EFFECTS OF POPULATION DENSITY ON HORN DEVELOPMENT IN BIGHORN RAMS

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Abstract: Trophy hunting is a management goal for many populations of ungulates and has important implications for conservation because of the economic value of trophy males. To determine whether population density affected horn growth of males, a marked population of bighorn sheep (*Ovis canadensis*) in Alberta, Canada, was studied for 27 years. For the first 9 years, population density was kept stable by removing adult females; afterwards, the numbers of ewes and yearlings tripled before beginning to decline. Horns were measured during repeated captures of marked rams. As the number of adult ewes and yearlings increased, ram horns were shorter and thinner because of decreased horn growth before 4 years of age. Some compensatory horn growth may have occurred at 5 years of age. The effects of population density on horn growth ceased when rams left the nursery groups to join all-male groups. Doubling of male numbers had no detectable effect on net annual horn growth of males ≥4 years old. Spring precipitation had no apparent effect on horn growth of males 3–4 years old, and had a minor positive effect on horn base circumference for rams 5–6 years old. The proportion of rams 6–7 years old that attained 4/5 of a curl decreased from 61–73% at low density to 33–35% at high density. When bighorn sheep populations increase to a density where intraspecific competition in nursery herds affects horn development of young rams, limited ewe harvests may prevent a decrease in size of horns of mature males.

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Much of the economic value of many ungulates derives from hunters' willingness to pay for harvesting large-horned or large-antlered ("trophy") males. Nonresident hunters in Alberta pay over $10,000 U.S. in permit and guiding fees to hunt bighorn sheep males, and higher sums are paid for hunting trophy sheep in Asia. Auctioning of "special" permits to hunt bighorn rams is a fundraising strategy used by many North American jurisdictions (Erickson 1988), and provinces or states reputed to produce large-horned rams generally obtain higher bids. In 1995 and 1996, 2 Alberta bighorn permits were auctioned for a total of $425,000 U.S. Factors affecting the size of horns are therefore of interest to wildlife managers, and horn size is also of general interest to conservation biology because of the potential to use trophy hunts to fund conservation and habitat protection.

Horn size of wild sheep is well known to vary among populations, often because of differences in climate and soil characteristics (Geist 1971, Shackleton 1973). Little is known, however, of what causes the wide differences among individuals and cohorts within a population, although spring precipitation may have a positive effect on horn growth (Bunnell 1978). Studies of bighorn sheep (Jorgenson et al. 1993*b*), moose (*Alces alces*; Solberg and Sæther 1994), and red deer (*Cervus elaphus*; Clutton-Brock and Lonergan 1994, Buckland et al. 1996) have shown that increases in total population size often do not result in greater numbers of adult males in the population, but such increases may retard the growth of horns and antlers. In a study of white-tailed deer (*Odocoileus virginianus*), however, major changes in density did not affect antler size (Shea et al. 1992). Population density would affect the development of horns and antlers only if density became sufficiently high to decrease resource availability and increase intraspecific competition.

In this paper, we explore the relation between population density and horn development in bighorn rams in a marked population where the number of adult ewes was first ma-

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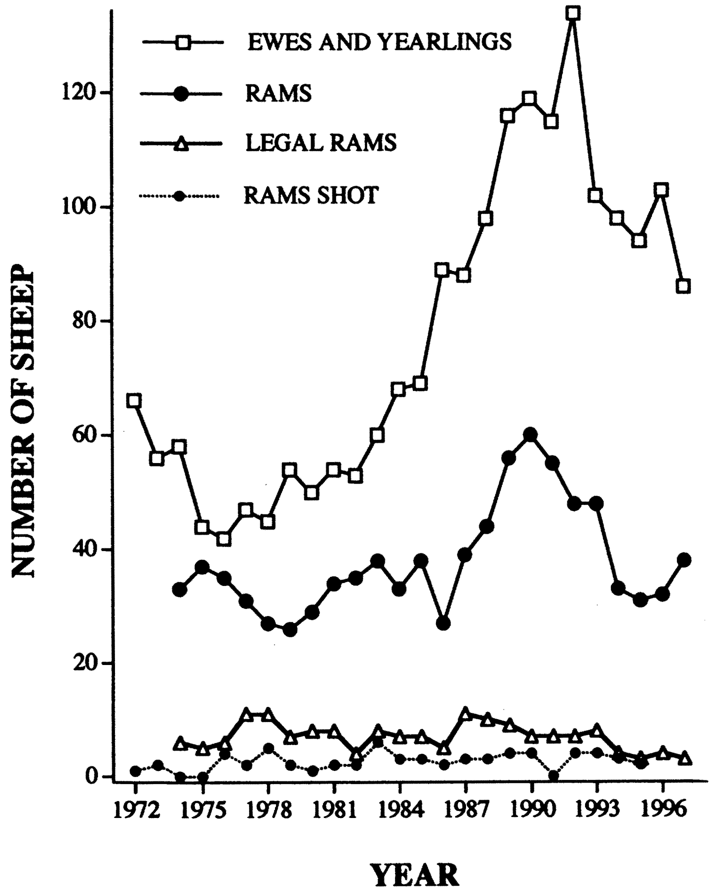

