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Research Article

Harvest Regulations and Artificial Selection on Horn Size in Male Bighorn Sheep

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ABSTRACT Wild sheep in North America are highly prized by hunters and most harvest regulations restrict legal harvest to males with a specified minimum horn curl. Because reproductive success is skewed toward larger males that are socially dominant, these regulations may select against high-quality, fast-growing males. To evaluate potential selective effects of alternative management strategies, we analyzed horn increment measures of males harvested over 28 yr (1975–2003) in 2 bighorn sheep (*Ovis canadensis*) ecotypes in British Columbia, Canada. Using mixed-effect models we examined variation in hunter selection for horn size, early horn growth, and male age under different harvest regulations (Full Curl, Three Quarter Curl, Any Ram). Under all regulations, males with the greatest early horn growth were harvested at the youngest ages, before the age at which large horns influence reproductive success. Early growth decreased with harvest age and until ≥7 yr of age it was greatest in males harvested under Full Curl regulation. Permit type (General vs. Limited Entry Hunt) and hunter origin (British Columbia Resident vs. Non-Resident) had little effect on horn size of harvested males. Full Curl regulations increased the average age of harvested males by <1 yr relative to Three-Quarter Curl regulations. Age-specific horn measures in the California ecotype harvested under Three-Quarter Curl regulations declined over time but we observed no temporal declines in the Rocky Mountain ecotype, primarily harvested under Full Curl regulations. Management strategies that protect some males with greater early horn growth or provide harvest refuges to maintain genetic diversity are likely to reduce potential for negative effects of artificial selection.

KEY WORDS artificial selection, bighorn sheep, British Columbia, harvest regulations, horn growth, management strategies, *Ovis canadensis*, trophy hunting.

Heritability of fitness-related traits presents a conundrum for management of species subject to selective harvest. If heritable traits positively correlated with fitness also are correlated with harvest probability, harvest can become an artificial selection on morphology and on life histories, with potential consequences for population productivity, genetic diversity, and persistence (Festa-Bianchet 2003, Fenberg and Roy 2008). This phenomenon is well documented in fish stocks that have been over-fished and begin reproducing at a younger age and smaller size (Jennings et al. 1998, Ernande et al. 2004, Olsen et al. 2004, Swain et al. 2007). In polygynous ungulates where mate choice and intrasexual competition are influenced by secondary sexual characteristics, large horns and antlers can be a key factor in reproductive success (Coltman et al. 2002, Preston et al. 2003). The size of such traits is thought to be correlated with individual quality, with larger individuals typically having greater fitness (Fitzsimmons et al. 1995, Moller and Alatalo 1999, Kruuk et al. 2002). Harvest regulations targeting large phenotypes may remove high-quality individuals and favor smaller or slower-growing individuals (Jachmann et al. 1995, Coltman et al. 2003).

Bighorn sheep (*Ovis canadensis*) management is typically focused on harvest of males with horns that meet a minimum degree of curl (Hebert and Evans 1991). Under some regulations, a male with rapidly growing horns can be legally harvested at 3 yr or 4 yr of age (Festa-Bianchet 1989, Jorgenson et al. 1993). Conversely, males with small horns may never become legal for harvest (Jorgenson et al. 1998). In bighorn males, body mass and horn size are heritable fitness-related traits positively correlated with social rank (Coltman et al. 2005, Pelletier and Festa-Bianchet 2006). Whereas a few top-ranked older males use tending tactics to defend and mate with many females annually, the success of subordinate males using alternate mating tactics is not correlated with social rank or horn size (Hogg and Forbes 1997, Coltman et al. 2002). Subordinates may collectively sire 40–50% of lambs in a given year but individual success of subordinates is low and many do not mate at all over a rut (Hogg and Forbes 1997, Coltman et al. 2002). In a herd of 100–120 sheep at Ram Mountain, Alberta, Canada, the most dominant male sired over a third of the lambs born annually and one male sired a quarter of all lambs born over a 6-yr period (Coltman et al. 2002). Large horn size also is genetically correlated with high offspring birth weights and survival (Coltman et al. 2005). A male with rapidly growing horns and the genetic potential to achieve high social status may however become legal to harvest at 4 yr of age and could experience negative selection through trophy hunting several years before its large horns will facilitate high mating success (Festa-Bianchet et al. 2006).

