AN EXAMINATION OF THE PATTERNS OF GROWTH AND THE INFLUENCE OF THE ENVIRONMENT ON HORN GROWTH OF MOUNTAIN GOATS (*Oreamnos americanus*) OF BRITISH COLUMBIA

By

Matthew A. Clarke

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Name: Matthew A. Clarke

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Examining Committee:

____
Supervisor: Dr. Michael Gillingham
Professor, Ecosystem Science and Management Program

____
Second Reader: Dr. Katherine Parker
Professor, Ecosystem Science and Management Program

____
Program Chair: Dr. Kathy Lewis
Professor, Ecosystem Science and Management Program

Date Approved: ___________________________________

ABSTRACT

Horn growth of mountain goats (*Oreamnos americanus*), is dependent on environmental conditions, and is related to measures of body condition such as mass and chest girth, allowing inference into the differences in growth conditions across wide geographic expanses. The regional patterns and the influence of environmental variables on the horn growth of mountain goats were examined using data acquired through the British Columbia Ministry of Environment, from the mandatory harvest reporting program for mountain goats. Several metrics of horn growth were examined, and a Michaelis-Menton non-linear-model was fit to the data to identify regional patterns of horn growth. Spatial data for environmental variables were combined with each mountain goat record and forward stepwise regression was used to identify parameters influencing horn growth. Differences in growth were identified among regions, where mountain goats of coastal habitats had longer, more symmetrical horns compared to goats from interior habitats. The factors influencing horn growth of mountain goats differed depending on the response variable used. Rainfall tended to be positively related to horn growth. Measures of primary productivity such as Normalized Difference Vegetation Index (NDVI) tended to be negatively related to horn growth. The environmental variables influencing horn growth were consistent with the geographic patterns associated with regional horn growth. The patterns of horn growth differed somewhat from goats in other studies, indicating that management of mountain goats needs to consider differences in growth conditions. Additionally, understanding the influences of environmental factors will enable wildlife managers to better meet conservation objectives by altering regulations during periods of unfavourable growth conditions.

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ACKNOWLEDGEMENTS

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INTRODUCTION[1]

The range of landscape and climatic conditions are highly variable over the broad expanse of British Columbia (Meidinger and Pojar 1991). Species require a specific combination of nutritional (Couturier et al. 2009), climatic (Jacobson et al. 2004, Couturier et al. 2009) and landscape features (Côté and Festa-Bianchet 2001a) in order to be present in an area. When the appropriate combination of forage, climatic conditions and landscape features are present, individual growth rates are likely high and populations are likely to grow (Côté and Festa-Bianchet 2001a, Festa-Bianchet et al. 2004, Couturier et al. 2009). When these resources are insufficient, as is often the case in winter for temperate regions, populations may decline or individuals may move to different locations in an effort to optimize the availability of these resources (Fox et al. 1989, Poole et al. 2009).

At a finer scale, these resources dictate the success of individual organisms, and animals will often seek out the area for which the availability of resources is optimized for a given life-history stage (Rettie and Messier 2000, Poole et al. 2007). In the case of caribou (*Rangifer tarandus*) and moose (*Alces alces*), calving habitats are often chosen at least in part due to a lack of predators, although the distances migrated to reach those habitats may differ (Rettie and Messier 2000). Alternatively, mountain goats (*Oreamnos americanus*) may choose habitats in close proximity to escape terrain in order to avoid predation events (Côté and Festa-Bianchet 2001a).

Climatic conditions also influence the success and persistence of animals. Habitats where climatic conditions are mild favour the survival of animals, whereas conditions that are

[1] Data used in this study were collected as part of the BC Ministry of Environment's mandatory harvest reporting program for mountain goats. In this thesis, I use 'we' to reflect the involvement of others, namely Michael Gillingham in various aspects of this work.

cold and harsh tax the energy reserves and result in reduced fitness and survival (Jacobson et al. 2004). In temperate regions, winter is considered to be the limiting season, where survival is reduced due to the harsh conditions and lack of nutritional resources (Jacobson et al. 2004).

The amount of nutrition available to an individual is often an important factor in habitat choice of animals, as it dictates their ability to survive, compete and successfully reproduce (Gates et al. 1986, Barboza and Reynolds 2004). In the case of males, access to sufficient forage may allow them to increase in size and develop sufficient secondary sexual characteristics such that they may be able to exclude other individuals from access to limited resources and mating opportunities (Asleson et al. 1996, Weckerly 1998). In the case of females, access to sufficient forage may allow them to produce and maintain healthy offspring, thereby increasing their fitness (Côté and Festa-Bianchet 2001a,b, Couturier et al. 2009).

Sexual dimorphism in size is common in most species, especially for species with intraspecific competition for reproductive opportunities (Weckerly 1998). Sexual dimorphism arises early and is maintained throughout an organism’s life (Côté et al. 1998, Weckerly 1998). Interestingly, sexual dimorphism does not necessarily indicate intersexual social dominance. Festa-Bianchet and Côté (2008) documented aggressive interactions between female and male mountain goats where the female, though much smaller, was the aggressor. It is likely that sexual dimorphism results from females choosing large males with superior competitive abilities (Weckerly 1998). In addition to size, sexual dimorphism may also take the form of secondary sexual characteristics (Weckerly 1998, Schmidt et al. 2007)

In many ungulates, the most notable secondary sexual characteristics are antlers or horns displayed by either one or both sexes (Geist 1966). When displayed by both sexes, there is typically sexual dimorphism in size (Côté et al. 1998, Schmidt et al. 2007). Horns are permanent structures found on bovids consisting of a bony core surrounded by a keratinous sheath that grow continuously throughout the life of an animal (Geist 1966, Hoefs and Nowland 1997, Côté et al. 1998). Horns may be used for predator defence (Stankowich and Caro 2009), but are more often associated with intraspecific competition for reproductive opportunities and dominance (Côté et al. 1998, Weckerly 1998, Festa-Bianchet and Côté 2008).

The evolution of horns likely reflects their use in intrasexual dominance displays or competitions for breeding opportunities. Large horns, characteristic of Bighorn rams (*Ovis canadensis*) or Dall rams (*Ovis dalli*) reflect the style of aggressive interactions where males compete through horn-to-horn contact (Geist 1964, Côté et al. 1998). For these animals, large horns constitute an evolutionary advantage, allowing individuals with relatively massive horns to experience greater mating success. In contrast, species with interactions that do not involve horn-to-horn contact, such as mountain goats, are more likely to exhibit different growth forms (Côté et al. 1998).

The growth of horns can reveal important information about the life history of an animal. Horns are not shed annually like antlers, rather they grow throughout the life of the animal, and annual growth rings formed during seasonal periods of slow growth are useful for providing age estimates (Smith 1988). The growth rate of horns is most rapid in the first few years of life and is often reduced in older individuals, although the extent of this reduction is species specific (Hoefs and Nowland 1997, Côté et al. 1998.) In addition, brooming, or the wear of horn tips, increases with age (Bunnell 1978). As a result, the oldest individuals in a population may not have the largest horns (Côté et al. 1998, Festa-Bianchet and Côté 2008).

The relatively short and sharp horns of mountain goats begin to grow at birth. The first increment tends to be the longest, and the first annulus is made at 1.5 years, after which annuli represent yearly growth (Festa-Bianchet and Côté 2008). Horns of males increase in length and circumference more rapidly than do those of females during the first year of horn growth, whereas horns of females grow at a faster rate than those of males during the second and third years (Côté et al. 1998). Due to a longer first increment, males will typically have longer horns than females (Côté et al. 1998, Festa-Bianchet and Côté 2008). Mountain goat horns continue to grow throughout the life of the animal, although the rate of horn accumulation decreases with age (Cowan and McCrory 1970, Côté et al. 1998). At five years of age, the growth rates decline and yearly growth increments for both sexes are small and consistent (Côté et al. 1998, Smith 1988). Horns are typically symmetrical; asymmetry however, may indicate reduced fitness, especially in female goats (Côté and Festa-Bianchet 2001b). Those goats in a stable developmental environment tend to show less asymmetry than goats in unstable environments (Côté and Festa-Bianchet 2001b).

