

Assessing how morphology of female desert bighorn sheep varies with climate in the Mojave
Desert of California

by
Jose Alberto Torres

A THESIS

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In partial fulfillment of
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(Honors Associate)

Presented March 8, 2023
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AN ABSTRACT OF THE THESIS OF

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Abstract approved: _____

Clinton W. Epps

Understanding how spatial variation in climate correlates with phenotypic variation among individuals may offer insights about local adaptation, population performance, and species' response to climate change. Desert bighorn sheep (*Ovis canadensis nelsoni*) in the Mojave Desert of southern California experience a broad range of temperature and aridity, inhabiting mountain ranges with maximum elevations of 284—2417 m. I used data collected by California Department of Fisheries and Wildlife from 1978-2020 to assess variation in morphology among female desert bighorn sheep across 20 mountain ranges. Those data included horn length, horn circumference, body length, chest girth, metatarsal length, and neck circumference measurements. I tested the association of morphological measurements with environmental predictors (elevation, precipitation, and ambient temperature) using general linear models (GLMs) and principal component analysis (PCA) to determine whether climate was associated with morphology. I found that body length, chest girth, metatarsal length, and neck measurements were positively correlated with elevation and precipitation and negatively correlated with temperature. Horn length and circumference was best explained by a curvilinear relationship, where horn size was maximized at intermediate elevation and temperatures. I concluded that desert bighorn sheep morphology varies with climatic conditions, potentially due to local adaptation and differences in nutrition.

Key Words: Morphology, phenotypic variation, local adaptation, *Ovis canadensis nelsoni*, Mojave Desert

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Honors Baccalaureate of Science in Fisheries, Wildlife, and Conservation project of Jose Alberto Torres presented on March 8, 2023.

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

Jose Alberto Torres, Author

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Assessing how morphology of female desert bighorn sheep varies with climate in the Mojave Desert of California

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Abstract

Understanding how spatial variation in climate correlates with phenotypic variation among individuals may offer insights about local adaptation, population performance, and species' response to climate change. Desert bighorn sheep (*Ovis canadensis nelsoni*) in the Mojave Desert of southern California experience a broad range of temperature and aridity, inhabiting mountain ranges with maximum elevations of 284—2417 m. I used data collected by California Department of Fisheries and Wildlife from 1978-2020 to assess variation in morphology among female desert bighorn sheep across 20 mountain ranges. Those data included horn length, horn circumference, body length, chest girth, metatarsal length, and neck circumference measurements. I tested the association of morphological measurements with environmental predictors (elevation, precipitation, and ambient temperature) using general linear models (GLMs) and principal component analysis (PCA) to determine whether climate was associated with morphology. I found that body length, chest girth, metatarsal length, and neck measurements were positively correlated with elevation and precipitation and negatively correlated with temperature. Horn length and circumference was best explained by a curvilinear relationship, where horn size was maximized at intermediate elevation and temperatures. I concluded that desert bighorn sheep morphology varies with climatic conditions, potentially due to local adaptation and differences in nutrition.

Introduction:

Intraspecific variation in morphology for mammals can be driven by many factors including temperature and latitude, according to ecological theories such as Bergmann's rule (1847) (Ashton et al. 2000; Meiri and Dayan, 2003) and Allen's rule (1877). For example, bushy-tailed woodrats (*Neotoma cinerea*) showed evidence for intraspecific variation in skull morphology along a climate gradient (Cordero and Epps 2012). Species living in the desert have evolved specialized morphological and behavioral adaptations that increase their survival in the harsh desert environment. Allen's (1877) rule indicates that appendages (e.g., legs, ears) tend to be longer in warmer environments which helps dissipate heat (Rocha et al. 2021). African elephants (*Loxodonta africana*) likewise demonstrate morphological adaptation to the desert environment, where the increased size of their pinnae allow them to dissipate excess heat (Phillips and Heath 1992). Desert animals have been observed to use three main thermoregulation strategies depending on their body size to manage heat stress. The evaders-evaporators-endurers concept was proposed to show this relationship. Animals with smaller body mass (small surface area to volume ratios) have higher evaporation rates and evade the heat of the day in burrows and are

mostly nocturnal, while other species use estivation (summer sleep) to avoid the hottest periods of the year (Willmer et al. 2005). Medium size animals have evolved physiological traits to combat water loss through evaporation. For instance, the development of the carotid rete vascular network provides a cooling mechanism for blood going to the brain. Some larger animals such as the camel (*Camelus dromedarius*) and the oryx (*Oryx beisa*) are extremely desert adapted and have evolved multiple physiological traits to endure high heat environments (Willmer et al. 2005). All of these strategies may be accompanied by morphological changes.

Bighorn sheep (*Ovis canadensis*) are ungulates living in desert and alpine habitats in western North America and have adapted to extreme environments. There are three subspecies of bighorn sheep. Rocky Mountain (*O. c. canadensis*) and Sierra Nevada bighorn sheep (*O. c. californiana*) are adapted to high elevation ecosystems. Desert bighorn sheep (*O. c. nelsoni*), however, are generally adapted for the hot, arid deserts of the American Southwest and thus face different physiological constraints around water and thermoregulation demands. Desert bighorn sheep use the combination of behavioral, physiological, and morphological traits for thermoregulation and water balance (Cain et al. 2006). Desert bighorn sheep are smaller in body size when compared to their northern counterparts, as predicted by Bergman's rule (Bergmann 1847). Desert bighorn also have longer extremities, including ears and horns on females, following Allen's rule (McCutchen 1981). Female Rocky Mountain bighorn sheep average 71 kg (Blood et al. 1970), whereas female desert bighorn average 48 kg (Hansen 1980).

Bighorn sheep are characterized by large horns in males, which serve important purposes in mate choice, foraging, heat management, and defense. Horn size may also be important for female bighorn sheep. Wehausen (1991) described intraspecific variation of horn size in female bighorn sheep of both desert and Sierra Nevada subspecies, concluding that even over a relatively small spatial scale (California), females in northern populations had smaller horns than those farther south. Reasons for horn size variation in the Caprinae family have long been debated. Picard et al. (1994) noted that male Barbary sheep (*Ammotragus lervia*) endured much higher metabolic costs than females, which they attributed to loss of heat through the increased surface area of the horns of the males. Thus, cold temperatures likely constrain horn size in females, to reduce loss of heat during winter (Wehausen and Ramey 1993). However, large horns could be advantageous in hot climates as a means of dispersing excess heat (Hoefs 2000). For instance, Taylor (1966) demonstrated that Toggenberg goats (*Capra hircus*) have highly vascularized horns, suggesting their importance for regulating body temperature through blood flow. Wehausen (1991) argued that larger horns on female desert bighorn sheep also could have evolved as tools for opening barrel cactus (*Ferocactus cylindraceus*), which has been hypothesized to be an important source of water in the Mojave Desert. Horn size in male bighorn sheep is under strong pressure as a sexually selected trait and is important for male-male competition for the opportunity to mate. More research has been conducted on male horn size, with variation attributed to selection for large-horned rams by hunters (Coltman et al. 2003), or a combination of factors including age, genetics, and nutrition (Monteith et al. 2018).