High trophy hunting pressure was linked to declines in breeding values (a measure of expected effects of genes passed on to offspring) of both male body mass and horn length over 30 yr in the Ram Mountain population in Alberta (Coltman et al. 2003). Despite controversy over their importance to sustainable harvest strategies in other jurisdictions (Festa-Bianchet and Lee 2009), these results highlight a pragmatic question of relevance to conservation: which management strategies are most effective in reducing

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the risk of artificial evolutionary changes in male phenotype and fitness?

To assess potential selective effects on horn development under a variety of regulations, we examined whether early horn growth, horn length, and age of harvested males varied with harvest regulation. In British Columbia, Canada, bighorn sheep have primarily been hunted under Full Curl minimum, Three-Quarter Curl minimum, and Any Male regulations. Availability of long-term data on horn growth measures from compulsory inspection of harvested bighorns provided an opportunity to evaluate possible phenotypic responses to artificial selection across multiple populations of 2 bighorn ecotypes, managed under varied harvest regulations. Our objectives were to estimate variation in hunter selection for male horn size, early horn growth, and harvest age according to regulations. We also evaluated the influence of hunter origin (British Columbia Resident vs. Non-Resident), and permit restrictions through a quota system, on horn size and harvest age. We examined temporal trends in horn size, horn growth, and age of harvested males for evidence of long-term phenotypic responses to each hunting regulation.

STUDY AREA

We used horn growth measures recorded during compulsory inspection of harvested bighorns in British Columbia, 1975–2003. Our sample included California bighorn sheep (*O. canadensis californiana*, hereafter CBS) in the southern interior, and Rocky Mountain bighorn sheep (*O. canadensis canadensis*, RMBS) on the western slopes of the Rocky Mountains (Shackleton 1999). Although these 2 groups may be allopatric ecotypes of *O. canadensis canadensis* (Wehausen and Ramey 2000), they were managed separately. Native populations occupied geographically distinct ranges and differed in horn size and in age-specific horn growth patterns (Shackleton 1999; Demarchi et al. 2000*a*,*b*).

The number of CBS in British Columbia was estimated at 3,600 in 1998, an increase from 1,185 in 1960 but a decline from nearly 4,700 in 1990 (Demarchi et al. 2000*a*, Ministry of Water Land and Air Protection 2004). California bighorns existed in populations of 5–470 individuals distributed among 5 metapopulations, 2 of which include small isolated populations in northern Washington, USA. British Columbia's RMBS were part of a metapopulation of approximately 18,000 bighorn sheep along the Rocky Mountains of British Columbia, Alberta, and northern Montana (Demarchi et al. 2000*b*). The estimated total in British Columbia was 3,000 in 1996, the highest count in recent history (Ministry of Water Land and Air Protection 2004). Both ecotypes have declined in numbers since the mid-1990s (Ministry of Water Land and Air Protection 2004).

METHODS

Bighorn sheep were harvested in 23 Wildlife Management Units (WMUs; CBS: $n = 12$; RMBS: $n = 12$; one WMU includes both ecotypes). Male harvest regulations were based on minimum horn curl. In different WMUs and at different times, seasons were opened for Any Male >1 yr old; Three-Quarter Curl minimum; Full Curl minimum; and Mature male. In 1975 "Mature" defined males whose horns reached ≥7/8th curl; more recently this definition included males with ≥1 horn tip extending upwards beyond the forehead-nose bridge when viewed from the side. After 1975, Mature male harvest regulations were only applied in part of one WMU during 1999–2002. Therefore, we pooled males harvested under a Mature regulation with Full Curl males. Harvests were managed through 2 types of permit. General permits limited harvest by each hunter to 1 male bighorn sheep but the total number of permits sold to British Columbia Residents was not restricted. Limited Entry Hunt (LEH) permits involved a quota specific to a WMU or subsection of a WMU and were allocated by lottery. Non-Residents of British Columbia were required to engage a licensed guide to hunt bighorn sheep. Guide-outfitters were allocated annual permits under a quota system specific to each tenure area in WMUs open to sheep hunting by Non-Residents. Hunting seasons usually started in August and ended in October. There were spatial and temporal differences in both the definition of legal male and whether an unlimited number of permits were available for a given area; details are presented in Hengeveld (2008).