Upon attainment of a maximum horn length, male mountain goat horns may be 10-20% greater in length, and somewhat greater in circumference compared to female mountain goat horns, although this does not take into account body size, which is much greater for males (Côté et al. 1998, Festa-Bianchet and Côté 2008). Horn length and circumference in mountain goats also provide information on body size and condition, and are positively correlated to weight, chest girth, and hind foot length (Côté et al. 1998). These correlations mean that individuals with large horns tend to be the larger individuals in the populations, indicating that horns may be used as a surrogate for body measures in mountain goats (Côté et al. 1998).

The degree of reproductive fitness in polygynous species may be reflected in the sex ratio of their offspring where more male offspring indicates higher reproductive fitness (Trivers and Willard 1973). Reproductive fitness in most ungulates is typically highest when the animal is at its prime (5-6-yr old), and is lower for older or younger individuals. This is not the case, however, for mountain goats (Côté and Festa-Bianchet 2001c). In mountain goats, offspring size, fitness and potential reproductive success are positively correlated with maternal mass, age and social rank (Côté and Festa-Bianchet 2001c). Further, females of higher social rank are more likely to produce male offspring, which are more energetically costly to rear than females as a result of sexual dimorphism (Côté and Festa-Bianchet 2001c). Although more costly to raise, maternal experience increases the likelihood of offspring survival (Côté and Festa-Bianchet 2001c). Males produced by high-quality mothers are more likely to reproduce than those produced by low-quality mothers, indicating greater fitness of older females.

The lack of sexual dimorphism, and the higher level of reproductive fitness in older mountain goats, creates a management dilemma when it comes to managing the harvest of mountain goats. In contrast to natural predation, anthropogenic harvest typically targets the largest individuals of a species, which, in the case of mountain goats, are often the individuals with the greatest reproductive potential (Côté and Festa-Bianchet 2001c, Schmidt et al. 2007). These harvests are typically constrained by sex, where the largest individuals are typically males (Schmidt et al. 2007). In species with little sexual dimorphism, such as mountain goats, harvest of the largest individuals may include mature females (British Columbia Ministry of Environment, in preparation). Due to the unique reproductive biology of mountain goats, the harvest of mature females has much greater impacts on population dynamics than for other ungulates (Côté and Festa-Bianchet 2001c). For example, non-selective harvest of individuals greater than two years of age cannot be maintained at levels >1% (Hamel et al. 2006), posing potential management problems. Better understanding of the reproductive biology of mountain goats has led the British Columbia provincial government to propose regulations designed to reduce the harvest of dominant females (British Columbia Ministry of Environment, in preparation).

In British Columbia, historic management practices resulted in declines in mountain goat populations in the 1960s. These declines resulted from several factors including increased access, a lack of understanding of mountain goat biology, the low management priority of the species, and a philosophy of maximizing harvest (Phelps et al. 1983, British Columbia Ministry of Environment, in preparation). Following the population declines, hunting closures and restrictions were implemented to increase mountain goat populations. Currently, much of the mountain goat harvest in BC is regulated by limited-entry-hunting opportunities, although areas with restricted access are still managed under general open seasons (British Columbia Ministry of Environment, in preparation). Additionally, all mountain goats harvested in British Columbia must be inspected. These inspections provide information to actively evaluate the estimated population size and monitor the proportion of females in the harvest (British Columbia Ministry of Environment, in preparation). Although management of mountain goats is improving, there is a lack of information on the differences in growth conditions across British Columbia, which may influence management decisions.

Most studies of mountain goats have relied on relatively small sample sizes from small geographic areas (e.g., Côté et al. 1998, Festa-Bianchet and Côté 2008). Mandatory harvest reporting of all mountain goats harvested in BC since the 1970s has been an integral part of mountain goat population management. These reports document the age, sex, horn growth and locations of every mountain goat legally killed in British Columbia and provide an extensive history of mountain goat harvest throughout a large geographic range. No other such datasets exist that allow comprehensive examination of horn growth in mountain goats. In this study, horns of mountain goats were examined to determine if differences in length, symmetry, and patterns of growth could be attributed to regions with entirely different environmental characteristics. We hypothesized that regions with favourable biotic and abiotic conditions would produce the largest, most symmetrical horns, most rapid growth rates and highest amount of horn accumulation after annulus four. In addition to the examination of horn growth, we also wanted to identify the environmental variables that influenced the growth of horns. As horn growth is positively associated with body mass, chest girth, and hind foot length, the results of the horn-growth analyses relate back to factors influencing the condition of mountain goats across British Columbia.

METHODS

Data acquisition and screening

Raw data for the horn growth of mountain goats were acquired from Christopher Addison, a Biometrician of the Fish and Wildlife branch of the British Columbia Ministry of Environment. Horn-growth data are collected annually through mandatory harvest reporting of all mountain goats harvested legally in British Columbia. The information collected from these reports includes biological information such as the total horn length, basal circumference, the length from the tip of the horn to each annulus, brooming, sex and the age as determined by the inspector. Additionally, each record includes the date, management unit, nearest landmark, and grid location representing the location of the harvest to the nearest km. Grid locations are provided by the hunter, who indicates the location of the kill on a map. From this location, grid coordinates and the nearest landmark are determined. Collection of these data began in the 1970s as a response to declining populations of goats in many areas of the province (British Columbia Ministry of Environment, in preparation). This project examined data collected between 1976 and 2009 throughout British Columbia.

Portions of the spatial analysis required several Geographical Information Systems (GIS) layers. The provincial Wildlife Management Unit (WMU) layer was obtained through the Provincial Data Management Warehouse, accessed through www.lrdw.ca. A layer describing the current provincial goat range was provided by Kim Poole (Aurora Wildlife Research, 2305 Annable Rd, Nelson BC V1L 6K4) who is currently working on the Provincial Goat Management Plan.

The data layers required for querying environmental variables for each goat record were obtained from Garth Mowat and David Pritchard (Mowat et al. 2004). These layers include actual evapotranspiration (cell size 5839 m; the amount of water lost through vegetation), rainfall (cell size 3937 m; the amount of precipitation falling as rain over an area), ruggedness (cell size 682 m; a categorical variable essentially measuring the change in elevation over distance) Normalized Difference Vegetation Index (NDVI) (cell size 1000 m; a surrogate for productivity), and temperature (mean annual temperature data). Additionally, Vegetation Continuous Field (VCF) layers (cell size 500 m) were used and consisted of the percent treed, percent bare, percent herb and percent water, which essentially described the proportion of the landscape covered by each of these attributes. The VCF layers were developed at the University of Maryland and can be accessed at (http://glcf.umiacs.umd.edu/data/modis/vcf).

Prior to analyses, harvest records were screened to reduce erroneous records in the dataset. Initially, all records were spatially screened. To import the data into ArcMap GIS software (ESRI 2008), the grid locations required transformation into points that could be used as UTM coordinates. Grid easting and northing coordinates provided in each harvest record were multiplied by 1000 to obtain the equivalent UTM easting and northing coordinates. This provided the location in UTM, accurate to the nearest km. As British Columbia encompasses several UTM zones, records from each zone were imported into the GIS separately, and the projection was defined for the appropriate UTM zones. Following defining the projections of the records for each UTM zone, all records were reprojected into a single layer using the BC Albers coordinate system (Figure 1). This coordinate system is used by the British Columbia government to minimize the distortion associated with other coordinate systems, which occurs across the broad expanse of British Columbia. Following reprojection into the BC Albers coordinate system, Albers coordinates were added to each harvest record using Hawth's tools (Beyer 2004) in order to facilitate transition between the GIS and STATA (version 9.2, StataCorp 2006).

