Management and Conservation

Decrease in Horn Size and Increase in Age of Trophy Sheep in Alberta Over 37 Years

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ABSTRACT Long-term data (1974–2011) from harvested bighorn rams (*Ovis canadensis*) in Alberta, Canada, suggested a reduction in horn size and in the proportion of trophy rams in the provincial population over time. Age at harvest increased over time, suggesting slower horn growth. Rams that experienced favorable environmental conditions early in life had rapid horn growth and were harvested at a younger age than rams with slower horn growth. Guided nonresident hunters did not harvest larger rams than residents, suggesting that few large rams were available. Resident hunter success declined in recent years. Despite an apparently stable population, successive cohorts produced a decreasing harvest of trophy rams. We suggest that unrestricted harvest based on a threshold horn size led to a decline in the availability of trophy rams. That decline is partly an inevitable consequence of selective hunting that removes larger rams. Although our analysis does not establish that evolution of smaller horns caused the observed decline in both horn size and harvest of trophy rams, we suggest that intensive trophy hunting may have artificially selected for a decrease in horn growth rate. © 2013 The Wildlife Society.

KEY WORDS artificial selection, bighorn sheep, horn size, sampling bias, time series, trophy hunting, ungulates.

Many studies have shown the ecological impacts of human activities, particularly through habitat loss and fragmentation, overexploitation, and introduction of exotics (Estes et al. 2011). Less attention has been paid to the possible evolutionary impacts of human activities, despite recent evidence that those activities can have substantial consequences on fitness and lead to evolutionary change (Allendorf and Hard 2009, Darimont et al. 2009). Human harvests may affect evolution in fish (Edeline et al. 2009, Hutchings 2009), mammals (Coltman 2008), and plants (Law and Salick 2005), sometimes reducing population growth (Swain et al. 2007). Trophy hunting, where males with large horns, antlers, or tusks are selectively removed, presents a particularly interesting case of possible artificial selection because in many species (but not all; see Mainguy et al. 2009, Rughetti and Festa-Bianchet 2010) harvest pressure and sexual selection have opposing effects on these sexually selected traits (Jachmann et al. 1995, Coltman et al. 2003, Garel et al. 2007, Mysterud 2011).

Long-term, individual-based monitoring of bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, revealed that rams with rapidly growing horns had reduced life expectancy and reproductive success compared to rams with slow-growing horns, because hunters selectively removed young, large-horned rams (Coltman et al. 2003). In that population, horn size declined substantially over 30 years partly through density dependence (Jorgenson et al. 1998) and partly through artificial selection (Coltman et al. 2003, Bonenfant et al. 2009). However, whether environmental changes and selective hunting affected ram horn phenotype over the entire province was unknown. The selective effect of the trophy hunt would increase with harvest intensity, yet harvest rates are difficult to calculate because no reliable data exist on the availability of harvestable rams. The number of licenses sold to Alberta residents is unlimited, and the harvest is only limited by the ability of hunters to find trophy rams. The provincial bighorn sheep population likely increased in the late 1970s and early 1980s, and has been stable or slightly increasing over the past 25 years (Jorgenson 2008). Hunter success rate should vary according to the availability of trophy rams.

Trophy hunts are by definition selective and may have an evolutionary effect if they target traits with inheritable components, as is the case for horn size in bighorn sheep (Coltman et al. 2005). Selective effects are likely to be

strengthened if hunters cannot harvest small-horned rams, and if young rams with rapidly growing horns become targets several years before their large horns improve their reproductive success (Coltman et al. 2002, 2003). The definition of trophy sheep prevalent in most of Alberta over the last 4 decades allows ram horns to reach the legal minimum of 4/5 curl at 4–6 years of age (Pelletier et al. 2012), yet large horns improve the reproductive success of rams beginning at 6–7 years of age (Coltman et al. 2002, Festa-Bianchet et al. 2004). Rams with rapidly growing horns therefore become vulnerable to hunting 1–3 years before they experience the fitness benefits of large horns.

Little is known about possible differences in age and size of trophy animals taken by resident versus nonresident hunters in North America. Nonresident hunters must engage the services of professional guides. They may harvest animals with larger horns, because guides generally have better logistic organization than resident hunters. In British Columbia, however, no difference was found in horn size of rams of the Rocky Mountain ecotype taken by resident and guided nonresident hunters, whereas nonresidents killed rams of the California ecotype with slightly smaller horns than those taken by residents (Hengeveld and Festa-Bianchet 2011). For roe deer (*Capreolus capreolus*) in Poland, nonresident hunters took larger-antlered males than residents, mostly because they hunted earlier and in areas known to produce deer with large antlers (Mysterud et al. 2006).