Heads of harvested males have been subject to compulsory inspection since 1975. Measurements recorded during most inspections included horn base circumference, cumulative annual growth increments (length from the tip of the horn to each successive annulus, up to 12 yr of age), total horn length, and age at death estimated by counting horn annuli (Geist 1966). Data included the WMU where the male was harvested, permit type (General or LEH), and hunter origin (British Columbia Resident or Non-Resident). We calculated annual horn growth increments (the distance between successive growth annuli) from the cumulative horn growth measures. When both horns were measured, we based our analyses on the horn that had the most complete measurement data, the longest total length, or if all else was equal, the longest first increment, suggesting less horn tip wear. We pooled males harvested at ≥10 yr into one 10+ age class due to small sample sizes (45 males ≥11 yr for each ecotype).

A common error in measurements, particularly for older males with heavily worn horn tips, is to record the sum of growth increments 1 (lamb growth) and 2 (yearling growth) as a single first increment. This error produces a large first-year growth measure and a smaller than average measure for subsequent increments. Because we could not know which large first increment measures were erroneous, we included all complete records in the analyses ($n = 3{,}402$ males). To control for possibly erroneous first-year growth measures, we repeated horn growth analyses excluding the largest 5% of first increment measures (CBS: >185 mm; RMBS: >250 mm).

We analyzed age-specific horn growth patterns for each ecotype using data from hunting and non-hunting mortality. We compared age-specific annual horn growth increments, base circumference, and total length between ecotypes using independent sample *t*-tests and one-way analyses of variance. We used linear regression and Pearson correlations to test for compensatory growth by males with less horn growth early in life.

We used linear mixed-effect modeling to assess variation in total horn length, early horn growth, and harvest age as a function of harvest regulation (Any Male, Three-Quarter Curl, Full Curl). Total horn length analyses used data for males harvested at $\geq$3 yr of age, as only 4 males were harvested as 2-yr-olds under minimum horn curl regulations. We defined early horn growth as the cumulative growth during the second and third year of life. Measures of the first horn increment are biased because breakage of the horn tips likely increases with age (Bunnell 1978). We did not consider horn increments grown after the third year because males with large early horn growth can attain Three-Quarter Curl at age 3 yr and Full Curl at age 4 yr. Because males with greater early growth are at risk of harvest, horn increments for harvested males aged $\geq$4 yr may be biased towards males with less early growth.

We assessed the effect of harvest regulation on the 3 response variables using all legal hunter-harvested CBS males with horn measurement and harvest age data from WMUs that had >30 male harvest records. No comparison among regulations was possible for RMBS because nearly all animals (98.7%) were taken under Full Curl regulations. We compared the relationship between horn growth and harvest age among regulations for CBS, and between ecotypes for males harvested under Full Curl regulation. We also used linear mixed-effect modeling to assess variation in total horn length, early horn growth, and harvest age as a function of permit type (General, LEH), hunter origin (British Columbia Resident, Non-Resident), and harvest year (1975–2003). These analyses included only CBS males legally harvested under Three-Quarter Curl regulations and RMBS males legally harvested under Full Curl regulations. For analyses of temporal trends we pooled males into 3–5-yr-old and $\geq$6-yr-old age groups due to small sample sizes for some harvest ages and years.

We treated WMUs as independent populations and included them as a random effect in all models to account for spatial variation in horn growth. To control for year effects, we included cohort (birth yr) as a random effect in horn length and growth models (Beckerman et al. 2003, Postma 2006). We did not include cohort in harvest age models because the last few years of data were biased to young harvest ages. We also excluded cohort from temporal trend models because of autocorrelation with harvest age and year. We tested all models using R (Version 2.7.2, www.R-project.org, accessed 23 Sep 2008), with the LME4 mixed-effects package (Version 0.999375-28, www.lme4.r-forge.r-project.org, accessed 9 Feb 2009) to estimate regression coefficients, confidence intervals for estimated parameters, and overall model deviance. We selected the most parsimonious model by retaining significant terms identified through a backwards stepwise procedure that assessed random effects first and then fixed effects. We assessed significance of random factors with a chi-square test to evaluate the change in restricted maximum likelihood deviance between the full model and a null model where we removed the random factor (Hox 2002, Steele and Hogg 2003). The difference in deviance for 2 nested models has a chi-square distribution with degrees of freedom equal to the difference in the number of parameters estimated. Random effects were significant unless otherwise noted. We assessed significance of fixed terms by calculating simultaneous 95% highest posterior density (HPD) confidence intervals for estimated regression coefficients using a Markov chain Monte Carlo (MCMC) sampling method with 10,000 repetitions. The parameters were significant at $\alpha = 0.05$ if the confidence interval for the estimate did not include zero. We obtained *P* values by creating a cumulative distribution of the MCMC sampling estimates and testing probability that estimated regression coefficients differed from zero (Faraway 2006).