Spatial screening consisted of two phases. Initial screening involved removing those points for which the recorded harvest location did not coincide with the management unit on the harvest record. To accomplish this, each point was queried to obtain the value for the game management unit. Then using STATA, categorical variables were created to indicate whether the projected location of the record was where it was reported to be, that is, if the management unit the coordinates placed the record in was the same as that on the harvest record. If the record was not in the appropriate location (n = 1695), it was dropped from the analysis. Additionally, records that were not within the projected provincial mountain goat range (n = 4025) were labelled with categorical variables in STATA. These records were used for regional comparisons, but were dropped from analysis of the environmental variables influencing horn growth. The records that remained were the most likely to represent records with accurate locations.

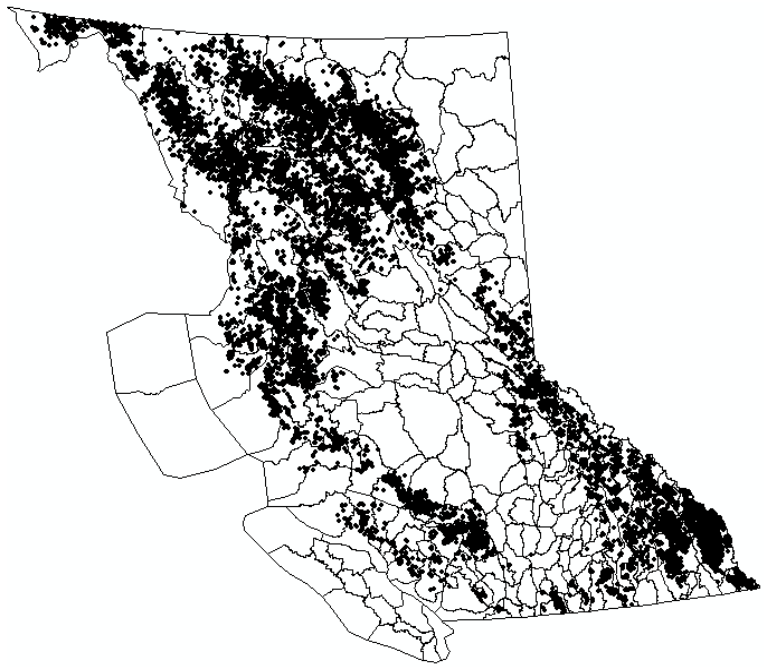

Figure 1. Mountain goat records from mandatory harvest reporting records in British Columbia following spatial screening. Underlying map is the Wildlife Management Units (WMU). Both the records for horn growth and the WMUs are projected in BC ALBERS.

Following spatial screening, the horn-growth records were screened to remove erroneous records from the dataset. A visual basic macro in Microsoft Excel 2007 was developed by Michael Gillingham to check and remove erroneous records from the dataset as necessary. Screening with the macro included checking the age reported by the inspector to see if they corresponded to the age of the horn as determined by adding one to the number of increments reported for the horn, and checking if the age was the same for the left and right horns. Horns with brooming were identified and only used for circumference measurements. Horns were checked to ensure that the total length was longer than the longest increment, and also checked to ensure that the length of each increment was increasing, as measurements were taken from the tip of the horn to each annulus and should increase with each increment. Another check done by the macro was to identify which records had all measurements for a given goat recorded. Additionally, the macro identified duplicate records. Duplicate records were identified as those records where the growth measurements were completely identical, although the location, sex, date, or other qualitative attributes were not necessarily identical. The problems identified by the Excel macro are outlined in Table 1.

Table 1. Summary of identified errors within the harvest data set used in the analysis. Erroneous records account for more than half of the total mountain goat harvest records

	Sex			
Problem	F	M	U	Total
None	3202	6907	76	10185
Duplicate Record	386	1377	11	1774
No Data	519	1222	8	1749
Base and Length Only	3003	7504	59	10566
No Age	613	889	19	1521
Length and Horn Age Only	104	280	1	385
Base Only	124	386	2	512
Length Incorrect	113	236	4	353
Base and Horn Age Only	52	98	1	151
Insufficient Data	14	23	0	37
Total	8130	18922	181	27233

The macro labelled each problem and created new variables for the horn records to ease analysis. Unless otherwise stated, the variables that were created by the macro were used in the analysis. Where both the left and right horns had measurements, the macro created variables for age, length to each annulus, basal circumference, and total length from the left horn. Otherwise, when only one horn had measurements, the side for which measurements were taken was used to construct the above variables.

Duplicate records and those with insufficient data were dropped from the analysis, as were records where sex was unknown (n = 181). Records were considered to have insufficient data if there were no horn measurements, although age, sex or location information may have been present. The removed records provided no reliable information for the analyses. Those records with unreasonable values for horn growth or age were also removed from the analysis. Unreasonable values for horn growth included records reporting total length >500 mm, or circumferences of <65mm, while unreasonable values for age included records indicating the age of the goat was >30 years. In general, only those records with no problems identified were used (Table 1). When other errors were discovered in the dataset, they were identified and/or deleted depending on their severity.

Examination of patterns and variation in horn growth

The examinations of patterns and differences of horn growth in mountain goats were unlikely to be sensitive to differences unless goat records were split into smaller regions to account for the highly variable climatic conditions that exist throughout mountain goat range in British Columbia. Game management units from four regions were selected to be representative of distinct climatic and environmental conditions based on the Biogeoclimatic Ecosystem Classification (BEC) system used in British Columbia. (Meidinger and Pojar 1991). Subunits 6-15, 6-9, 6-10, 6-11, and 6-3 from the Skeena region, were selected to be representative of the Coastal Western Hemlock, and Mountain Hemlock biogeoclimatic zones, which are generally considered to be mild with high precipitation. Subunits 3-33, 3-16, 5-5, and 5-4 from the Chilcotin were selected to be representative of the Interior Douglas Fir, Alpine Tundra, Mountain Hemlock, Mountain Spruce, and Ponderosa Pine biogeoclimatic zones, which are typically characterized by dry conditions and relatively cold winters. Subunits 4-25, 4-24 and 4-23 were selected to represent the Engelmann Spruce Subalpine Fir, Alpine Tundra, Mountain Spruce and Ponderosa Pine biogeoclimatic zones of the Kootenays, which tend to be somewhat intermediate in their climate. Subunits 7-51, 7-50, 7-41 and 7-42 were selected to represent the Spruce, Willow and Birch, and Alpine Tundra biogeoclimatic zones of Northwestern BC, where conditions may be relatively harsh. The subunits were selected using STATA and identified by creating a new categorical variable listing the comparison regions. In ArcMap GIS, the management units were joined with their associated biogeoclimatic zones using the union tool to summarize the climatic conditions of the comparison regions. A full description of these biogeoclimatic zones can be found in Meidinger and Pojar (1991).

Several new variables were constructed to characterize the basic patterns of horn growth in mountain goats. To address growth rates in mountain goats, growth variables were constructed representing the growth during each year. The variable representing growth to annulus one was simply the length of the first increment. Growth of subsequent years was determined by subtracting the length of the previous year from each increment, and these new variables were added to the dataset using STATA. To address asymmetry in mountain goats, only records with measurements for both right and left horns were included in the analysis. The difference between the length of horns at annulus four, as well as the difference between basal circumference were calculated and the new variables were added to the dataset using STATA. To examine whether the amount of horn growth at older ages was substantial in relation to the total horn growth, the growth in years six, seven, and eight were summed, then divided by the sum of growth in the first five years. The resulting proportional value was added to the dataset again using STATA. To determine whether the first increment was always the largest, the data were ranked by age using STATA.

