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COHORT VARIATION IN HORN GROWTH OF DALL SHEEP RAMS IN THE SOUTHWEST YUKON, 1969-1999

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Abstract: Horn growth of 2481 Dall sheep (*Ovis dalli*) rams was measured as part of harvest assessment in the southwest Yukon for cohorts born between 1969 and 1992. Estimated volumes for annual horn growth increments were based on measurements of annual horn segment lengths and their annual base circumferences. Poor horn growth was observed in 1972, 1982, and 1992 in rams of all age classes, except lambs. In general, lambs showed little variability between years, because growth during the first summer is negligible compared to subsequent years and horn tips of older rams are worn. Above-average horn growth was observed in 1977, 1978, 1989, 1994, 1995, and 1996 for rams from all cohorts. At 8 years there were significant between-cohort differences in total horn volume depending on year of birth. Good or poor years have dramatic cumulative effects on horn growth, depending on the age and growth stage of the cohorts when good or poor growth years occur. Over 31-years (1969-1999) there was a significant '10-year' periodicity in horn growth, which was consistent across all age classes and all cohorts during this period. Annual horn growth increments appear to provide an integrated climate signal that is related to precipitation and temperature cycles which likely influence plant productivity. This predictable pattern provides a context for the Yukon's sheep management program.

Key words: Dall sheep rams, *Ovis dalli*, Yukon, horn growth, cohort variation, periodicity

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Climate variability has a strong influence on survival, reproduction, and population size of mountain sheep (e.g. Douglas and Leslie 1986, Portier et al.1998). In the case of Dall sheep in Yukon and Alaska, poor lamb survival and recruitment were recorded during cold winters with high snowfall (Burles et al. 1984, Heimer and Watson 1984). Warmer and drier weather during summer was positively correlated with higher lamb production during the following season (Dry Creek, Alaska; Heimer and Watson 1986), and Hoefs (1984) demonstrated significant correlations between summer forage production on winter ranges, lamb survival during the following winter, and lamb production the following spring. Barichello and Carey (1988) concluded that winter snow conditions may play an important role in dynamics of sheep in the central Yukon based on observations of poor survival and reproduction following deep snows in winter 1982-83. While the impacts of particularly severe seasons are usually evident, it is often difficult to determine the longer-term effects of climate variation on mountain sheep populations because suitable census data are not available.

In addition to affecting lamb production and survival, climatic variability also has a significant influence on growth and condition of sheep. Ram horn growth is a potentially significant indicator of condition in sheep and goats (Geist 1971, Picton 1994, Festa-Bianchet et al. 1997, Côté et al. 1998, Picard et al. 1999), and horn growth has been used as a measure of response to climate, stress (measured as fluctuating asymmetry), and population bottlenecks (loss of genetic variability) (Picton 1994). There is also direct evidence that horn growth is limited by the availability of resources. In the Yukon, Hoefs and Nowlan (1997) demonstrated an almost two-fold difference in horn growth between captive and wild Dall sheep, indicating that resource availability plays a significant role in patterns of horn growth.

Growth of sheep horns provide a detailed proxy record for quantifying the effects of climatic variability on sheep, as the annual increment in horn size is a reflection of integrated climatic conditions influencing forage availability. In this study we examined patterns of horn growth of Dall sheep rams harvested in the southwest Yukon. Variability in patterns of growth are interpreted in relation to climatic variability on conditions in alpine sheep range, and we discuss potential underlying causes and long-term consequences of cohort variation in horn growth in this population.

STUDY AREA

The study area was located in the Ruby Ranges, southwest Yukon. The Ruby Range Mountains are located along the southwestern margin of the central Yukon Plateau, and they formed part of a southern arm of the intermittently ice-free Beringian land mass during the last glaciation (Hughes et al. 1968). This range consists of older, rolling mountains with generally continuous alpine meadows and discrete boulder fields (Oswald and Senyk 1977). These ranges are vegetated by characteristic alpine meadow species, have a short growing season (60-90 days), and low nutrient soils typical of alpine soils in general (Price 1971, McIntire 1999). Most of this area lies in the precipitation shadow of the St. Elias Mountains, and treeline occurs at about 1,200 m. In the valley bottom, average annual precipitation is 190-285 mm and average annual temperature is –4º C (Environment Canada, Burwash Landing meteorological station). Within the annual census area (part of the entire management zone), the sheep population has declined from approximately 900 adults (rams and ewes) in the early 1980s, to only about 600 adults by 1999, however the causes of this decline are not known (YTG, unpublished data). Harvest has remained relatively constant during this period. There is some preliminary evidence that available habitat may be declining (Weir and Hik 2001).