RESULTS

We analyzed 4,416 records of males (CBS: $n = 2{,}628$; RMBS: $n = 1{,}788$) from 1975 to 2003 (2003 data were incomplete), including legal hunter harvest (CBS: $n = 2{,}029$; RMBS: $n = 1{,}349$), illegal harvest, and opportunistic collection of horns from sheep found dead or, in rare cases, killed for animal control purposes. We excluded from analyses all records that were duplicated ($n = 16$); were missing horn measurements ($n = 91$), male age ($n = 152$), or harvest location ($n = 38$); had an estimated age that did not correspond with the number of annuli measures ($n = 690$); or had obvious errors such as biologically impossible growth increment values ($n = 27$). Data included 3 CBS males harvested as 2-yr-olds under Three-Quarter Curl regulations. Full Curl harvest included 1 2-yr-old RMBS, 18 3-yr-old RMBS, and 7 3-yr-old CBS. To reach legal horn curl definition at 2 yr or 3 yr of age requires exceptional growth. Although we suspect that these records were erroneous, we had no a priori reason to exclude them from analyses. Of the RMBS males harvested at $\leq$4 yr of age, 70% were harvested from one WMU with greater than average horn growth. These very young males accounted for 0.8% of our total sample. In 1975–2003, 74.6% of harvested CBS males were harvested under Three-Quarter Curl regulation (17.5% as LEH permits); 98.7% of RMBS were harvested under Full Curl regulation (3.8% as LEH permits).

Both ecotypes had similar age-specific horn growth patterns, with the longest increments in the second (yearling) growth year (Fig. 1A). By age 4, male horns averaged >75% (CBS: 78.9%; RMBS: 76.3%) of mean horn length of males aged $\geq$12 yr (CBS: $\bar{x} = 881$ mm, SD = 69.9, $n = 16$; RMBS: $\bar{x} = 944$ mm, SD = 101.9, $n = 10$). Horn increment length differed between ecotypes at all ages ($P \leq 0.001$); CBS had longer first (+11 mm, SE = 2.8) and second (+18 mm, SE = 2.7) increments relative to RMBS whereas the reverse was true for ages 3–10 yr. California bighorns had smaller horn bases than RMBS after age 2 yr (Fig. 1B). Males with greater early horn growth also had greater horn growth in later years; for ages 2–10 yr successive growth increments were positively correlated