To examine the variability of horn growth among the comparison regions, a Michaelis-Menton equation was fit to the growth records of each comparison region using SAS 9.2 (SAS Institute 2009) The Michaelis-Menton model is developed using the equation;

$$Y = \frac{A \times X}{B + X}$$

Where Y = horn growth (mm) and X = elapsed time (years). This equation contains two parameters, one describing the estimated maximal horn length (parameter A) and the other, a parameter which may be used to infer the amount of time required for horns to achieve half of their total growth (parameter B). These parameters were compared by sex and comparison region. These steps allowed for examination of the patterns and differences in horn growth in mountain goats of British Columbia.

To determine if horn growth differed among selected comparison regions, data for the length of the horns at the fourth increment were square transformed to meet normality and homogeneity of variance assumptions. ANOVA with Bonferonni post hoc comparisons were used to discern differences in the length at increment four for the comparison regions.

To identify whether horns were symmetrical in all comparison regions, the difference variable constructed from the left and right horns for increment four and basal circumference was used. This analysis was limited to differences of <20 mm, as in our initial analyses, there were numerous values with unreasonably high values. The presence of these values demonstrates why the Excel macro was required for checking the records and creating new variables from the original harvest record. Differences >20 mm most likely represented erroneous records and for that reason they were excluded from the analysis. Length and basal symmetry were examined by sex among comparison regions, with 95% confidence intervals around mean values to identify regions where horns were asymmetrical.

To understand which increment tended to be the largest for horn growth, the horn-growth data were ranked by age based on the amount of growth between each increment using the STATA command ROWRANKS. Ranked data were then summarized by sex and comparison region. To understand the amount of growth that occurred after age five, another variable was constructed by summing the growth after annulus four and dividing this by the sum of the growth to the fourth annulus. Only goats with ages $\geq$eight years were used in this portion of the analysis. The mean and 95% confidence intervals were calculated by sex for each comparison region.

Analysis of environmental and climatic influences on horn growth

Mountain goat home range is highly variable, and depends on the amount of available habitat (Côté and Festa-Bianchet 2003). Côté and Festa-Bianchet (2003) indicate that summer home ranges are typically small (5 km^2), although they also indicated that annual home ranges may be as large as 25 km^2. The quality of forage is higher during summer months (Côté et al. 1998), and due to the availability of forage, the majority of horn growth occurs on summer ranges. Unfortunately, hunting season dates overlap with the mountain goat rut, and as such, male mountain goats may exhibit much greater movements than during other times of the year. It is, therefore, important that the home range be expanded to include these greater movements.

Goat records were imported into ArcMap GIS software (ESRI 2008) and each point was buffered with a 1.7841-km radius buffer using Hawth's Tools (Beyer 2004) to create a 10-km^2 buffer that would include an area the size of a summer range where most of the resources for horn growth were likely to be obtained. This buffer also accounted for the greater movement associated with the mountain goat rut (Côté and Festa-Bianchet 2003). Again using Hawth's tools, 20 points were randomly selected from within the 10-km^2 buffer (Figure 2). These 20 points were then queried using Hawth's Tools Intersect Points tool (Beyer 2004) against the layers for actual evapotranspiration, percent bare, treed, herb and water (from VCF), rainfall, ruggedness, NDVI, and temperature. This resulted in 20 records per individual goat record. The resulting data table was imported into STATA.

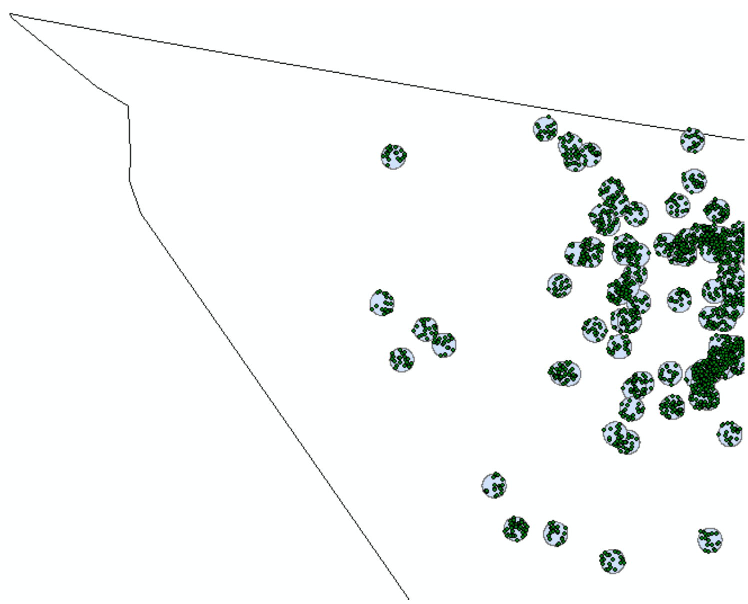

Figure 2. Northwestern corner of British Columbia with buffered locations and the 20 randomly selected points within the buffered zone. These points were queried for environmental variables and merged with the existing records for horn growth.

A STATA COLLAPSE command was used to generate the mean value for each of the 20 random points for each horn record for all continuous variables (i.e., NDVI, rainfall, temperature, VCF layers, evapotranspiration). As ruggedness was a categorical variable with values ranging from one to seven, the median was used instead of the mean. These collapsed values were then merged into the STATA file for use in understanding which factors influenced horn growth.

Identifying which environmental or climatic variables influenced horn growth was accomplished using stepwise regression. Stepwise regression was chosen as it provides the model that best describes which variables are important to horn growth. Further, predicting models using an information theoretic approach across the wide geographic range of British Columbia is complicated and would detract from the ability to describe the variables influencing horn growth.

Three different response variables were used in the stepwise regression. Length at the fourth annulus was one response variable, chosen based on the results of the initial analysis, which indicated minimal horn growth after the fourth annulus. Basal circumference was chosen as the second response variable, as basal circumference is representative of the growth throughout the animal's life. Finally, length to annulus one was the third response variable, chosen as it is the annulus where growth tends to be most rapid, and variability is potentially easier to detect.

Descriptor variables included those metrics described above. Forward Selection stepwise regression in STATA was used, where a variable required a minimum p-value of 0.10 for inclusion. We selected a p-value of 0.10 to ensure that any variables which influenced horn growth would not be missed. To identify any problems of multi-colinearity in the descriptor variables, the Variance Inflation Factor (VIF) was calculated for the stepwise regressions using STATA. A VIF <5 was considered to indicate no issues with colinearity. Examination of residual plots was conducted to identify whether any problems existed within the data. Outliers that represented incorrect points, whether they were duplicates or unreasonable values, were dropped from the overall analysis. Outliers that represented valid points for animals were retained for the stepwise regressions.

RESULTS

Examination of patterns and variation in horn growth

Horn growth to increment four significantly differed among comparison regions ($F_{3,359}$ = 8.50, P < 0.0001). Specifically, females in the northeast region were smaller than the females goats in the Skeena (Bonferroni post hoc tests; Table 2). Additionally, females from the Skeena were larger than those in the Chilcotin (Table 2). No other significant differences were found for females in other regions. Male mountain goat horns were longest in the Skeena and Kootenay regions, and shortest in the Chilcotin and Northeast regions (Table 2). The length of horns at annulus four did not differ between males and females, except in the northeast comparison region, where males were slightly larger than females ($F_{1,550}$ = 4.15, P = 0.0420) (Table 2).

Table 2. Length (mm) at increment four of male and female mountain goats in the comparison regions. Means of females sharing the same superscript indicate no difference in length to increment four for females. Means of males sharing the same superscript indicate no difference in length to increment four for males. All comparisons were conducted using Bonferroni post hoc tests for differences.