Fig. 1. Size and composition in June of the Ram Mountain population of bighorn sheep, 1972–97: number of ewes and yearlings of both sexes, rams ≥2 years old, rams with horns describing 4/5 of a curl or more (legal rams are ≥4 yr old), and legal rams shot by hunters. Only full-curl rams were legal after 1995.

nipulated to simulate a "nontrophy" hunting season (Jorgenson et al. 1993*b*) and then allowed to more than triple. Like most sexually dimorphic ungulates (Main et al. 1996), adult bighorn sheep are sexually segregated through much of the year (Geist 1971), but young males remain with "nursery" groups (comprising females, lambs, yearlings of both sexes, and some 2- and 3-year-old males) and gradually join male groups at 2–4 years of age (Festa-Bianchet 1991). Therefore, we expected that the number of females and yearlings would affect the development of horns of males up to 3 years of age, and that the number of adult males would affect horn development of rams ≥4 years old.

STUDY AREA AND METHODS

We studied bighorn sheep at Ram Mountain, Alberta, Canada (52°N, 115°W; elevation 1,082–2,173 m), where a capture and marking program began in 1971. Further details on the study area and capture methods can be found in Jorgenson et al. (1993*b*). Ram Mountain is an isolated outcrop separated from the main Rocky Mountain range by about 30 km of coniferous forest. The study area includes about 38 km^2 of alpine and subalpine habitat used by bighorns.

We captured sheep from late May to early October in a corral trap baited with salt. Ewes were marked with canvas collars and rams with Allflex ear tags (Allflex USA, Dallas/Fort Worth Airport, Texas, USA). Most rams ≥3 years old were caught once or twice in most summers, but very few were captured after July.

After 1975, >90% of the sheep ≥1 year old had been marked; therefore, our estimates of population size were based on total counts (Fig. 1). We counted sheep by noting the identity of all those caught at the trap, seen at the trap, and seen during foot searches of the study area. Because of the open habitat and long field season, we were very efficient at finding marked sheep: using capture–mark–recapture models, we estimated the probability of missing a marked sheep in a given year was <0.5% for ewes and <5% for rams (Jorgenson et al. 1997); almost all rams missed had emigrated to a nearby mountain. Therefore, our population estimates are very accurate.

Captured rams were restrained by hand and hog-tied. For each horn, we used a measuring tape to determine the total length along the outside curvature and base circumference (mm). Further details on capture procedures and frequency of captures are in Festa-Bianchet et al. (1996). Between 1972 and 1980, 12–24% of adult ewes were removed (Jorgenson et al. 1993*b*).

Rams with horns describing at least 4/5 of a curl (legal rams) were hunted from late August through October. The Alberta hunting regulations define a legal ram under the 4/5ths rule as "a male sheep with horns, 1 of which is of sufficient size that a straight line drawn from the most anterior point of the base of the horn to the tip of the horn passes in front of the eye when viewed in profile." Any Alberta resident hunter could purchase a trophy sheep license; therefore, harvest was limited only by availability of legal rams. In 1996, the definition of legal ram in the study area was increased to full curl. There were no full-curl rams in either 1996 or 1997; in this paper, "legal" always refers to rams with horns ≥4/5 of a curl. Beginning in 1974, we noted whether each marked ram seen in the study area was legal or not. To assess the effects of population size on the age-specific proportion of rams that were legal, we considered the years 1975–87 as "low density" ($\bar{x}$ = 59 ewes and yearlings/yr), and the years 1988–97 as "high density" ($\bar{x}$ = 107 ewes and yearlings/yr).

