REGIONAL AND CLIMATIC INFLUENCES ON GROWTH OF MOUNTAIN GOAT HORNS IN SOUTHWESTERN MONTANA

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Abstract: Because free-ranging mountain goats (*Oreamnos americanus*) are difficult to study, efforts to increase our understanding of population status and responses to environmental stressors from hunter-harvested horns may be valuable despite ad hoc sampling and limited data. As in other ungulates, the investment young mountain goats make in horn growth generally responds to body condition. We used data routinely collected by the Montana Department of Fish, Wildlife and Parks on harvested mountain goats in the southwestern Montana region during 1981–1998 to examine patterns in horn growth as affected by location, time period, and climatic variables. Our sample was limited to goats in which yearly growth increments (up to the fourth summer of life) were recorded; we quantified horn growth by approximate volume. We used site-specific temperature and precipitation data obtained from Parameter-elevation Regressions on Independent Slopes Model (PRISM), and site-specific Normalized Difference Vegetation Index (NDVI) data from Advanced Very High Resolution Radiometer satellites in an exploratory investigation of trends with yearly meteorological conditions. Age-specific horn growth varied among mountain ranges within the region, and was greater among introduced than native populations. Overall trophy size and age-at-harvest showed few trends with time. In one population in which both indices declined significantly (Crazy Mountains), age-specific horn growth did not change while aerial population trend counts and kid:nanny ratios increased dramatically, suggesting that hunters sampled unselectively from an increasingly larger and younger population. In contrast to previous work, we found little evidence for compensatory horn growth within the first 3 growth increments; our use of volume rather than length may explain this difference. Yearly patterns in precipitation and temperature explained little of the variation in annual horn growth; however, we found weak indications that horn growth was positively correlated with mean NDVI, and negatively correlated with the rate of NDVI increase in early spring, as well as with maximum September temperature. Documentation of growth increments from hunter-harvested mountain goats may aid managers in discriminating among plausible competing hypotheses related to population performance.

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***Key words*:** annual increment, climate, growth, horns, hunting, Montana, mountain goat, *Oreamnos americanus*.

Many mountain goat (*Oreamnos americanus*) populations in Montana, particularly native populations, have recently been faring poorly (Carlsen and Erickson 2008, Koeth 2008). Whereas regulated harvest levels may have been excessive in earlier years through the 1980s, most jurisdictions have now reduced harvest quotas substantially; over-hunting thus seems an unlikely explanation. Remaining hypotheses for the slow response to conservative harvests seen among some mountain goat populations include increasing human disturbance in winter, and changes in vegetation resulting from climate change. In particular, mountain goats are sensitive to warmer summers, but are also dependent on the short-term flush of alpine vegetation in summer to sustain them through the long winter period (Bailey 1991, Côté and Festa-Bianchet 2001a).

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Patterns of horn growth may also be informative to managers interested in regional variation in habitat quality (Foster 1978, McDonough et al. 2006, Clarke 2010). In Montana, mountain goats exist in both native and introduced populations, and the latter populations have generally shown greater resilience to harvest (Swenson 1985). The potential for artificial selection produced by selective hunting for larger-horned bighorn sheep (*Ovis canadensis*) has generated interest (Coltman et al. 2003, Festa-Bianchet 2003, Hengeveld and Festa-Bianchet 2011, Mysterud 2011), but not been investigated specifically in mountain goats. Whether or not annual horn growth within individuals is compensatory is relevant to the potential for artificial selection: if growth is not compensatory, animals producing small horns when young will still have relatively small horns when old, whereas if animals compensate for poor horn growth in early years later on, older animals will feature greater uniformity in horn size. Thus, compensatory growth would limit the opportunity for artificial selection based on horn size (Rughetti and Festa-Bianchet 2010).

In addition to generating insights into responses to harvest, data provided by regulated hunts, and thus already on hand, may assist our understanding of how goats interact with climate by providing insight into patterns of yearly body growth associated with broad-scale measures of vegetation and weather. Mountain goat horns grow throughout their lives, with most growth occurring during the first two years and progressively less thereafter (Brandborg 1955, Côté et al. 1998). Length and circumference of goat horns vary by age and sex, but are also highly correlated with body mass and chest girth (Bunnell 1980, Côté et al. 1998), so may act as proxies for body condition generally. Importantly, Festa-Bianchet and Côté (2008) found that among yearling goats at Caw Ridge, AB, horn growth was positively associated with indices of spring forage quality, suggesting that goats responded to annual variation in habitat conditions by allocating more resources to horns in good years. Pettorelli et al. (2007) found that rapid spring green-up accompanied by rapid senescence typical of warmer summers was associated with lower mass gain among mountain goat kids. Horn growth among young nannies at Caw Ridge was lower in years they lactated than years not tending a kid (Festa-Bianchet and Côté 2008). Among alpine ibex (*Capra ibex*), Giacometti et al. (2002) found relationships between horn growth and ambient spring temperature as well as spring plant phenology. Similarly, Hik and Carey (2000:88) found substantial annual variation in horn growth among Dall sheep (*Ovis dalli*) rams, and concluded that "annual horn growth increments appear to provide an integrated climate signal that is related to precipitation and temperature cycles which likely influence plant productivity."