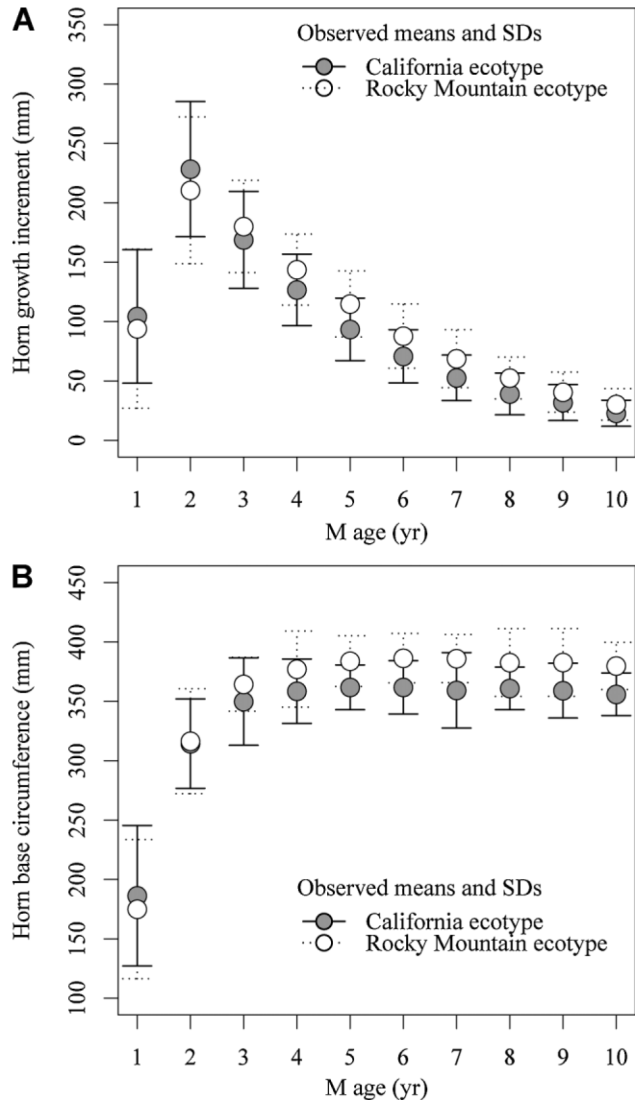

Figure 1. Age-specific [A] annual horn growth increments (mm) and [B] horn base circumference (mm) of California ($n = 1{,}817$) and Rocky Mountain ($n = 884$) ecotype bighorn sheep males. Figures include all males with complete horn measurement and age data from compulsory inspection of legally and illegally harvested males and opportunistic horn collections in British Columbia, Canada, 1975–2003.

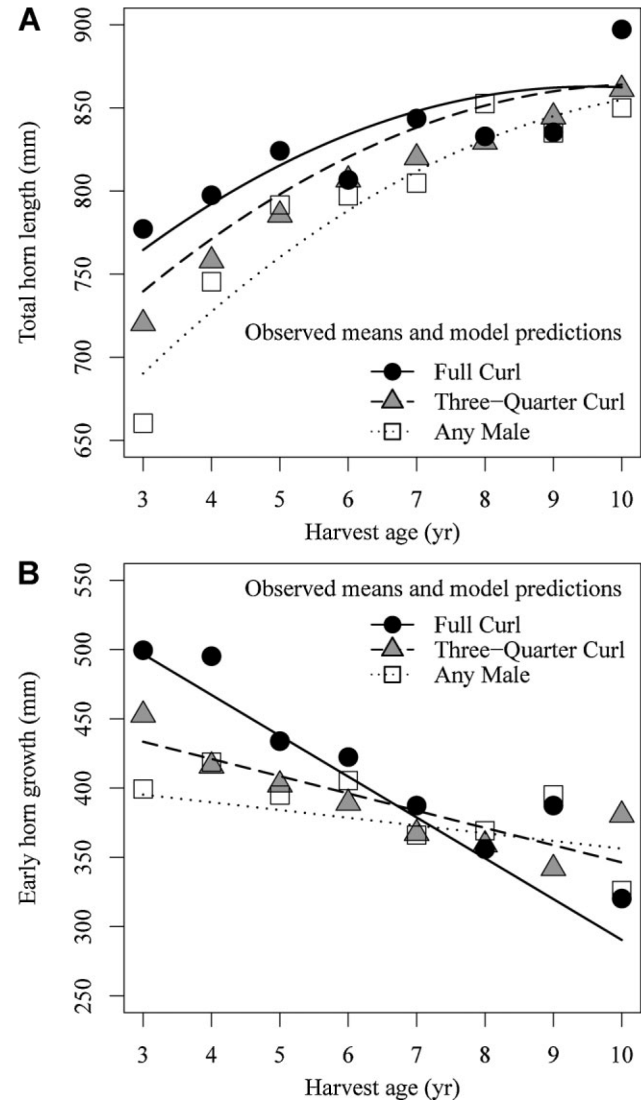

Figure 2. Linear mixed-effects models of [A] total horn length (mm) and [B] cumulative early horn growth during the second and third year of life (mm) of hunter-harvested California ecotype bighorn sheep males as a function of harvest age (yr) and harvest regulation (Three-Quarter Curl reference category, Any Male, Full Curl) in British Columbia, Canada, 1975–2003. We included Wildlife Management Unit (WMU) and cohort as random effects. We limited analyses to males harvested at $\geq$3 yr of age; we pooled harvest ages $\geq$10 yr. [A] $n = 1{,}529$ males, 37 cohorts, 11 WMUs; [B] $n = 1{,}415$ males, 37 cohorts, 11 WMUs. Some model predictions appear skewed from observed means because mixed models account for unequal sample sizes and variation in horn size among WMUs and cohorts.