Data presented here represent 850 captures of 179 rams ≥3 years old between 1971 and 1997. Legal rams were at risk of hunting mortality, and natural mortality of adult rams was 13–40%, increasing with age (Jorgenson et al. 1997). As a result, our sample size decreased with ram age, from 132 3-year-olds to 31 rams ≥8 years old. We adjusted individual horn length and base circumference to 5 June via individual linear growth rates for rams caught more than once during the period 25 May–1 August, and via age-specific linear regressions of horn length or base circumference on capture date for rams caught only once in a year. Horn length can be affected by wear of the tips ("brooming") during social interactions (Geist 1971), and rams >4 years old can have varying amounts of horn removed by brooming. The longer horn was used for analysis of horn length. For base circumference, the mean of the 2 horns was used for analyses. We calculated annual changes in horn length or base circumference by subtracting the measurement adjusted to 5 June at age x from the same measurement at age $x + 1$, therefore ignoring any effects of horn tip wear between years. We used this measure of net incremental horn growth, rather than measuring horn length between successive annuli, because we were interested in the management implications of the effects of population density. The actual size of the ram's horns is of interest to a hunter, not the horn growth that could be measured by the annual growth annuli.

To determine whether population density affected horn development, we used linear regressions. We first compared horn measurements with the average number of ewes and yearlings during the first 3 years of a ram's life. We then compared the net change in horn length or base circumference during a year to the number of adult rams in the same year. Lambs were excluded from measures of population size because their effect on forage availability was likely much less than that of older sheep: by mid-September, lambs are only about 40% of the mass of adult ewes (Festa-Bianchet et al. 1996). In addition, while the winter mortality of yearlings and adult ewes did not vary much from year-to-year (Jorgenson et al. 1997), lamb survival was highly variable (Festa-Bianchet et al. 1997): the number of lambs could decrease by >70% over 12 months, with most of the mortality taking place in October–May, when we were not on the study area. Therefore, we could not assign a specific value to the number of lambs in the population during some years. Furthermore, because bighorn sheep are limited to traditional areas near escape terrain (Geist 1971), population size and population density are closely correlated: sheep in our study population did not expand the area they used as a response to population growth (J. T. Jorgenson, unpublished data).

Our analyses included 21 rams born in 1968–71. To compare horn growth and population density during the first 3 years of life for these rams, we assumed numbers of ewes and yearlings in 1968–71 and numbers of rams in 1971–73 were the same as the average for 1972–75. This assumption is justified because censuses of the study area by Alberta Fish and Wildlife in 1968–73 suggested a stable population.

The statistical comparison of horn size or growth with population size for different age classes was problematic. First, comparisons of total horn length or base circumference of different age classes were not independent, because the same rams usually were remeasured every year, and horn size at a given age is not independent of horn size 1 year earlier. Second, as rams became older, our sample became biased toward smaller-horned rams because the larger-horned rams were more likely to become legal and therefore to be removed from the sample via harvest. This bias was likely stronger at low density because rams 4–6 years old were more likely to be legal at low versus high population density (see Results). To partly overcome these statistical and sampling problems, we adjusted the level of α to 0.01 for net annual increments in horn size, where we compared population density to horn measurements for 5 age classes. For total horn length and base circumference, we compared density to horn measurements for 7 age classes and adjusted α to 0.007 to avoid increasing our probability of Type I error beyond the 5% threshold.

Because horn growth could be affected by availability of growing vegetation, we used linear regression to compare year-to-year changes in horn length and base circumference to precipitation from 15 May to 15 July, the main growing season at Ram Mountain, and to total precipitation in May–August each year. Weather data were collected by Environment Canada at the Nordegg Ranger Station, approximately 20 km from Ram Mountain. Weather data were available for only 16 of the 20 years between 1975 and 1994.

Rams orphaned by ewe removals had smaller horns than nonorphans at 4–5 years of age (Festa-Bianchet et al. 1994). We ignored the effects of orphaning (6.7% for length and 3% for base circumference) because we were interested in the effects of a potential management strategy of controlling the number of ewes, which would most likely involve the removal of some lactating ewes (and orphaning of some lambs) during a fall hunting season.