Region	Sex	Observations	Mean	Std. Error
Northeast	F	138	204.77^{a}	1.82
Skeena	F	116	216.52^{b}	1.78
Chilcotin	F	77	205.95^{a}	2.11
Kootenay	F	32	213.63^{ab}	3.74
Northeast	M	414	208.84^{c}	0.89
Skeena	M	205	217.73^{d}	1.32
Chilcotin	M	139	208.47^{c}	1.55
Kootenay	M	103	216.21^{d}	2.2

Horn growth was not complete after annulus four, although it was relatively minor in most instances (Table 3). In some instances, between 3.90 and 8.89% of horn length was accumulated after annulus four (Table 3). Females in the Chilcotin grew the least after annulus four, with 1.62-3.49% of horn growth occurring during the later increments (Table 3); however, there were only six observations for this comparison. Males from the Kootenays displayed the greatest amount of growth after annulus four, with 4.18-8.94% of total horn length deposited (Table 3).

Table 3. Proportion of total horn growth occurring after age 5.5 for mountain goats in comparison regions.

Region	Sex	Mean	Std. Error
Northeast	F	0.046	0.004
Northeast	M	0.048	0.001
Skeena	F	0.056	0.004
Skeena	M	0.063	0.003
Chilcotin	F	0.026	0.004
Chilcotin	M	0.051	0.007
Kootenay	F	0.064	0.011
Kootenay	M	0.066	0.012

In the majority of instances, horn growth was greatest for the first increment of mountain goats for all regions (Table 4). In some instances, the growth of the first increment was not the largest, although these instances were rare and did not appear to be influenced by sex or the region the goats came from (Table 4). Rankings >1 indicate that the growth of the first increment was not the largest of all increments on the horn (Table 4).

Table 4. Horn growth of mountain goats ranked by the amount of growth occurring in the first year. A rank of one indicates that the first increment was the longest. A ranking of two or more indicates that the growth in the first year was not the highest.

			Rank			
Region	Sex	Observations	1	2	3	4
Northeast	F	342	306	28	8	0
Skeena	F	416	394	13	8	1
Chilcotin	F	206	191	8	7	
Kootenay	F	103	101	1	1	
Northeast	M	980	893	76	10	1
Skeena	M	645	622	18	5	0
Chilcotin	M	354	338	15	1	
Kootenay	M	250	243	6	1	

Horn growth was symmetrical when all of British Columbia was considered in the analysis (95% confidence intervals for the difference between the length of the left and right horns included zero). When comparison regions were used for the analysis, however, asymmetry in horn length at increment four was found for male and female goats of the Kootenays, and male goats of the Northeast comparison region (Table 5). For the examination of asymmetry in circumference measurements, female goats in the Chilcotin comparison region were found to have significant differences between the left and right horns (Table 6).

Table 5. Asymmetry of mountain goat horn length across comparison regions. Asymmetry was the difference (mm) between the right and left horns at increment four. Mean values with superscript NS indicate that the confidence interval included zero. Mean values with superscript S indicate that confidence intervals did not include zero.

Region	Sex	Observations	Mean	Std. Error	Lower 95%CI	Upper 95%CI
Chilcotin	F	124	0.331^{NS}	0.517	-0.693	1.354
Chilcotin	M	217	-1.092^{NS}	0.687	-2.447	0.263
Kootenay	F	323	-3.096^{S}	0.982	-5.028	-1.164
Kootenay	M	644	-2.339^{S}	0.615	-3.547	-1.13
Northeast	F	134	-0.328^{NS}	0.625	-1.565	0.909
Northeast	M	330	-1.324^{S}	0.52	-2.347	-0.301
Skeena	F	75	0.093^{NS}	0.775	-1.45	1.637
Skeena	M	118	-1.619^{NS}	1.62	-4.827	1.59

Growth rates as determined by the parameters provided by the Michaelis-Menton models were variable across the province. All horns grew in asymptotic fashion (Michaelis-Menton, all $P < 0.001$) for both sexes in all comparison regions. The model parameter A, which represents the potential maximal horn growth to age seven, was greatest for females of the Skeena region, and smallest for females of the Kootenay region (Table 7). Males of the Skeena region had the largest A parameter values, while males in the Chilcotin were the smallest (Table 7). The model parameter B for the Michaelis-Menton equation represented the age at which half of the total horn growth (A) was achieved. Parameter B was highest for female goats in the Skeena and Chilcotin, while it was highest for males in the Skeena and Northeast regions (Table 7).

Table 6. Differences in circumference (mm) between horns of mountain goats for comparison regions. Mean values with superscript NS indicates that the confidence interval included zero. Mean values with superscript S indicates that confidence intervals did not include zero.

Region	Sex	Observations	Mean	Std. Error	Lower 95%CI	Upper 95%CI
Northeast	F	155	0.335[NS]	0.186	-0.032	0.703
Skeena	F	83	0.096[NS]	0.334	-0.569	0.762
Chilcotin	F	138	0.486[S]	0.240	0.011	0.960
Kootenay	F	343	-0.216[NS]	0.274	-0.754	0.323
Northeast	M	384	0.063[NS]	0.193	-0.316	0.441
Skeena	M	133	0.188[NS]	0.250	-0.307	0.683
Chilcotin	M	230	0.170[NS]	0.188	-0.200	0.539
Kootenay	M	730	0.100[NS]	0.199	-0.291	0.491

Table 7. Horn-growth parameters from the Michaelis-Menton growth models. The model parameter A is a measure of the maximal horn growth (mm), and B is the age at which half of the horn growth is completed. Parameters sharing the same superscripts did not differ from each other.

Region	Sex	A	Lower 95%CI	Upper 95%CI	B	Lower 95%CI	Upper 95%CI
Northeast	M	291.6[a]	279.1	304	1.92[c]	1.655	2.185
Northeast	F	286.2[ab]	262.8	309.6	1.947[c]	1.438	2.456
Skeena	M	312.2[a]	294.8	329.7	2.21[c]	1.844	2.576
Skeena	F	326.3[a]	294.7	357.9	2.616[c]	1.933	3.3
Chilcotin	M	263.2[b]	255.6	270.8	1.247[d]	1.094	1.401
Chilcotin	F	286.5[ab]	264.7	308.3	2.053[c]	1.569	2.537
Kootenay	M	286.3[ab]	269.1	303.6	1.638[cd]	1.288	1.988
Kootenay	F	275.9[ab]	246.3	305.5	1.432[cd]	0.836	2.028

Analysis of environmental and climatic influences on horn growth

Examination of the residual plots indicated that linear multiple regressions models were appropriate for the data. In two instances, there were distinct clusters in the residuals (Figure 3). These points were examined to determine their validity. If the points represented reasonable values as described in the methods, they were retained in the analysis. If points represented obvious data errors, they were removed from the analysis. In addition, there were no problems with colinearity as all VIF values were <5.

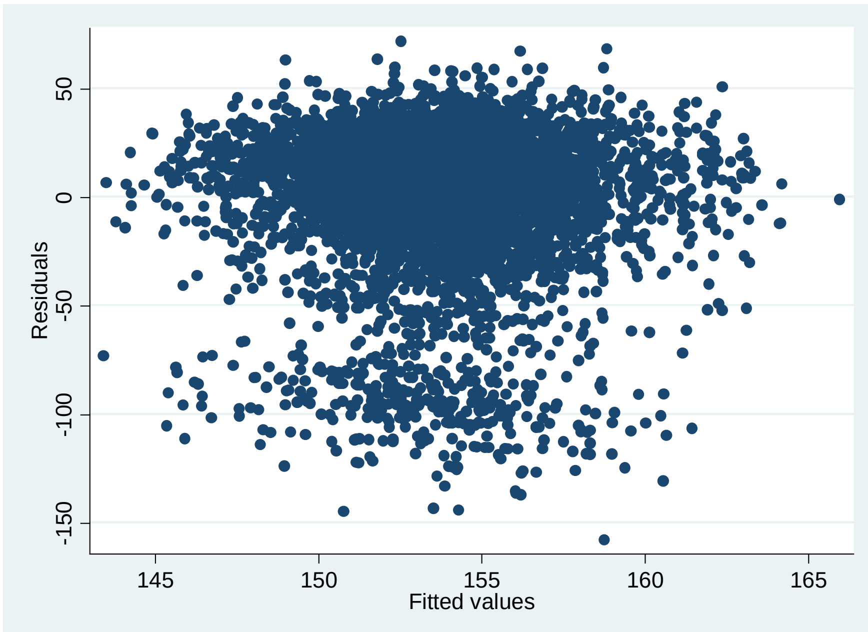

Figure 3. Residuals from stepwise regressions for increment one of male mountain goats. The cluster of points with low residual values (<75) were considered valid points, and represent those records for which horn growth was <100 during the first year of growth.