We used hunter harvest registration data to examine the following hypotheses: 1) that patterns of horn growth would conform to previously reported patterns in which mountain goats in introduced populations would display more vigorous growth than in native populations (despite these introductions having been made approximately 50 to 70 years ago; Swenson 1985, McCarthy 1996, Lemke 2004); 2) as reported by Côté et al. (1998) and Festa-Bianchet and Côté (2008), that horn growth would be compensatory within the first few annuli (i.e., we would observe negative correlations between growth in successive years within individual goats); and 3) that age-at-harvest would be a negative function of early horn growth (suggesting that hunters might selectively remove animals with faster-growing horns). We also examined 4) time-series within populations with sufficient data for evidence of trends in horn size at harvest, age-at-harvest, and horn growth (standardized by sex and age).

With these variables controlled, we then explored the data for evidence of yearly effects that were explainable by reference to climate variables similar to those that have been postulated as affecting mountain goat body mass and survival (Côté and Festa-Bianchet 2001a, Pettorelli et al. 2007). We hypothesized that horn growth would be positively correlated with annual growing season precipitation; we investigated numerous hypothetical relationships between horn growth and annual growing season temperature. We further expected to observe that horn growth would be a positive function of integrated NDVI (normalized difference vegetation index) during the growing season (Pettorelli et al. 2005, Hamel et al. 2009), and, following Pettorelli et al. (2007), negatively associated with the slope of increasing NDVI during early spring green-up.

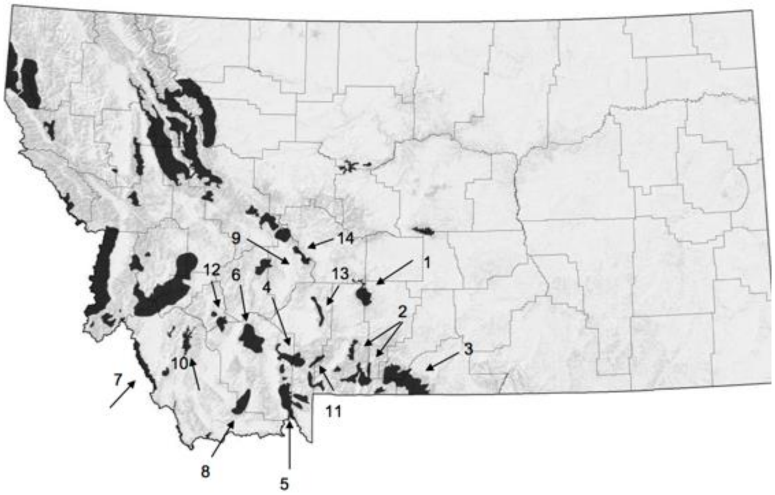

Fig. 1. Map of Montana, USA, showing approximate mountain goat ranges as of 2002 (adapted from Carlsen and Erickson 2008). Numbered arrows show ranges in southwestern Montana that provided hunter-harvested horns for this study: (1) Crazy Mountains; (2) Absaroka Mountains; (3) Beartooth Mountains; (4) Spanish Peaks; (5) Madison Range; (6) Tobacco Root Range; (7) Beaverhead Range; (8) Snowcrest Mountains (9) Elkhorn Mountains; (10) Pioneer Mountains; (11) Gallatin Range; (12) Highland Mountains; (13) Bridger Mountains; (14) Big Belt Mountains. All except 7, 10, and 14 are introduced goat herds.

METHODS

Study Area

We assigned goats horns to a total of 14 mountain ranges in southwestern Montana (Fig. 1) based on the hunting district (HD) in which they were harvested (Table 1). Because we had no information on possible exchange of individuals among these mountain ranges we initially treated them as geographically isolated; however, statistical tests (see below) supported combining these 14 into 5 groups of populations.