(CBS: $r = 0.295$–0.790, $P \leq 0.001$; RMBS: $r = 0.431$–0.555, $P < 0.004$). Males with greater early growth had longer total horn length at harvest (CBS: $r = 0.154$, $t_{1,740} = 6.480$, $P \leq 0.001$; RMBS: $r = 0.121$, $t_{843} = 3.537$, $P \leq 0.001$), independent of harvest age (CBS: $P = 0.056$; RMBS: $P = 0.316$). Greater early growth also was correlated with greater horn base circumference at harvest (CBS: $r = 0.174$, $t_{1,675} = 7.215$, $P \leq 0.001$; RMBS: $r = 0.079$, $t_{830} = 2.292$, $P = 0.022$), although the relationship weakened for older males due to an interaction of base circumference and harvest age (CBS: -0.1 mm/yr, SE $= 0.04$, $P = 0.024$; RMBS: -0.2 mm/yr, SE $= 0.05$, $P \leq 0.001$; Fig. 1B). There was no directional asymmetry in total length (CBS: $t_{974} = 0.536$, $P = 0.592$; RMBS: $t_{506} = -0.801$, $P = 0.423$).

On average horns of CBS males harvested under Three-Quarter Curl regulation were 66 mm longer than for males harvested under Any Male regulation (SE $= 15.8$, $HPD_{Lower} = -97.5$, $HPD_{Upper} = -33.7$, $P \leq 0.001$; Fig. 2A). Horn length of males harvested under Full Curl regulations was on average 36 mm longer than for males harvested under Three-Quarter Curl rule (SE $= 18.6$, $HPD_{Lower} = -0.2$, $HPD_{Upper} = 71.4$, $P = 0.046$). An interaction of the Any Male regulation and harvest age on horn length indicated that the difference in horn length among regulations decreased with increasing age at harvest ($+6$ mm/yr, SE $= 2.5$, $HPD_{Lower} = 0.7$, $HPD_{Upper} = 10.5$, $P = 0.017$; Fig. 2A). Mean early growth in males harvested under Full Curl regulation was 114 mm greater (SE $= 26.3$, $HPD_{Lower} = 61.5$, $HPD_{Upper} = 165.3$, $P \leq 0.001$) than for males harvested under the Three-Quarter Curl rule, which had 59 mm greater early growth (SE = 20.9, $HPD_{Lower} = -101.3$, $HPD_{Upper} = -16.3$, $P = 0.008$) than males harvested under Any Male regulations (Fig. 2B). Relative to Three-Quarter Curl regulation, the interaction of regulation and age was positive under Any Male (+7 mm/yr, SE = 3.3, $HPD_{Lower} = 0.2$, $HPD_{Upper} = 131.4$, $P = 0.039$) and negative under Full Curl harvest (−17 mm/yr, SE = 4.1, $HPD_{Lower} = -25.5$, $HPD_{Upper} = -9.3$, $P \leq 0.001$), indicating that the greatest effect of regulations on early horn growth was at the youngest harvest ages (Fig. 2B). By excluding the largest 5% of first increment measures, the interaction between harvest age and the Any Male regulation disappeared ($HPD_{Lower} = -1.1$, $HPD_{Upper} = 12.6$, $P = 0.105$), but that between harvest age and Full vs Three-Quarter Curl remained significant (−12 mm/yr, SE = 4.4, $HPD_{Lower} = -21.0$, $HPD_{Upper} = -3.9$, $P = 0.005$). Overall, early growth decreased with harvest age and until ≥7 yr of age early growth was greatest in males harvested under Full Curl regulation (Fig. 2B). Under Full Curl regulation for harvest ages 4–10 yr early horn growth decreased with harvest age by 26 mm/yr in CBS (SE = 4.3, $HPD_{Lower} = -36.7$, $HPD_{Upper} = -18.8$, $P \leq 0.001$) and 22 mm/yr in RMBS (SE = 1.9, $HPD_{Lower} = -25.3$, $HPD_{Upper} = -17.5$, $P \leq 0.001$; Fig. 3).

Most (65%) harvested males were <8 yr old (Fig. 4). Mean harvest age of CBS (n = 1,624 M, 11 WMUs) under a Three-Quarter Curl regulation (5.8 yr, SE = 0.2, $HPD_{Lower} = 5.3$, $HPD_{Upper} = 6.2$, $P \leq 0.001$) was greater than under Any Male (−0.7 yr, SE = 0.2, $HPD_{Lower} = -1.0$, $HPD_{Upper} = -0.3$, $P \leq 0.001$) and less than under Full Curl harvest (+0.4 yr, SE = 0.2, $HPD_{Lower} = 0.04$, $HPD_{Upper} = 0.8$, $P = 0.027$). Mean harvest age for RMBS taken under Full Curl regulation was 6.9 yr (SE = 0.3, $HPD_{Lower} = 6.3$, $HPD_{Upper} = 7.6$, $P \leq 0.001$, n = 998 M, 8 WMUs).