An analysis of sport-harvested bighorn rams in British Columbia revealed temporal changes consistent with hunter-induced selection for small horns (Hengeveld and Festa-Bianchet 2011), similar to results for European mouflon (*O. aries*) in France (Garel et al. 2007) and for Iberian wild goat (*Capra iberica*) and Barbary sheep (*Ammotragus lervia*) in Spain (Pérez et al. 2011). For Iberian wild goat, a decrease in horn size over 18 years was accompanied by an increase of about 4 years in the average age of harvested males, suggesting that males took longer to become what hunters considered a trophy. The average age of trophy-harvested Barbary sheep males, however, decreased by about 6 months over 9 years, possibly because high hunting pressure led to males being shot as soon as they approached trophy size (Pérez et al. 2011). In British Columbia, no age trend was found at harvest for bighorn sheep of the California ecotype over 28 years. The average age of harvested Rocky Mountain rams increased by about 0.7 years, yet their average horn length did not change (Hengeveld and Festa-Bianchet 2011). Together, temporal trends in age and horn size of harvested animals may provide information on age-specific horn growth, although when harvests are based upon a minimum degree of horn curl, declining trends would be underestimated by horn measurements of harvest animals (Pelletier et al. 2012). Analyses of long-term data from harvested trophy-hunted males, however, remain relatively rare even though this information is often collected by management agencies (Wishart 2012). We analyzed records of more than 7,000 trophy-harvested bighorn rams in Alberta over 37 years to test for temporal trends in age and horn size, and compare the size and age of rams harvested by

Alberta residents and by guided nonresident hunters. We sought to test the hypothesis that, because of high harvest pressure and a phenotypically defined minimum horn size, rams harvested in recent years would be older and have smaller horns than rams harvested a few decades ago.

METHODS

Hunting Regulations and Data Collection

Over the period of data collection (1974–2011), nearly all populations of bighorn sheep in Alberta outside protected areas were hunted under a 4/5 minimum-curl regulation. The season began in late August or early September and usually closed at the end of October. Any Alberta resident could purchase a license for trophy sheep and harvest 1 ram with at least 1 horn where a straight line drawn from the most anterior point of the base of the horn to the tip of the horn extended beyond the anterior edge of the eye when viewed in profile (picture in Pelletier et al. 2012). Rams fitting this definition are referred to as legal rams. The 4/5-curl definition of legal ram was adopted in 1968. A resident who harvested a ram could not buy a trophy sheep license the following year. In addition, about 80 licenses were available yearly to nonresidents, who must engage the services of a guide. Nonresidents were also limited to harvesting legal rams and could only hunt in specific areas, generally north of the Bow River, which flows between Banff and Calgary (Fig. 1). The hunting season for nonresidents opened
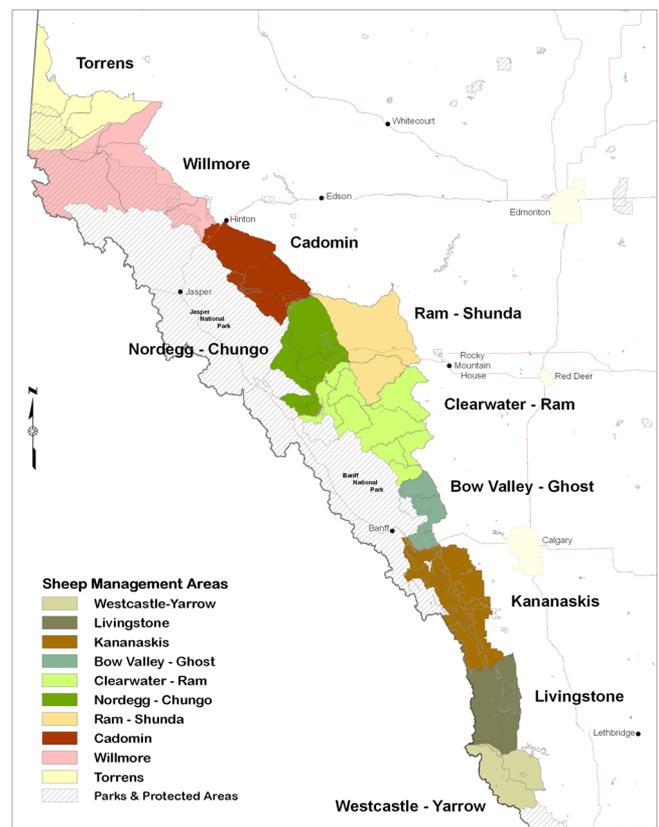
Figure 1. Sheep Management Areas (SMAs) in Alberta. Boundary lines inside each area refer to Wildlife Management Units.

approximately 1 week later and closed about 2 weeks earlier than the season for residents.

Hunters were required to submit the head of harvested rams for compulsory inspection and measurement. Alberta Fish and Wildlife personnel estimated the age of the ram based on horn annuli and measured total length along the outside curvature and base circumference of both horns. They also noted the Wildlife Management Unit (WMU) where the hunter harvested the ram and the hunter's residency status.