RESULTS

The number of adult rams increased a few years after cessation of ewe removals but then declined while the number of ewes continued to increase (Fig. 1). The number of ewes more than tripled, while the number of rams only doubled. As we previously reported (Jorgenson et al. 1993*b*), numbers of legal rams and number shot by hunters were independent of number of ewes. About 40% of legal rams were shot each year, for a yearly harvest of 0–6 rams (Fig. 1).

The mean number of ewes and yearlings in the first 3 years of life had a negative effect on total horn length of rams up to 7 years of age and on horn base circumference to 6 years of age (Table 1, Fig. 2). However, the relation between number of ewes and yearlings during a ram's first 3 years of life and the net annual increments in horn length changed with the ram's age. Population size had a negative effect on net horn growth for 3-year-olds but had no effect on the change in base circumference for the same age class (Table 1). The net increases in horn length for 5-year-olds and in base circumference for 4-year-olds appeared positively related to the number of ewes and yearlings in the first 3 years of life, although for 5-year-olds the *P*-value obtained was less than the Bonferroni-adjusted value necessary to reject the null hypothesis at $\alpha = 0.05$ (Table 1, Fig. 3). The number of ewes and yearlings did not affect net horn growth of rams $\geq$6 years old (Table 1).

Population size affected the proportion of rams whose horns grew to 4/5 of a curl (Fig. 4). Less than 10% of 4-year-olds and <30% of 5-year-olds were legal, and the proportion of legal 4- and 5-year-olds changed little with population size. The proportion of rams aged 6–9 years that were legal, however, was substantially lower at high versus low density (Fig. 4). The average age of rams shot by hunters was 6.2 years at both levels of density considered in Figure 4.

We expected that number of adult rams in the population would affect horn development of rams $\geq$4 years old, as rams >3 years old spent most of their time in male groups (Festa-Bianchet 1991). Our analyses, however, did not reveal any influence of ram numbers on net annual changes in length or base circumference for rams aged 4–8 years (Table 2).

To attempt to explain the considerable residual variance in horn growth once we accounted for population size (Fig. 3), we compared ram

Table 1. Regression statistics of the average numbers of adult ewes and yearlings in the first 3 years of life on the size and development of horns of bighorn rams 3–10 years old at Ram Mountain, Alberta. Only age classes with samples ≥10 are reported. Note that because of repeated comparisons, only P-values of <0.007 for length and base measurements, and <0.01 for increment measurements are considered significant.

Horn measurement	Ram age (yr)	n	Slope	r^2	P
Length	3	132	−0.127	0.258	<0.001
	4	113	−0.161	0.335	<0.001
	5	89	−0.177	0.419	<0.001
	6	66	−0.158	0.356	<0.001
	7	34	−0.082	0.228	0.004
	8	25	−0.026	0.015	0.562
	9–10	20	−0.067	0.078	0.233
Base	3	132	−0.055	0.18	<0.001
	4	113	−0.067	0.32	<0.001
	5	89	−0.037	0.16	<0.001
	6	66	−0.039	0.203	<0.001
	7	34	−0.002	0.002	0.823
	8	25	−0.009	0.014	0.567
	9–10	20	−0.023	0.056	0.313
Net length increment to the following year	3	93	−0.031	0.116	0.001
	4	73	−0.007	0.009	0.434
	5	58	0.026	0.141	0.037
	6	26	0.017	0.046	0.293
	7	16	0.013	0.017	0.629
	8	10	0.055	0.281	0.115
Base increment to the following year	3	93	−0.004	0.004	0.543
	4	73	0.028	0.335	<0.001
	5	59	0.009	0.047	0.099
	6	27	0.008	0.057	0.232
	7	16	−0.017	0.155	0.131
	8	10	−0.002	0.007	0.824

horn growth to total precipitation from mid-May to mid-July. For rams 3 and 4 years old, precipitation in late spring and early summer had no effect on horn growth (examining net annual increments in both total length and base circumference; $P > 0.490$). For rams 5 and 6 years old, precipitation had no relation with horn length increments ($P > 0.400$) but a slight positive relation with changes in base circumference (5-year-olds: $r^2 = 0.12$, slope = 0.011, $P = 0.033$, $n = 38$; 6-year-olds: $r^2 = 0.23$, slope = 0.009, $P = 0.045$, $n = 18$). However, there was no significant effect of both precipitation and population density in multiple regressions: for horn measurements and age classes with an effect of the number of ewes and yearlings, precipitation did not explain any additional variance ($P > 0.501$). Similarly, the number of ewes and yearlings did not explain any additional variance in the increment of base circumference for either 5- or 6-year-old rams when entered into a stepwise multiple regression with precipitation in mid-May to mid-July ($P > 0.324$). Precipitation from May to August did not explain any more variance in horn increment than precipitation from mid-May to mid-July.