Body size within desert bighorn sheep might also be influenced by climate, as climate plays an important role in nutrition and forage quality for desert bighorn sheep. Diet quality and lamb

recruitment in the Mojave Desert are strongly linked to precipitation (Wehausen 2005, Epps et al. 2004). Population extinction risk of desert bighorn sheep in the 20th century in California was strongly negatively correlated with elevation and precipitation (Epps et al. 2004), whereas genetic diversity, a signal of population size and stability, was positively correlated with those factors (Epps et al. 2006); both studies suggest that climate could be a strong selective force. Local adaptation is now recognized as an important component of bighorn sheep management and conservation (Wehausen 1991; Wiedmann and Sargeant 2014; Bleich et al. 2018). Morphological adaptation associated with variation in climate could be particularly important to understand as climate changes rapidly (Warrington and Waterman 2022). However, to my knowledge, no study has systematically evaluated how variation in horn or body size for female bighorn sheep reflects potential adaptation to climate variation within subspecies.

In this thesis, I evaluated morphological variation in desert bighorn sheep from Southern California and assess how horn and body measurements vary with climate. I used a 42-year (1978-2020) dataset of morphological measurements of desert bighorn sheep collected by California Department of Fish and Wildlife (CDFW) to evaluate two hypotheses. *Hypothesis 1:* Female desert bighorn sheep body size differs among 20 populations I evaluated due to variation in habitat conditions, such as elevation and forage quality. *Predictions:* Because larger females in higher, colder mountain ranges would have a thermoregulatory advantage for keeping warm (e.g., as predicted by Bergman's Rule), and may occupy higher habitat quality because elevation and precipitation are positively correlated (Epps et al. 2004, Epps et al. 2006, Creech et al. 2016), I predict that females in populations that occupy higher elevation ranges will have larger body sizes than those in populations within lower elevation ranges. *Hypothesis 2:* The horn size (length and circumference) of ewes will also differ among populations along an elevational gradient. I predict that horn size will be negatively correlated with elevation and positively correlated with maximum temperature due to the increased surface area of larger horns in warmer low elevation areas that could act as a heat dispersal mechanism. However, while I expect larger horns to be advantageous in the hottest, low-elevation ranges, those populations are likely limited by nutrition quality where energy is used to maintain body mass and for reproduction, rather than increasing investment in appendages such as horns. Therefore, I also consider an alternate predication that horn size could be largest at moderate elevations and temperatures.

Methods:

Study Area

The study area included 20 mountain ranges that contained populations of desert bighorn sheep in Southeastern California. Mountain ranges were distributed across the Mojave, Sonoran, and Great Basin Deserts, ranging from latitudes 33.521° to 37.879° (Figure 1). Maximum elevations of mountain ranges in my study area ranged from 1055m (South Bristol Mountains) to 4325m (White Mountains). Temperatures in the Mojave Desert range from -15°C to 38°C (Dibblee 1967). The Mojave Desert is characterized by winter rainfall with summer monsoons. From 1893-2001, average precipitation during the winter was 95 mm/year and ranged 27–249 mm/year. Average precipitation during the summer was 35 mm/year and ranged 1–125 mm/year.

Precipitation variation is strongly affected by El Niño Southern Oscillation (ENSO) and La Niña. El Niño is the process by which the equatorial Pacific warm pool is pushed towards the Eastern Pacific bringing with it rainfall. La Niña is an opposite pattern where a cool water oceanic pool is found in the Eastern Pacific, resulting in less rainfall (Clarke 2014). During my study period the years 1983, 1992, and 1993 had the highest precipitation averages during the winter. During the summer, the years 1983 and 1984 had the highest precipitation averages (Hereford et al. 2006). Vegetation in the Mojave Desert includes creosote bush (*Larrea tridentata*), catclaw acacia (*Senegalia greggii*), iodine bush (*Allenrolfea occidentalis*), rabbitbush (*Ericameria* sp.), brittlebush (*Encelia farinosa*), Joshua tree (*Yucca brevifolia*), banana yucca (*Yucca baccata*), and barrel cactus (*Ferocactus cylindraceus*). Mid-sized to large mammalian species in the study area include mule deer (*Odocoileus hemionus*), desert bighorn sheep, feral burros (*Equus asinus*), domestic cattle (*Bos taurus*), American badger (*Taxidea taxus*), kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), mountain lion (*Felis concolor*), and bobcat (*Lynx rufus*) (Walker and Landau 2018).

Morphological Measurements

CDFW personnel or contractors captured female bighorn sheep from 1978-2020 as part of ongoing management and research projects. Captures before 2013 were conducted solely by CDFW using internally approved procedures and guidelines. Captures from 2013-2020 likewise used CDFW-approved procedures and guidelines, but in Mojave populations also were approved by the National Park Service Institutional Animal Care and Use Committee (ACUP PWR_MOJA_Epps.Powers_DesertBighorn_2013.A3, 2013-2015; PWR_MOJA_Epps.Powers_DesertBighornSheep_2016.A3, 2016-2019; PWR_DEVA.JOTR.MOJA_Epps.Galloway_DesertBHS_2019.A3, 2019-2020) and the Oregon State University Institutional Animal Care and Use Committee (IACUC-2019-0017, 2019-2020).

Morphological measurements were collected at time of capture and recorded on data collection sheets. In the earliest captures (1978-1983), only gross and net weight were recorded, where net weight was estimated by subtracting the mass of any capture equipment still attached to the bighorn when gross weight was recorded. Weights were determined by suspending animals on a scale under a tripod. Over the course of the study period more measurements were added to the collection process. The 7 morphological measurements I focused on for this study were maximum horn length (MHL), maximum horn circumference (MHC), body length (BL), neck circumference beneath jaw (NCBJ); neck circumference mid-neck (NCMN); chest girth (CG), and metatarsal length (ML) (Figure 2). Horn measurements were taken with a flexible measuring tape. MHL was measured as the longest horn measurement taken from the base to the tip of the horn on both sides; MHC was the largest circumference measured around the base of the horn for both sides. BL was measured from tip of the nose to the tail base. Neck circumference measurements were taken beneath jaw (NCBJ), and mid-neck (NCMN). Chest girth was measured around the chest area behind front legs. Age was estimated by using horn growth rings and tooth eruption patterns (Wehausen and Ramey 1993).

Metatarsal length (ML) was measured with tape from 2001-2018, but calipers (Haglof Mantax Blue 40cm) were employed in most captures starting in 2015, with some individuals measured

by both methods. Because measurements can vary between these methods, I used linear regression to generate an equation to correct all measurements to the caliper scale for all individuals (n = 82) where both methods were employed (Figure 3). I screened the data to remove cases where significant measurement error by either method appeared likely, removing one individual for which $1 - [\text{caliper measurement}] / [\text{tape measurement}]$ was $>10\%$ (n=1). Caliper measurements appeared to be consistently lower, and my corrective equation was

$$[\text{Caliper measurement}] = 0.8899[\text{tape measurement}] + 3.3064.$$

I examined the distribution of each measurement type, and graphed all measurements against age, to identify extreme outliers. Questionable measurements were reviewed by CDFW staff (R. Ianniello) and corrected using original data sheets when possible. I removed measurements that could not be verified and were deemed biologically unrealistic from the analysis.

Bighorn sheep conservation efforts have resulted in a series of translocations of desert bighorn sheep among populations within California. To account for this, I reviewed database records as well as translocations within the study area described in the Western Association for Fish and Wildlife Agencies master translocation database (Wild Sheep Working Group 2015). I used that database to confirm the origin of individuals for cases where the capture database noted that animals were translocated but did not specify origin. Notes from data collection sheets were also used to identify if an individual had been translocated but lacked further information as to origin. I removed individuals from the analysis if I was unable to verify mountain range of origin, as morphological characteristics recorded at time of capture for translocation would reflect the mountain range of origin rather than destination. For analysis, translocated individuals were assigned to their mountain range of origin.