By definition, legal rams are not a random sample of the population, because they must have horns describing 4/5 of a curl. Both size and shape of the horns determine whether or not a ram can be legally harvested. A dataset of harvested individuals would underestimate a possible negative trend in horn size over time because small-horned rams cannot be harvested (Pelletier et al. 2012). For Dall's sheep (O. dalli) in the Yukon and bighorn sheep in British Columbia, horn growth rate is negatively correlated with harvest age; rams shot at 4–5 years of age have horn growth in their first few years of life about 30% greater than those shot at 10 years of age or older (Loehr et al. 2006, Hengeveld and Festa-Bianchet 2011). Unfortunately, horn increments were not measured in Alberta. The bias in the hunter-killed sample compared to the overall population likely decreases with ram age, because although only exceptionally well-developed rams can be legal at 4–5 years of age, most rams are legal by the time they reach 8 years (see Results Section). Some rams, however, never reach legal status. Accounting for these biases in the interpretation of harvest-derived data is essential.

To examine how horn length and ram age affected the probability of attaining legal status, we used data from 2 long-term studies in Alberta where legal status was assessed yearly on marked rams by experienced observers. Data on age and legality were available from Sheep River and Ram Mountain, whereas data on yearly horn length were only available from Ram Mountain (Jorgenson et al. 1998).

Data Analyses

The harvest dataset was first checked by Alberta Fish and Wildlife biologists to remove entries with missing horn measurements, ram age, or obvious errors, such as wrong Wildlife Management Unit or harvest outside the hunting season. We excluded illegally harvested rams (primarily sheep that did not meet the legal definition) from analyses. We also excluded rams taken by First Nations, as subsistence harvest is not restricted by horn size nor based on licensing requirements. That process removed 7% of entries, leaving about 7,100 rams of known age and horn size. To account for possible geographic variation in horn size, we considered 8 Sheep Management Areas (SMA; Fig. 1), delineated by Fish and Wildlife biologists based on genetic differences and local knowledge of barriers to movement (Alberta Fish and Wildlife, unpublished data). Each SMA consisted of several WMUs, which may vary in regulations such as season opening date, definition of legal ram, permitted weapons, and whether or not nonresidents were allowed to hunt. Generally, rams are larger in the southern than in the northern half of the province, with the exception of SMA Cadomin (Fig. 1), which also produces large rams. The registration database classifies hunters as Alberta residents or nonresidents. We restricted analyses of effects of hunter residency to WMUs where hunting by nonresidents was allowed, during times when both types of hunters could hunt. No areas are reserved for nonresident hunters. From 1996, the definition of legal ram was changed from 4/5 to full curl in 3 WMUs. We excluded from analyses rams harvested in those units after regulations were changed. We also excluded rams harvested during late season hunts based on a draw of a small number of permits that were instituted in a few WMUs in 2005 and later.

We used the monthly values of the Pacific Decadal Oscillation averaged from April to September (summer PDO) to assess the effects of environmental variability on horn growth (Loehr et al. 2010). Most horn growth occurs during the first 4 years of life (Jorgenson et al. 1998). Therefore, to select the time period to consider for PDO effects, we calculated mean PDO while harvested rams were in different ranges of age between birth and 4 years (0–4, 1–4, 0–3, 1–3, 0–2, 1–2, and 2–3). We then used the Akaike's Information Criterion (AIC) to evaluate which period best fit horn length and base circumference of rams. As both measurements are influenced by age at harvest (Hengeveld and Festa-Bianchet 2011), we compared a model including PDO with a model including only age at death (Table S1, available online at www.onlinelibrary.wiley.com). From this model selection, we retained the average PDO when rams were aged 1–4 for subsequent analyses.

We analyzed age at death, horn length, and base circumference using linear mixed effect models (Pinheiro and Bates 2000) including SMA as a random effect to account for both regional differences in horn size and changes in the distribution of the harvest over the years of the study. To calculate cohort-specific harvest, we summed harvested rams by year of birth. This analysis included only cohorts from 1970 to 2000, that would have been completely harvested over the period of monitoring. Rams born in 1970 would have been 4 years old at the start of the time series, those born in 2000 would have been 11 years old in 2011. Rams $\geq$12 years old made up only 2.4% of the harvest; therefore, our analyses are unlikely to be biased by a few very old rams from the 1999–2000 cohorts that may have been harvested after 2011. All analyses were implemented in R version 2.15 (R Development Core Team 2012).

RESULTS

Between 1974 and 2011, harvested rams showed a slight and nonlinear decrease in horn length, smaller base circumference, and an increase in age (Table 1). The temporal trend in horn length was quadratic, reflecting a slight increase in 1974–1985 and a decrease from about 1986 (Fig. 2A), while the decrease in base circumference appeared linear (Fig. 2B). For the entire dataset, horn base circumference and length were weakly correlated ($r = 0.35$; $P < 0.0001$). Between 1980 and 2010, horn length for 6-year-old rams decreased by approximately 3 cm, or 3.5%. Average age increased from

Table 1. Temporal trends in horn length (cm), horn base circumference (cm), and age at death (years) for bighorn rams shot in Alberta, 1974–2011. Estimates are from linear mixed effect models accounting for Sheep Management Area as a random effect. To assess the effects of environmental variability, we calculated the average summer Pacific Decadal Oscillation (PDO) while rams were aged between 1 and 4 years. Sample sizes differ as not all measurements were available for all rams.