Data Collection

We collated and screened mandatory harvest report forms from successful mountain goat hunters maintained at Montana Fish, Wildlife, and Parks (MFWP) Region 3 headquarters in Bozeman, MT, selecting only those that met the following criteria: 1) growth increment lengths and circumferences were recorded consistently with MFWP instructions (i.e., outermost growth increment considered youngest, lengths and circumferences logically consistent with each other; 2) the documented age estimated from annuli was consistent with recorded annulus measurements; and 3) no additional concerns were raised from indications on the data form (e.g., broken or excessively worn horns) that data would be unreliable. Earliest records came from goats harvested in 1982; documentation of annual growth increment records ceased in 1998 (annuli were not documented for all harvested goats after 1998). To minimize influence of broken or distorted horns, we used the larger of the right or

Table 1. Mountain ranges, whether mountain goats were introduced or native, years included in sample, and sample sizes by number of goat horns and horn increments.

Mountain range	Introduced or native	Years represented (annulus growth)	Number of horns	Number of increments
Crazy Mountains	I	1983-98	20	51
Absaroka Mountains	I	1976-97	75	200
Madison Mountains	I	1973-85	39	100
Native Populations (Beaverhead, Pioneers, Big Belts)	N	1972-85	22	63
Other Introduced Populations (Beartooths, Spanish Peaks, Tabacco Roots, Snowcrest, Elkhorn, Gallatin, Bridgers)	I	1971-96	21	58
Total		1971-98	177	472

left horns (and thus did not examine asymmetry; Picton 1994, Côté and Festa-Bianchet 2001b, Clarke 2010). We calculated the age at birth as the year of harvest minus the estimated age. Teeth were collected and aged using cementum annuli (Mattson Laboratories, Milltown, MT) for only 24 of the 177 useable samples. Ages from cementum annuli were identical to those previously estimated from increments in 12 cases, and differed by 1 year in an additional 5. We replaced ages estimated from horn increments with those estimated from teeth in all 24 cases. We had no way to independently verify the accuracy of horn measurements or age.

Although we also examined lengths and circumferences of horns, we chose approximate volume as the best single metric to reflect the energetic investment made by goats in somatic horn growth. For total horn volume and volume of the first growth increment (i.e., corresponding to kid and yearling growth; Brandborg 1955, Côté et al. 1998), we used the equation for conical volume:

$$\text{volume} = r^2 \pi L / 3$$

where *r* equals the radius at the horn (or increment) base, in cm, and *L* equals the length of the horn (or increment), in cm (Foster 1978, Hik and Carey 2000). For volume of the second and third growth increments, we used the equation for conical frusta:

$$\text{volume} = \frac{\pi L (R^2 + Rr + r^2)}{3}$$

where *R* and *r* are the radii of the 2 annuli bounding the growth increment (Hik and Carey 2000).

Climate Variables

Having first considered the effects of sex, age, and region, we investigated possible relationships between horn growth and 6 climatic variables: i) total integrated mean weekly NDVI during the growing season (Julian days 129-258 [May 9-September 15, except one day earlier during the leap years of 1992 and 1996]); ii) the maximum NDVI recorded during the growing season; iii) the slope of mean weekly NDVI on time during the first 5 weekly periods; and iv) the slope of mean weekly NDVI on time during the first 10 weekly periods. When used as a covariate for growth of mountain goat horns in mountain ranges other than the Crazy, Absaroka or Madison Ranges, we used the mean of the 3 values for the 3 sites; v) monthly accumulated precipitation during the vegetation growing season, and vi) maximum monthly temperature.