Horn growth to increment four of male mountain goats was positively influenced by temperature, rainfall, and herbaceous cover, and negatively influenced by ruggedness, evapotranspiration, and NDVI (Table 8). The linear model was significant ($P < 0.001$), although the fit of the data to the line of best fit was relatively poor ($R^2 = 0.0276$).

Table 8. Factors influencing the growth of horns to increment four on male mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Temperature	1.12	0.143	7.82	0.001
Rainfall	0.001	0.000	-3.6	0.001
Herb Cover	0.09	0.022	4.27	0.001
Ruggedness	-1.09	0.322	-3.37	0.001
Evapotranspiration	-0.02	0.006	-2.7	0.007
NDVI	-0.06	0.029	-2.21	0.027
Intercept	233.09	4.063	57.37	0.001

Similarly, the growth of horns of females to increment four was positively influenced by rainfall and temperature, and negatively influenced by the amount of bare ground and NDVI (Table 9). The stepwise regression was significant ($P < 0.001$), although as with the males, the fit of the data to the line of best fit was relatively poor ($R^2 = 0.0188$).

Table 9. Factors influencing the growth of horns to increment four on female mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Bare Ground	-0.083	0.031	-2.64	0.008
Rainfall	0.001	0.000	-3.82	0.001
Temperature	0.772	0.210	3.68	0.001
NDVI	-0.103	0.043	-2.39	0.017
Intercept	230.052	5.583	41.21	0.001

Growth during the first year of life of male mountain goats was positively influenced by temperature and rainfall and negatively influenced by the amount of bare ground, rugged terrain, and evapotranspiration (Table 10). When increment one was used for stepwise regressions, the regression for male mountain goats was significant ($P < 0.001$), although the fit of the data to the line of best fit was poor ($R^2 = 0.0084$).

Table 10. Factors influencing the growth of horns to the first increment on male mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Bare Ground	-0.056	0.020	-2.81	0.005
Ruggedness	-1.037	0.364	-2.85	0.004
Temperature	0.693	0.161	4.3	0.001
Evapotranspiration	-0.020	0.007	-2.98	0.003
Rainfall	0.001	0.000	-2.32	0.02
Intercept	169.579	2.727	62.18	0.001

Growth during the first year of life of female mountain goats was positively influenced by the proportion of treed and herb-covered landscape and negatively influenced by evapotranspiration, which was marginally significant (Table 11). Regression results were significant ($P < 0.001$), although the fit of the data to the line of best fit was poor ($R^2 = 0.008$).

Table 11. Factors influencing the growth of horns to the first increment on female mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Tree Cover	0.163	0.035	4.72	0.001
Herb Cover	0.090	0.045	1.99	0.047
Evapotranspiration	-0.017	0.010	-1.77	0.076
Intercept	137.197	4.220	32.51	0.001

Basal circumference of male mountain goats was positively related to temperature and rainfall, while negatively influenced by evapotranspiration, NDVI, ruggedness, and the proportion of the landscape that was treed (Table 12). The model was significant, but fit of the data to the line of best fit was relatively poor ($R^2 = 0.0245$).

Table 12. Factors influencing the basal growth of horns of male mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Temperature	0.754	0.063	11.91	0.001
Evapotranspiration	-0.009	0.003	-3.63	0.001
NDVI	-0.046	0.014	-3.33	0.001
Rainfall	0.001	0.000	-4.24	0.001
Ruggedness	-0.296	0.136	-2.18	0.029
Tree Cover	-0.018	0.009	-1.9	0.058
Intercept	147.128	1.811	81.24	0.001

Basal circumference of female mountain goat horns was positively related to evapotranspiration, rainfall and temperature (Table 13). The stepwise regression for basal circumference of female mountain goats was significant ($P < 0.0038$), but the fit of the data to the line of best fit was relatively poor compared to the regressions for males ($R^2 = 0.0048$).

Table 13. Factors influencing the basal growth of horns of female mountain goats in British Columbia. Factors were identified using stepwise regression.

Variable	Coefficient	Standard Error	T	P
Evapotranspiration	0.007	0.004	1.89	0.058
Rainfall	0.001	0.000	-3	0.003
Temperature	0.185	0.084	2.19	0.029
Intercept	107.476	1.232	87.23	0.001

DISCUSSION

Examination of patterns and variation in horn growth

The length, circumference and patterns of horn growth were linked to the region from which the mountain goats came. Although the differences between regions were not necessarily significant, goats from the Skeena management units had the largest mean length, both for the length comparisons at age five and for the parameter fit by the Michaelis-Menton growth models describing maximal length. Mountain goats of the Kootenays had horn lengths similar to the goats in the Skeena. Goats of the Skeena had symmetrical horns, whereas goats from the Kootenay region tended to have some degree of asymmetry. In contrast, goats from the Chilcotin management units grew the smallest horns, and although length was symmetrical, basal circumference was not. Chilcotin females were the only individuals to demonstrate any horn asymmetry in circumference.

Horn length is positively related to mass, hind foot length, and chest circumference (Côté et al. 1998), and so it is likely that the goats of the Skeena and Kootenay management units, which had the longest horns, are the largest of those in British Columbia. In contrast, the goats of the Chilcotin management units are likely smaller in mass, hind foot length and chest circumference, as goats from these areas tended to have smaller horns relative to those in other locations of the province (Côté et al. 1998). The environmental conditions of these regions differ greatly (Meidinger and Pojar 1991), with the Skeena likely being the most favourable to growth and survival. The mountain goats of the Chilcotin, however, face much different climatic conditions, which tend to be characterized by much drier and colder conditions (Meidinger and Pojar 1991) than those goats of the Skeena management units. The environmental stressors of the Chilcotin likely negatively influence growth, resulting in smaller animals (Côté et al. 1998). In addition to the regional differences, we identified sexual dimorphism in horn length at age five only in goats of northern British Columbia. The lack of sexual dimorphism in horn length has been identified elsewhere (e.g. Côté et al. 1998), but generally, sexual dimorphism in horn length is maintained until the animal is six years of age or greater (Côté et al. 1998).

The patterns of horn growth are related to environmental stressors, individual condition and reproductive status for mountain goats (Côté et al. 1998, Côté and Festa-Bianchet 2001b). Asymmetry in horns reflects the ability of the animal to undergo stable development, and is particularly useful in females for identifying individual quality (Côté and Festa-Bianchet 2001b). Horns of male and female Skeena goats were collectively symmetrical. The climatic conditions of the coastal management units comprising the Skeena region were moderated due to their proximity to the ocean, and as such were likely milder and wetter than those in other areas of the province (Meidinger and Pojar 1991), lending support to the conclusion that the environmental conditions of this region tended to be more stable and favourable to growth. In contrast, horns of female mountain goats of the Kootenays exhibited asymmetry in length, while horns of females in the Chilcotin management units displayed asymmetry in basal circumference. Asymmetry in these regions likely reflects the lack of a moderating influence on climatic conditions, resulting in much more variable and harsh conditions than those of coastal regions (Côté and Festa-Bianchet 2001b) and so these goats are faced with more stressors with which they must cope. This conclusion is corroborated by the fact that goats in the Chilcotin tended to have the shortest horns.

