 2015; O'Brien, 2016; Strauss et al., 2017; O'Brien et al., 2018, 2020). The carotid rete is a meshwork of cranial vasculature that anatomically and functionally replaces the internal carotid artery in supplying the brain (Daniel, Dawes & Prichard, 1953; Nickel & Schwarz, 1963; Kanan, 1970; Gillilan, 1974; Carlton & McKean, 1977; Schummer et al., 1981; Dieguez et al., 1983; Wible, 1984; Frackowiak, 2006; O'Leary, 2010; Frackowiak et al., 2015; O'Brien et al., 2018, 2020). It rests within the subdural cavernous venous sinus at the base of the forebrain (notably, the carnivoran rete resides in the pterygoid plexus; Daniel, Dawes & Prichard, 1953; Baker & Hayward, 1967; Baker, 1972, 1982; Mitchell et al., 1987; Caputa, 2004), which receives blood returning to the body from the nasal turbinates via the angularis oculi vein (Jessen et al., 1998). Nasal turbinates are bony, shelf-like structures within the nasal airway that are covered by a well-vascularized layer of mucosa. The cavernous venous sinus receives blood that has been cooled by the evaporation of water during inspiration (Negus, 1958; Walker et al., 1961; Romer and Parsons, 1986). Typically, respiration results in evaporative water loss. However, as air is inspired over the nasal turbinates, the moisture from the ambient air cools the surface of the turbinates via evaporation (Negus, 1958; Walker et al., 1961; Romer and Parsons, 1986). Upon exhalation, warmed and moistened air passes across these cooled turbinates and the moisture condenses. As a result, moisture is maintained within the nasal passages rather than being lost to the environment, and body water is conserved (Negus, 1958; Walker et al., 1961; Romer and Parsons, 1986). The thin vessel walls and high surface area of the rete allow for rapid counter-current heat exchange between warm arterial blood travelling to the brain from the central arteries and inspirationally-cooled venous blood draining from the nasal turbinates (Taylor, 1966; Baker & Hayward, 1967; Hayward & Baker, 1969; Taylor & Lyman, 1972; Baker &

Chapman, 1977; Baker, 1982; Johnsen et al., 1985; Mitchell et al., 1987; Johnsen & Folkow, 1988; Baker & Nijland, 1993; Mitchell et al., 2002; Maloney et al., 2007; Strauss et al., 2017; O'Brien et al., 2020), thus lowering the temperature of arterial blood perfusing the brain and generating selective brain cooling (Baker, 1982; Mitchell et al., 1987). Singular arteries within the cavernous sinus, such as an internal carotid artery, do not possess the vascular characteristics necessary to facilitate the same arterial blood cooling as the carotid retia (Nunneley & Nelson, 1994; Nelson & Nunneley, 1998).

In addition to their presence in almost all extant terrestrial artiodactyls (Ask-Upmark, 1935; Daniel, Dawes & Prichard, 1953; Baker & Hayward, 1968a,b; Finch, 1972; Gillilan, 1974; Carlton & McKean, 1977; Baker, 1982; Jessen & Feistkorn, 1984; Johnsen et al., 1987; Mitchell et al., 1987; Johnson & Folkow, 1988; Kuhnen & Jessen, 1991; Kuhnen & Mercer, 1993; Jessen et al., 1994; Kuhnen, 1997; Mitchell et al., 1997; Fuller et al., 1999; Maloney et al., 2002; Lust et al., 2007; Hébert et al., 2008; Hetem et al., 2012; Frackowiak et al., 2015; Kieltyka-Kurc et al., 2015; Strauss et al., 2016; O'Brien, 2016), well-developed carotid retia have also been described in feliform carnivores (Daniel, Dawes & Prichard, 1953; Baker & Hayward, 1967; Baker, 1972; Kamijyo & Garcia, 1975; Baker & Doris, 1982; Kier et al., 2019) and a rudimentary rete has been described in domestic dogs (Daniel, Dawes & Prichard, 1953; Magilton & Swift, 1967,1969; Gillilan, 1976; Baker & Chapman, 1977; White et al., 1983; Baker, 1984a). The full taxonomic breadth of the rete within Carnivora remains uninvestigated. However, CR-SBC is conspicuously absent in tragulids (Fukuta, 2007; O'Brien, 2015), hippos (O'Brien, 2016; Strauss et al., 2017), and sister taxon (*sensu* Hassanin et al., 2012), such as perissodactyls, primates, rodents and lagomorphs, and other large herbivores (ex: proboscideans) (Ask-Upmark, 1935; Sisson & Grossman, 1967; Gillilan, 1974; Jessen, 2001; Mitchell et al., 2002).

Historically, it was hypothesized that CR-SBC served to insulate the brain from thermal stress (Taylor, 1966; Baker & Hayward, 1967,1968; Magilton & Swift, 1968; Baker, 1972, 1989; Taylor & Lyman, 1972; Baker & Chapman, 1977; Mitchell et al., 1987); however, more recent studies have found this hypothesis to be invalid under both hot (Mitchell et al., 2002) and cold (Aas-Hansen et al., 2000) conditions. Instead, as Kuhnen and Jessen (1991) first proposed, the function of CR-SBC is now widely accepted as a mechanism for conserving body water (Kuhnen & Jessen, 1991; Jessen et al., 1998). CR-SBC achieves this by indirectly reducing the temperature of the hypothalamus (Strauss et al., 2017), the region of the brain that is primarily responsible for maintaining thermal homeostasis (Benzmger, 1973; Smiles et al., 1976; Mitchell et al., 1987; McKinley et al., 2008). In animals with CR-SBC, hypothalamic temperature is determined by the temperature of arterial blood that has already passed through the rete (Hayward et al., 1966; Strauss et al., 2015). Changes to hypothalamic temperature can significantly alter signals sent to the rest of the body in response to heat stress (Jessen & Kuhnen, 1996; Kuhnen, 1997). For example, if hypothalamic temperatures elevate, heat loss effectors, such as panting and sweating, become more pronounced (Mitchell et al., 1987). By cooling the hypothalamus, CR-SBC therefore counters these thermal responses, resulting in reduced evaporative water loss and conservation of body water (Taylor, 1970a,b; Taylor & Lyman, 1972; Robertshaw & Demi'el, 1983; Baker, 1984b; Jessen & Feistkorn, 1984; Kuhnen & Jessen, 1991; Kuhnen, 1997; Maloney & Mitchell, 1997; Aas-Hansen et al., 2000; Robertshaw, 2006; Fuller et al., 2007; Mitchell & Lust, 2008; Strauss et al., 2015, 2017; Fuller et al., 2016). As hyperthermia increases and evaporative cooling is attenuated by CR-SBC, heat load removal switches to non-evaporative cooling (Caputa et al., 1986; Laburn et al., 1988; Jessen et al., 1994, 1998; Kuhnen, 1997; Mitchell et al., 1997; Jessen et al., 1998; Fuller et al., 1999, 2005; Jessen, 2001; Maloney et al., 2002; Mitchell et al., 2002; Mitchell & Lust, 2008), such as radiation and convection (Jessen et al., 1998; Mitchell et al., 2002). Additional studies have found that CR-SBC becomes enhanced during periods of dehydration (Taylor, 1970a; Maloiy, 1973; Finch & Robertshaw, 1979; Baker & Doris, 1982; Baker & Nijland, 1993; Baker, 1984a,b, 1989; Dmi'el, 1986; Nijland & Baker, 1992; Silanikove, 1994; Jessen et al., 1998; Mitchell et al., 2002; Fuller et al., 2007; Strauss et al., 2015). Water deprivation, including that brought on by environmental factors such as aridity, seems sufficient to upregulate CR-SBC (Hetem et al., 2012). Overall, suppression of evaporative cooling via CR-SBC, even under increasing dehydration and hyperthermia, implies that large-bodied mammals capable of this physiology prioritize conservation of body water over the maintenance of thermal homeostasis (Schmidt-Nielsen et al., 1956; Taylor, 1970a,b; Baker, 1989; Baker & Turlejska, 1989; Jessen et al., 1998; McKinley et al., 2008; Hetem et al., 2016). Thus, CR-SBC may release large bodied mammals from physiological constraints associated with evaporative water loss.

Given the known function of the rete as a mechanism of body water conservation, we hypothesize that CR-SBC releases large-bodied mammals from evolutionary water budget constraints that would otherwise be disadvantageous to large mammals in environments where water is scarce. To investigate this, we model the range of variance in water metabolism, via a proxy of tooth enamel $\delta^{18}O$ values, across individuals from species that possess a carotid rete against those without from three different environmental categories – arid, dry subhumid, and humid. Large-bodied mammals without CR-SBC are likely more constrained in their metabolism of water, so we expect to see a comparatively lower amount of variance in $\delta^{18}O$ values in mammals without a carotid rete. We further expect these differences in $\delta^{18}O$ to be of a higher magnitude within arid climates. As the environment becomes more humid (increased water availability), we expect to see this variation equalize between large mammals with and without CR-SBC. Essentially, we expect that as water availability increases (thereby removing the selective pressure of aridification), the selective advantage of CR-SBC will be reduced.