METHODS

Horn measurements

Measurements of Dall ram horn growth were collected from 1974 to1999 as part of annual harvest assessment in the southwest Yukon. These data include a total of 2481 individuals, however year of birth was known for only 1332. Of this sample, the number of individuals in each cohort ranged from 30 to186 individuals for year classes born between 1969 and 1992 (mean = 79 individuals). The age of each ram was determined by counting annual growth segments (Geist 1966, Hemming 1969). The length of annual growth segments were measured using a flexible tape measure placed along the frontal surface of the longer horn, and the lengths of all annual segments determined. The basal circumference of each annual segment was also measured. Measurements were made by conservation officers and biologists using standard methodology (Merchant et al. 1982, Barichello and Hoefs 1984).

Indices of Horn Size

Horn growth was calculated from linear measurements of annular length and circumference that were used to estimate horn segment volume. Volume of horn tips (age 1) were estimated as a cone ($V = \pi r^2 h/3$), while subsequent annual increments were estimated as conical fustra (Heimer and Smith 1975), such that Volume = $1/3 \pi h(R^2+Rr+r^2)$, where h is the estimated height and R and r are the respective base radii of the annual fustrum. Although horn tips were often broken or worn, resulting in inaccurate measurements (Hoefs and Nette 1982), the contribution of first year growth to the total horn volume of 8-year-old rams was less than 1%. Estimated volumes were adjusted using the correction factor of 0.544 ± 0.0033 (1 S.D.) calculated by Heimer and Smith (1975) in order to derive an estimate of true horn volume. A third estimate of horn growth, surface area estimated as annular circumference multiplied by the length of the annual increment (Picton 1994), was also calculated. It was highly correlated with volume ($r^2>0.95$, $p<0.05$) and we did not consider it further.

Horn volume was used in subsequent analyses of cohort growth differences because it provides a better approximation of the actual amount of horn tissue laid down each year than segment length or diameter. However, we include a summary of patterns of increase in length for comparison with volume increases. We focused our analysis of cumulative horn volume at age 8 because approximately 85% of all rams can be legally harvested at this age (Barichello and Carey 1990). Sample sizes for older rams decrease significantly. We have considered 8-year-old animals as reaching maturity. This criterion is also consistent with behavioural observations of wild sheep, including studies by Geist (1971) and Heimer and Watson (1986). Statistical analyses were based on estimates of true horn volume and conducted using SPSS v.10. Results are presented as means ± 1 S.E.M., unless otherwise indicated.