Spatial Data

To determine whether morphological variation in desert bighorn sheep was correlated with climate conditions in mountain ranges of origin, I used PRISM spatial climate datasets (30-year normals) to summarize three climate conditions predictive variables. For each mountain range represented in my dataset, I used a population-level polygon to describe the extent of bighorn sheep habitat (polygons provided by CDFW, updated from Epps et al. 2004, see also Figure 1). I used the PRISM 30-year normals dataset (raster, 800 m resolution) from 1981 to 2010 to extract average annual maximum temperature and average annual precipitation across those three decades (PRISM climate group 2021). The average annual temperature and precipitation conditions are modeled by the PRISM group using a digital elevation model (DEM). Using GIS, I calculated the spatial average annual maximum temperature (MT) and maximum annual precipitation (MAP) within each population polygon (Table 1). I also calculated the maximum elevation (ME) from a 30-m digital elevation model (USGS 2019) (Table 1). As in Epps et al. (2004), I used the maximum (rather than average or median) within each polygon under the assumption that bighorn sheep could move freely within each population to access resources and to reduce variation associated with slight differences in how population boundaries have been defined over time. Because my intent was to capture spatial variation in climate that would have

influenced morphology over longer time periods, I used 30-year normals (1981 – 2010) that reflected most of my sampling period.

Analysis (ANOVA, General Linear Models, PCA)

To visualize potential age-related effects on morphology, I plotted the relationship between age (0-15 years) with each of the morphological measurements using Microsoft Excel (Microsoft Corporation 2018). I determined that growth slowed after age 4 for all measurements. An example of this trend can be seen in the chest girth measurements (Figure 4). Consequently, I created a new dataset that only included measurement data for bighorn aged ≥ 4 years. I performed an analysis of variance (ANOVA) in SPSS Statistics 26 software (IBM Corp, 2019) for each measurement to determine if morphology varied by population across the 20 populations in my study. I used a Bonferroni correction for multiple comparisons, resulting in a significance level of 0.007 to achieve $\alpha = 0.05$ (Table 2).

Next, I conducted multiple linear regression to evaluate whether maximum elevation, maximum annual precipitation, or maximum temperature predicted variation in each morphological measurement. For each analysis, I used ΔAIC to determine the best fit model, where top models had between zero and two ΔAIC . All analyses hereafter were conducted using JMP Pro 16 (SAS, Inc). I further analyzed horn measurements using general linear models with linear and binomial fits, using ME and MAT as explanatory variables (Figure 5, 6, 7, 8).

Because morphological measurements are closely correlated, I used principal component analysis (PCA) to explore possible relationships among the measurement values. PCA cannot operate with null values, therefore any individuals with any missing morphometric data had to be removed from analysis. All 7 morphological measurements were included in the principal component analysis, and I used principal component 1 ($N = 117$), and principal component 2 ($N = 117$) for subsequent analysis. The first and second principal components were used as the response variable in two separate linear models with the three environmental predictor variables (MAT, MAP, and ME). The final model of best fit was selected using a stepwise Akaike information criterion (AIC).

Results:

The analysis of variance (ANOVA) of 7 morphological measurements demonstrated that means differed among the 20 populations (Table 2). After correcting for multiple comparisons using a strict Bonferroni criterion ($\alpha = 0.05$, $p_{critical} = 0.007$), all measurements varied significantly except maximum horn circumference (Table 2).

My environmental predictors were highly correlated. Maximum elevation was highly positively correlated with maximum precipitation ($r = 0.94$), and negatively correlated with maximum temperature ($r = -0.75$). Maximum precipitation and maximum temperature were also negatively correlated ($r = -0.76$).

Multiple linear regression models showed that maximum annual temperature (MAT) was the best environmental predictor for 3 of the 7 morphological measurements: body length, chest

girth, and metatarsal length declined with increasing temperature. Body length, chest girth, metatarsal length, neck circumference beneath jaw, and neck circumference mid-neck all showed positive relationships with maximum annual precipitation (MAP) and maximum elevation (ME). Maximum horn length (MHL) was best predicted by ME; horns were shorter as elevation increased. MHL also was positively associated with MAT and negatively associated with MAP. The best model for maximum horn circumference (MHC) included ME and MAT as predictors; as both elevation and precipitation increased, horn circumference decreased (Table 3).

The PCA plot for the first two principal components showed that morphological measurements could be separated into two distinct clusters: horn measurements (MHL and MHC) and body measurements (CG, BL, ML, NCMN, and NCBJ; Figure 9). Within the body measurement cluster, two pairs of measurements, body length and metatarsal length (BL and ML) and the two neck measurements (NCMN and NCBJ), were very closely correlated (Figure 9). The first principal component captured 36.7% of the variance, and the second principal component captured 21.7% of the variance. The formulas for these principal components were:

$$\text{Principal component 1} = (0.04*BL) + (0.08*CG) + (0.24*ML) + (0.13*NCBJ) + (0.13*NCMN) + (0.19*MHC) + (0.02*MHL) + (-35.73)$$

$$\text{Principal component 2} = (-0.02*BL) + (0.03*CG) + (-0.10 * ML) + (-0.09 * NCBJ) + (-0.09 * NCMN) + (0.47 * MHC) + (0.12 * MHL) + (-4.46)$$

PC1 generally represented the size variation within body measurements whereas PC2 represented the variation within horn measurements. Multiple linear regression analysis of these components as a function of the environmental predictors revealed that PC1 was best predicted by MAP and MAT (Table 4). PC1 was negatively associated with MAT, and positively associated with ME and MAP. PC2 was negatively associated with ME and MAP, and positively associated with MAT.

Maximum horn length decreased as elevation increased and displayed a slight curvilinear relationship (Figure 5). Similarly, maximum horn length was positively correlated with temperature with a curvilinear relationship having the best fit ($R^2 = 0.17$). Peak horn length occurred at intermediate temperature, with a maximum of about 26 °C (Figure 8). Maximum horn circumference also decreased as elevation increased but demonstrated no curvilinear relationship (Figure 6). Maximum horn circumference did not have a strong relationship with temperature, but still showed a slight curvilinear fit with peak maximum horn circumference at approximately 26 °C (Figure 7).

Discussion:

In this study of morphological measurements from desert bighorn sheep obtained during captures over a 42-year period, I found interpopulation variation that was associated with temperature, elevation, and precipitation. I observed a significant difference in population means almost all morphological measurements among the 20 populations in this study, which indicates that

morphological characteristics differed by population, potentially reflecting differences in environmental conditions at the mountain range scale. Specifically, I found that as maximum temperature increased, body length, chest girth, and metatarsal length decreased. These findings support my hypothesis that body size would decrease as temperature increases due to limited resources, forage quality, and Bergmann's rule. I expected that horn length would increase as temperature increased and elevation decreased due to their potential use for thermoregulation. My results supported this hypothesis in part, but also supported my alternate prediction: horn length and circumference best fit a curvilinear relationship, where horn measurements appear to be largest around an intermediate elevation of 1800 meters (Figure 4). In general, however, the longest horns were found at lower elevations, and maximum temperature was the best predictor of horn length (Figures 4, 5).

Body size varied as predicted, with larger female bighorn sheep occurring in higher, wetter, cooler mountain ranges. Mountain ranges at lower elevations have shorter growing seasons when compared to higher elevation ranges (Epps et al. 2004). The lack of high-quality forage availability due to less precipitation and hotter temperatures at lower elevation ranges may contribute to desert bighorn having smaller body sizes compared to higher elevation ranges. Saether et al.'s (1996) study on moose (*Alces alces*) found lowest body masses and growth in habitats with low food availability due to snow depth preventing access to forage.