Stable oxygen isotope ($\delta^{18}O$) analysis has commonly been used in paleoclimate reconstructions because $\delta^{18}O$ values of precipitation are sensitive to temperature, precipitation, humidity, and vapor transport (Dansgaard, 1954, 1964; Gat, 1980, 1996; Yurtsever & Gat, 1981; Ayliffe & Chivas, 1990; Rozanski et al., 1993; Kohn & Cerling, 2002; Vachon et al., 2010a,b; Welker, 2012; Liu et al., 2014; Winnick et al., 2014; Daniels et al., 2017; Bailey et al., 2019; Pederzani & Britton, 2019). Therefore, $\delta^{18}O$ values can serve as a proxy for regional terrestrial temperature and precipitation (Longinelli, 1984; Fricke et al., 1998; Fortelius et al., 2002; Levin et al., 2006; Koch, 2007; Eronen et al., 2010; Fraser & Theodor, 2013), wherein greater $\delta^{18}O$ values are indicative of more arid conditions (Dansgaard, 1964; Luz et al., 1984; Kohn, 1996; Yann et al., 2013). This includes the $\delta^{18}O$ composition of bioapatite, which is derived from tooth enamel. $\delta^{18}O$ values in enamel are affected by additional non-climatic variables, such as diet, metabolic rates, and water turnover (Longinelli, 1984; Luz et al., 1984; Bryant & Froelich, 1995; Kohn, 1996; Levin et al., 2006), with the primary determining factor being body water (Kohn & Cerling, 2002). Hypsodont (high-crowned) tooth enamel records multiple years of body water $\delta^{18}O$ composition, and records changes in consumed meteoric waters (Fricke et al., 1998; Kohn et al., 1998; Balasse, 2002; Passey & Cerling, 2002; Hoppe et al., 2004; Zazzo et al., 2012). While tooth enamel stable oxygen isotope analysis has been applied across a broad range of mammalian taxa, including those with (artiodactyls and carnivores) and without (perissodactyls, proboscideans, rodent, and lagomorphs) CR-SBC (MacFadden & Cerling, 1994; Fricke et al., 1998; MacFadden, 1998; Larson et al., 2001; Higgins & MacFadden, 2004; Feranec &

Macfadden, 2006; DeSantis et al., 2009; Feranec et al., 2010; Uno et al., 2013; Blumenthal et al., 2014), the presence of dentition capable of recording environmental parameters of interest on relevant timescales, as well as their abundance in the fossil record and large spatial and temporal range, makes artiodactyls ideal specimens to study as indicators of climate (Fraser et al., 2021). Levin et al. (2006) presented that $\delta^{18}O$ values of tooth enamel relative to meteoric water values can be used as an aridity index to separate the influences of temperature and precipitation by examining taxa with demonstrated sensitivity to water deficits (Levin et al., 2006; Yann et al., 2013), such as those possessing CR-SBC. The application of an aridity index allows for large-scale comparisons of relative aridity despite complex effects of climatic variables on $\delta^{18}O$ values of precipitation (Yann et al., 2013).

2. Materials and Methods

2.1 Materials: The dataset for this study (**Table 3.1**) is composed of $\delta^{18}O$ values of tooth enamel representing 6 families of Artiodactyla (Bovidae, Cervidae, Giraffidae, Suidae, Hippopotamidae, Camelidae), 3 families of Perissodactyla (Equidae, Rhinoceortidae, Tapiridae), Ursidae from Carnivora, as well as other large-bodied mammals that are within overlapping ecological communities, including Elephantidae, Hominidae, and Hylobatidae, for a total of 1256 specimens. Aridity indices (AI) – the ratio of annual precipitation to evaporation (UNEP, 1992; Williams & Balling, 1986; Gringof & Mersha, 2006) -- from the World Atlas of Desertification (WAD) (European Commission Joint Research Centre) were used with dataset $\delta^{18}O$ values to create three environmental categories: arid ($AI < 0.5$), dry subhumid ($0.5 < AI < 0.65$), and humid ($AI > 0.65$) (Middleton & Thomas, 1997). specimens that were from captive zoological collections were evaluated based on their endemic range.

Taxon	**CR**	**Average $\delta^{18}O$ values**
Aepyceros_melampus	1	33.93174792
Ailuropoda_melanoleuca	0	18.2
Alcelaphus_buselaphus	1	32.91461316
Beatragus_hunteri	1	32.82160489
Capra_sibirica	1	23.850152
Capra_walie	1	30.9527774
Cephalophus_callipygus	1	29.348072
Cephalophus_dorsalis	1	31.48624745
Cephalophus_leucogaster	1	30.60469034
Cephalophus_natalensis	1	27.23338184
Cephalophus_nigrifrons	1	28.32722559
Cephalophus_silvicultor	1	27.76922401
Cephalophus_weynsi	1	28.04008247
Ceratotherium_simum	0	33.98625346
Cervus_elaphus	1	27.7468028
Connochaetes_gnou	1	34.21235672
Connochaetes_taurinus	1	32.23126929
Damaliscus_korrigum	1	33.09234199
Damaliscus_lunatus	1	31.564421
Diceros_bicornis	0	31.02499593
Equus_burchellii	0	33.27143047
Equus_grevyi	0	37.64058813
Eudorcas_thomsonii	1	34.09027323
Giraffa_camelopardalis	1	35.17131849
Hippopotamus_amphibius	0	28.95712255
Hippotragus_niger	1	31.9630202
Hylobates_moloch	0	22
Hylochoerus_meinertzhageni	1	29.33607361
Kobus_ellipsiprymnus	1	32.41691367
Kobus_kob	1	34.74605994
Lama_guanicoe	1	33.061478
Litocranius_walleri	1	37.64158765
Loxodonta_africana	1	31.15051391
Loxodonta_cyclotis	0	27.50559202
Madoqua_kirkii	1	36.964982
Nanger_granti	1	33.56204265
Nanger_soemmerringii	1	33.849494
Neotragus_batesi	1	28.33645472
Okapia_johnstoni	1	30.37784152
Oreotragus_oreotragus	1	34.29558527
Oryx_beisa	1	34.89630401
Ourebia_ourebi	1	30.73879064
Ovis_ammon	1	24.2418788
Ovis_aries	1	22.4481824
Phacochoerus_aethiopicus	1	32.12027936
Phacochoerus_africanus	1	33.65604772
Philantomba_monticola	1	27.98044457
Pongo_pygmaeus	0	21.23333333
Potamochoerus_larvatus	1	29.75808463
Potamochoerus_porcus	1	26.52311575
Redunca_fulvorufula	1	31.84875463
Redunca_redunca	1	31.49155225
Rhinoceros_sondaicus	0	24.36666667
Rusa_unicolor	1	22
Sus_scrofa	1	22.5
Sylvicapra_grimmia	1	30.6503918
Symphalangus_syndactylus	0	23.2
Syncerus_caffer	1	32.23662734
Tapirus_indicus	0	20.55
Trachypithecus_cristatus	0	24.6
Tragelaphus_buxtoni	1	28.597835
Tragelaphus_eurycerus	1	29.4116417
Tragelaphus_imberbis	1	33.57166196

Tragelaphus_oryx	1	-10
Tragelaphus_scriptus	1	31.1975401
Tragelaphus_spekeii	1	30.12757397
Tragelaphus_strepsiceros	1	37.05571827
Ursus_arctos	0	23.8913864
Vicugna_pacos	1	22.95934677
Vicugna_vicugna	1	26.52069547

Table 3.1. *Dataset.* Includes genus-level taxonomy, presence/absence of carotid rete (CR), and average $\delta^{18}O$ values.

2.2 Methods:

2.2.1 Sample: Isotope data were grouped using two criteria: presence or absence of CR-SBC within arid, dry subhumid, and humid categories (for a total of 6 categories). Data were compared pair-wise within each environmental category. As the presence of CR-SBC requires the presence of a carotid rete -- and the absence of an internal carotid artery (O'Brien, 2016, Strauss et al., 2017) --, anatomical features can be used as binary indicators of CR-SBC physiology.

Abbreviations: Arid = A, Dry subhumid = DSH, Humid = H, Carotid Rete = CR, Internal Carotid Artery = ICA

2.2.2 Software: All analyses were performed in R (vs. 4.0.4). Packages used to complete analyses included *base R* (R Core Team, 2021), *FSA* (vs. 0.8.32; Ogle et al., 2021), *car* (vs. 3.0-10; Fox, Jordan, Sanford Weisberg, 2019), *conover.test* (vs. 1.1.5; Dinno, 2017), and *dplyr* (vs. 1.0.5; Wickham et al., 2021).