Variables	Coeff.	SE	P	N
Horn length				7,037
Age	4.501	0.220	<0.001	
Age^2	−0.149	0.014	<0.001	
Harvest year	21.802	3.934	<0.001	
Harvest year^2	−0.005	0.001	<0.001	
Horn base				7,030
Age	−0.047	0.013	<0.001	
Harvest year	−0.007	0.002	<0.001	
PDO	0.228	0.039	<0.001	
Age				7,107
Harvest year	8.860	1.208	<0.001	
Harvest year^2	−0.002	0.0003	<0.001	
PDO	−0.559	0.053	<0.001	

6.8 years to 7.5 years (Fig. 3A; $\beta = 0.017 \pm 0.003$, adjusted $R^2 = 0.49$, $P < 0.001$), mostly because of a decline in the proportion of males aged 4 or 5 years, from about 25% in the 1980s to less than 10% in recent years (Fig. 3B; $\beta = -0.0004 \pm 0.001$, adjusted $R^2 = 0.48$, $P < 0.001$). The database contained only 6 3-year-olds (less than 0.05% of the total). The summer PDO averaged over years 1–4 had a positive effect on horn base circumference, a strong negative effect on age at harvest, and no effect on horn length (Table 1). Although age at harvest had the expected positive and quadratic effect on horn length, it had a surprising negative effect on base circumference (Table 1; Fig. S1). Repeated measurements of live rams suggest that both horn length and base increase non-linearly with age, growing at a slower rate in older rams (Jorgenson et al. 1998).

For residents, the number of licenses sold and total harvest increased from 1974 to 1984 (Fig. 4). In 1987, the fee doubled from $20 to $40 and license sales declined. Harvest

of rams by resident hunters did not vary much between 1980 and 1992 and then declined (Fig. 4). Harvest increased with the number of licenses sold, but success rate declined (Table 2). Success rate averaged 7.2% and ranged yearly from 5.2% to 11.4%. Both harvest and success rate, however, declined over the last 15–20 years (Table 2). For example, for every 2,000 licenses sold in 1974, 124 rams would have been shot with a success rate of 6.8% (Table 2). For every 2,000 licenses sold in 2010, harvest would have been 107 rams (a 14% decline), for a success rate of 5.5%. Success of nonresidents averaged 48% (range 26–65%) and showed no temporal trend (data not shown). Most (mean 79%, yearly range 68–89%) of the harvest was by residents.

The number of rams harvested from each cohort first increased for cohorts born through the 1970s, declined for cohorts born in the 1980s, and remained low for cohorts born in the 1990s ($\beta = 634 \pm 295$, $P = 0.040$, $\beta^2 = -0.160 \pm 0.074$, $P = 0.039$, adjusted $R^2 = 0.27$). Rams harvested increased slightly for the most recent cohorts (Fig. 5). Assuming a constant provincial population of 6,000 bighorn sheep outside National Parks (Jorgenson 2008), production of harvested rams dropped by 35%, from 1 ram shot/year per 24 sheep for cohorts born in 1975–1982 to 1 ram per 37 sheep for cohorts born after 1990.

Residents harvested rams with larger bases and longer horns, but slightly younger than those taken by nonresidents (Table 3). As reported for the overall analysis (Table 1), the average summer PDO when rams were aged 1–4 years was associated with decreasing age at harvest and increasing base circumference.