RESULTS

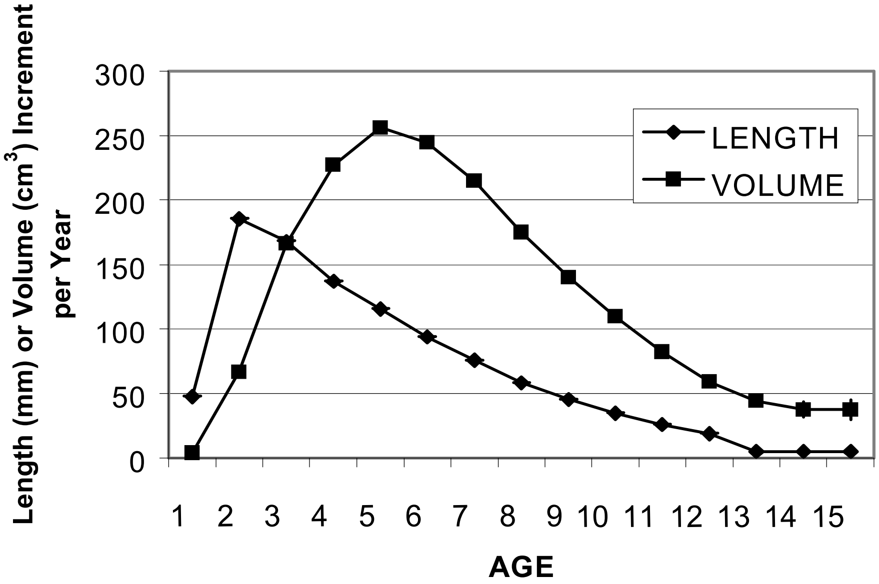
Patterns of horn growth

The pattern of horn growth exhibited by rams is consistent with the hypothesis that rapid acquisition of large horns is an important mating success strategy (Geist 1971). However, the apparent pattern of growth depends on how horn growth is characterized (Fig. 1). In terms of annual growth, maximum increments in horn length occur at a younger age than maximal estimates of horn volume (Fig 1A). Consequently the overall correlation between annual length and annual volume was low (linear regression: $r^2=0.121$, $p=0.268$). Annual increments of horn volume follow a quadratic pattern with maximum growth occurring during years 4 to 7, whereas annual increments in horn length decline after age 2. These patterns are very similar to those described by Heimer and Smith (1975). In the first year, horn growth is minimal, averaging about 7 cm^3 compared to 70 cm^3 in the following year. Cumulative length and volume (Fig. 1B) tend to reach a maximum between ages 8 and 10, and these cumulative measures are highly correlated (linear regression: $r^2 = 0.928$, $p<0.0001$). At age 8, the overall mean estimated horn volume of rams from all cohorts was 1298 ± 7 cm^3, while mean horn length was 826 ± 2 mm.

Cohort Variation in Horn Growth

Cohorts from 1969 to 1992 demonstrated significant variability in cumulative horn volume at 8 years (Fig. 2: ANOVA: $F_{23,1308} = 4.105$, $p < 0.0001$). Individual cohorts had horn volumes at 8 years that were up to 10% greater or less than the long-term mean volume (1298 cm^3). Horn length was also significantly different among cohorts during this 24-year period (Fig. 2: ANOVA: $F_{23,1317} = 2.864$, $p < 0.0001$), however the pattern was less variable, particularly during the 1980s. There was a significant correlation between horn volume and horn length at 8 years (linear regression: $r^2=0.463$, $p<0.0001$), indicating that both measures are showing similar patterns. However, horn volume is a more appropriate measure to use when analyzing cohort and annual variation.

A.



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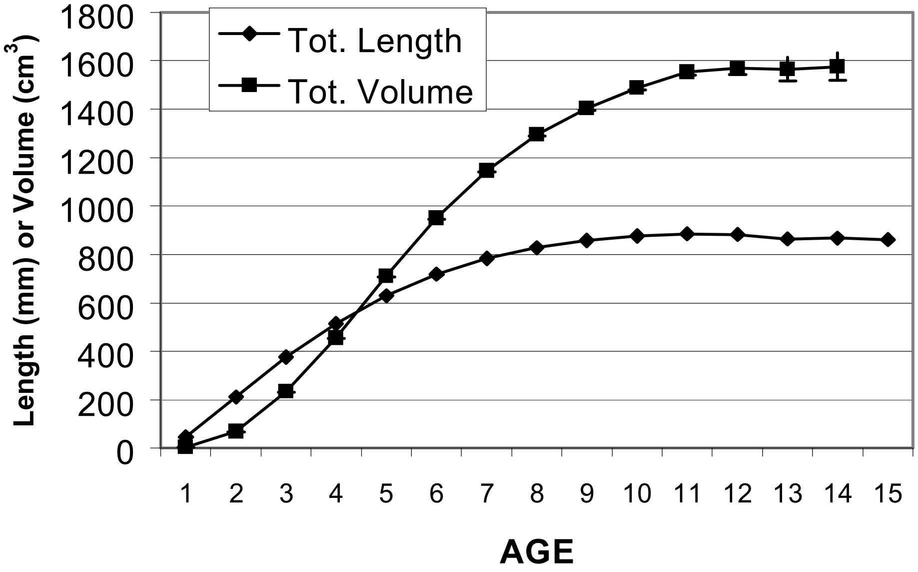

Fig. 1. (A) Annual increments and (B) cumulative increments of horn growth of Dall sheep rams measured as either length or volume (mean ± SEM). Sample sizes for each age group (1 through 15) are 1472, 2398, 2436, 2060, 2048, 1987, 1791, 1457, 1077, 664, 335, 135, 49,12 and 7, respectively.