When we compared total horn length and base circumference for all rams, it appeared that little horn growth took place for rams ≥7 years old (Fig. 5). To determine whether this apparent effect was due to the selective removal of larger-horned rams by hunters, we compared individual annual net incremental growth in horn length and base circumference. The horns of most rams appeared to increase in length with age, but base circumference did not seem to change after 6 years of age (Table 3).

DISCUSSION

There was a clear relation between number of ewes and yearlings in the population and size of rams' horns, suggesting that increased intraspecific competition within the nursery herd may have a negative effect on horn development. Although effects of population size during the first 3 years of life persisted until rams were at least 6–7 years old, our results clearly show that population size did not have a negative effect on horn growth for rams ≥4 years

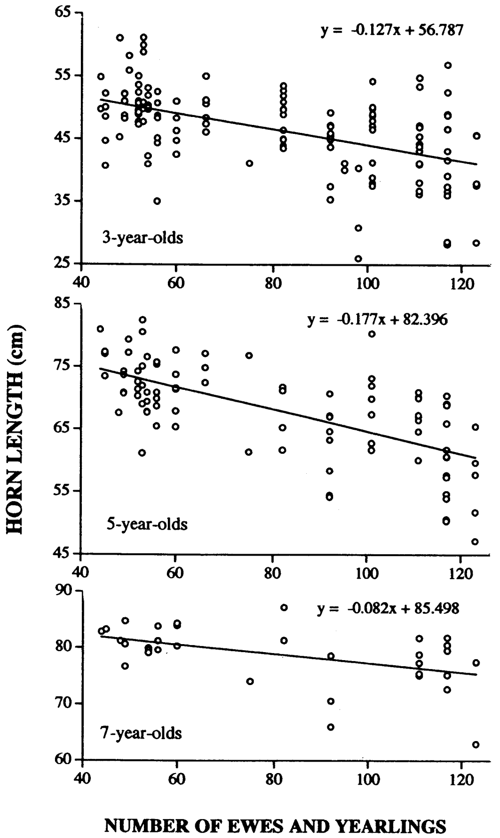

Fig. 2. Relation between average number of ewes and yearlings in the first 3 years of life and length of horns of bighorn rams aged 3, 5, and 7 years in the Ram Mountain population, 1971–97.

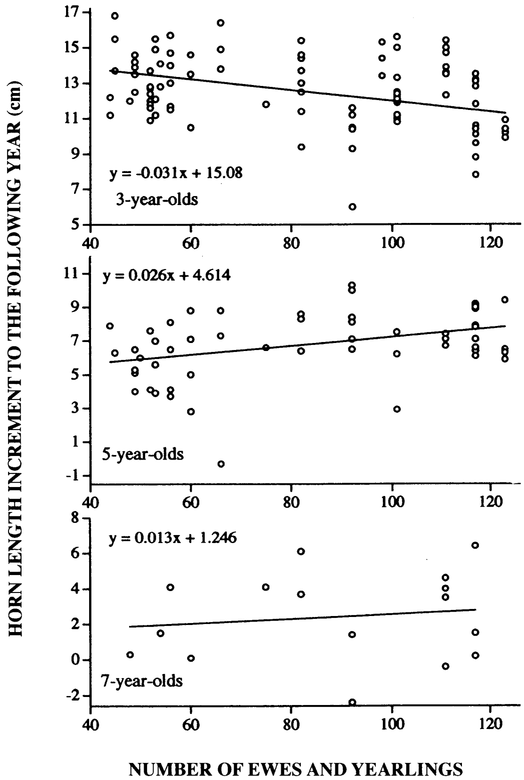

Fig. 3. Relation between the average number of ewes and yearlings in the first 3 years of life and the net change in horn length to the following year for bighorn rams aged 3, 5, and 7 years in the Ram Mountain population, 1971–97. Note changes in scale on the abscissa.

old. Most bighorn rams remain within nursery groups until 2 years of age and then gradually switch to male groups; by age 4, rams are found almost exclusively in male groups (Festa-Bianchet 1991). Other studies of wild sheep found rams that grew large horns in the first few years of life showed a decrease in the rate of horn growth during their later years relative to rams whose horns had relatively poor growth in early life (Bunnell 1978). We found a similar trend, apparently caused by the effects of density: for 4- and 5-year-old rams, at least, population density during the first 3 years of life appeared to have a slight positive effect on net annual horn growth. However, by 4 years of age, rams in our study population had already completed about 80% of horn growth (Fig. 5), and the minor amount of greater horn growth at high density after rams left the nursery groups did not compensate the negative effect of density on horn growth in early life.