The probability to fit the definition of legal ram increased with both horn length and base circumference but was most closely associated with length (Fig. 6). Horn length and circumference explained respectively 42% and 19% of the deviance (horn length: 0.25 ± 0.03, $Z = 7.593$, $P < 0.001$, circumference: 0.41 ± 0.07, $Z = 6.151$, $P < 0.001$). At Ram Mountain, a third of rams ≥8 years old were not legal, whereas only 5% of Sheep River 8-year-old rams were not
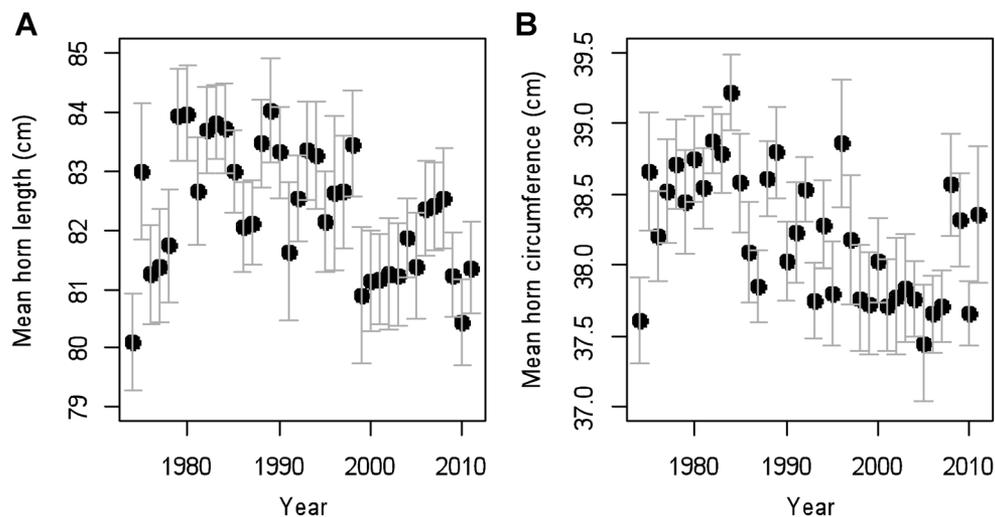
Figure 2. Mean (±SE) horn length (A) and horn base circumference (B) of 6-year-old bighorn sheep rams harvested in Alberta between 1974 and 2011. Results were similar for other age classes, 6 years was the modal age at harvest.
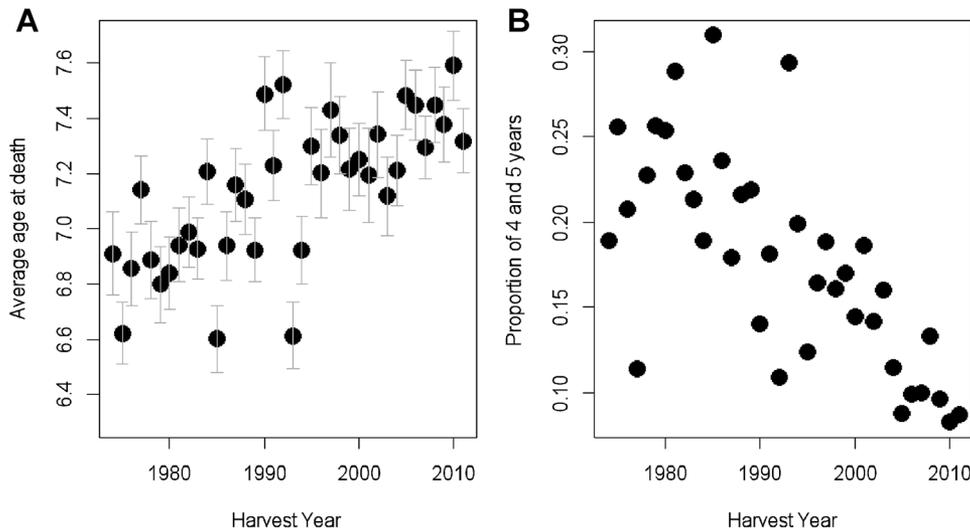
Figure 3. (A) Average age (±SE) of bighorn rams harvested in Alberta, 1974–2011. (B) Proportion of rams (±SE) aged 4 or 5 years in the harvest each year.

legal (Fig. S2). These trends are biased because once rams reach legal status, some are harvested and exit the sample. For that reason, we do not provide a statistical analysis. Given that rams with only exceptionally developed horns could be legal at a young age, variability in horn length of harvested rams should increase with increasing age at harvest. As expected, coefficients of variation increased with age for horn length, but we found no clear effect of age on base circumference (Fig. S3).

DISCUSSION

Our results are consistent with the hypothesis that selective hunting contributed to a decrease in both horn size and availability of trophy rams (Coltman et al. 2003, Bonenfant et al. 2009, Festa-Bianchet and Lee 2009). The size and number of trophy rams harvested increased during the late 1970s and early 1980s, then declined. The initial increase in horn size between 1974 and 1980 was partly explained by an increase in PDO, which had very low values in 1970–1975.
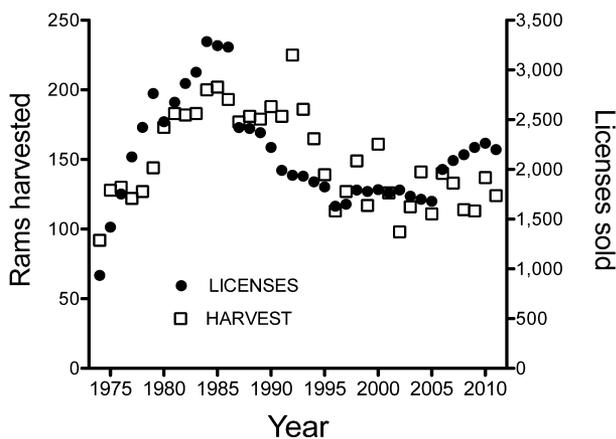
Figure 4. Number of trophy sheep licenses sold and harvest of bighorn rams in Alberta, 1974–2011, resident hunters only.

Better access to previously remote areas because the road network expanded, may also have allowed hunters to harvest some large rams. Resident hunter success rate also declined over recent years. Although the entire provincial bighorn sheep population was not regularly censused, partial censuses and expert opinion by wildlife biologists suggest that it likely increased between 1974 and 1985, possibly accounting for the initial increase in harvest. The provincial bighorn population has been stable over the last 25 years (Jorgenson 2008), but trophy ram harvest declined over that period. Multiple lines of evidence from our analyses suggest that the decline in harvest is caused by a decrease in the number of rams reaching legal status, as a result of a decline in horn growth rate.