2.2.3 Assumptions: Prior to analysis, isotope values within each of the 6 categories were tested for normality (statistically: Shapiro-Wilkes, {base} vs. 4.0.4; R Core Team, 2021; visually: quantile-quantile plot, {base}vs. 4.0.4; R Core Team, 2021; see **Appendix A**). Of the 6 bins of data, 3 groups of data were found to be statistically non-normal (arid-carotid-rete [$p_{CR.A}$= 2.334 x10^{-9}], arid-internal-carotid-artery [$p_{ICA.A}$= 3.079 x 10^{-8}], and dry-subhumid-carotid-rete [$p_{CR.DSH}$= 2.937 x 10^{-6}] groups), and 3 groups were found to be normal (dry-subhumid-internal-carotid-artery [$p_{ICA.DSH}$= 0.1297], humid-carotid-rete [$p_{CR.H}$= 0.4372], and humid-internal-carotid-artery [$p_{ICA.H}$= 0.08978]). Because of non-normal data distributions, along with sample size imbalances, we therefore employed non-parametric analyses.

2.2.4 Statistical Tests: A non-parametic ANOVA (Kruskal-Wallis; {base} vs. 4.0.4; R Core Team, 2021) and appropriate post-hoc test (Dunn test; {FSA} vs. 0.8.32; Ogle, Wheeler, & Dinno, 2021) were performed to test for differences in group-wise means (see **Appendix A**). For comparison, parametric individual pairwise t-test ({base} vs. 4.0.4; R Core Team, 2021) was also performed. Because evolutionary processes operate on trait and/or performance variance, our analytical focus is on the degree of $\delta^{18}O$ value spread about the mean (i.e. the variance), rather than a comparison of means alone (as in Kruskal-Wallis or ANOVA tests). We performed a non-parametric Conover Squared Ranks Test ({conover.test} vs. 1.1.5; Dinno, 2017) to test for differences in $\delta^{18}O$ value variance between rete presence and absence within all three environmental categories. Levene's parametric test for homogeneity of variance ({car} vs. 3.0-10; Fox & Sanford, 2019) was also performed to corroborate results of the non-parametric analyses. Given the unevenness of sample size across environmental categories (N_{A}= 637, N_{DSH}= 219; N_{H} = 400) and rete presence ($N_{CR.A}$ = 454, $N_{ICA.A}$ = 183, $N_{CR.DSH}$ = 156, $N_{ICA.DSH}$ = 63, $N_{CR.H}$ = 316, $N_{ICA.H}$ = 84) data were randomly subsampled to equalize sample sizes ({dplyr} vs. 1.0.5; Wickham et al., 2021) and the analyses were repeated to verify results.

3. Results

The results of the Kruskal-Wallis test and post-hoc Dunn test (see **Table 3.2, Fig. 3.1**) found that there were significant differences in mean $\delta^{18}O$ values across all environments (p_{A} = 1.79 x 10^{-8}, p_{DSH} = 0.00661, p_{H} = 0.0264). Under a comparative parametric individual pairwise t-test, only mean $\delta^{18}O$ values under arid conditions were significant (p_{A} = 1.23 x 10^{-8}), and those within dry subhumid and humid environments were found to be non-significant (p_{DSH} = 0.0511, p_{H} = 0.07). The Conover Ranked Sum test for non-parametric comparison of variance in $\delta^{18}O$

values found significant differences in variance within arid ($p_A = 0$) and dry subhumid environments ($p_{DSH} = 0.025$), and non-significant variance in humid environments ($p_H = 0.116$). Conversely, under a parametric Levene's test for homogeneity, variance was significant in arid ($p_A = 1.35\text{E-}08$) and humid ($p_H = 1.8 \times 10^{-4}$) environments, and non-significant in dry subhumid environments ($p_{DSH} = 0.733$).

p-values

Environmental Categories	**Dunn Post-Hoc Test**	**Individual Pairwise T-test**	**Levene's Test**	**Conover Ranked Sum Test**
Arid	1.79×10^{-8}	1.23×10^{-8}	1.35×10^{-8}	0
Dry Subhumid	0.00661	0.0511	0.733	0.025
Humid	0.0264	0.07	0.00018	0.116

Table 3.2. *Reported p-values from stable oxygen isotope (δ^{18}O) analysis of tooth enamel.* Reported data include comparison of mean δ^{18}O values both in non-parametric (Dunn Post-Hoc test) and parametric (individual pairwise t-test) analysis, and comparison of variance δ^{18}O of values across environments in both non-parametric (Conover Ranked Sum test) and parametric (Levene's test for Homogeneity of Variance) analysis.

Analysis was repeated with data subsampled to adjust for discrepancies in sample size between individuals with and without a rete in each environmental group. The results of the Kruskal-Wallis test and post-hoc Dunn Test with subsampled data found significant differences in mean δ^{18}O values in arid environments only ($p_A = 0.00778$) and those within dry subhumid and humid were non-significant ($p_{DSH} = 0.94059$, $p_H = 0.44244$). Under a comparative parametric individual pairwise t-test, mean δ^{18}O values under arid ($p_A = 2.714 \times 10^{-7}$) and dry subhumid ($p_{DSH} = 0.03329$) conditions were significant, and those within humid environments were found to be non-significant ($p_H = 0.0894$). The Conover Ranked Sum test for non-parametric comparison of variance in δ^{18}O values found significant differences in variance only within arid ($p_A = 0.004$), and non-significant variance in dry subhumid ($p_{DSH} = 0.475$) and humid environments ($p_H = 0.221$). Conversely, under a parametric Levene's test for homogeneity, variance was significant in arid ($p_A = 6.082 \times 10^{-6}$) and humid ($p_H = 0.008785$) environments, and non-significant in dry subhumid environments ($p_{DSH} = 0.2879$).