We studied the effects of population density on ram horn development in a hunted population. Our sample of rams available for measuring was affected by hunting mortality, which was clearly biased toward large-horned rams because Alberta hunting regulations use a morphological definition of which rams can be harvested and prohibit the harvest of small-horned rams. In addition, a hunter faced with a choice of >1 legal ram will likely shoot the largest-horned animal. Therefore, as age increased, the sample of surviving rams ≥5 years old was progressively biased toward small-horned individuals. Furthermore, this bias was almost certainly stronger at low population density because a much greater proportion of rams, particularly among those aged 6 and 7 years, was legal at low versus high density. In an unhunted population, the effects of density on horn size of older rams likely would be stronger than those we

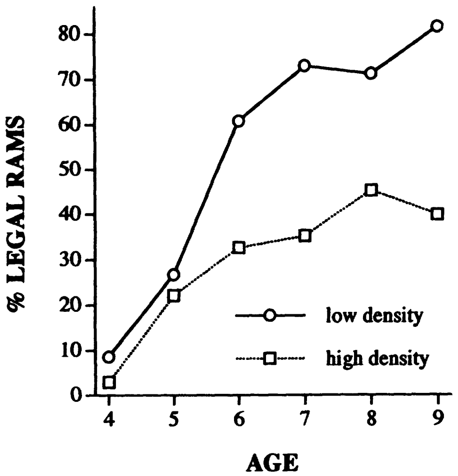

Fig. 4. Proportion of bighorn rams 4–9 years old at Ram Mountain whose horns described at least 4/5 of a curl and were classified as legal during years of low density (1975–87) and years of high density (1988–97). Sample sizes for low-density years were 70, 56, 46, 26, 14, and 11 for 4–9-year-olds. For high-density years, sample sizes were 68, 63, 49, 34, 22, and 10. Differences in the proportion of legal rams according to population density were significant for rams aged 6 years old ($G = 7.70$, $P < 0.006$) and 7 years ($G = 8.67$, $P < 0.006$).

found at Ram Mountain, where, at low density, several young, large-horned rams were removed by hunters. In hunted populations, it could be misleading to study the age-related changes in ram horn size by looking at average horn measurements of all rams. For example, while Figure 5 suggests little or no incremental horn growth took place after 7 years of age, Table 3 indicates horn length increased for most individual rams between 7 and 10 years.

Table 2. Regression statistics of the numbers of adult rams and the 1-year change in total length or in base circumference of the horns of bighorn rams aged 4–6 years old at Ram Mountain, Alberta. Note that because of repeated comparisons, only P-values <0.01 are considered significant.

	Ram age (yr)	n	Slope	r^2	P
Change in length	4	73	−0.005	0.001	0.813
	5	58	0.027	0.02	0.291
	6	26	0.029	0.012	0.587
	7	16	−0.009	0.001	0.901
	8	10	0.049	0.018	0.715
Base circumference	4	73	0.020	0.024	0.195
	5	59	−0.029	0.066	0.050
	6	27	−0.009	0.007	0.671
	7	16	0.035	0.101	0.231
	8	10	0.057	0.347	0.073