My observation that horns were smaller for female desert bighorn sheep at high elevations followed expectations based on comparison across subspecies, given that increased surface area of horns at higher elevation where temperatures are lower could pose a significant risk for heat loss. However, horn size also declined slightly for populations that experienced the highest temperatures. Although I expected that more surface area of larger horns would be beneficial in the hottest environments, it is possible that there is a limitation in food availability preventing horns from maximum growth. This may be due to limited resources found at these higher temperature/lower elevation ranges (Epps et al. 2004). Indeed, Marco Festa-Bianchet et al. (2004) found that when food was scarce, male bighorn allocated metabolic resources to maintenance rather than horn growth. While the largest horns in my study were observed on a small number of females at the lowest elevation ranges, averages were not largest at those elevations. I believe that larger horns would be beneficial at the high temperature/low elevation ranges for feeding and competition with other bighorn. For instance, I have observed that females with larger horns push smaller females away from resources such as the barrel cactus. However, nutritional constraints from the environment or competition may limit growth for the majority of individuals. Wehausen (1991) hypothesized that the larger horns in females may have evolved due to their function as tools to break open barrel cactus (*F. cylindraceus*). Barrel cactus is an important food and water source which desert bighorn depend on year-round, and larger horns are more effective at breaking open the barbed barrel cactus (Wehausen 1991). Future research could evaluate the relationship between horn length and feeding behavior and determine whether ewes that have bigger horns can consistently better break open and defend barrel cactus resources against other bighorn.

My results support the findings of Wehausen and Ramey (1993): their study did not find support for larger horns being strongly selected for heat dissipation when comparing Mojave Desert ewes to ewes from the Sonoran Desert, which is hotter. Yet, it is important to note that longest horn length recorded in my study was from a ewe in the lowest elevation/highest temperature mountain range (Figure 7). Properly testing the heat distribution hypothesis would likely require direct measurements of body heat and horn size. In my study, while I could not compare the horn sizes of desert bighorn in the Sonoran Desert due to available morphometric data, future studies could include these other populations using elevation as a predictor to further test this hypothesis. Wehausen (1991) noted larger horns require energy allocated to horn growth, and thus could come at a cost as those resources are diverted away from reproduction and growth. As the climate warms, if energy allocation is shifted to meet increased thermoregulation demands, I might observe a decline in reproduction (births, lamb survival, and lamb recruitment).

The database used for this study, while extensive, had limitations. Data collection for this study occurred over a long period of time (1978-2020) and was transcribed from field data sheets to a digital database, which creates the potential for data transcription errors. Incorrect measurements are sometimes recorded by data collection team, as animal captures can be a very confusing process. I verified questionable measurements with CDFW staff and removed those I was unable to verify. I only included females who ≥ 4 years to minimize age effects in my analysis; Wehausen and Ramey (1993) found that limiting analysis to females of an age ≥ 4 years eliminated age effects. Determining age of a desert bighorn sheep is error-prone in the field, particularly when relying on horn annuli, although tooth eruption patterns are also used and are considered more reliable for animals up to 4 years of age. Blood et al. (1970) also found that females body measurements grow up until the age of at least 4, but they likewise concluded that age could not be accurately determined after age 4.

In conclusion, in my study of morphological variation in desert bighorn sheep, I found support of Bergmann's rule for body measurements and some support for Allen's rule with respect to horn size (Table 3). Females were larger in higher elevation, cooler mountain ranges. Females in warmer, low, and mid-elevation mountain ranges had the longest horns, although horns showed a curvilinear relationship suggesting resource availability as well as thermoregulation may play an important role in the development of these appendages. The results of this study suggest that adaptations that would be beneficial for thermoregulation may be constrained by the lack of resources. As climate continues to change, there is further need for understanding how this will impact overall fitness.

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Tables:

Table 1. Summary of maximum elevation (ME), maximum annual precipitation (MAP), and maximum temperature (MT) for mountain ranges/populations of bighorn sheep included in this study from Southern California (n = 20). Elevation data originated from a 30-m digital elevation model (DEM) used to calculate the maximum elevation within each polygon (USGS 2020). MAP and MT data from 30-year normals (1981 – 2010) that reflected the majority of my sampling period. Temperature and precipitation values from PRISM datasets were represented as rasters with a resolution of ~800 m.

Mountain range	ME (m)	MAP (mm)	MT (°C)
Avawatz Mountains	1862	233.05	28.95
Cady Mountains	1396	166.82	29.91
Castle Mountains / Piute Range	1769	286.63	26.26
Cushenberry	2497	611.68	22.49
Eagle Crags	1651	232.99	27.01
Eagle Mountains	1619	189.72	29.91
Granite / Old Dad Mountains	2054	223.07	27.58
Kelso Peaks / Marl / Old Dad Mountain	1498	207.88	28.83
Kingston Range / Mesquite Mountain	2220	325.39	26.37
Marble Mountains	1163	154.64	30.45
N. Bristol Mountains	1188	181.22	29.90
Newberry, Rodman, and Ord Mountains	1918	323.46	28.02
Old Woman / Piute Mountains	1610	260.08	30.44
Orocopia Mountains / Mecca Hills	1152	143.78	31.61
Panamint Buttes / Hunter Mountain	2260	307.18	30.86
Panamint Range	3352	510.54	32.26
S. Bristol Mountains	1055	145.23	30.77
Turtle Mountains	1297	282.70	29.78
White Mountains	4325	637.80	21.83
Wood / Hackberry Mountains	1885	214.74	24.90

Table 2. Summary of ANOVA test for differences in mean of body measurements for female bighorn sheep across 20 populations throughout the southern California desert from 1978 to 2020. I used a Bonferroni correction with an α of 0.05 and a critical value of 0.007 to determine significance.

Morphological measurement	Sample size	df	F-statistic	Sig
Body length	174	17	4.44	<0.007**
Chest girth	226	20	21.11	<0.007**
Metatarsal length	123	11	2.57	0.006*
Neck circumference beneath jaw	133	14	6.67	<0.007**
Mid-neck circumference	128	14	4.49	<0.007**
Maximum horn circumference	184	19	1.68	0.045
Maximum horn length	181	19	2.42	0.002*

*Statistically significant value.

**Significance value significantly below critical value of 0.007.

Table 3. Summary of general linear models with female bighorn sheep morphological measurements body length (BL), chest girth (CG), metatarsal length (ML), neck circumference beneath jaw (NCBJ), neck circumference mid-neck (NCMN), max horn length (MHL), and max horn circumference (MHC) as the response variables for the 20 selected populations across the southern California desert covering years (1978-2020). Models use maximum temperature (MT), maximum annual precipitation (MAP), and maximum elevation (ME) as predictors with best model having lowest Δ AIC. Models have superscripts (+,-) indicating directionality of each predictor.