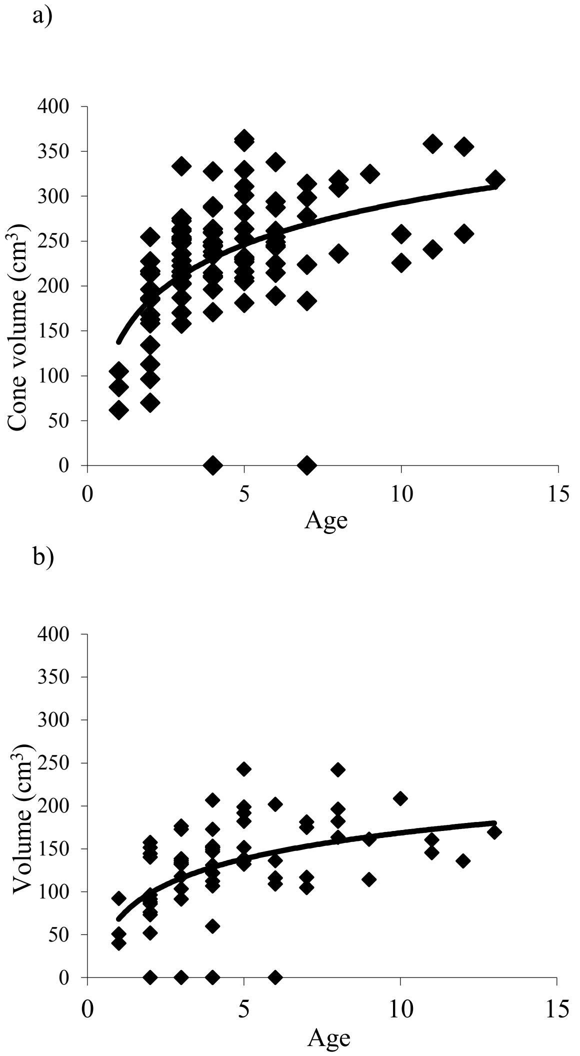

Fig. 2. Volume of male (a) and female (b) mountain goat horns with age at hunter harvest, southwestern Montana mountain ranges, 1971–1998.

We obtained NDVI data at the 1-km^2 pixel resolution from Advanced Very High Resolution Radiometer (AVHRR) satellites (http://phenology.cr.usgs.gov/ndvi_avhrr.php) centered at 3 locations (Crazy Mountains: 46.018°, -110.277°, elevation 3,418 m; Absaroka Mountains: 43.950°, -109.333°, elevation 3,653 m; Madison Range: 45.158°; -111.479°, elevation 2,556 m) for the years 1989–1998. AVHRR data were not available for earlier years, and Landsat Multispectral Scanner (MSS) data proved to be too inconsistent (e.g., cloud cover too great) to be useful. Each individual NDVI record consisted of the mean daily NDVI during weekly periods. We obtained estimates of monthly precipitation and maximum monthly temperature for the same 3 sites at the 2.5 minute resolution scale from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) model (Daly et al. 2008) for the years 1971–1998 (http://prismmap.nacse.org/nn/, accessed December 8, 2011). We created new annual temperature and precipitation variables by combining monthly means across combinations of months during the growing season (April–October).

MFWP conducted aerial surveys for the Absaroka and Crazy Mountains during only a few years covered by the horn data (see Lemke (2004) for methods); we were thus unable to include them in formal analyses relating mountain goat population density to horn growth variables.

STATISTICAL ANALYSES

To investigate patterns of growth with age, we regressed total horn volume at harvest on age for each sex. To examine differences in horn growth among mountain ranges, we used one-way and 2-way ANOVA with i) total volume at death and ii) volume of the first and second growth increments as response variables, and mountain range as a blocking variable. When overall ANOVA tests were significant, we used Tukey (HSD) multiple comparison procedures to group populations.

Previous studies of mountain goat horns had found weak signals of compensatory growth within the first 3 growth increments. The presence of compensatory growth within individuals would generate auto-correlation if analyses were conducted on individual increments without including the animal as a random factor. Thus, we tested for these animal effects separately for males and females, for increment length, circumference, and volume within each mountain range with sufficient data, by regressing older growth increments on younger ones (e.g., Festa-Bianchet and Côté 2008). As detailed below, we concluded that the first 3 growth increments measured by volume were independent, and thus conducted subsequent analyses using increments (rather than goat horns) as experimental units. To facilitate comparisons among mountain ranges, sexes, and increment ages, we transformed each growth increment to its standardized *z*-value by subtracting it from its sex × age × mountain range-specific mean and dividing by the corresponding standard deviation. We used least-squared multiple regression to model horn growth on age-at-harvest and on time in years.