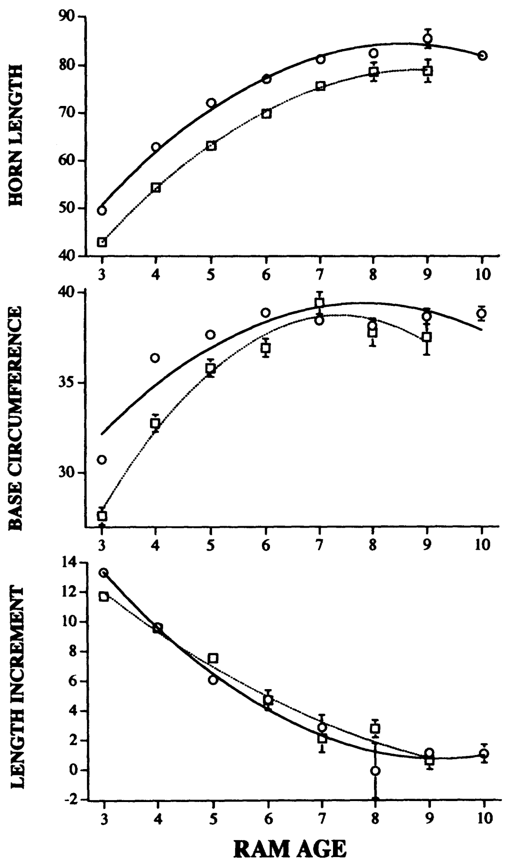

Fig. 5. Average horn length, base circumference, and increase in horn length to the following year for bighorn rams at Ram Mountain, 1972–97. All measurements are in centimeters. Rams born during low-density years (before 1986) are indicated by circles and a continuous line, and rams born during high-density years (1986 and later) are indicated by squares and a dotted line. The 10-year-old age class at low density includes all rams aged 10–12 years. Standard errors are indicated when sufficiently large to be shown within the figure's resolution. Second-degree polynomial regressions through the averages are included only to illustrate differences between high and low density measurements.

During our study, number of rams did not increase as much as number of ewes (Fig. 1), partly because harvesting of rams continued while ewe removals stopped. Ram population size, within the limits reached during this study, had little effect upon annual horn growth of rams ≥4 years old. Therefore, it appears that intraspecific competition was not very high within bands of rams during our study.

MANAGEMENT IMPLICATIONS

In populations of bighorn sheep at high density, limited ewe removals could prevent density-dependent decreases in size of horns of big-

Table 3. Net incremental increase in total horn length or in base circumference to the following year for bighorn sheep rams 6–10 years old at Ram Mountain, 1972–97. Rams 9 and 10 years old were combined to increase sample size.

Age (yr)	Total length (cm)				Base circumference (cm)			
	n	Change	Paired *t*	*P*	*n*	Change	Paired *t*	*P*
6	26	4.71	10.297	<0.001	26	0.12	0.649	0.522
7	16	2.42	3.869	<0.002	16	−0.25	0.914	0.375
8	10	1.61	1.813	0.103	10	−0.17	0.739	0.479
9–10	10	1.26	4.268	0.002	10	0.30	1.068	0.313

horn rams. Similar results could be expected in other ungulate species. A reduction in ewe numbers, however, will have a positive effect on the growth of ram horns only if intraspecific competition for resources within nursery groups limits horn development. At Ram Mountain, lower growth of horns on young rams was associated with several population responses that suggested increased intraspecific competition, including lower mass of yearlings (Festa-Bianchet et al. 1995), delayed age of primiparity (Jorgenson et al. 1993*a*), and increased lamb mortality (Bérubé et al. 1996). Although predators such as gray wolves (*Canis lupus*) and mountain lions (*Puma concolor*) were occasionally seen, evidence of predation on bighorn sheep at Ram Mountain has been only anecdotal. Predation did not prevent our study population from increasing following cessation of ewe removals.

Situations similar to our study are likely to occur in many populations of ungulates managed for trophy production in Europe and parts of North America where large predators are rare or absent. However, in populations limited by factors independent of resource abundance, such as predation (Wehausen 1996, Ross et al. 1997) or disease (Wehausen et al. 1987), removal of adult females is unlikely to have any effect on the development of horns or antlers in males. In at least 1 case (Shea et al. 1992), a drastic decrease in density did not affect antler development in white-tailed deer, possibly because the decrease had no effect on intraspecific competition. Ewe hunting seasons were first proposed as a tool to decrease the probability of pneumonia epizootics, but we have shown that ewe removals may increase horn growth of young rams. At high population density at Ram Mountain, there were several indications that resources were limited (Bérubé et al. 1996, Festa-Bianchet et al. 1997, Jorgenson et al. 1997). We suspect that ewe removals in populations that are below carrying capacity would have no effect on ram horn development.