The rates of horn growth were highly variable, although the time required to accumulate half of the total horn length (parameter B of the Michaelis-Menton models) was longest in the Skeena management units. In contrast, the goats of the Chilcotin management units required much less time to grow half of their overall length (Table 8). This is potentially due to the difference in length of the horns, where horns of goats from the Skeena management units tended to be longer (parameter A) than those of the Chilcotin goats. Therefore, the difference in time to grow the horns may be related to the length of the horns (Côté et al. 1998). Alternatively, those goats of the Skeena may have simply grown more in later years than goats from the Chilcotin management units. This conclusion is supported by the results of the analysis on the amount of horn growth accumulated after age five (Table 3).

The growth of mountain goat horns during the first year and a half of life is considered to be the most rapid, and growth rates decrease in subsequent years (Côté et al. 1998). Rapid growth for young animals may be related to the development of dominance hierarchies (Fournier and Festa-Bianchet 1995, Côté et al. 1998). The results of our analyses support the conclusion that the growth of the first increment is the longest. In some instances, however, the growth between the second and third annuli exceeded the growth occurring to the first annulus, which has not been documented in other studies of mountain goat horns (e.g., Cowan and McCrory 1970, Côté et al. 1998). Growth has been observed to depend on environmental conditions for Dall sheep (Bunnell 1978), and on disease for other species (Scott 1988). It is, therefore, possible that the reduced growth during the first year is the result of disease or environmental stochasticity. When horn growth is relatively slow during the first year, that is when horns do not grow as much as expected, growth in subsequent years is higher than expected (Côté et al. 1998), indicating that overall horn length may not be negatively affected by a single season of poor growth.

Mountain goats at Caw Ridge in Alberta were reported to have shorter and consistent annual increments after age five (Côté et al. 1998). Our analyses indicate similar patterns in growth, where the majority of horn growth was accumulated during the first four years of life. In our analyses, horn growth continued, although the amount of horn accumulation was relatively minor after age five. Male mountain goats from the Kootenay management units were found to grow the most after age five, with 4.18-8.94% of the total horn length accumulated after age five.

Interestingly, the horn length of mountain goats of the Kootenay comparison regions were not the largest horns of all goats examined. This may be due to slower growth during some portion of the first five years of the goat's life, which may result in greater horn growth for older animals (Côté et al. 1998).

The patterns of mountain goat horn growth in this analysis were similar to those of Caw Ridge in Alberta, although there were deviations and distinct patterns in growth among the regions examined. In particular, our analyses supported the conclusions by Côté et al. (1998) that the first increment of mountain goats tends to be the largest. Côté et al. (1998) did not find a link between precipitation and horn growth, although they acknowledged that their sample size was small and indicated the need to take other variables into considerations. In our analyses, we selected regions characterized by different climatic conditions, and identified differences in horn growth among regions. These results support our initial predictions that the horn growth of mountain goats is dependent on the climatic and biological characteristics of their habitats. By linking the differences in horn growth to the mass, chest girth, and other characteristics (Côté et al. 1998) of the mountain goats in a region, we can hypothesize directional differences in size and condition, and that those differences depend on the environment in which the animal developed.

Analysis of environmental and climatic influences on horn growth

The analysis of the variables that influenced horn growth revealed that the parameters explaining horn growth differed by sex. In all instances, models for females included fewer variables than those for males. This is contrary to expectations, as females have additional nutrient demands placed on them, notably gestation and lactation. The habitat utilization of females differs greatly from that of males, especially during the summer when horn growth takes place (Festa-Bianchet and Côté 2008). Females tend to occupy alpine habitats to a much greater extent than males, and move greater distances (Festa-Bianchet and Côté 2008), perhaps in part as a predator avoidance strategy (Festa-Bianchet and Côté 2008). For this reason, perhaps females are less dependent on the specific combinations of resources in an area. Rather, they rely on covering sufficient area to optimize the combination of resources. Alternatively, males tend to be much larger than females (Côté et al. 1998, Côté and Festa-Bianchet 2001a), and so the greater number of variables in these models may be related to body size.

In addition, the parameters explaining horn growth differed depending on the response variable used. The factors that influenced growth of basal circumference and length to increment four can be considered as those factors influencing the majority of horn growth occurring over the life of a mountain goat. The results of our analysis and those of Côté et al. (1998) indicate that horn growth is minor after age five, and so the growth to this point indicates the parameters that are required to grow large, both in body size and horn length. Alternatively, the growth to the first increment is more characteristic of the conditions faced by the goats during the first year and a half of life (Côté et al. 1998). The influence of environmental variables on growth during this first increment may be less important than maternal quality, where a high-quality mother may increase the growth of her offspring (Côté and Festa-Bianchet 2001a), and may be able to provide sufficient nutrition even during difficult years.

The factors contributing positively to horn growth of both male and female mountain goats to age five included temperature and rainfall. The positive influence of temperature and rainfall on horn growth corroborates those results from the analysis on regional differences in horn growth, where goats from the Skeena management units tended to be largest. This indicates that when temperatures are milder, and precipitation is available to support primary productivity

(Bunnell 1978), animals are able to allocate more resources to horn growth. These results contradict those of Côté et al. (1998), who indicated that rainfall was not significantly related to horn growth, although they acknowledged the need to examine rainfall on a larger scale than was done in their study. Alternatively, NDVI was negatively related to horn growth of both males and females. This is contrary to our expectations, as NDVI represents plant productivity (Couturier et al. 2009), and was used to provide an index of the amount of forage available to the animals. The NDVI layer identifies all primary productivity, and includes conifers and other vegetation which is unavailable as forage for mountain goats. Perhaps if a layer describing the difference in NDVI over several months (as in Walker et al. 2007) were used, the forage available to goats would be better represented.

As in the model for growth to age five, basal circumference was positively influenced in both models by rainfall and temperature. Additionally, evapotranspiration was in both models, but the influence was positive for females and negative for males. This may reflect differences in sexual preference of habitat type. Festa-Bianchet and Côté (2008) indicated that male mountain goats spent a greater proportion of time in forested areas than females, in which case, evapotranspiration would be from conifers and other unpalatable forage. Females, occupying the spaces above the tree line (Festa-Bianchet and Côté 2008) would be positively influenced by evapotranspiration, which would more likely represent edible forage. This inference assumes that the animals were occupying habitats characteristic of sexual preferences for the time of year they were harvested, and that the goats across British Columbia utilize habitats in a similar manner to goats at the Caw Ridge study site in Alberta (Festa-Bianchet and Côté 2008). The use of forested habitats is supported by the fact that both NDVI and the proportion of the landscape that was treed also contributed negatively to basal circumference of mountain goat horns.

The only parameter in both models describing horn growth to increment one was evapotranspiration, which was of similar magnitude and direction for both sexes. As indicated previously, the growth to increment one may be more determined by maternal quality than environmental parameters. In this instance as immature goats of both sexes would be in nursery groups (Festa-Bianchet and Côté 2008), we would expect similar parameters to be in both models but this was not the case. Differences in growth of males and females during this time must be considered, especially as females do not have the same nutritional requirements, as they are neither preparing to rear offspring (Côté and Festa-Bianchet 2001b), nor increasing in size at the same rate as males (Côté et al. 1998). Male and female mountain goats increase in mass at a rapid rate following weaning (Côté and Festa-Bianchet 2001a, 2001b), with females and males reaching roughly 65 and 52% of their maximal mass respectively by age two (Gendreau et al. 2005). Although the proportion of total mass reached is less for males, they are generally much larger at maturity than females (Côté and Festa-Bianchet 2001a , Gendreau et al. 2005) and so males may require more resources during this period, which would explain why the models for males had more parameters.