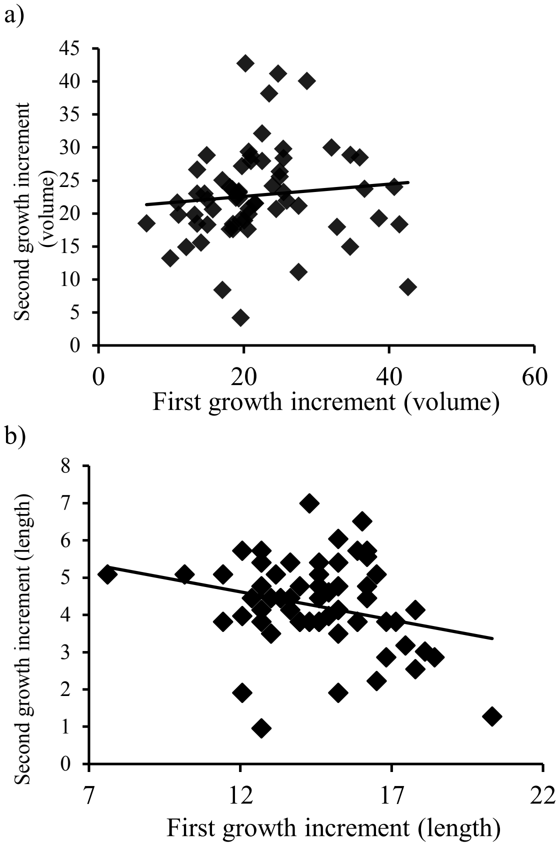

Fig. 3. Scatterplot showing second growth increment on first growth increment for female mountain goats, SW Montana, 1971–1998. (a) Horn volume: second increment = 0.078 + 0.112 (first increment); $F = 0.48$, df = 1,62; $P = 0.49$, $r^2 = 0.008$. (b) Horn length: second increment = 6.507 – 0.159 (first increment); $F = 5.55$, df = 1,65; $P = 0.02$, $r^2 = 0.079$.

To examine associations of horn growth with climatic variables, we used least-squared multiple regression with *z*-transformed annual increment as the response variable. Because these latter series of analyses were exploratory and not premised on clearly articulated *a priori* hypotheses relating climatic variables to horn growth, probability values may not be reliable and results should be viewed with caution. We used the software

Table 2. Regressions of volume of older on younger growth increments (GI) of mountain goats in 3 independent mountain goat populations, southwestern Montana, 1988-1999. Shown are mountain range name, sex, specific regression, regression slope (β), F statistic, probability value (P), and coefficient of determination (r^2). Models denoted with (*) suggest compensatory growth; models denoted with (**) suggest an individual animal effect.

Mountain range group	Sex	Regression	β	F	P	r^2
Absaroka	M	GI 2 on GI 1	-0.015	0.01	0.904	0.001
		GI 2+3 on GI 1	-0.179	1.43	0.241	0.047
		GI 3 on GI 2*	-0.255	4.48	0.043	0.130
	F	GI 2 on GI 1	0.349	2.07	0.162	0.071
		GI 2+3 on GI 1	0.081	0.11	0.746	0.005
		GI 3 on GI 2	0.022	0.02	0.884	0.001
Crazy	M	GI 2 on GI 1**	0.776	6.60	0.026	0.375
		GI 2+3 on GI 1	0.100	0.06	0.811	0.008
		GI 3 on GI 2	0.164	0.79	0.399	0.090
	F	GI 2 on GI 1	0.329	0.16	0.713	0.052
		GI 2+3 on GI 1	-0.374	0.06	0.828	0.030
		GI 3 on GI 2	0.223	0.58	0.526	0.225
Madison	M	GI 2 on GI 1	-0.008	0.00	0.963	0.001
		GI 2+3 on GI 1	0.134	0.41	0.534	0.036
		GI 3 on GI 2	-0.052	0.05	0.831	0.004
	F	GI 2 on GI 1	0.078	0.48	0.492	0.008
		GI 2+3 on GI 1	0.023	0.02	0.889	0.001
		GI 3 on GI 2**	0.275	7.79	0.007	0128

package Statitix7 (Analytical Software, Tallahassee, FL).

RESULTS

1. Patterns of Growth

As previously documented (Brandborg 1955, Côté et al.1998, Festa-Bianchet and Côté 2008), horns of both sexes grew asymptotically, with most growth occurring in the first few years (Fig. 2a, 2b). Using the relationships total volume = intercept + ln(age), horns of males had grown to a mean of approximately 72% of their asymptotic 10-year-old volume by the end of their fourth summer (i.e., the first 3 growth increments). Females had attained approximately 59% of their estimated 10-year volume by this time. Although asymptotic horn lengths at age 10 were similar for males (predicted $\bar{x}$ = 24.0 cm) and females (predicted $\bar{x}$ = 24.2 cm), volume of the stouter male horns was approximately twice that of females by the end of the third summer. Female horns subsequently grew at a somewhat faster pace so that at age 10, volume of male horns was roughly 1.5 time that of female horns.

2. Variation Among Mountain Ranges

Goat horn sizes varied among mountain ranges within the southwestern Montana study area (one-way ANOVA for volume of the first growth increment among males ($F = 2.45$, df = 11,93, $P = 0.010$) and females ($F = 7.00$, df = 8,60, $P < 0.001$)). First growth increments among females in the Spanish Peaks (43.0 cm^2) and Crazy Mountain ranges (37.2 cm^2) were significantly ($\alpha = 0.05$) greater than those in the Absaroka (22.0 cm^2), Madison (19.1 cm^2) and Pioneer mountain ranges (15.2 cm^2). No other pairwise comparisons were significant. The 3 native goat populations (Beaverheads, Pioneers, Big Belts) considered as a group, had smaller first growth increments ($\bar{x}$ = 40.5 cm^2, SE = 3.93) than introduced populations among males ($\bar{x}$ = 48.7 cm^2, SE = 1.44; $t = -2.25$, 103 df, $P = 0.027$) but this trend was not significant among females ($\bar{x}$ = 19.6 cm^2, SE = 2.81 vs. $\bar{x}$ = 22.8 cm^2, SE = 1.05; $t = -1.20$, 67 df, $P = 0.234$). Sample sizes for the Spanish Peaks, Pioneers, Beaverhead, Big Belts, and all other introduced populations were small, however. Thus, we conducted subsequent analyses by considering goats as belonging to one of 5 mountain range groups: 1) Crazy Mountains, 2) Absaroka Mountains, 3) Madison Mountains, 4) native populations, 5) all other introduced populations.