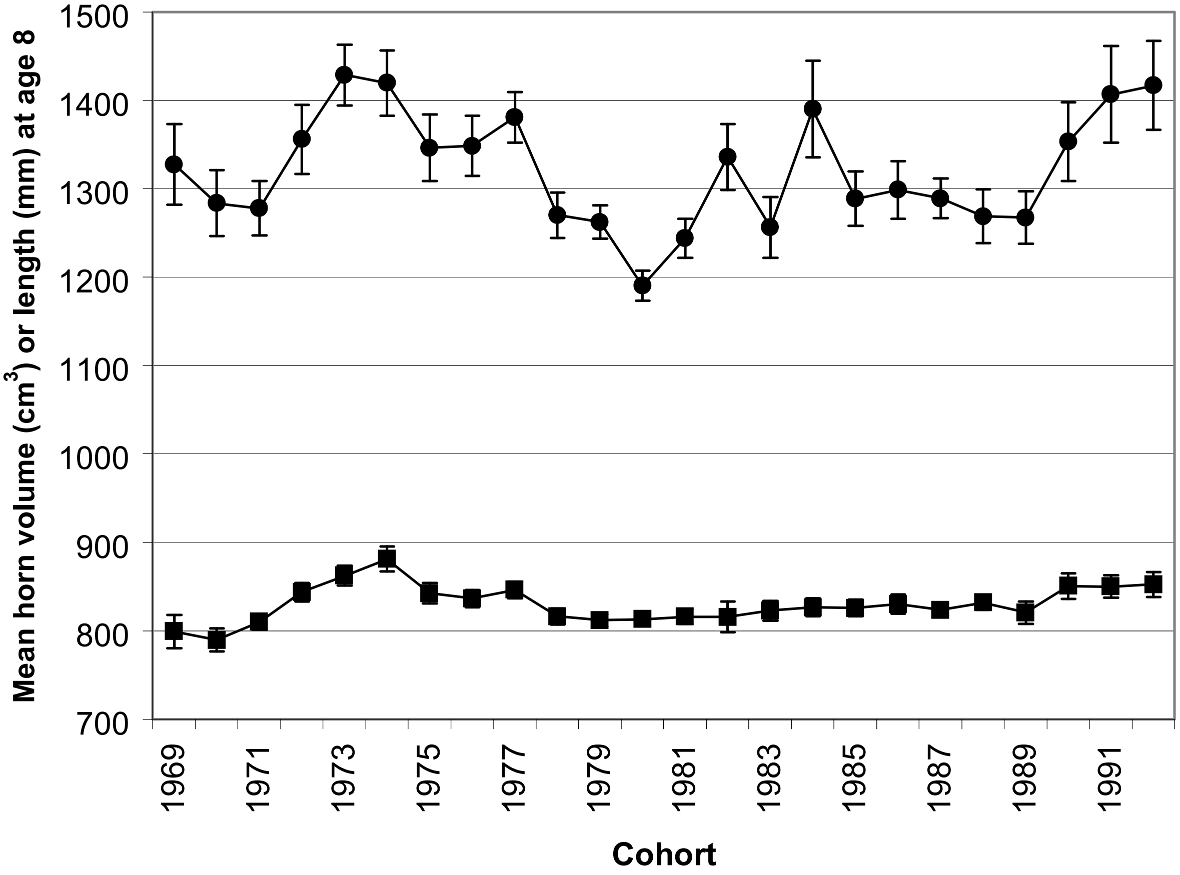

Fig. 2. Variation in horn volume (circles) and length (squares) of Dall sheep rams at age 8 for each cohort from 1969 to 1992 (mean ± SEM). Samples sizes are 11, 31, 53, 52, 52, 25, 32, 43, 57, 90, 131, 146, 78, 41, 46, 67, 59, 59, 89, 60, 44, 37, 19, and 10 for cohorts 1969 to 1992 respectively.

The greatest difference in horn volume at 8 years was between cohorts born in 1973 and 1980. Mean horn volume for rams in these two cohorts were significantly different (Tukey HSD test; $p<0.0001$) by almost 250 cm^3 (Fig. 2). This large difference at 8 years can be largely accounted for by age-specific differences in horn growth. The 1973 cohort experienced significantly greater increases in volume during years 3 to 7 than the 1980 cohort, however, after the eighth year this pattern was reversed (Fig. 3A). Nevertheless, since annual increments decrease after age 5 (Fig. 1A), rams surviving beyond age 8 years in the 1973 cohort typically had larger horns than older rams from the 1980 cohort. For instance, at age 13 horn volume for the 1973 cohort was 1760±175 cm^3 (N=2) compared to 1707±99 cm^3 (N=3) for the 1980 cohort, although the difference was no longer statistically significant (Fig. 3A). However, very few animals survive to this age in the region (Hoefs and Cowan 1979). Horn length also shows a similar overall pattern (Fig. 3B), such that annual increases in horn length for 3- and 4-year-old rams are significantly less for the 1980 cohort than the 1973 cohort, and there is little opportunity to 'catch-up' later in life.