The decrease over time in the proportion of harvested rams aged 4 or 5 years implies that horn growth slowed, so that rams take longer to become legal. An increase in age over time was reported for trophy-harvested Iberian wild goats (Pérez et al. 2011) in Spain and Rocky Mountain bighorn rams in British Columbia (Hengeveld and Festa-Bianchet 2011). In contrast, reduced postwar harvest of red deer (*Cervus elaphus*) in Hungary led to an increase in antler length and number of tines of the very largest harvested stags (Rivrud et al. 2013). Because the antlers of only the largest stags were measured, however, it is unclear

Table 2. Yearly harvest of bighorn rams and success rate by Alberta residents as a function of the number of permits sold and year, 1974 to 2011.

Variables	Coeff.	SE	P
Harvest			
Licenses sold	0.032	0.007	<0.001
Harvest year	0.059	0.012	<0.001
Harvest year^2	−0.147	0.032	<0.001
Success rate			
Licenses sold	−0.002	0.0003	<0.001
Harvest year	−24.90	6.439	<0.001
Harvest year^2	−0.006	0.002	<0.001
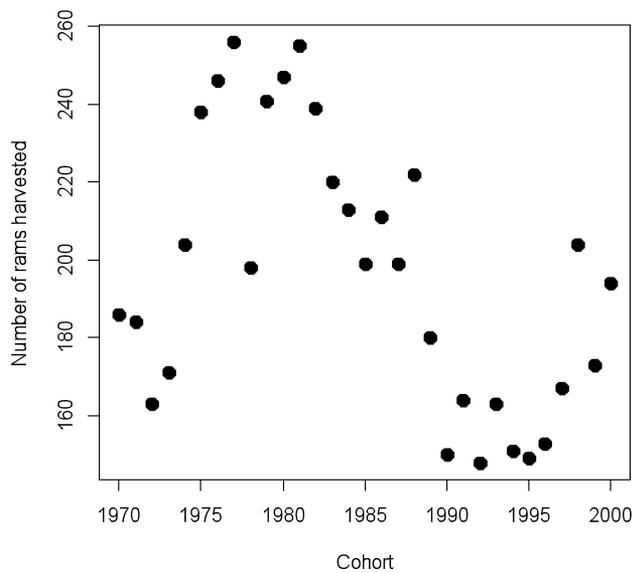
Figure 5. The number of rams harvested in Alberta in 1975–2011 from cohorts born from 1970 to 2000.

how different harvest strategies affected antler size at the population level (Pelletier et al. 2012).

In Alberta, the alternative that hunters stopped harvesting legal young rams seems unlikely given the very low success rate. However, data on the proportion of hunters that choose not to harvest a legal ram that they may encounter would be informative. Slower horn growth rate also may result from high population density, as reported at Ram Mountain in the 1980s and early 1990s (Jorgenson et al. 1998). That explanation appears unlikely, because the effect on horn growth at Ram Mountain required a doubling of population

Table 3. Effect of hunter residency on age, horn base circumference, and horn length of a subset of bighorn rams harvested in Alberta, 1974 to 2011. Estimates are from linear mixed effects models including as random effects the 5 Sheep Management Areas where nonresident hunters could hunt. Analyses are restricted to 4,392 rams taken when both groups of hunters were allowed to hunt. To assess the effects of environmental variability, we calculated the average summer Pacific Decadal Oscillation (PDO) while rams were aged between 1 and 4 years.

Variables	Coeff.	SE	P
Age			
Harvest year	9.262	1.583	<0.001
Harvest year^2	−0.002	0.0004	<0.001
PDO	−0.550	0.069	<0.001
Hunter origin[a]	−0.163	0.059	0.040
Horn base			
Age	−0.054	0.016	<0.001
Harvest year	3.657	1.714	0.033
Harvest year^2	−0.001	0.0004	0.033
PDO	0.166	0.074	0.025
Hunter origin[a]	0.308	0.063	<0.001
Horn length			
Age	4.018	0.290	<0.001
Age^2	−0.120	0.018	<0.001
Harvest year	20.541	3.518	<0.001
Harvest year^2	−0.005	0.001	<0.001
Hunter origin[a]	1.305	0.190	<0.001

[a] The category of reference is nonresidents.

size, whereas in general the provincial population appears stable. Changes in sex ratio through intense removals of mature males may also affect the level of male–male competition, reducing sexual selection (Mysterud et al. 2008), but we have no reliable data on temporal trends in sex ratio for the provincial population.

An increase in age at which rams become legal would reduce the availability of legal rams, because more would be lost to natural mortality. Monitoring of marked rams in 2 populations in Alberta suggests that 19–27% of 4-year-olds would die of natural causes before reaching age 6 (Loison et al. 1999). After accounting for age, our analyses also suggest a decline in horn length and base circumference over the last 2 decades. Compared to 20–30 years ago, a greater proportion of rams may possibly now die without their horns ever attaining legal status; however, we currently cannot test this hypothesis. We underscore that rams that do not reach legal status cannot enter our sample, because harvesting them is illegal. We previously showed (Pelletier et al. 2012) that horn measurements of harvested rams would underestimate a decrease in horn size by 10–15%. Therefore, the actual decrease in horn size of bighorn rams in Alberta in recent years was likely greater than suggested by our results.