Permit type and hunter origin had small, uncorrelated effects on total horn length for CBS males harvested under Three-Quarter Curl regulation (n = 1,202 M, 33 cohorts, 9 WMUs). LEH permit holders and Non-Resident hunters harvested males with slightly shorter horns (−25 mm, SE = 8.3, $HPD_{Lower} = -44.5$, $HPD_{Upper} = -8.2$, $P = 0.001$; and −12 mm, SE = 3.6, $HPD_{Lower} = -19.0$,

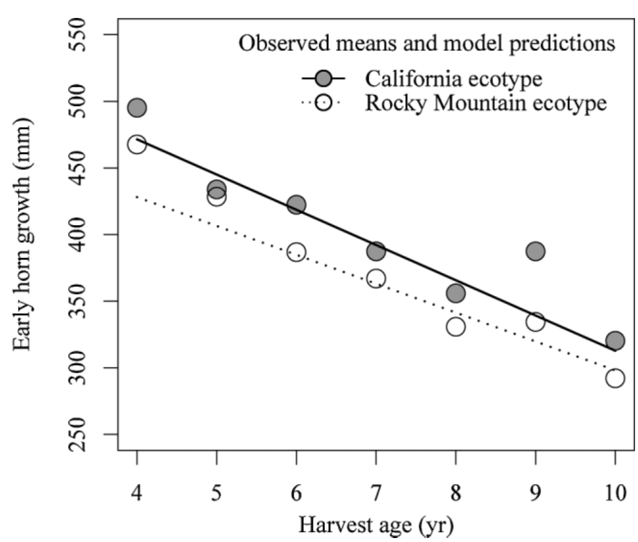

Figure 3. Linear mixed-effects models of cumulative early horn growth during the second and third year of life (mm) of hunter-harvested California ecotype (n = 119 M, 31 cohorts, 8 Wildlife Management Units [WMUs]) and Rocky Mountain ecotype (n = 629 M, 32 cohorts, 8 WMUs) bighorn sheep males as a function of harvest age (yr) in British Columbia, Canada, 1975–2003. We included WMU and cohort as random effects. We limited analyses to males harvested at ≥4 yr of age under Full Curl harvest regulation; we pooled harvest ages ≥10 yr. Some model predictions appear skewed from observed means because mixed models account for unequal sample sizes and variation in horn size among WMUs and cohorts. Random effects were significant for the Rocky Mountain ecotype only.