Response	Model	Δ AIC
BL (n=174)	MT ⁽⁻⁾ *	0
	MT ⁽⁻⁾ *, MAP ⁽⁻⁾	2.08
	ME ⁽⁻⁾ , MT ⁽⁻⁾ *	2.09
	MT ⁽⁻⁾ , MAP ⁽⁻⁾ *, ME ⁽⁺⁾ *	4.20
	MAP ⁽⁺⁾ *	4.77
	ME ⁽⁺⁾ *	6.29
	MAP ⁽⁺⁾ , ME ⁽⁺⁾	6.83
CG (n=224)	MT ⁽⁻⁾ *	0
	MT ⁽⁻⁾ , ME ⁽⁻⁾ *	0.33
	MT ⁽⁻⁾ *, MAP ⁽⁻⁾	0.98
	MT ⁽⁻⁾ *, ME ⁽⁻⁾ , MAP ⁽⁺⁾ *	2.39
	MAP ⁽⁺⁾ *	12.70
	ME ⁽⁻⁾ , MAP ⁽⁺⁾	14.35
	ME ⁽⁺⁾ *	15.15
ML (n=123)	MT ⁽⁻⁾ *	0
	MT ⁽⁻⁾ *, MAP ⁽⁻⁾	0.06
	MT ⁽⁻⁾ *, MAP ⁽⁻⁾ , ME ⁽⁺⁾	1.18
	ME ⁽⁺⁾ *	1.82

NCBJ (n=132)	ME ⁽⁻⁾ , MT ⁽⁻⁾	2.13	
	MAP ^{(+)*}	3.50	
	MAP ⁽⁻⁾ , ME ⁽⁺⁾	3.71	
	ME ^{(+)*} , MAP ^{(-)*} , MT ^{(-)*}	0	
	ME ^{(+)*}	3.68	
	ME ^{(+)*} , MAP ⁽⁻⁾	3.73	
	ME ^{(+)*} , MT ⁽⁻⁾	4.94	
	MT ^{(-)*}	14.31	
	MT ^{(-)*} , MAP ⁽⁻⁾	16.43	
NCMN (n=128)	MAP ^{(+)*}	23.38	
	ME ^{(+)*}	0	
	ME ^{(+)*} , MT ⁽⁻⁾	1.92	
	ME ^{(+)*} , MAP ⁽⁻⁾	1.93	
	ME ^{(+)*} , MT ⁽⁻⁾ , MAP ⁽⁻⁾	3.43	
	MT ^{(-)*}	6.14	
	MAP ^{(+)*}	6.53	
	MT ⁽⁻⁾ , MAP ⁽⁺⁾	6.98	
	MHL (n=179)	ME ^{(-)*}	0
ME ^{(-)*} , MAP ⁽⁺⁾		1.81	
ME ^{(-)*} , MT ⁽⁻⁾		2.05	
ME ^{(-)*} , MAP ⁽⁺⁾ , MT ⁽⁻⁾		3.92	
MAP ^{(-)*}		5.91	
MAP ^{(-)*} , MT ⁽⁺⁾		7.99	
MT ^{(+)*}		20.49	
MHC (n=181)		ME ^{(-)*} , MT ^{(-)*}	0
		MT ^{(-)*} , ME ^{(-)*} , MAP ⁽⁺⁾	2.11
	MT ^{(-)*} , MAP ^{(-)*}	4.37	
	ME ^{(-)*}	9.04	
	ME ⁽⁻⁾ , MAP ⁽⁺⁾	10.26	
	MAP ^{(-)*}	11.53	
	MT ⁽⁺⁾	18.74	

*Confidence intervals do not overlap zero showing significance in directionality.

Table 4. Principal component analysis summary of 7 bighorn morphological measurements with principal components 1 and 2 as response variables and southern California environmental factors maximum temperature (MT), maximum annual precipitation (MAP), and maximum elevation (ME) as predictors. Directionality of correlation indicated with (+) for positive correlation and (-) for negative correlation.

Response Variable	Model	Δ AIC
Principal component 1 (n=110)	MAP ⁽⁻⁾ , MT ^{(-)*}	0
	MT ^{(-)*}	0.82
	ME ⁽⁺⁾ , MAP ⁽⁻⁾ , MT ^{(-)*}	2.06

Principal component 2 (n=110)	MT ^{(-)*} , ME ⁽⁻⁾	2.22
	ME ^{(+)*}	8.28
	MAP ^{(+)*}	9.01
	ME ⁽⁺⁾ , MAP ⁽⁺⁾	10.30
	MT ^{(-)*} , ME ^{(-)*}	0
	ME ^{(-)*} , MAP ⁽⁻⁾ , MT ^{(-)*}	1.56
	ME ^{(-)*}	8.69
	ME ^{(-)*} , MAP ⁽⁺⁾	9.43
	MT ^{(-)*} , MAP ^{(-)*}	25.24
	MAP ^{(-)*}	27.22
MT ^{(+)*}	47.29	

*Confidence intervals do not overlap zero showing significance in directionality.

Table 5. Summary of means for the 7 bighorn morphological measurements body length (BL), chest girth (CG), metatarsal length (ML), neck circumference beneath jaw (NCBJ), neck circumference mid-neck (NCMN), horn length (HL), and horn circumference (HC) analyzed in this study measurements are in centimeters.

	BL		CG		HL		HC		ML		NCBJ		NCMN	
	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Avawatz Mountains	149.0	144.78 - 152.4	91.0	90.2 - 91.44	32.4	31.8 - 33	15.4	13.97 - 17.1	NA	NA	NA	NA	NA	NA
Cady Mountains	145.5	145.5 - 145.5	93.3	92.3 - 94.8	34.0	31 - 36.8	15.2	14.9 - 15.9	27.6	27.6 - 27.6	31.8	31.8 - 31.8	35.3	35.3 - 35.3
Castle Mountains/Piute Range	146.8	139 - 153	99.5	90 - 109.5	38.5	32.1 - 44.5	16.0	13.5 - 17.7	26.9	26 - 28	35.1	33 - 37	37.8	33.5 - 41
Cushenberry	145.5	132 - 158	98.8	93 - 108	33.3	30 - 37	16.2	13.5 - 18	26.4	24.7 - 28.2	33.9	30 - 36	36.4	32 - 41
Eagle Crags	147.3	147.3 - 147.3	97.8	97.8 - 97.8	23.5	23.5 - 23.5	13.7	13.7 - 13.7	NA	NA	27.9	27.9 - 27.9	37.1	37.1 - 37.1
Eagle Mountains	NA	NA	97.4	91.4 - 103	34.9	31 - 39	15.4	15 - 17	NA	NA	NA	NA	NA	NA
Granite/Old Dad Mountains	140.0	140 - 140	95.6	92.7 - 98.5	35.1	30.5 - 40.6	15.8	14.6 - 17.1	26.3	25.5 - 27	34.0	33 - 35	36.4	36.5 - 37
Kelso Peaks/Marl/Old Dad Mountain	138.9	118.1 - 151.1	92.8	80 - 106	34.3	24.4 - 42.5	16.0	14 - 18	25.9	20.2 - 28.2	33.3	29 - 38	35.3	31.5 - 41
Kingston Range /Mesquite Mountain	136.6	130 - 141	97.8	94 - 100.8	30.5	24.5 - 37	15.7	14.5 - 16.8	25.7	21.5 - 27.2	35.1	34.5 - 36	37.5	35.8 - 40
Marble Mountains	140.6	125 - 155	97.2	92 - 103	35.3	28 - 80	15.2	12.5 - 16.5	26.6	24.9 - 28.5	33.1	30.5 - 36	35.0	31 - 37
N. Bristol Mountains	149.0	149 - 149	97.0	97 - 97	34.0	34 - 34	15.0	15 - 15	NA	NA	32.5	32.5 - 32.5	38.5	38.5 - 38.5
Newberry, Rodman, and Ord Mountains	143.1	135 - 151	99.3	92-106.5	34.0	29.5 - 42	15.1	13.8 - 16.5	27.1	25.8 - 28	33.0	29.5 - 34.6	35.3	33.2 - 38
Old Woman / Piute Mountains	144.7	135 - 155	96.8	90.2- 113	35.5	20.9 - 42	16.2	14.3 - 17.8	NA	NA	31.0	27.5 - 33	38.2	33.7 - 49.8
Orocopia Mountains/Mecca Hills	152.4	147 - 160	95.5	89 - 102	39.0	33 - 50	17.1	15 - 23	NA	NA	NA	NA	NA	NA
Panamint Buttes/Hunter Mountains	139.6	129 - 154	93.5	88 - 98.5	28.8	25.5 - 30.5	15.3	14.5 - 15.5	NA	NA	NA	NA	NA	NA
Panamint Range	128.6	125.7 - 132.7	92.2	87 - 100.3	36.3	25.4 - 90.2	14.6	13.8 - 15.9	22.8	22.8 - 22.8	33.4	33.4 - 33.4	33.0	33 - 33
S. Bristol Mountains	137.3	137 - 137.5	96.0	91 - 101	26.3	25 - 27.5	14.8	14.5 - 15	26.7	26.4 - 26.9	31.7	31 - 32.5	34.5	34 - 35
Turtle Mountains	NA	NA	94.0	91.4 - 96.52	44.5	44.5 - 44.5	14.9	13.33 - 16.5	NA	NA	NA	NA	NA	NA
White Mountains	147.5	133 - 160	98.4	87 - 108	29.0	22 - 34.5	15.5	13 - 26	27.1	22.4 - 29.1	37.9	(30 - 53)	39.7	(35 - 48)
Wood/Hackberry Mountains	140.9	136.5 - 150.5	100.8	95 - 110.25	39.2	34.5 - 43	16.4	15 - 17.3	27.2	26.6 - 27.6	35.0	(32.5 - 37.5)	35.6	(33.5 - 38.5)