3. Compensatory Growth Within Young Individuals

We found little evidence of compensatory growth within the first three growth increments, as measured by approximate horn volume, in either male or female mountain goats (Table 2). Of 18

Table 3. Regressions of length of older on younger growth increments (GI) of mountain goats in two independent mountain goat populations, southwestern Montana, 1988-1999. Shown are mountain range name, sex, specific regression, regression slope (β), probability value (P), F statistic, and coefficient of determination (r^2). Models denoted with (*) suggest compensatory growth; models denoted with (**) suggest an individual animal effect. Models with neither effect significant are not shown.

Mountain range group	Sex	Regression	β	F	P	r^2
Horn length						
Absaroka	M	GI 2 on GI 1*	-0.267	10.65	0.002	0.214
		GI 2+3 on GI 1*	-0.325	12.23	0.001	0.283
Madison	M	GI 2 on GI 1*	-0.257	9.81	0.006	0.380
Horn radius						
Absaroka	M	GI 2 on GI 1 **	0.674	78.10	< 0.000	0.661
		GI 2+3 on GI 1 **	1.240	121.06	< 0.000	0.614
Madison	M	GI 2 on GI 1 **	0.761	27.56	<0.000	0.663

linear models regressing volume of an older (or combination of two older) growth increments on a younger one (3 tests × 3 goat populations × 2 sexes), only 1 was significantly negative (Absaroka males; increment 3 on increment 2) as would be expected if compensatory growth occurred, and this model explained only 13% of the variation. Slopes for 12 of the 18 models were positive (although only 2 were significant). Thus, growth of horn volume during ages 2 and 3 were largely independent of growth occurring during the preceding 2 or 3 years. We took advantage of this independence to conduct further analyses using growth increment (rather than individual goats) as our experimental units.

Examination of these same regressions using horn length (c.f., Côté et al 1998, Toïgo et al. 1999, McDonough et al. 2006, Festa-Bianchet and Côté 2008) suggested that previous reports of early compensation in horn growth may have resulted from this choice of metric (Fig. 3, Table 3). In 3 cases, regressions that displayed no trend for volume were significantly negative for length (Table 3), but significantly positive for radius. No other models testing increment length against earlier increment lengths were significant.

4. Early Growth and Age-at-Harvest

Males with faster growing horns early in life (as measured by volume) were harvested at younger ages than those with slower growing horns (normalized increment volume = 0.236–0.049 [age at harvest]; $F = 4.34$, df = 1, 282, $P = 0.038$). However, this relationship explained very little of the total variation ($r^2 = 0.015$), and was not significant among females.

5. Trends With Time

With one exception, we failed to find evidence of mountain range-specific temporal trends of age-at-harvest (accounting for sex), total volume at harvest (accounting for sex and age), or growth increment (all $P > 0.16$). The exception occurred in the Crazy Mountains, where age-at-harvest declined during the period 1990–1996 from a predicted mean of ~ 8 yrs in 1982 to <4 yrs in 1996 (linear regression of age on year: $\beta_1 = -0.728$, male effect $\beta_2 = 0.0128$; 2,17 df, $F = 6.76$, $P = 0.018$). However, this increasing youthful harvest was not accompanied by a decrease in trophy size (horn size on year, accounting for factors sex and age: $\beta = 0.025$, 2,17 df, $t = 0.14$, $P = 0.891$), or by a decrease in growth increment with time (increment Z score on time, $\beta = 0.037$, 1,49 df, $t = 0.53$, $P = 0.600$).

6. Climatic Variables

In general, the independent climatic variables we were able to examine supported our hypotheses, but added relatively modest amount of explanatory power to base models describing variation in relating z-transformed horn growth increments. Models that included precipitation and/or temperature improved model fit over those lacking these variables, but only slightly.