Ewe removals do not appear to affect the availability of legal rams: a 3-fold increase in number of ewes and yearlings was accompanied by an ephemeral increase in number of rams and no change in number of legal rams (Fig. 1). Other studies of ungulates have reported that increases in population size are usually accompanied by a decrease in the proportion of adult males in the population (Clutton-Brock et al. 1991, Clutton-Brock and Lonergan 1994, Buckland et al. 1996). Where natural mortality of adult females is insufficient to prevent increases in numbers, removal of some adult females to maintain populations at moderate density could prevent a density-dependent decrease in horn or antler size without decreasing the availability of mature males.

Management strategies such as ewe removals that aim to increase or prevent a decrease in horn size of harvested rams are incompatible with unlimited-entry hunts for trophy males, unless hunters are only allowed to take rams from the very oldest age classes. Otherwise, as we previously noted (Jorgenson et al. 1993*b*), hunters would harvest more young rams in populations limited by ewe removals, but those rams would be well short of maximum horn size. In bighorn sheep populations located in accessible areas of Alberta, most rams are shot in the year they become legal (J. T. Jorgenson, personal observation). At Ram Mountain, for example, of 8 rams that had horns of 4/5-curl by age 4, 7 were shot at 4.5 years of age. In another Alberta population where ram horns generally grow faster than at Ram Mountain, 2 rams had 4/5-curl horns at 3 years and 4 4-year-olds were legally shot in 1982–91 (Festa-Bianchet 1989). Rams shot as 4 or 5 years old rams are well short of their horn growth potential (Fig. 5). Given that high harvests of mature males may have negative effects on survival of younger males (Heimer et al. 1984, Jorgenson et al. 1997) and that trophy hunting may reduce genetic variability in a population (Hartl et al. 1991, Fitzsimmon et al. 1995), we recommend that management of trophy species should direct the harvest to a limited proportion of mature males that are near the end of their natural lifespan. For bighorn sheep, harvest should be directed to rams ≥8 years old. A "full-curl" restriction on rams that can be harvested would probably achieve this management goal, and we are currently assessing the consequences of an experimental "full-curl" hunting restriction on survival and development of mature males at Ram Mountain. We suspect manipulating the age of rams taken by hunters will have a greater effect on the availability of trophies than will manipulations of ewe numbers.

Long-term data on horn length for known-age rams within a single population or geographic area, such as are routinely obtained at hunter check stations or through compulsory registration, could be used to evaluate trends in horn growth for different populations. A persistent decrease in horn length of harvested rams could indicate high intraspecific competition within nursery herds. When coupled with census data, long-term data on horn length could be used to set ewe harvest quotas or to decide whether or not to institute ewe culling programs. Similar considerations could apply to other ungulates managed for trophy production.

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LONG-TERM RANGE FIDELITY IN ROCKY MOUNTAIN ELK

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Abstract: The validity and utility of applying results of home range analysis to long-term wildlife management objectives depends on the assumption that populations remain relatively faithful to such ranges over time, but such an assumption is rarely investigated analytically. We evaluated the home range fidelity of elk (*Cervus elaphus*) in 3 populations in southcentral Montana and northwestern Wyoming via comparison of home range use, size, and boundaries in 2 different time periods, 1979–82 and 1988–91, using 265 locations of 15 elk and 971 locations of 23 elk. Range use changed significantly in 2 of 3 populations between time periods ($P < 0.01$), but total size of home range (95% minimum convex polygon) changed in only 1 population ($P < 0.05$). Significant seasonal changes in elevational use accompanied changes in range boundaries and use in every season. Distances between radiocollared elk located simultaneously decreased in all seasons in 2 populations ($P < 0.05$), suggesting increasing herd cohesion and social stability. Changes in range use in different time periods consistently tended to increase spatial separation of populations of elk and to reduce densities of elk. Range boundaries of populations were fluid over time, suggesting boundaries and use of home ranges of larger populations of elk should be systematically reinvestigated at intervals of ≤ 10 years if accurate estimation of these parameters is important to management.

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Many investigations of elk home range and dispersal have shown elk to be strongly faithful to seasonal and annual ranges (Knight 1970, Craighead et al. 1972, Craighead et al. 1973, Shoesmith 1979, Edge and Marcum 1985). Relatively sudden, long-distance movements from traditional range to new areas have been documented (Craighead et al. 1972, Rickard et al. 1977) and, less commonly, there is circumstantial evidence of significant shifts in traditional migration routes and seasonal ranges (Smith and Robbins 1994). However, few studies (Craighead et al. 1972, Craighead et al. 1973, Shoesmith 1979, Smith and Robbins 1994) have

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