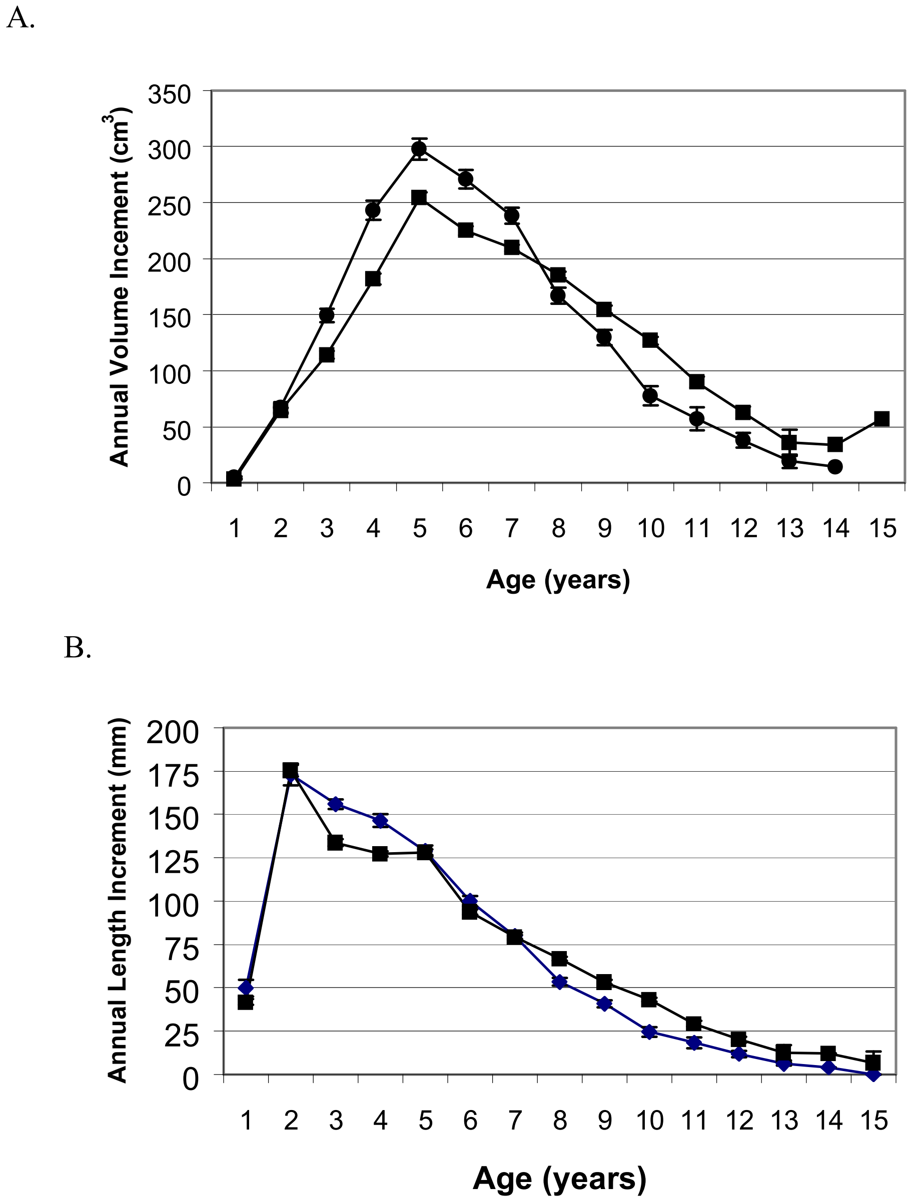

Fig. 3. Age specific differences in patterns of horn development and growth for Dall sheep rams born in 1973 (circles) and 1980 (squares) based on increments of (A) volume or (B) length.

To examine the long-term pattern of cohort variation in horn growth, deviations from the estimated overall (1969-1999) mean horn volume at each age were calculated for each age class in each year as an index of annual variation in horn growth (Fig. 4). These results clearly show periodic variation in growth that is strikingly consistent among cohorts and age-classes over the 30-year period of these records. In some years all individuals, regardless of age class or cohort have above-average growth, and in other years all individuals have below-average growth. A serial autocorrelation of this short time series identified the strongest periodicity for intervals of 10-years. Although there is some variability between age classes and cohorts (see Fig.4), the overall pattern is highly significant.