The strongest association of (standardized) horn increment volume with climatic variables

Table 4. Results from best-fitting linear models relating standardized horn growth increment to mountain-range specific temperature and precipitation variables. Both sexes were modeled. (a) first 3 growth increments (i.e., through age 4), $F = 3.18$, $P = 0.024$, $r^2 = 0.025$; (b) first 2 growth increments only, $F = 3.95$, $P = 0.009$, $r^2 = 0.042$.

a)

Predictor	β	SE	t	P
Constant	0.0582	0.0532	1.09	0.275
June maximum temp	0.2719	0.0903	3.01	0.003
September maximum temp	-0.1537	0.0670	-2.30	0.022
April-August precipitation	0.1436	0.0703	2.04	0.042

b)

Predictor	β	SE	t	P
Constant	0.0784	0.0619	1.27	0.206
June maximum temp	0.3707	0.1079	3.44	0.001
September maximum temp	-0.1790	0.0803	-2.23	0.027
April-August precipitation	0.1749	0.0809	2.16	0.031

Table 5. Results from best-fitting linear models relating standardized horn growth increment to mountain-range specific NDVI and temperature variables. Both sexes were modeled, shown are models with first two growth increments only (a) $F = 5.44$, $P = 0.006$, $r^2 = 0.124$; (b) $F = 3.49$, $P = 0.035$, $r^2 = 0.083$

a)

Predictor	β	SE	t	P
Constant	0.4358	0.1343	0.24	0.002
Mountain-range specific mean NDVI during April-October	0.4652	0.1522	3.06	0.003
Maximum September temperature	-0.9433	0.3149	-3.00	0.004

b)

Predictor	β	SE	t	P
Constant	1.2226	0.4744	2.58	0.012
Mountain-range specific mean NDVI during April-October	0.2607	0.1230	2.12	0.037
NDVI slope during first 5 bi-weekly periods of growth season	-3.707	1.6317	-2.27	0.026

was found by modeling it as a positive function of mountain-range specific precipitation during April–August of the year of growth, a positive function of maximum temperature in June, and a negative function of maximum temperature in September (Table 4). These relationships were slightly stronger when limiting the response variable to the first 2 growth increment, but even then, explained only about 4% of total variation. No variables were significant when modeled in isolation.

In models considering NDVI (which extended back only as far as growth year 1989), horn growth was consistently positively (albeit not always-significantly) associated with growing season NDVI and negatively associated with maximum temperature during September (Table 5a); these relationships were strengthened when examining only the first two growth increments, and excluding animals killed at age >6. We found some evidence that early horn growth was negatively associated with the slope of increasing NDVI during the first 5 (but not the first 10) bi-weekly periods in each year's growing season (Table 5b). As with models examining only temperature and precipitation however, explanatory power was weak even for models that were statistically significant.

DISCUSSION

As also noted by Hik and Carey (2000) for Dall sheep, mountain goats required more years to approach their asymptotic horn size when measured by volume than by length. Thus, the suggestion from our data that goats in southwestern Montana grew more slowly than in Alberta (where nearly all growth had taken place by age 4; Côté et al 1998), is likely an artefact of the choice of metric.

Despite modest sample sizes, we detected differences in early horn growth rates among mountain goats living in different ranges within southwestern Montana. We lacked ancillary data with which to explore causes for these differences (e.g., population density, [e.g., Pérez et al. 2011], habitat [McDonough et al. 2006, Clarke 2010], genetics), but note that most comparative studies have found population-specific differences in growth rates, body size, and/or resilience to harvest rates (Côté and Festa-Bianchet 2003, McDonough et al. 2006, Clarke 2010). We found that the 3 native populations in southwestern Montana were characterized by slower rates of horn growth than nearby introduced populations. The reasons that introduced populations generally grow more vigorously than native populations remains unclear; one hypothesis to consider is that introduced populations that have persisted long enough to be studied represent those inhabiting relatively productive habitats (Guenzel 1980).

Perhaps because horns of mountain goats are relatively small and hunter selectivity assumed to be modest, the species has not been the focus of concerns regarding potential artificial selection from hunting (c.f., Coltman et al. 2003, Festa-Bianchet 2003, Hengeveld and Festa-Bianchet 2011, Mysterud 2011). We detected no signals that would be consistent with a decline in horn size attributable to artificial selection. That said, our results regarding compensation, as well as the relationship between early growth and age-at-harvest, suggest that mountain goats may not be as immune to potential artificial selection as previously assumed, should harvest pressure, hunter selectivity, and trait heritability be sufficiently strong.