The negative temporal trends in horn size remained after accounting for age and summer PDO; the latter had a positive effect on horn base circumference of young rams. We were puzzled to find no effect of PDO on horn length, considering that a positive effect was reported for Dall's sheep in the Yukon (Loehr et al. 2010). Because the definition of legal rams is affected mostly by horn length, and a much greater proportion of asymptotic size is reached by age 4–5 for circumference than for length (Jorgenson et al. 1998), in the harvest sample the effects of PDO are more easily detectable on base circumference than on horn length. The effects of PDO are likely not detected on horn length because more rams from cohorts that experienced favorable environmental conditions become legal at an early age (Table 1). Rams that develop rapidly are harvested at a younger age (Loehr et al. 2006, Hengeveld and Festa-Bianchet 2011). At Ram Mountain, rams born at low population density had rapid horn growth and many were harvested when aged 4 or 5 years (Jorgenson et al. 1998). Rams from cohorts that experienced favorable environmental conditions (high average PDO) during their first 4 years were harvested at a younger age than those that developed more slowly. Rams from cohorts experiencing rapid early growth that survive to be harvested at ages 6 or older would be smaller than the average for their cohort and would appear to have average horn length for these ages. Harvest-induced survival bias may be weaker in cohorts that developed under poor environmental conditions, because few rams from those cohorts are legal at 4 and 5 years of age. Regardless of environmental conditions during early development, only rams with exceptionally large horns are legal at 4 or 5 years (Fig. S2). That contention is supported by the positive relationship between coefficient of variation in horn length and age at harvest (Fig. S3); among young rams (aged 4–6 years), those with average-sized horns cannot enter the
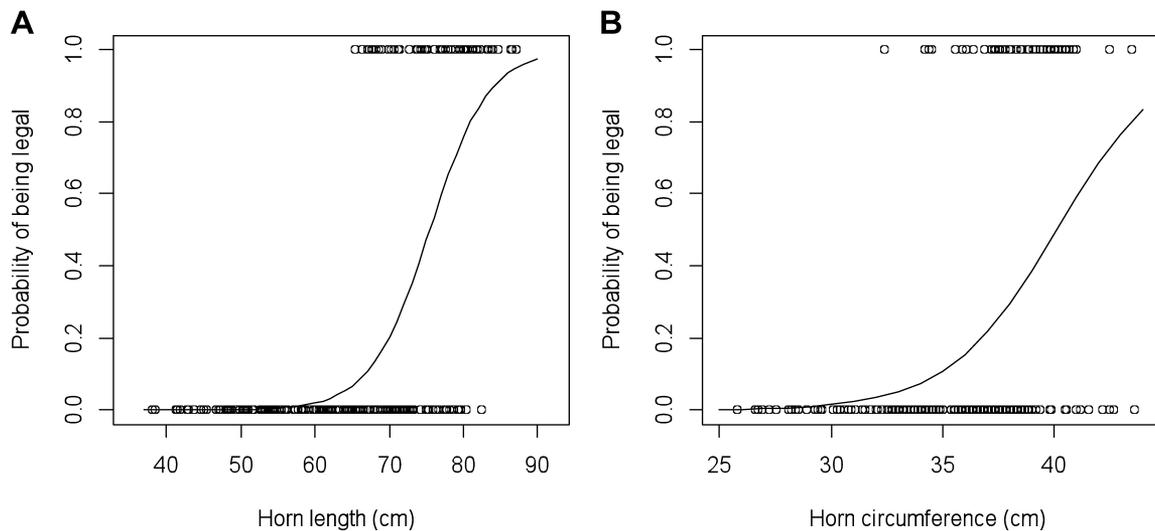
Figure 6. Probability that a bighorn ram will be legal as a function of (A) horn length and (B) horn base circumference. Data are from 296 marked rams at Ram Mountain, Alberta (1983–2006).

harvested sample. For example, the average horn length of harvested 4-year-olds in Alberta was 16% greater than that of all 5-year-olds live-captured at Ram Mountain. With increasing age, more opportunities occur for rams with different horn lengths to reach legal status, and the coefficient of variation increases. The effect of age on horn length in harvested rams should be weaker than in the overall population; young rams would be a positively biased sample, and old rams a negatively biased sample as longevity declines with horn size because of the trophy hunt (Bonenfant et al. 2009).

In British Columbia, bighorn rams with rapid horn growth early in life were harvested at younger ages than those with slower horn growth (Hengeveld and Festa-Bianchet 2011). Hunters selectively removed the rams with the largest horns before they could reach an age at which large horns increase mating success (Coltman et al. 2002). Similar results from Dall's sheep in the Yukon support this contention and suggest that hunter selection directly opposes sexual selection (Loehr et al. 2006). Selective harvest may have led to the artificial evolution documented in the isolated population at Ram Mountain (Coltman et al. 2003). Because annuli measurements were not available for rams harvested in Alberta, we could not compare early horn growth with age at harvest. The weak but negative relationship between harvest age and horn base circumference, however, suggests that a similar age-related selection may occur in Alberta; rams with rapidly growing horns are harvested at a young age, whereas those with smaller horns survive longer. Horn base circumference normally increases through life (Jorgenson et al. 1998).