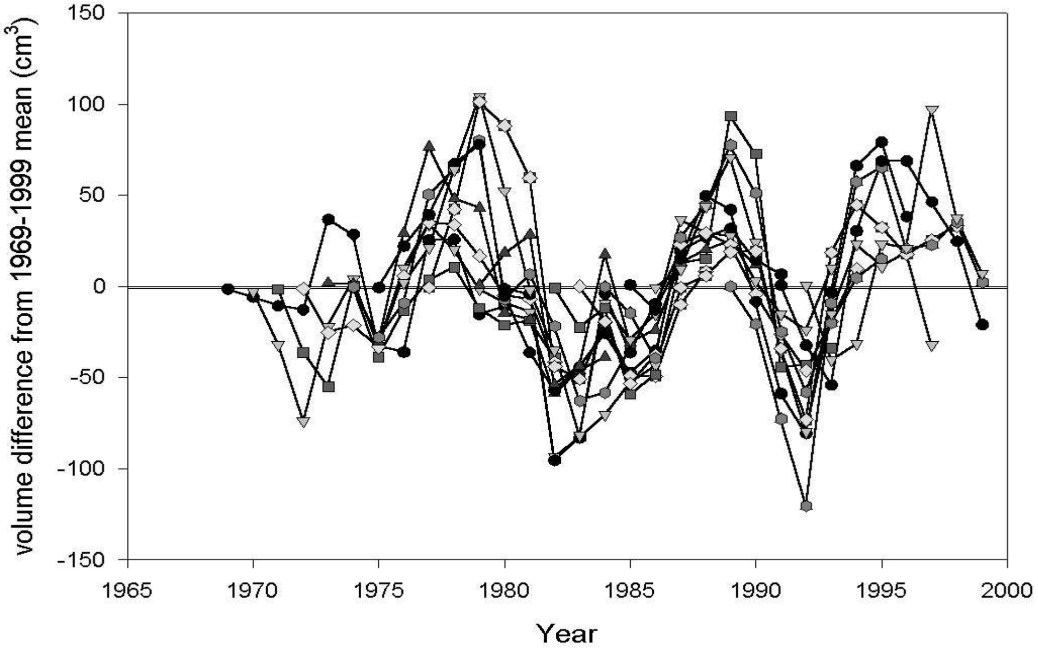

Fig. 4. Patterns of interannual variation in the horn growth (volume as cm^3) of individuals of each age class and cohort (1969-1999). Values are calculated as the difference between the annual and long-term mean values for each age/cohort class. Individual symbols and lines follow the difference in horn volume through each age class for each cohort, therefore the points in a given year indicate the deviation for all age classes of all cohorts living during that year.

Effect of Conditions in Birth Year on Horn Volume at Maturity

The results displayed in Fig. 4 strongly support a hypothesis that cohort variation in horn growth is periodic, with a frequency of approximately 10 years. In light of the patterns of age-specific annual growth rates described in Fig. 1, this periodic pattern raises the possibility that certain cohorts may experience better or poorer conditions for growth in a manner that is highly predictable, given the average life-span of rams in this population.

We defined a poor season as one that was characterized by below-average growth of all individuals in all cohorts and a good season as one during which horn growth was above-average for all rams, based on the deviations shown in Fig. 4. The cumulative differences between growth of all age classes in a given year and the long-term mean for each age class provided an index of values that indicate above- or below-average conditions. When these indices of conditions in a birth year are used to predict horn volume at age eight, the results show, surprisingly, that rams born in poor horn growth years will eventually have the largest horns at 8 years (Fig. 5).

Conversely, males born during relatively good years are likely to experience poor growth during years of maximum horn accretion, and therefore have smaller horns at 8 years. For example, rams born during one of the worst horn growth summers on record (1992) were among the larger horned cohorts at 8 years (see Fig. 2). This relationship (Fig. 5) is only marginally significant (linear regression: $r^2=0.122$, $p=0.101$), but the biological implications for hunters, outfitters, and managers are not trivial.