Compensation in horn length, as demonstrated by Festa-Bianchet and Côté (2008) weaken the potential for artificial selection (as shown further by Rughetti and Festa-Bianchet 2010 for the closely related alpine chamois (*Rupicapra rupicapra*)), because all individuals would tend, over time, toward similar horn sizes. Although our data confirmed weak compensation in horn length in early growth increments, we found no evidence of compensation in horn volume. Mountain goats with large volume horns when young thus have large volume horns when older. To the degree this is heritable and hunters respond to horn volume rather than length, this suggests the potential for artificial selection.

Given the small differences in size among horns of adult males, we were surprised by our finding that faster growing horns were associated with being harvested at a younger age. Thus, male mountain goats predisposed toward growing larger horns were removed at slightly younger ages than those with slower growing horns, potentially reducing their reproductive success. This suggests some selectivity among hunters, who may target males with stouter or longer horns, independent of the billy's age. While this also suggests the potential for hunter-mediated selection against faster horn growth, this effect would appear to be quite weak. In addition to explaining only a negligible percentage of variation in early growth (<2%), the fitted relationship suggested that whereas males harvested at ~ age 4 or 5 grew horns at close to mean rates early in life, even a billy harvested at the relatively old age of 10 had earlier produced horn volume only 0.25 standard deviation units below the mean, suggesting little scope for hunter-selection. Thus, that we observed only the potential — but no evidence — of artificial selection on goat horn size suggests that hunter selectivity, harvest intensity, or both would have to be stronger than was evidently the case for it to be manifested on a population-wide scale.

In general, our data provided no evidence of systematic trends of either age-at-harvest or horn growth with time that would suggest overharvest. The one exception was in the Crazy Mountains, where we observed a negative trend of both horn total volume at harvest and age-at-harvest during the 1990–1996 period for which we had increment data, superficially tending to suggest overharvest. However, age-specific horn volume did not decline during these years, which we would have expected had genetic or climatic effects been having a deleterious effect on this population. As well, the Crazy Mountain goat population increased markedly prior to and during these years, total horn volume at harvest did not continue to decline after these years (T.O. Lemke and K. Loveless, Montana Department of Fish and Wildlife, unpublished data), and the population was newly exposed to hunting following a 14-year cessation. Thus our interpretation is that hunters in the early 1990s encountered a Crazy Mountain goat population with a relatively large number of old males, and as recruitment continued to increase, hunters harvested from an increasingly younger age structure. We point this out to emphasize the importance of interpreting simple hunter-harvest statistics (e.g., age-at-harvest) within the appropriate context: without information on the status of this population prior and subsequent to our years of horn annulus data, we could easily have misinterpreted these trends.

Our data provided only weak support for our *a priori* hypotheses regarding climate's potential effect on horn growth. Exploratory analyses suggested that horns tended to grow faster in years with more precipitation and more vegetation biomass (as indexed by mean NDVI during the growing season). Horn growth tended to be negatively associated with higher temperatures in September, and faster spring green-up (early slope of NDVI). Although our best models were statistically significant, they explained relatively little variation. That said, non-significant slopes of all climatic variables remained consistent among all models, and all were consistent with what we would have expected had these climate-related hypotheses been more strongly supported. These analyses do not resolve questions regarding the future of mountain goats in the face of climate change, but offer some tantalizing hints that concerns expressed by Pettorelli et al. (2007) deserve additional consideration. Mean and maximum NDVI values estimated at the mountain top location used to index the Absaroka population have declined in recent years (1989–2010), and spring green-ups (as indexed by the slope of NDVI increase) have become faster (unpublished data). Thus it is possible that horns may be giving us some indication mountain goats are being stressed by these climatic trends.

In contrast to horns from mountain sheep (Bunnell 1978, Hik and Carey 2000, Festa-Bianchet et al. 2004) and alpine ibex (Giacometti et al. 2002), the first growth increment of mountain goat horns spans 2 growing seasons, which clouds the ability to detect yearly effects early in life. Our power to detect effects of annual changes in meteorological conditions was also compromised by errors in aging of goat horns (Foster 1978); whereas small errors in measurements would not necessarily have a large impact, a difference of only a year in aging the goat from annuli could easily have had the effect of changing the relative growth recorded from a climatologically favorable to an unfavorable year (or vice versa), and thus induce considerable noise in the data.

For mountain goats, body size is a more important determinant of reproductive success than horn size (Côté et al. 1998, Festa-Bianchet and Côté 2008). Thus, we were not surprised to find weak relationships with hunting- and climate-related explanatory variables. That said, our investigation did add some insight into these populations' responses to both. With climate change and artificial selection hypotheses yet untested, mountain goat populations being challenged by multiple stressors, and funds for engaging in in-depth ecological studies limited, we suggest that management agencies would do well to obtain data from harvested horns, including measuring length and circumference of annuli, as well as ageing goats using cementum annuli from teeth.

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