Figures:

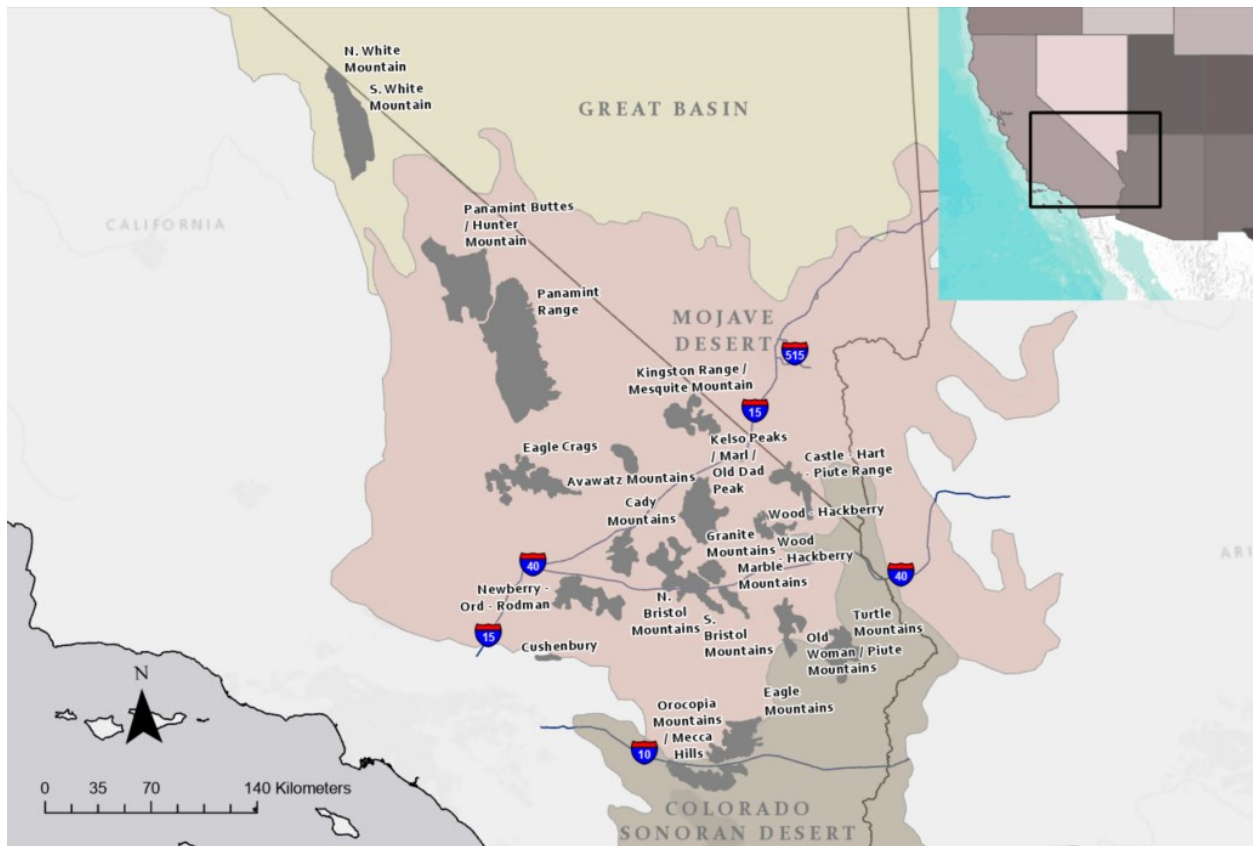


Figure 1 Study area in Southern California with individual mountain ranges/populations of bighorn sheep ($n = 20$) analyzed in this study highlighted, shapefile for desert boundaries from (USGS 2006).