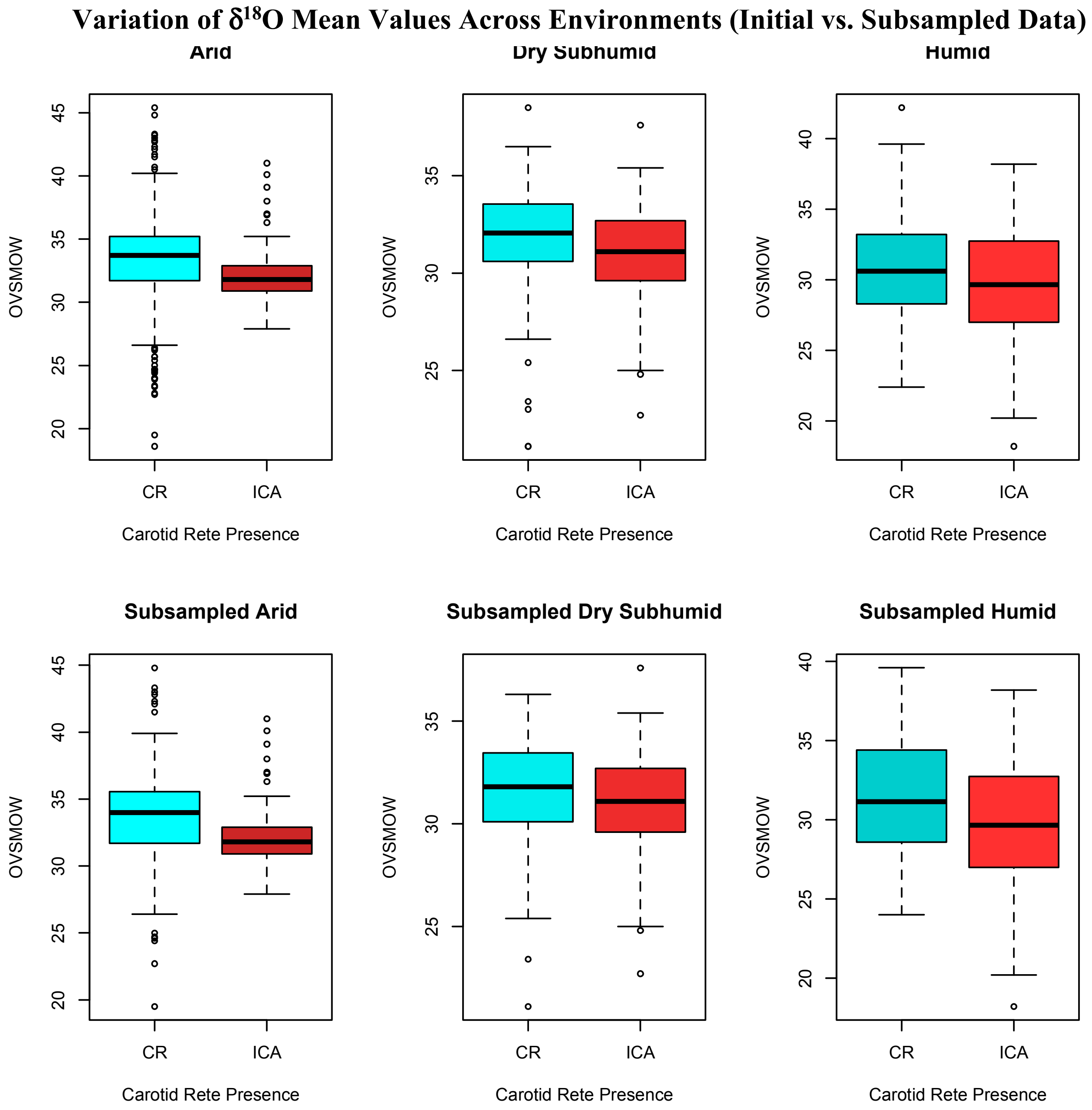

Figure 3.1. *Results of a non-parametric comparison of variance of mean $\delta^{18}O$ isotope values* (see also **Table 3.2**). A Conover Ranked Sum Test found that variance of values was significant in arid and dry subhumid environments, and non-significant in humid environments. When analysis was repeated with subsampled data to adjust for discrepancies in sample size between species with and without a rete in each environmental group (see also **Table 3.3**), significance was consistent across arid and humid categories, and non-significant in dry subhumid environments.

4. Discussion

Given the known function of CR-SBC as a mechanism of water conservation, we hypothesized that CR-SBC releases large-bodied mammals from water budget constraints that would otherwise canalize water metabolism in environments where water is scarce. In this study, we investigated both the mean distribution of $\delta^{18}O$ enamel values and a comparison of the variance of $\delta^{18}O$ values across three distinct environmental categories and in individuals with and without a carotid rete. CR-SBC affects individual performance within an environment, decoupling mean distribution and variance of $\delta^{18}O$ values (**Table 3.2, Fig. 3.1**). Therefore, the emphasis of this analysis is the comparison of the variance of $\delta^{18}O$ values, rather than the differences in group-wise means. The results of the analysis (**Table 3.2, Fig. 3.1**), show there is a comparatively higher, and statistically significant, amount of variance of $\delta^{18}O$ values in mammals possessing the rete than those without, especially within arid climates, that begins to equalize as environmental water availability increases. Within more arid environmental categories, the amount of variation of mean $\delta^{18}O$ values of individuals belonging to species with CR-SBC exceeds that of those without (**Fig. 3.1**). Concurrently, as water availability increases, variance equalizes as the selective advantage of CR-SBC becomes less influential. These results were corroborated when the data were subsampled and the analysis was performed again (**Table 3.3, Fig. 3.1**).

Within arid environments, water scarcity exerts a selective pressure in which utilizing body water for evaporative cooling may be more disadvantageous than developing hyperthermia (Schmidt-Nielsen et al., 1956; Taylor, 1970a,b; Baker, 1989; Baker & Turlejska, 1989; Jessen et al., 1998; McKinley et al., 2008; Hetem et al., 2016). Therefore, the inhibition of evaporative cooling by CR-SBC, and consequent conservation of body water and reduction of metabolic load of thermoregulation, offers a selective advantage in such arid environments (Jessen et al., 1998; Fuller et al., 2014). While attenuation of evaporative cooling does result in hyperthermia, this actually facilitates the switch to non-evaporative cooling. When body temperature is higher than external temperatures, heat load is dispelled passively through nonevaporative means (Mitchell, 1987), and body water is further conserved. Therefore, CR-SBC may be used to facilitate the use of non-evaporative cooling, supplemented by behaviors, like shade-seeking and temporal niche switching (Jessen et al., 1998; Hetem et al., 2012; Fuller et al., 2014), to reduce heat stress and evaporative water loss.

	Dunn Post-Hoc Test	**Individual Pairwise T-test**	**Levene's Test for Homogeneity of Variance**	**Conover Ranked Sum Test**
Arid	0.00778	2.714×10^{-7}	6.082×10^{-6}	0.004
Dry Subhumid	0.9405947	0.03329	0.2879	0.475
Humid	0.442436	0.0894	0.008785	0.221

Table 3.3. *Reported p-values from randomly subsampled data*. Data presented include comparison of mean $\delta^{18}O$ values both in non-parametric (Dunn Post-Hoc test) and parametric (individual pairwise t-test) analysis, and comparison of variance $\delta^{18}O$ of values across environments in both non-parametric (Conover Ranked Sum test) and parametric (Levene's test for Homogeneity of Variance) analysis.

The utilization of CR-SBC has previously been proposed as a mechanism that has allowed for expansion of large-bodied mammals capable of this physiology into arid environmental extremes, from hot deserts to freezing tundras (Mitchell & Lust, 2008; Strauss et al., 2017). Conversely, species that do not possess the carotid rete are far more limited in their thermal and hydrological niches. All wild perissodactyl species and non-CR-SBC artiodactyls, such as tragulids, inhabit environments with low seasonality (little temperature variation), and/or reside near predictable sources of environmental water (Whittow et al., 1977; Skinner & Smithers, 1990; Fuller et al., 2000; Lust et al., 2007; Mitchell & Lust, 2008). Without CR-SBC physiology, non-rete taxa are dependent on low variation in ambient temperature to maintain their body temperature (Whittow et al., 1977). Thus, our analysis, as well as previous literature, supports CR-SBC as a selectively advantageous physiology in arid environments, where water availability is limited, as primarily a water-saving feature that is most useful in preventing dehydration in those species that possess it.

While CR-SBC is highly efficient in conserving body water, there are other physiological mechanisms that provide a similar benefits. Common mechanisms include the reduction of water content in feces and urine volume (Maloiy et al., 1979), particularly in arid-adapted artiodactyls (Taylor & Lyman, 1967; Li et al., 1982; Louw & Seely, 1982; Mohamed et al., 1988). This is made possible as a result of reduced glomerular filtration rates and renal plasma flow (Siebert & Macfarlane, 1971; Maloiy et al., 1979; Wilson, 1989), as well extended loops of Henlé (Schmidt-Nielsen & O'Dell, 1961; Louw & Seely, 1982; McNab, 2002) relative to temperate species. Additionally, the selective influence of CR-SBC is confounded by a nearly complete taxonomic overlap within Artiodactyla of CR-SBC and foregut fermentation, otherwise known as rumination (Janis, 1976, 2007; Gentry, 2000; Vrba & Schaller, 2000; Hassanin & Douzery, 2003; Clauss & Rössner, 2014; DeMiguel et al., 2014). Rumen contains a water reservoir that serves as a buffer against dehydration (Silanikove, 1994; Cain et al., 2006), and may provide a selective advantage in dry environments when compared to non-ruminant ungulates. However, O'Brien (2018) found that CR-SBC was significantly associated with artiodactyl diversification, whereas rumination was non-significant, when investigating CR-SBC across Ferungulata (artiodactyls, perissodactyls, and carnivorans).

The evolutionary history of CR-SBC within Artiodactyla and Perissodactyla has been the primary focus of investigations of the rete in deep time. Artiodactyl diversity has increased since the Eocene (~55-45 mya ago) whereas that of non-rete sister taxa, namely perissodactyls, has decreased (Mitchell & Lust, 2008; Strauss et al., 2017). Previous studies have suggested that climatic changes, specifically aridification events, such as the Early Eocene climatic optimum (Bininda-Edmonds et al., 2007), are likely the source of this contrast (Vrba, 1995; Merceron et al., 2010; Cantalapiedra et al., 2011; Demiguel et al., 2014; Strauss et al., 2017). The presence of CR-SBC has been proposed as an influential factor that allowed artiodactyls to proliferate and expand into myriad habitats, overcoming past global aridification (Mitchell & Lust, 2008; Janis, 2009; O'Brien, 2016); however, its exact emergence in the fossil record is unknown. Osteological correlates associated with the presence of the carotid rete, and, therefore, CR-SBC, have been established by previous studies (O'Brien, 2015, 2016; O'Leary, 2016). In artiodactyls that possess an internal carotid artery rather than a carotid rete, such as tragulids and hippotamids, the presence of the internal carotid artery is indicated by the presence of a groove on the rostromedial wall of the tympanic bulla and a corresponding groove on the body of the basioccipital (O'Brien, 2015; O'Leary, 2016); these grooves are absent in artiodactyls that possess a carotid rete, and, therefore, their absence can be correlated with the presence of a carotid rete and CR-SBC (O'Brien, 2015, 2016).