The results of this study represent valid patterns, consistent with expectations of the factors influencing horn growth of mountain goats. Although we are confident that as many errors were identified and removed from the dataset as was possible, the data quality of the harvest records was extremely poor. Following screening, only one third of the data were useable. Unfortunately, we could not develop a set of screening criteria for every error in the dataset, and as such, even after the extensive screening, erroneous records were still being identified and removed from the analysis. Due to the many errors in the dataset, we cannot help but consider that certain variables may be incorrectly entered. In short, while the analyses on the patterns and factors influencing horn growth are valid, more attention needs to be directed towards all aspects of data collection, entry, and reporting. These errors need to be examined and accounted for prior to any major shift in management.

MANAGEMENT IMPLICATIONS

The mountain goats of British Columbia demonstrated similar patterns of horn growth to those of Caw Ridge, Alberta. There were important differences however, which indicates that care must be taken when extrapolating growth data from populations of mountain goats of Caw Ridge to goats in other areas of North America. Unlike the goats of Caw Ridge (Côté et al. 1998), the goats in our analyses did not exhibit sexual dimorphism in horn length at five years of age, except for those in northern BC. This emphasizes the difficulty identifying differences in male and female mountain goats, and points to the difficulties managing the harvest of these animals, especially when considering their unique reproductive biology (Côté and Festa-Bianchet 2001c).

The links between horn growth and location identified in this study are important to the conservation and management of mountain goats in British Columbia. Mountain goats do not grow in a uniform fashion across the province, and management of consumptive and non-consumptive forms of recreation should consider these differences. For example, if we consider mountain goats in dry areas with relatively harsh winters, such as those from the management units we selected to represent the Chilcotin, we might expect the observed differences in growth to extend to population growth. This indicates that the mountain goats of these regions may be able to sustain a much lower harvest level, or that they may require longer to recover from disturbance events compared to goats from areas where growth is somewhat better.

The models for horn growth provided an idea of those parameters important for horn growth, but the fit of the models was poor, and so the predictive capacity is also poor. An understanding was gained of the importance of temperature and precipitation on mountain goat growth, and may allow wildlife managers to be more restrictive on harvest allocations when extremely cold winters or prolonged periods without precipitation occur. Future studies should attempt to utilize more detailed GIS layers as they become available and incorporate access and harvest rates into the models in an attempt to improve the predictive capacity of these models and better understand the environmental influences on growth.

LITERATURE CITED

Asleson M., E. Hellgren, and L. Varner. 1996. Nitrogen requirements for antler growth and maintenance in white-tailed deer. Journal of Wildlife Management 60:744-752.

Barboza, P. and P. Reynolds. 2004. Monitoring nutrition of a large grazer: muskoxen on the Arctic refuge. International Congress Series 1275:327-333.

Beyer, H.L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

British Columbia Ministry of Environment. In preparation. Mountain goat management plan for British Columbia.

Bunnell, F. 1978. Horn growth and population quality in Dall sheep. Journal of Wildlife Management 42:764-775.

Côté, S.D., and M. Festa-Bianchet. 2001a. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230-238.

Côté, S.D., and M. Festa-Bianchet. 2001b. Life-history correlates of horn asymmetry in mountain goats. Journal of Mammalogy 82:389-400.

Côté, S.D., M. Festa-Bianchet, and K. Smith. 1998. Horn growth in mountain goats (*Oreamnos americanus*). Journal of Mammalogy 79:406-414.

Côté, S.D., and M. Festa-Bianchet. 2001c. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). Behavioural Ecology and Sociobiology 49:260-265.

Côté, S. D., M. Festa-Bianchet. 2003. Mountain goat. Pages 1061–1075 *in* Wild mammals of North America: biology, management, and conservation. G. A. Feldhamer, B. Thompson, and J. Chapman, editors. The John Hopkins University Press, Baltimore, Maryland.

Couturier, S., S. Côté, R. Otto, R. Weladh, and J. Huot. 2009. Variation in calf body mass in migratory caribou: The role of habitat, climate and movements. Journal of Mammalogy 90:442-452.

Cowan, I.M., and W. McCrory. 1970. Variation in the mountain goat, *Oreamnos americanus* (Blainville). Journal of Mammalogy 51:60-73.

ESRI. 2008. Environmental Systems Research Institute Inc., Redlands, California.

Festa-Bianchet, M., D. Coltman, L. Turelli, and J. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resources availability. Behavioural Ecology 15:305-312.

Festa-Bianchet, M., and S.D. Côté. 2008. Mountain goats: ecology, behavior and conservation of an alpine ungulate. Island Press pp 48-118.

Fournier, F., and M. Festa-Bianchet. 1995. Social dominance in adult female mountain goats. Animal Behaviour 49:1449-1459.

Fox, J., C. Smith, and J, Schoen. 1989. Relation between mountain goats and their habitat in southeastern Alaska. United States Department of Agrigulture General Technical Report PNW-GTR-246.

Gates, C., J. Adamczewski, and R. Mulders. 1986. Population dynamics, winter ecology and social organization of Coats Island caribou. Arctic 39:216-222.

Geist, V. 1964. On the rutting behavior of the mountain goat. Journal of Mammalogy 45:551-568.

Geist, V. 1966. The evolution of horn like organs. Behaviour 27:175-214.

Gendreau, Y. S.D. Côté, and M. Festa-Bianchet. 2005. Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). Behaviour Ecology and Sociobiology 58:237-246.

Hamel, S., S. Côté, K. Smith, and M. Festa-Bianchet. 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. Journal of Wildlife Management 70:1044-1053.

Hoefs, M., and U. Nowlan. 1997. Comparison of horn growth in captive and free-ranging Dall's rams. Journal of Wildlife Management 61:1154-1160.

Jacobson, A.R., A. Provenzale, A. Von Hardenberg, B.Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598-1610.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia, Special Report Series. Research Branch, Ministry of Forests, Victoria, BC, Canada.

Mowat, G., D.C. Heard, and T. Gaines. 2004. Predicting grizzly bear (*Ursus arctos*) densities in British Columbia using a multiple regression model. B.C. Ministry of Water, Land and Air Protection, Victoria, BC. 16pp.

Phelps, D.E., R. Jamieson, and R.E. Demarchi. 1983. The history of mountain goat management in the Kootenay region of British Columbia. B.C. Fish and Wildlife Branch, Cranbrook. Bulletin. B-20. 35pp.

Poole, K.G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139-150.

Poole, K., K. Stuart Smith, and I. Teske. 2009. Wintering strategies by mountain goats in interior mountains. Canadian Journal of Zoology 87:273-283.

Rettie, W.J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466-478.

SAS Institute. 2009. SAS version 9.2 for Windows. SAS Institute, Cary.

Schmidt, J., J. Ver Hoef, and R. Bowyer. 2007. Antler size of Alaskan moose *Alces alces gigas*: effects of population density, hunter harvest and use of guides. Wildlife Biology 13:53-65.

Scott, M.E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology 2:40-56.

Smith, B. 1988. Criteria for determining age and sex of American mountain goats in the field. Journal of Mammalogy 69:395-402.

Stankowich, T., and T. Caro. 2009. Evolution of weaponry in female bovids. Proceedings of the Royal Society of Biological Sciences 276:4329–4334.

StataCorp, L.P., 2006. Stata 9.2 for Windows. StataCorp, College Station.

Trivers, R., and D. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90-92.

Walker, A.B.D., K.L. Parker, M.P. Gillingham, D.D. Gustine, and R.J. Lay. 2007. Habitat selection and movements of Stone's sheep in relation to vegetation, topography and risk of predation. Ecoscience 14:55-70.

Weckerly, F. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79:33-52.