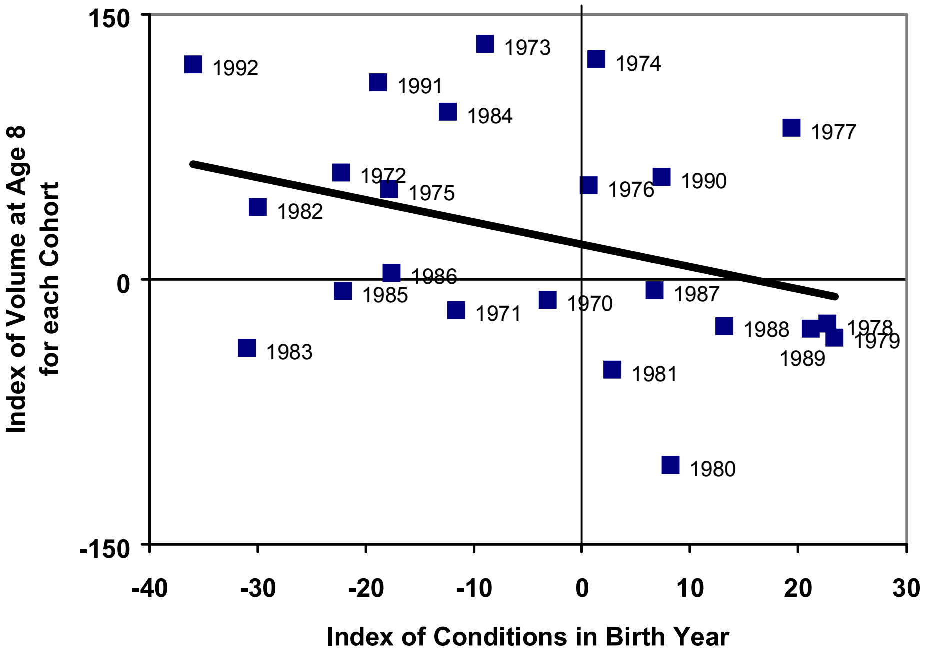

Fig. 5. Relationship between index of conditions in birth year and index of horn volume at age 8 for each cohort from 1970 to 1992. Indices are based on cumulative differences in horn growth from long-term mean values for each age/cohort group. Negative values indicate below-average conditions in the year of birth (x-axis), or below-average horn volume at age 8 (y-axis).

DISCUSSION

Overall, patterns of horn growth of Dall sheep rams over 30 years indicate strong interannual variation with a periodicity of approximately 10 years. Depending on the year of birth, individual rams will have different trajectories of horn growth during the first decade of life. These strong cohort effects in horn growth were also detected in an earlier examination of horn growth data from this region (Bunnell 1978, Mindek 1989), and these authors suggested that cohort effects on early horn growth were compensated for by better growth in later years. While this may be true for animals that live for at least 10-12 years, relatively few animals reach this age in the Yukon. In alpine ibex, Toigo et al. (1999) observed that environmental effects during the first year influenced horn growth of males, and that these animals were unable to compensate for poor growth during later years, emphasizing the importance of cohort effects in this population.

Another possible explanation for our results is that horn growth is dependent on population density as suggested by Geist (1971). Heimer and Smith (1975) also speculated that density-dependent nutrition might influence population quality for Dall sheep, however this hypothesis was refuted in subsequent studies (see Heimer and Watson 1986, Heimer 1999). The density of the sheep population in the Ruby Range during the past 30 years is probably well below historical numbers (J. Johnson, personal communication), and has declined since 1980 (Carey et al. unpublished data). Although cohort-related effects may be related to density in some populations of bighorn sheep (*Ovis canadensis*), Jorgenson et al. (1998) showed that population density only influenced horn growth of young rams

(<4 years age). During this time males are still associated with nursery bands, and higher intraspecific competition for resources may limit horn growth. The effects of density disappeared once rams joined all-male groups. In our analyses, Dall sheep rams of all age classes showed correlated changes in horn growth (Fig. 4), indicating that changes in relative density of nursery herds associated with interannual variability in reproductive success could not explain the periodic patterns of growth in the southwest Yukon.

The basis for the observed periodic variation in ram horn growth appears to be mediated through the influence of annual climatic conditions on primary productivity of alpine habitats utilized by sheep for forage. Hoefs and Brink (1978) found that precipitation during the summer growing season was correlated with primary productivity of sheep range. Summer productivity was also directly correlated with reproduction during the following season (Hoefs 1984). In our study area in the Ruby Range the relationship between ewe: lamb ratios and an index of summer weather conditions (the deviation of June to August minimum temperature from average minimum temperature, multiplied by summer precipitation), was positive and significant (linear regression: $r^2 = 0.642$, $p=0.002$, $N=11$; Carey et al., unpublished data). Several authors (e.g. Hoefs and Brink 1978, Mindek 1989) have attempted to describe particular environmental conditions associated with poor growth, but this analysis is difficult at present without knowing more about how variation in environmental conditions influence vegetation productivity (D. Hik, unpublished data). However, several recent studies have demonstrated that large-scale weather variation can influence synchronization and periodicity of population dynamics of large mammals including Soay sheep (*Ovis aries;* Grenfell et al. 1998, Milner et al. 1999) and red deer (*Cervus elaphus;* Forchhammer et al. 1998).