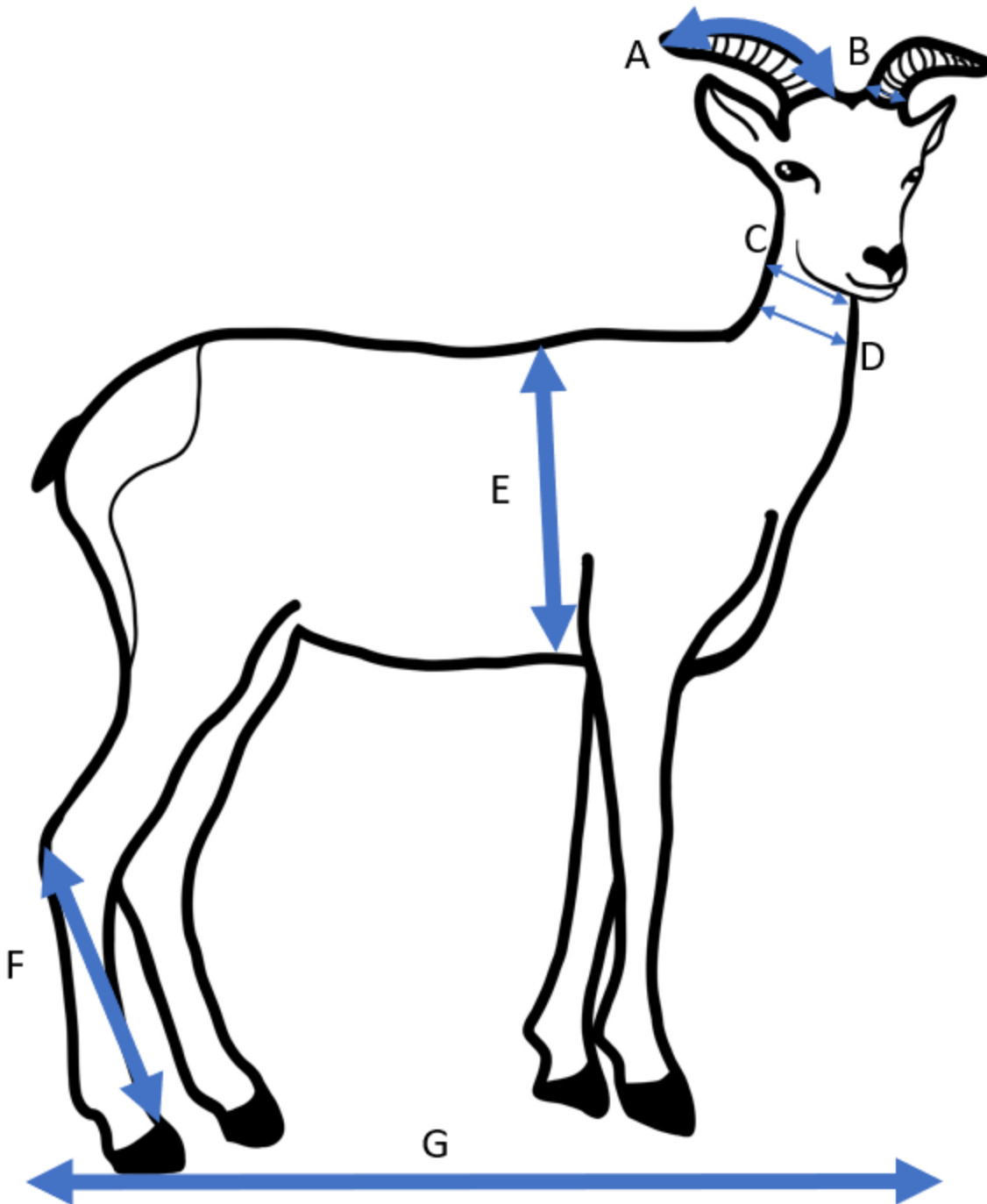


Figure 2. Morphological measurements collected and analyzed of desert bighorn sheep (n=7) using a flexible tape and calipers. Max horn length (A), max horn circumference (B), neck circumference beneath jaw (C), neck circumference mid neck (D), chest girth (E), metatarsal length (F), and body length (G).

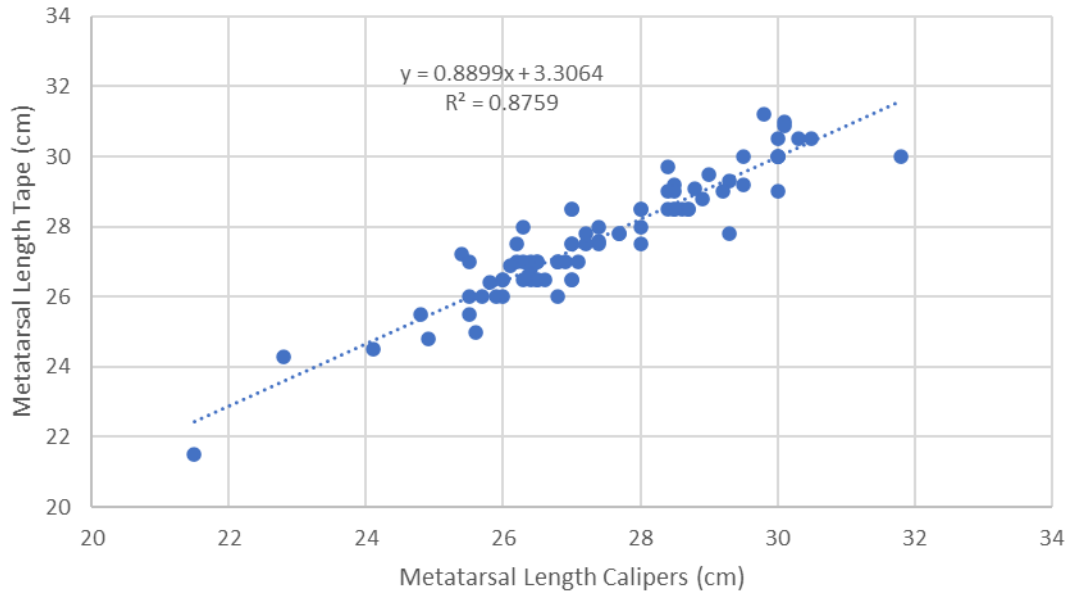


Figure 3. Relationship between metatarsal tape (y-axis) and caliper (x-axis) measurements for male and female bighorn sheep of Southern California desert populations where both methods were employed (n= 82) one outlier (BHS_1601) was removed from analysis due to not meeting criteria of a maximum of 10% difference between the two measurements bringing down total to n=81.



Figure 4. Visual example of chest girth growth stabilizing after age 4, including female bighorn sheep captured in southern California from 1978-2020 (N=512).

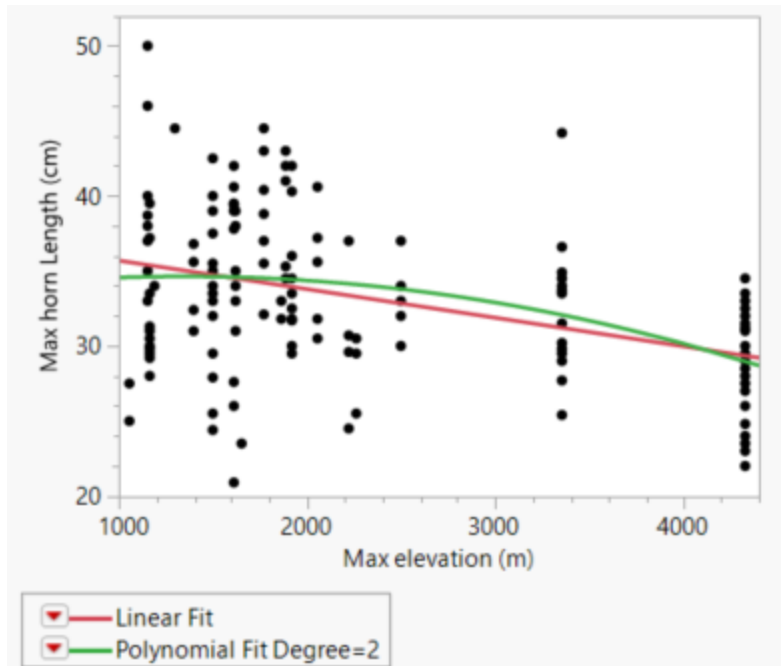


Figure 5 Female bighorn sheep maximum horn length relationship with elevation (n = 179), linear fit formula (max horn length = $37.597801 - 0.001966 * \text{max elevation}$) ($R^2 = 0.20$); polynomial fit formula (max horn length = $37.384401 - 0.0014385 * \text{max elevation} - 6.3749^{-7} * (\text{max elevation} - 2475.67)^2$) ($R^2 = 0.21$).