However, similarly detailed evolutionary histories of the rete are missing for other taxa that possess it, namely carnivorans. Within their evolutionary histories, carnivorans and artiodactyls have often occupied the same ecological communities, and, therefore, may have needed to be able to withstand the same environmental conditions. Developmental studies of the carotid rete in artiodactyls have found that there are differential developmental pathways for the rete across taxonomic families, suggesting that the presence of the rete may be homoplastic in Artiodactyla (O'Brien et al., 2020). Similar ecological conditions may have driven the evolution of a carotid rete, and, consequently, CR-SBC in carnivorans; however, as present studies of the carnivoran rete are limited to domestic cats and dogs (Daniel, Dawes & Prichard, 1953; Baker & Hayward, 1967; Baker, 1972; Kier et al., 2019), this hypothesis remains untested. Carnivorans also lack robust osteological correlates for the rete as exist within Artiodactyla, and further studies are needed to investigate the taxonomic breadth of CR-SBC in extant taxa as well as within the fossil record. Additional studies are also needed to investigate variance of $\delta^{18}O$ values, both within Carnivora and across Ferungulata.

5. Conclusion

Previous studies have established that CR-SBC provides a selective advantage to those species that possess it in environments where water availability is limited and risk for dehydration is high (Kuhnen & Jessen, 1991; Jessen et al., 1998; Hetem et al., 2012; Fuller et al., 2014). The aims of this study were to investigate whether CR-SBC was not only selectively advantageous, but also provided a release from constraint imposed by the environment, specifically aridity. However, it is noted that the dataset for this study primarily focuses on ungulates, and covers the carnivoran rete only within two species of Ursidae; therefore, results should be analyzed within a primary context of Artiodactyla and Perissodactyla. Within this framework, the results of the analysis (**Table 3.2, Table 3.3, Fig. 3.1**) corroborate the release of environmentally-imposed constraint via CR-SBC. Within more arid environmental categories, the amount of variation of mean $\delta^{18}O$ values of individuals belonging to species with CR-SBC exceeds that of those without. Concurrently, as water availability (i.e. humidity) increases, variance equalizes as the selective advantage of CR-SBC becomes less influential. Future studies investigating the physiological capabilities of the rete should focus on three primary areas of interest: 1) the relationship between CR-SBC and physiologies that conserve body water evolved concurrently in artiodactyls, such as rumination; 2) the presence of CR-SBC in the fossil record of Artiodactyla via established osteological correlates (O'Brien 2015,2016; O'Leary, 2016); 3) CR-SBC in Carnivora, both in extant taxa and in the fossil record.