In the southwest Yukon, the deviation from the long-term mean volume in ram horn growth is also broadly synchronized and correlated with the cycle in snowshoe hare (*Lepus americanus*) numbers from the adjacent boreal forest (see Krebs et al. 2001). A bivariate spectral analysis of these two time series found that periodicities of 11 years were strongest, and that cross-correlation analysis indicated that the strongest relationship occurred with a lag of –2 years ($r = 0.5741$, $p < 0.05$; Hik and Carey, unpublished data). This relationship essentially implies that the periodic pattern observed in horn growth precedes the hare cycle by two years, consistent with the suggestion that growth or condition is a more sensitive indicator of environmental conditions than adult survival, which may remain high even in years when individuals are in poor condition (Hik 1995). More significantly, the periodicity of horn growth and the correlation with the snowshoe hare cycle provides support for the hypothesis that there is a general underlying climate-mediated influence on herbivore growth and survival in this northern region (Sinclair et al. 1993).

In the southwest Yukon the observed periodicity in horn growth may provide a strong terrestrial signal of inter-decadal climatic variability associated with large-scale oceanic phenomena such as the Pacific Decadal Oscillation, and these periodic anomalies in atmospheric flow over the Pacific Ocean may have profound consequences for the weather of North America, particularly during winter (Bond and Harrison 2000). The length of the sunspot cycle also correlates well with indicators of terrestrial climate in the Northern Hemisphere (Friis-Christensen and Lassen 1991, Fligge et al. 1999), although inclusion of other factors such as volcanic dust and greenhouse gases improves the relationship (e.g. D'Arrigo et al. 1999). While the direct link between climate cycles and sunspots is still uncertain (Waple 1999), there is a clear need to examine specific mechanisms that link climate, vegetation dynamics, habitat quality and productivity, and the demography and growth of terrestrial wildlife population in the Yukon.

Although several attempts have been made to link weather directly to observed variation in horn growth, this is difficult without knowing details of what factors influence plant productivity. Mysterud et al. (2000) have similarly discussed the need to carefully evaluate impacts of specific local weather conditions on forage productivity before firm conclusions can be drawn between climatic periodicity and dynamics of northern ungulates. Ongoing studies in the Ruby Range suggest that net annual primary productivity of alpine meadows is most strongly influenced by the timing of snow-melt, however summer temperature and precipitation are also important (D. Hik, unpublished data). Winter conditions may also restrict access to forage on winter range (Goodson et al. 1991), which could influence the correlation between summer productivity and horn growth.

Several attempts have been made to correlate specific changes in temperature and precipitation with primary productivity (e.g. Hoefs and Brink 1978, Mindek 1989), however there is no clear relationship and horn growth is probably a better bio-indicator of average conditions in this region than generalized weather records. As well, strong temperature inversions occur in Yukon mountains (Burn 1994), and therefore climate records from the valley bottom may not be representative of climate at higher elevations, particularly in winter (D. Hik, unpublished data). While the instrumental climate record is probably too short to detect clear patterns, a significant 11-year periodicity has been observed for both precipitation and temperature based on a 250-year time series analysis of ice-core records (1736-1986) from the summit of Mt. Logan, only 100 km west of the Ruby Range study area (Holdsworth et al. 1992).

MANAGEMENT IMPLICATIONS

While the prevailing wisdom is that northern sheep populations are self-regulatory and thus tend to manage themselves (Geist 1971, Hoefs 1984), the results of these analyses emphasize several important management implications for the southwest Yukon. First, there is a distinct cohort effect on horn growth that is broadly predictable because it is correlated with larger-scale climate patterns that operate on decadal and multi-decadal scales, even though the precise ecological mechanisms are unknown. Geist (1971) suggested that variation in horn growth in North American wild sheep was an indication of the quality of a population, such that more rapid horn growth and more massive horns at any given age would be characteristic of high quality populations. In the case of Dall sheep in the southwest Yukon, periodic climate-mediated effects appear to influence horn growth of rams in specific cohorts. Therefore, selective removal of large-horned rams by hunters should have no influence on the genetic quality of a population, or on the potential of the population to produce more rams with fast-growing horns.

Second, our results suggest that large rams will only be produced periodically in the Ruby Range populations. The largest rams will come from cohorts born during poor summers, further confounding the potential for producing many large rams at any time in this population because there is lower lamb survival during poor summers. These rams may in fact be harvested at a younger age because they experience more rapid horn growth (Fig. 3). By age 12 or 13 years there is very little difference in the size of horns of individuals born in good or poor seasons.

Finally, we suggest that other jurisdictions consider programs for measuring annual horn growth of harvested rams. This detailed information may allow sheep horns to serve as valuable bioindicators of interannual variation in the quality of sheep habitat. The underlying causes of this variability may not be easily explained, but without measurements of annual growth it is impossible to even ask these questions. Estimates of volume based on measurements of length and basal circumference provide superior information than measurements of length alone.

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