Unexpectedly, nonresident hunters harvested rams with horns slightly smaller than those harvested by residents. Nonresident hunters employ guides and typically have access to more remote areas. We suggest that they did not take larger-horned rams than those shot by residents because few large rams are available. Data on the proportion of legal rams that survive the hunting season would be very informative but are unavailable. The positive relationship between licenses sold and total harvest by residents suggests that some legal rams survive the hunting season, otherwise the relationship between number of licenses and harvest would reach a plateau. On the other hand, the negative effect of number of licenses on success rate implies that hunters compete for a limited pool of legal rams. More importantly, once the number of licenses was accounted for, resident success rate declined in recent years, suggesting a decrease in the availability of legal rams.

A recent analysis of the Boone & Crockett records revealed that the size of bighorn sheep horns submitted in recent decades showed a slight increase (Monteith et al. 2013). Submission to the Boone & Crockett book, however, is voluntary and listing requires a minimum score. Rams submitted for listing come from multiple jurisdictions with different harvesting regimes and hunting pressure. Only exceptionally large horns are listed, and ram age is not included. Hunter-harvested rams overall provide a biased estimation of temporal trends in horn size (Pelletier et al. 2012), and the Boone & Crockett records are even more biased. Their relevance to our results or to any actual trends in horn or antler size of different species is unknown. For example, our analysis of 7,100 harvested rams reveals a temporal decline in horn size in bighorn rams in Alberta, yet 1 ram harvested in a previously unhunted area in central Alberta in 2000 had the highest score ever recorded for a Rocky Mountain bighorn sheep.

The relationships between horn size and legal status are worthy of additional investigation because selective hunting may affect the evolution of both horn size and shape (Festa-Bianchet and Lee 2009). Although length is a major determinant of legal status, differences in shape may also affect it, as suggested for European mouflon (Garel et al. 2007) and by the wide overlap of legal and not legal rams with horns of 66–80 cm (Fig. 6A). Future research

should assess whether horn length varied according to the age at which a ram first became legal, because as horns grow, they may change in shape as well as in size.

Cohorts born in the late 1970s generally led to greater ram harvests than more recent cohorts, and many of the rams from earlier cohorts were harvested at young ages. Harvest biases affect cohort analyses as well; rapid horn growth will lead to more harvested rams because more rams will become legal at a young age, and be shot before they are exposed to much natural mortality. Differences in horn growth among cohorts will also bias the apparent relationship between age and horn size because more large rams will be shot early in life from cohorts with rapid growth. Data on horn size for older rams may therefore originate mostly from slow-growing cohorts.

The idea that killing large-horned rams may favor small-horned rams remains controversial (Loehr et al. 2006). In some ungulates, relationships between horn or antler size, male age, and reproductive success are not as strong as in wild sheep, so that the evolutionary effects of selective removals of large-horned males may be weak (Rughetti and Festa-Bianchet 2010, Rivrud et al. 2013). Some analyses in Coltman et al. (2003) may have overestimated the genetic component of the temporal decline in horn size (Postma 2006). We attempted to control for environmental conditions during early development by using summer PDO. Our results suggest that favorable environmental conditions during the first 4 years of life lead to a decrease in the age at which rams are harvested, possibly increasing the selective effect of the trophy hunt. To properly manage bighorn sheep, we must distinguish between selection and evolution. Although our analysis does not establish that evolution of smaller horns is responsible for the observed decline in both horn size and harvest of trophy rams in Alberta, it implicates artificial selection as 1 cause of those declines.

MANAGEMENT IMPLICATIONS

Unlimited availability of resident licenses, combined with a legal minimum horn curl definition to limit harvest may or may not have evolutionary consequences, but inevitably leads to selection; rams surviving the hunt on average have smaller horns than the pre-hunt population. Rams typically can become legal at any age after 4 years, and horn size increases with age. Therefore, a heavily hunted population with low escapement will have fewer and smaller rams than one that is lightly hunted. The rut starts in late November, so only rams that survive the hunting season can breed. The evolutionary effect of selective hunting would be correlated with harvest pressure on large-horned rams, and may be partly countered by post-hunt immigration from refuge areas (Tenhumberg et al. 2004). The minimum-curl regulation with unrestricted entry allows any Alberta residents to hunt bighorn sheep, and assumes that escapement of adult males will avoid any impact on population dynamics. Our analysis suggests that this management strategy reduces the availability of trophy rams and may have an undesirable genetic impact. Adaptive management would involve a reduction in ram harvests, in line with bighorn management in other jurisdictions (Festa-

Bianchet and Lee 2009). Our work underlines the usefulness of long-term records of age and horn size of harvested bovids, which would be improved by measuring horn increments in addition to length and circumference. Even when harvested animals are a biased sample, once that bias is taken into account, long-term monitoring allows the detection of trends in age and horn size that are of interest to managers.

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