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APPENDIX A

```
##############  PREVALENCE OF CAROTID-RETE-MEDIATED SELECTIVE BRAIN
 COOLING ACROSS ARIDITY INDICES##################
##############        KATHERINE SLENER       ##################
##############     DATE THESIS SUBMITTED    ##################
##############  EXECUTED IN R vs. 4.0.4  ##################

#Clear workspace:
rm(list=ls())

#Set libraries
library(car)#car version 3.0-10
library(dplyr)  #v.s. 1.0.5
library(FSA)    #FSA version 0.8.32
library(conover.test)       #vs. 1.1.5


############################################################
#############################################################
#############################################################
##set working directory
# Upload data for Discrete Character Analysis + boxplots:
data<-read.csv("Rainfall_Rete_Isotope_Categorical_AI.csv", header=TRUE)
head(data)
summary(data)
nrow(data) #1256
#############################################################
#############################################################
######Data husbandry

#####For each variable, find the group specific sample size, mean, median,
 and mode. Test variable for normality.

#####Write function for mode:
getmode <- function(v) {
 uniqv <- unique(v)
 uniqv[which.max(tabulate(match(v, uniqv)))]
}
```

```
###Arid subset
#Arid w/ CR Partition
Arid_CR<-subset(data, Combined_State == "A.CR") #Base R
nrow(Arid_CR)    ##454

 ##Arid w/ CR Summary Statistics:
 #Get Arid CR standard deviation
 sd.A_CR<-sd(Arid_CR$o_vsmow)     ##stats (base R)
 sd.A_CR  ##3.632889

 #Get Arid CR mean
 mean.A_CR<-mean(Arid_CR$o_vsmow)    #Base R
 mean.A_CR   ##33.36432

 # Get Arid CR median
 median.A_CR<-median(Arid_CR$o_vsmow)    #stats (base R)
 median.A_CR ##33.7

 #Get A CR mode

 mode.A_CR <- getmode(Arid_CR$o_vsmow) #stats (base R)
 mode.A_CR   ##34.2

 #Normal Distribution - Non-Parametric
 qqnorm(Arid_CR$o_vsmow) #stats (base R)      #Not normal
 shapiro.test(Arid_CR$o_vsmow)   #stats (base R)
 #W = 0.96251, p-value = 2.334e-09   #Not normal
 hist(Arid_CR$o_vsmow, col=rainbow(14))      #a little skew

#Arid w/ ICA Partition
Arid_ICA<-subset(data, Combined_State == "A.ICA")
nrow(Arid_ICA)   ##183

 #Get Arid ICA standard deviation
 sd.A_ICA<-sd(Arid_ICA$o_vsmow)  ##stats (base R)
 sd.A_ICA        ##1.991667

 #Get Arid ICA mean
 mean.A_ICA<-mean(Arid_ICA$o_vsmow) #Base R
 mean.A_ICA  ##32.15792

 #Get Arid ICA median
 median.A_ICA<-median(Arid_ICA$o_vsmow)  #stats (base R)
 median.A_ICA        ##31.8

 #Get Arid ICA mode
 mode.A_ICA <- getmode(Arid_ICA$o_vsmow) #stats (base R)
 mode.A_ICA  ##30.9

 #Normal Distribution
 qqnorm(Arid_ICA$o_vsmow) #stats (base R)     #Not normal
 shapiro.test(Arid_ICA$o_vsmow) #stats (base R)
 #W = 0.92302, p-value = 3.079e-08 #Not normal
```

```
 #Plot
 hist(Arid_ICA$o_vsmow, col=rainbow(14))


##### Dry Sub-Humid Dataset

##Dry Sub-Humid CR Partition
DrySubHumid_CR<-subset(data, Combined_State == "DSH.CR")
nrow(DrySubHumid_CR) #156

 #Get Dry Sub-Humid CR standard deviation
 sd.DSH_CR<-sd(DrySubHumid_CR$o_vsmow)   #stats (base R)
 sd.DSH_CR #2.726287

 #Get Dry Sub-Humid CR mean
 mean.DSH_CR<-mean(DrySubHumid_CR$o_vsmow)   #stats (base R)
 mean.DSH_CR #31.81154

 #Get DSH CR median
 median.DSH_CR<-median(DrySubHumid_CR$o_vsmow)   #stats (base R)
 median.DSH_CR #32.05

 #Get DSH CR mode
 mode.DSH_CR <- getmode(DrySubHumid_CR$o_vsmow) #stats (base R)
 mode.DSH_CR #31.4

 #Normal Distribution
 qqnorm(DrySubHumid_CR$o_vsmow)  #stats (base R)         #Not normal
 shapiro.test(DrySubHumid_CR$o_vsmow)        #stats (base R)
 #W = 0.93894, p-value = 2.937e-06       #Statistically not normal

 hist(DrySubHumid_CR$o_vsmow, col=rainbow(14))       #visually not normal


##DSH ICA Partition
DrySubHumid_ICA<-subset(data, Combined_State == "DSH.ICA")
nrow(DrySubHumid_ICA) #63

 #Get Dry Sub-Humid ICA standard deviation
 sd.DSH_ICA<-sd(DrySubHumid_ICA$o_vsmow) #stats (base R)
 sd.DSH_ICA  #2.777356

 #Get Dry Sub-Humid ICA mean
 mean.DSH_ICA<-mean(DrySubHumid_ICA$o_vsmow) #stats (base R)
 mean.DSH_ICA #30.99841

 #Get DSH ICA median
 median.DSH_ICA<-median(DrySubHumid_ICA$o_vsmow) #stats (base R)
 median.DSH_ICA #31.1

 #Get DSH ICA mode
 mode.DSH_ICA <- getmode(DrySubHumid_ICA$o_vsmow) #stats (base R)
 mode.DSH_ICA #32.6
```

```
 #Normal Distribution
 qqnorm(DrySubHumid_ICA$o_vsmow) #stats (base R) ##Not normal
 shapiro.test(DrySubHumid_ICA$o_vsmow) #stats (base R)
 #W = 0.97019, p-value = 0.1297  #Normal

 #Plot
 hist(DrySubHumid_ICA$o_vsmow, col=rainbow(14))


##### Humid Subset

### Humid CR Partition
Humid_CR<-subset(data, Combined_State == "H.CR")
nrow(Humid_CR) #316

 #Get Humid CR standard deviation
 sd.Hum_CR<-sd(Humid_CR$o_vsmow)         #stats (base R)
 sd.Hum_CR      #3.384844

 #Get Humid CR mean
 mean.Hum_CR<-mean(Humid_CR$o_vsmow)     #stats (base R)
 mean.Hum_CR #30.78987

 #Get Humid CR median
 median.Hum_CR<-median(Humid_CR$o_vsmow)         #stats (base R)
 median.Hum_CR #30.6

 #Get Humid CR mode
 mode.H_CR <- getmode(Humid_CR$o_vsmow) #stats (base R)
 mode.H_CR #30.3

 #Normal Distribution
 qqnorm(Humid_CR$o_vsmow) #Normal        #stats (base R)
 shapiro.test(Humid_CR$o_vsmow)      #stats (base R)
 #W = 0.99521, p-value = 0.4372  #Normal

 #Plot
 hist(Humid_CR$o_vsmow, col=rainbow(14))


##Humid ICA Partition
Humid_ICA<-subset(data, Combined_State == "H.ICA")
nrow(Humid_ICA) #84

 #Get Humid ICA standard deviation
 sd.Hum_ICA<-sd(Humid_ICA$o_vsmow) #stats (base R)
 sd.Hum_ICA  #4.634624

 #Get Humid ICA mean
 mean.Hum_ICA<-mean(Humid_ICA$o_vsmow)   #stats (base R)
 mean.Hum_ICA #29.80476

 #Get Humid ICA median
 median.Hum_ICA<-median(Humid_ICA$o_vsmow)   #stats (base R)
```

```
 median.Hum_ICA #29.65

 #Get Humid ICA mode
 mode.H_ICA <- getmode(Humid_ICA$o_vsmow)    #stats (base R)
 mode.H_ICA #27.8

 #Normal Distribution
 qqnorm(Humid_ICA$o_vsmow) #Not Normal   #stats (base R)
 shapiro.test(Humid_ICA$o_vsmow)
 #W = 0.97422, p-value = 0.08978     #Normal

 #Plot
 hist(Humid_ICA$o_vsmow, col=rainbow(14))

################################################################
################################################################
#################           Analysis        ###################
################################################################
################################################################

#########Differences in Oxygen Isotopes ##########

####Arid Environments
#Make category vector
CR.ICA.A<-c(rep("CR", nrow(Arid_CR)), rep("ICA", nrow(Arid_ICA)))
CR.ICA.A
length(CR.ICA.A) #637   #Base R

OVSMOW.A<-c(Arid_CR$o_vsmow, Arid_ICA$o_vsmow)
length(OVSMOW.A) #637       #Should match length of CR.ICA.A

Arid.Dat<-as.data.frame(cbind(CR.ICA.A, OVSMOW.A))
head(Arid.Dat)
#  CR.ICA.A OVSMOW.A
#1       CR     39.9
#2       CR     43.2
#3       CR     43.3
#4       CR     27.6
#5       CR       43
#6       CR     23.9

#Make dataframe numeric
Arid.Dat$OVSMOW.A <- as.numeric(as.character(Arid.Dat$OVSMOW.A))

##Levene's test
Lev.arid<-leveneTest(OVSMOW.A~CR.ICA.A, data=Arid.Dat) #Package: car
Lev.arid
#Levene's Test for Homogeneity of Variance (center = median)
#       Df F value    Pr(>F)
#group   1  33.121 1.348e-08 ***
#      635
#---
#Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
##t test
t.arid <- t.test(OVSMOW.A~CR.ICA.A, data=Arid.Dat, var.equal=FALSE)
    #stats (base R)
t.arid
#   Welch Two Sample t-test
#
#data:  OVSMOW.A by CR.ICA.A
#t = 5.3553, df = 579.07, p-value = 1.233e-07
#alternative hypothesis: true difference in means is not equal to 0
#95 percent confidence interval:
# 0.7639486 1.6488387
#sample estimates:
# mean in group CR mean in group ICA
#          33.36432          32.15792

##Plot
boxplot(OVSMOW.A~CR.ICA.A, data=Arid.Dat, col=c("cyan",
 "firebrick3"),main="Oxygen Isotopes Across Arid Environments")

#################################

###Dry Subhumid
#Make a category vector
CR.ICA.DSH<-c(rep("CR", nrow(DrySubHumid_CR)), rep("ICA",
 nrow(DrySubHumid_ICA)))
CR.ICA.DSH
length(CR.ICA.DSH) #219

OVSMOW.DSH<-c(DrySubHumid_CR$o_vsmow, DrySubHumid_ICA$o_vsmow)
length(OVSMOW.DSH) #219

DSH.Dat<-as.data.frame(cbind(CR.ICA.DSH, OVSMOW.DSH))
head(DSH.Dat)
#  CR.ICA.DSH OVSMOW.DSH
#1         CR       34.6