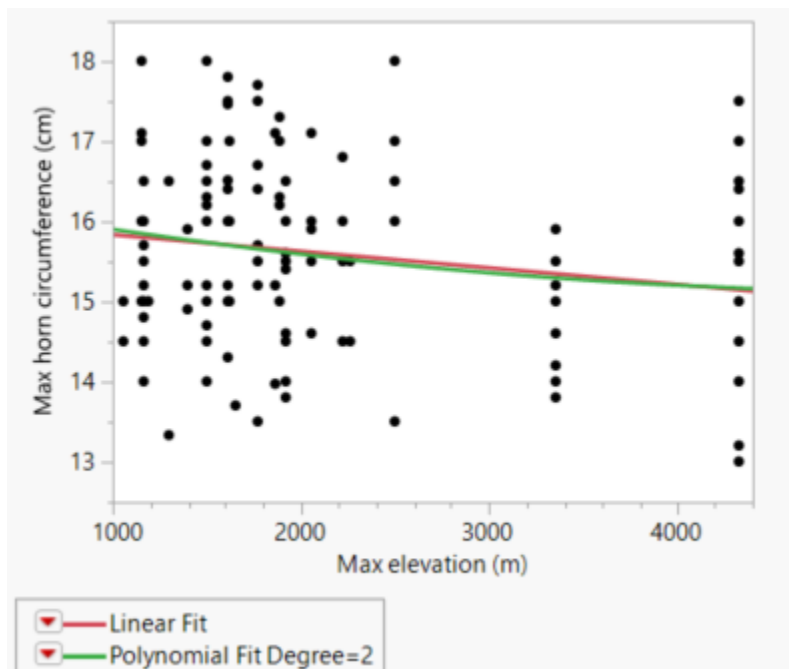


Figure 6. Female bighorn sheep maximum horn circumference relationship with elevation (n = 181), linear fit formula (max horn circumference = $16.037156 - 0.000207 * \text{max elevation}$) ($R^2 = 0.052$); polynomial fit formula (max horn circumference = $16.052656 - 0.000236 * \text{Max elevation} + 3.8363^{-8} * (\text{max elevation} - 2462.3)^2$) ($R^2 = 0.053$).

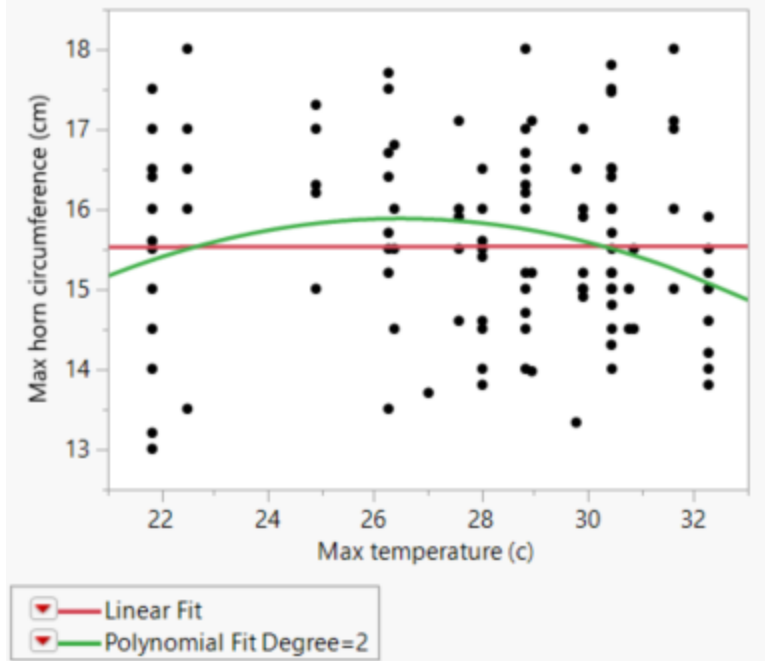


Figure 7. Female bighorn sheep maximum horn circumference relationship with temperature ($n = 181$), linear fit formula (max horn circumference = $15.501045 + 0.0009731 * \text{max temp}$) ($R^2 = 1.12e-5$); polynomial fit formula (max horn circumference = $16.800562 - 0.0343807 * \text{max temp} - 0.0239082 * (\text{max temp} - 27.2019)^2$) ($R^2 = 0.045$).

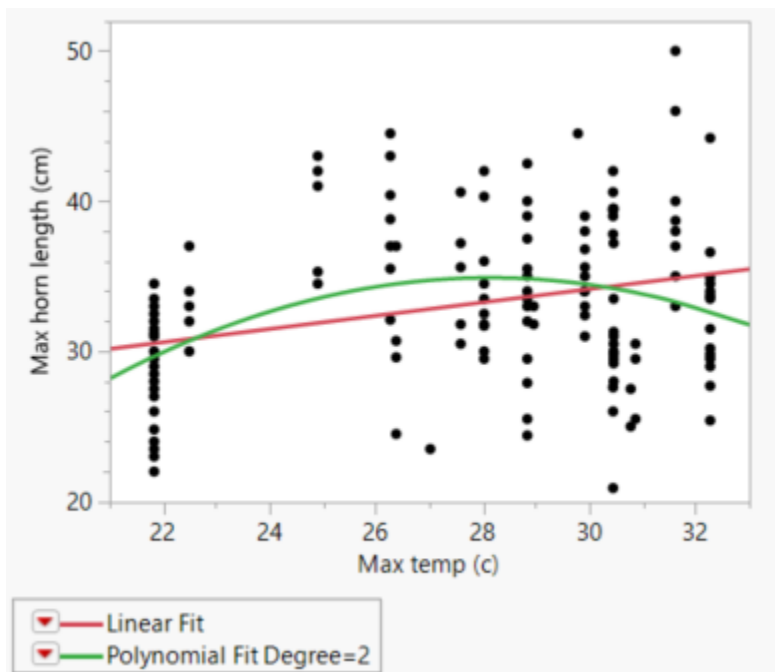


Figure 8. Female bighorn sheep maximum horn length relationship with temperature ($n = 179$), linear fit formula (max horn length = $20.872928 + 0.4424079 * \text{max temp}$) ($R^2 = 0.11$);

polynomial fit formula (max horn length = $27.644833 + 0.2626738 * \text{max temp} - 0.1321229 * (\text{max temp} - 27.135)^2$ ($R^2 = 0.17$).

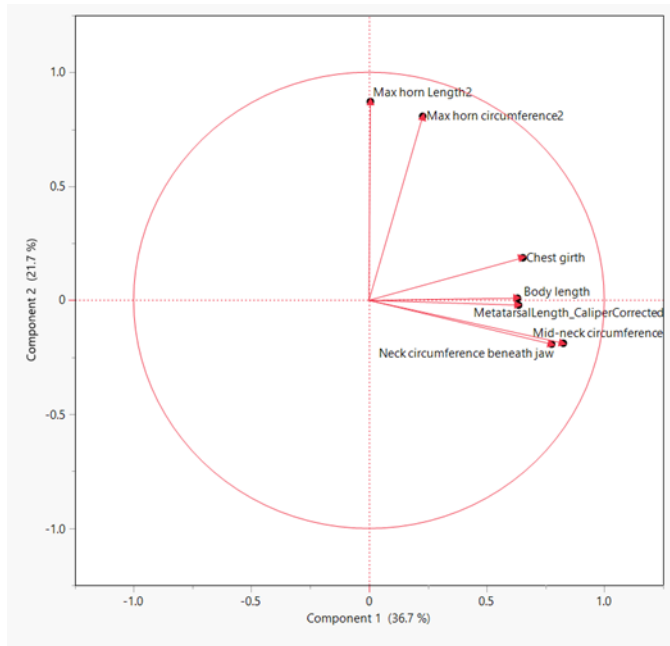


Figure 9. Principal component analysis results showing 7 morphological measurements for desert bighorn sheep collected from 20 populations in southern California from 1978 to 2020, including max horn length (MHL), max horn circumference (MHC), chest girth (CG), body length (BL), metatarsal length (ML), neck circumference mid-neck (NCMN), and neck circumference beneath jaw (NCBJ).