#2         CR       31.8
#3         CR       32.2
#4         CR       32.2
#5         CR       32.6
#6         CR       33.6

#Make dataframe numeric
DSH.Dat$OVSMOW.DSH <- as.numeric(as.character(DSH.Dat$OVSMOW.DSH))

##Levene's Test for Homogeneity of Variance (center = median)
Lev.DSH<-leveneTest(OVSMOW.DSH~CR.ICA.DSH, data=DSH.Dat)
Lev.DSH
#Levene's Test for Homogeneity of Variance (center = median)
#       Df F value Pr(>F)
#group   1  0.1168 0.7329
#      217

##t-test
t.DSH <- t.test(OVSMOW.DSH~CR.ICA.DSH, data= DSH.Dat, var.equal=FALSE)
```

```
t.DSH
#   Welch Two Sample t-test
#
#data:  OVSMOW.DSH by CR.ICA.DSH
#t = 1.9716, df = 112.81, p-value = 0.0511
#alternative hypothesis: true difference in means is not equal to 0
#95 percent confidence interval:
# -0.003954901  1.630206427
#sample estimates:
# mean in group CR mean in group ICA
#        31.81154          30.99841

#Plot
boxplot(OVSMOW.DSH~CR.ICA.DSH, data=DSH.Dat, col=c("cyan2",
 "firebrick2"),main="Oxygen Isotopes Across Dry Subhumid Environments")
#################################

###Humid
#Make a category vector
CR.ICA.H<-c(rep("CR", nrow(Humid_CR)), rep("ICA", nrow(Humid_ICA)))
CR.ICA.H
length(CR.ICA.H) #400

OVSMOW.H<-c(Humid_CR$o_vsmow, Humid_ICA$o_vsmow)
length(OVSMOW.H) #400

H.Dat<-as.data.frame(cbind(CR.ICA.H, OVSMOW.H))
head(H.Dat)
#  CR.ICA.H OVSMOW.H
#1       CR     22.5
#2       CR     36.1
#3       CR     27.6
#4       CR     28.8
#5       CR     29.1
#6       CR     30.3

#Make dataframe numeric
H.Dat$OVSMOW.H <- as.numeric(as.character(H.Dat$OVSMOW.H))

##Levene's test
Lev.Hum<-leveneTest(OVSMOW.H~CR.ICA.H, data=H.Dat)
Lev.Hum
#       Df F value    Pr(>F)
#group   1  14.333 0.0001768 ***
#      398
#---
#Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

##t-test
t.Hum <- t.test(OVSMOW.H~CR.ICA.H, data= H.Dat, var.equal=FALSE)
t.Hum
#data:  OVSMOW.H by CR.ICA.H
#t = 1.8231, df = 107.64, p-value = 0.07106
#alternative hypothesis: true difference in means is not equal to 0
```

```
#95 percent confidence interval:
# -0.08597848  2.05620150
#sample estimates:
# mean in group CR mean in group ICA
#          30.78987          29.80476



######Kruskal-Wallace (non-parametric ANOVA) & post-hoc (Dunn Test)
###1. Query what type of data it is
sapply(data,class)
#       AI          Rete        Combined_State        o_vsmow
#   "factor"    "factor"    "factor"      "numeric"

###2. Run Kruskal-Wallis
kruskal.test(o_vsmow~Combined_State, data = data)
#data:  o_vsmow by Combined_State
#Kruskal-Wallis chi-squared = 160.49, df = 5, p-value <2.2e-16

### 2. Run post-hoc Dunn Test
##install library(FSA)
dunnTest(o_vsmow~Combined_State, data = data)
#       Comparison          Z      P.unadj        P.adj
#1      A.CR - A.ICA  5.2198940 1.790256e-07 2.148307e-06
#2     A.CR - DSH.CR  5.2162013 1.826297e-07 2.008926e-06
#3    A.ICA - DSH.CR  0.2480315 8.041100e-01 8.041100e-01
#4    A.CR - DSH.ICA  5.6413146 1.687567e-08 2.193837e-07
#5   A.ICA - DSH.ICA  2.0632462 3.908924e-02 2.345355e-01
#6  DSH.CR - DSH.ICA  1.8379231 6.607373e-02 3.303687e-01
#7       A.CR - H.CR 11.1007248 1.244307e-28 1.866460e-27
#8      A.ICA - H.CR  3.8343975 1.258724e-04 1.258724e-03
#9     DSH.CR - H.CR  3.3638797 7.685504e-04 5.379853e-03
#10   DSH.ICA - H.CR  0.3971787 6.912357e-01 1.000000e+00
#11     A.CR - H.ICA  8.0020189 1.223956e-15 1.713538e-14
#12    A.ICA - H.ICA  3.7435507 1.814380e-04 1.632942e-03
#13   DSH.CR - H.ICA  3.4458953 5.691708e-04 4.553367e-03
#14  DSH.ICA - H.ICA  1.1519149 2.493560e-01 9.974241e-01
#15     H.CR - H.ICA  1.1175268 2.637692e-01 7.913075e-01

##Results Summary
#Arid -- very significant (A.CR - A.ICA  5.2198940 1.790256e-07 2.148307e-
 06)
#DSH -- somewhat significant (1.8379231 6.607373e-02 3.303687e-01)
#Hum -- least significant (1.1175268 2.637692e-01 7.913075e-01)

#Run Conover Rank Sum Test (nonparametric equality of variances)
conover.test(data$o_vsmow, data$Combined_State, alpha=0.05)

#  Kruskal-Wallis rank sum test
#data: x and group
#Kruskal-Wallis chi-squared = 160.4873, df = 5, p-value = 0
#
#
#                           Comparison of x by group
```

```
#                                (No adjustment)
#Col Mean-|
#Row Mean |       A.CR      A.ICA     DSH.CR    DSH.ICA       H.CR
#---------+-------------------------------------------------------
#   A.ICA |   5.578356
#         |    0.000Hu0*
#         |
#  DSH.CR |   5.574410   0.265064
#         |    0.0000*     0.3955
#         |
# DSH.ICA |   6.028717   2.204934   1.964137
#         |    0.0000*    0.0138*    0.0249*
#         |
#    H.CR |   11.86303   4.097714   3.594885   0.424453
#         |    0.0000*    0.0000*    0.0002*     0.3357
#         |
#   H.ICA |   8.551536   4.000629   3.682533   1.231019   1.194270
#         |    0.0000*    0.0000*    0.0001*     0.1093     0.1163
#
#alpha = 0.05
#Reject Ho if p <= alpha/


 #########################################################################
 ######
#############Subsample
 Data##########################################################
##########################################################################
 #####
##subsampling = resampling is an empirical way to derive sampling
 distributions

######Arid
##CR Partition
subsample_Arid_CR<-sample_n(Arid_CR, size=nrow(Arid_ICA), replace=FALSE)
 #package(dplyr)
nrow(subsample_Arid_CR) #183
nrow(subsample_Arid_CR) == nrow(Arid_CR) #FALSE     #Should be FALSE; IF
 TRUE, your new dataset is the SAME as your old dataset
nrow(subsample_Arid_CR) == nrow(Arid_ICA) #TRUE  #Should be TRUE; IF FALSE
 <- objective not met
##ICA Parition
  subsample_Arid_ICA<-sample_n(Arid_ICA, size=nrow(Arid_ICA),
 replace=FALSE)
nrow(subsample_Arid_ICA) == nrow(Arid_CR)
#[1] FALSE
nrow(subsample_Arid_ICA) == nrow(Arid_ICA)
#[1] TRUE
##Combined
subsample_CR.ICA.A<-c(rep("CR", nrow(subsample_Arid_CR)), rep("ICA",
 nrow(subsample_Arid_ICA)))
length(subsample_CR.ICA.A) #366
```

```
subsample_OVSMOW.A<-c(subsample_Arid_CR$o_vsmow,
 subsample_Arid_ICA$o_vsmow)
length(subsample_OVSMOW.A) #366
subsample_Arid.Dat<-as.data.frame(cbind(subsample_CR.ICA.A,
 subsample_OVSMOW.A))
head(subsample_Arid.Dat)

#Make data numeric
subsample_Arid.Dat$subsample_OVSMOW.A <-
 as.numeric(as.character(subsample_Arid.Dat$subsample_OVSMOW.A))

###Re-run Analysis###
##Levene Test
subsample_Lev.arid<-leveneTest(subsample_OVSMOW.A~subsample_CR.ICA.A,
 data=subsample_Arid.Dat) #package(car)
subsample_Lev.arid
#Levene's Test for Homogeneity of Variance (center = median)
#       Df F value   Pr(>F)
#group   1  34.335 1.04e-08 ***
#      364
#---
#Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##Results differ from original analysis (THIS IS GOOD)

##t-test
subsample_t.arid <- t.test(subsample_OVSMOW.A~subsample_CR.ICA.A,
 data=subsample_Arid.Dat, var.equal=FALSE)   #stats (base R)
subsample_t.arid
#Welch Two Sample t-test
#
#data:  subsample_OVSMOW.A by subsample_CR.ICA.A
#t = 4.116, df = 280.83, p-value = 5.071e-05
#alternative hypothesis: true difference in means is not equal to 0
#95 percent confidence interval:
# 0.6623243 1.8764735
#sample estimates:
# mean in group CR mean in group ICA
#         33.42732          32.15792

##Results differ from original analysis

######DrySubHumid
##CR Partition
subsample_DrySubHumid_CR<-sample_n(DrySubHumid_CR,
 size=nrow(DrySubHumid_ICA), replace=FALSE)
nrow(subsample_DrySubHumid_CR) #63
nrow(subsample_DrySubHumid_CR) == nrow(DrySubHumid_CR) #FALSE
    #Should be FALSE; IF TRUE, your new dataset is the SAME as your old
 dataset
nrow(subsample_DrySubHumid_CR) == nrow(DrySubHumid_ICA) #TRUE    #Should
 be TRUE; IF FALSE <- objective not met
##ICA Partition
```

```
subsample_DrySubHumid_ICA<-sample_n(DrySubHumid_ICA,
 size=nrow(DrySubHumid_ICA), replace=FALSE)
nrow(subsample_DrySubHumid_ICA) == nrow(DrySubHumid_CR)
#[1] FALSE
nrow(subsample_DrySubHumid_ICA) == nrow(DrySubHumid_ICA)
#[1] TRUE
subsample_CR.ICA.DSH<-c(rep("CR", nrow(subsample_DrySubHumid_CR)),
 rep("ICA", nrow(subsample_DrySubHumid_ICA)))
length(subsample_CR.ICA.DSH) #126
subsample_OVSMOW.DSH<-c(subsample_DrySubHumid_CR$o_vsmow,
 subsample_DrySubHumid_ICA$o_vsmow)
length(subsample_OVSMOW.DSH) #126
subsample_DrySubHumid.Dat<-as.data.frame(cbind(subsample_CR.ICA.DSH,
 subsample_OVSMOW.DSH))
head(subsample_DrySubHumid.Dat)

#Make data numeric
subsample_DrySubHumid.Dat$subsample_OVSMOW.DSH <-
 as.numeric(as.character(subsample_DrySubHumid.Dat$subsample_OVSMOW.DSH))

###Re-run Analysis###
##Levene Test
subsample_Lev.DrySubHumid<-
 leveneTest(subsample_OVSMOW.DSH~subsample_CR.ICA.DSH,
 data=subsample_DrySubHumid.Dat) #package(car)
subsample_Lev.DrySubHumid
#Levene's Test for Homogeneity of Variance (center = median)
#       Df F value Pr(>F)
#group   1  0.9664 0.3275
#      124

##t-test
subsample_t.DrySubHumid <-
 t.test(subsample_OVSMOW.DSH~subsample_CR.ICA.DSH,
 data=subsample_DrySubHumid.Dat, var.equal=FALSE)    #stats (base R)
subsample_t.DrySubHumid
#   Welch Two Sample t-test
#data:  subsample_OVSMOW.DSH by subsample_CR.ICA.DSH
#t = 2.9857, df = 120.78, p-value = 0.003426
#alternative hypothesis: true difference in means is not equal to 0
#95 percent confidence interval:
# 0.4615069 2.2781756
#sample estimates:
# mean in group CR mean in group ICA
#         32.36825          30.99841

##Results differ from original analysis

######Humid
##CR Parition
subsample_Humid_CR<-sample_n(Humid_CR, size=nrow(Humid_ICA),
 replace=FALSE)
nrow(subsample_Humid_CR) #84
nrow(subsample_Humid_CR) == nrow(Humid_CR) #FALSE
```

```
nrow(subsample_Humid_CR) == nrow(Humid_ICA) #TRUE
##ICA Partition
subsample_Humid_ICA<-sample_n(Humid_ICA, size=nrow(Humid_ICA),
 replace=FALSE)
nrow(subsample_Humid_ICA) == nrow(Humid_CR) #[1] FALSE
nrow(subsample_Humid_ICA) == nrow(Humid_ICA) #[1] TRUE
#Combined
subsample_CR.ICA.H<-c(rep("CR", nrow(subsample_Humid_CR)), rep("ICA",
 nrow(subsample_Humid_ICA)))
length(subsample_CR.ICA.H) #168
subsample_OVSMOW.H<-c(subsample_Humid_CR$o_vsmow,
 subsample_Humid_ICA$o_vsmow)
length(subsample_OVSMOW.H) #168
subsample_Humid.Dat<-as.data.frame(cbind(subsample_CR.ICA.H,
 subsample_OVSMOW.H))
head(subsample_Humid.Dat)

#Make data numeric
subsample_Humid.Dat$subsample_OVSMOW.H <-
 as.numeric(as.character(subsample_Humid.Dat$subsample_OVSMOW.H))

###Re-run Analysis###
##Levene Test
subsample_Lev.Humid<-leveneTest(subsample_OVSMOW.H~subsample_CR.ICA.H,
 data=subsample_Humid.Dat) #package(car)
subsample_Lev.Humid
#Levene's Test for Homogeneity of Variance (center = median)
#       Df F value  Pr(>F)
#group   1   4.177 0.04256 *
#      166
#---
#Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##Results differ from original analysis

##t-test
subsample_t.Humid <- t.test(subsample_OVSMOW.H~subsample_CR.ICA.H,
 data=subsample_Humid.Dat, var.equal=FALSE)  #stats (base R)
subsample_t.Humid
#Welch Two Sample t-test
#data:  subsample_OVSMOW.H by subsample_CR.ICA.H
#t = 2.1316, df = 157.72, p-value = 0.03459
#alternative hypothesis: true difference in means is not equal to 0
#95 percent confidence interval:
# 0.1009325 2.6490675
#sample estimates:
# mean in group CR mean in group ICA
#         31.17976          29.80476

##Results differ from original analysis

######Kruskal-Wallis & Dunn Test
###Define Combined State
CombinedState <- data$Combined_State
```

```
head(CombinedState)

###Subsample Combined State Data
subsample_CombinedState <- sample(CombinedState)
length(subsample_CombinedState) #1256
### Subsample OVSMOW
OVSMOW <- data$o_vsmow
OVSMOW
subsample_OVSMOW<-sample(OVSMOW)
length(subsample_OVSMOW) #1256
### Combined
subsample_Dat<-as.data.frame(cbind(subsample_CombinedState,
 subsample_OVSMOW))
head(subsample_Dat)
head(data)

###Make data numeric
subsample_Dat$subsample_OVSMOW <-
 as.numeric(as.character(subsample_Dat$subsample_OVSMOW))
# Query what type of data it is
sapply(subsample_Dat,class)
#subsample_CombinedState        subsample_OVSMOW
#             "character"               "numeric"

###Run Kruskal-Wallis
kruskal.test(subsample_OVSMOW~subsample_CombinedState, data =
 subsample_Dat)
#data:  subsample_OVSMOW by subsample_CombinedState
#Kruskal-Wallis chi-squared = 7.7877, df = 5, p-value = 0.1683


### Dunn Pos-Hoc Test
dunnTest(subsample_OVSMOW~subsample_CombinedState, data = subsample_Dat)
#        Comparison           Z     P.unadj     P.adj
#1      A.CR - A.ICA  2.66129249 0.007784131 0.1167620
#2     A.CR - DSH.CR  1.03543354 0.300466489 1.0000000
#3    A.ICA - DSH.CR -1.25660882 0.208895321 1.0000000
#4    A.CR - DSH.ICA  0.63200029 0.527386689 1.0000000
#5   A.ICA - DSH.ICA -1.01358937 0.310778732 1.0000000
#6  DSH.CR - DSH.ICA -0.07452240 0.940594720 1.0000000
#7       A.CR - H.CR  1.27592305 0.201982721 1.0000000
#8      A.ICA - H.CR -1.50230215 0.133019093 1.0000000
#9     DSH.CR - H.CR -0.02676027 0.978650943 1.0000000
#10   DSH.ICA - H.CR  0.06164717 0.950843811 1.0000000
#11     A.CR - H.ICA -0.00684106 0.994541666 0.9945417
#12    A.ICA - H.ICA -1.77431250 0.076011474 1.0000000
#13   DSH.CR - H.ICA -0.71606108 0.473953632 1.0000000
#14  DSH.ICA - H.ICA -0.51469377 0.606767026 1.0000000
#15     H.CR - H.ICA -0.76808696 0.442435522 1.0000000

###Conover Ranked Sum Test
conover.test(subsample_Dat$subsample_OVSMOW,
 subsample_Dat$subsample_CombinedState, alpha=0.05)
#  Kruskal-Wallis rank sum test
```

```
    #data: x and group
    #Kruskal-Wallis chi-squared = 7.7877, df = 5, p-value = 0.17
    #

    #                           Comparison of x by group
    #                                (No adjustment)
    #Col Mean-|
    #Row Mean |       A.CR      A.ICA     DSH.CR    DSH.ICA       H.CR
    #---------+-------------------------------------------------------
    #   A.ICA |   2.664265
    #         |    0.0039*
    #         |
    #  DSH.CR |   1.036590  -1.258012
    #         |     0.1501     0.1043
    #         |
    # DSH.ICA |   0.632706  -1.014721  -0.074605
    #         |     0.2635     0.1552     0.4703
    #         |
    #    H.CR |   1.277348  -1.503980  -0.026790   0.061716
    #         |     0.1009     0.0664     0.4893     0.4754
    #         |
    #   H.ICA |  -0.006848  -1.776294  -0.716860  -0.515268  -0.768944
    #         |     0.4973     0.0380     0.2368     0.3032     0.2210
    #
    #alpha = 0.05
    #Reject Ho if p <= alpha/2


    ##########Panel all Plots
    attach(mtcars)
    par(mfrow=c(2,3))
    boxplot(OVSMOW.A~CR.ICA.A, data=Arid.Dat, col=c("cyan",
     "firebrick3"),main="Arid", xlab = "Carotid Rete Presence", ylab =
     "OVSMOW")
    boxplot(OVSMOW.DSH~CR.ICA.DSH, data=DSH.Dat, col=c("cyan2",
     "firebrick2"),main="Dry Subhumid", xlab = "Carotid Rete Presence", ylab =
     "OVSMOW")
    boxplot(OVSMOW.H~CR.ICA.H, data=H.Dat, col=c("cyan3",
     "firebrick1"),main="Humid", xlab = "Carotid Rete Presence", ylab =
     "OVSMOW")
    boxplot(subsample_OVSMOW.A~subsample_CR.ICA.A, data=subsample_Arid.Dat,
     col=c("cyan", "firebrick3"),main="Subsampled Arid", xlab = "Carotid Rete
     Presence", ylab = "OVSMOW")
    boxplot(subsample_OVSMOW.DSH~subsample_CR.ICA.DSH,
     data=subsample_DrySubHumid.Dat, col=c("cyan2",
     "firebrick2"),main="Subsampled Dry Subhumid", xlab = "Carotid Rete
     Presence", ylab = "OVSMOW")
boxplot(subsample_OVSMOW.H~subsample_CR.ICA.H, data=subsample_Humid.Dat,
    col=c("cyan3", "firebrick1"),main="Subsampled Humid", xlab = "Carotid Rete
    Presence", ylab = "OVSMOW")
```

VITA

Katherine Wallace Slenker

Candidate for the Degree of

Master of Science

Thesis: INVESTIGATIONS OF ECOMORPHOLOGICAL FEATURES UNDER ARIDIFICATION: CRANIAL HEADGEAR AND CAROTID-RETE-MEDIATED SELECTIVE BRAIN COOLING

Major Field: Biomedical Sciences

Biographical:

Education:

Completed the requirements for the Master of Science in Biomedical Sciences at Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma in July, 2022.

Completed the requirements for the Bachelor of Arts at Case Western Reserve University, Cleveland, Ohio in May, 2020.

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Presentations:

2022	Slenker KW, Woodward, H, O'Brien, HD. Osteohistology of Antilocaprid Horncores. Oklahoma State University Research Days, Tulsa, OK, Feb. 23.
2022	Slenker KW, Woodward, H, O'Brien, HD. Osteohistology of Antilocaprid Horncores. Society for Integrative and Comparative Biology, Phoenix, AZ, Jan 5.
2021	Slenker KW, O'Brien, HD. Presence of Selective Brain Cooling in Carnivorans. Oklahoma State University Research Days, Tulsa, OK, Feb. 22.