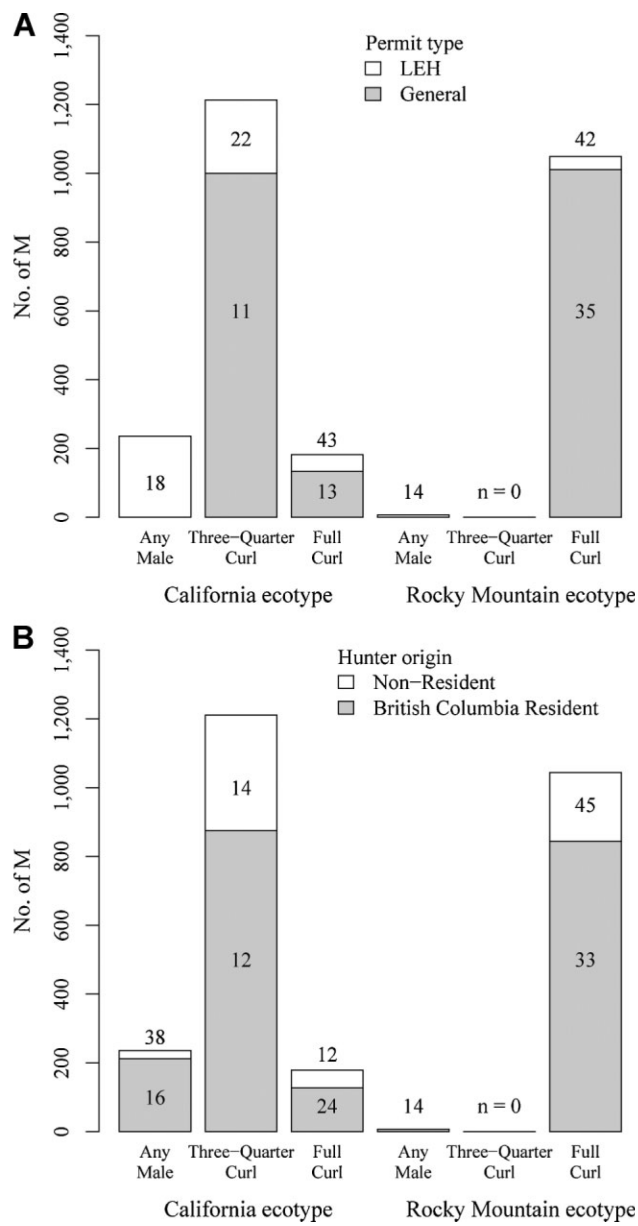

Figure 4. Sample size by [A] permit type (General vs. Limited Entry Hunt [LEH]) and [B] hunter origin (British Columbia Resident vs. Non-Resident) of California (n = 1,631) and Rocky Mountain (n = 1,056) ecotype bighorn sheep males harvested under Any Male, Three-Quarter Curl, and Full Curl regulations in British Columbia, Canada, 1975–2003. Percentage of males harvested at age ≥8 yr is given for each permit and hunter type, including all males for which harvest age was recorded.

Table 1. Linear mixed-effects model of total horn length (mm) of hunter-harvested California bighorn sheep males ($n = 1{,}165$) from 9 Wildlife Management Units (WMUs) in British Columbia, Canada, as a function of harvest year (1975–2003) and harvest age group (3–5-yr-old reference category, $\geq$6 yr). Males were harvested under Three-Quarter Curl regulation.

	Estimate	SE	HPD[a] lower	HPD upper	*P*-value
Fixed effects					
Intercept	780.6	7.0	765.1	796.8	$\leq$0.001
Yr	−1.0	0.4	−1.8	−0.2	0.007
Age $\geq$6 yr	54.2	8.0	38.4	69.9	$\leq$0.001
Yr $\times$ age $\geq$6 yr	−0.2	0.5	−1.2	0.9	0.761
			Variance		SD
Random effects					
WMU			108.7		10.4
Residual			3,096.2		55.6

[a] HPD = 95% highest posterior density intervals derived from Markov chain Monte Carlo sampling of the estimated model coefficients.

$\text{HPD}_{\text{Upper}} = -5.1$, $P \leq 0.001$, respectively) at all harvest ages compared to British Columbia Resident hunters under a General permit. Non-Resident hunters harvested CBS males with slightly less early horn growth than did British Columbia Resident hunters, at all harvest ages (−15 mm, SE = 5.1, $\text{HPD}_{\text{Lower}} = -24.7$, $\text{HPD}_{\text{Upper}} = -4.4$, $P = 0.004$). There was an interaction between permit type and hunter origin on early horn growth such that Non-Residents harvested males with greater early horn growth (+26 mm, SE = 11.9, $\text{HPD}_{\text{Lower}} = 9.1$, $\text{HPD}_{\text{Upper}} = 56.6$, $P = 0.028$) only when compared to British Columbia Resident LEH permit holders. There was a marginal effect of permit type but not of hunter origin on total horn length of RMBS males harvested under Full Curl regulations ($n = 981$ M, 33 cohorts, 8 WMUs); horns of LEH males averaged 22 mm longer (SE = 11.5, $\text{HPD}_{\text{Lower}} = 0.9$, $\text{HPD}_{\text{Upper}} = 44.7$, $P = 0.049$) than for General permit males. There was no effect of permit type ($P = 0.186$) or hunter origin ($P = 0.284$) on early horn growth of Full Curl RMBS. For both ecotypes, early horn growth model results were similar when we excluded the largest 5% of first increment values (CBS: $P < 0.027$; RMBS: $P > 0.148$).

Permit type and hunter origin did not directly affect harvest age of CBS males under Three-Quarter Curl regulation, but Non-Residents harvested older males (+0.6 yr, SE = 0.3, $\text{HPD}_{\text{Lower}} = 0.1$, $\text{HPD}_{\text{Upper}} = 1.2$, $P = 0.023$) when competing with British Columbia Resident LEH permit holders. Rocky Mountain bighorn males harvested by Non-Resident hunters under Full Curl regulation were on average 0.4 yr older (SE = 0.1, $\text{HPD}_{\text{Lower}} = 0.1$, $\text{HPD}_{\text{Upper}} = 0.6$, $P = 0.001$) than those harvested by British Columbia Residents. A nearly significant effect of permit type on harvest age of RMBS suggested that males harvested under LEH permits were slightly older (+0.6 yr, SE = 0.3, $\text{HPD}_{\text{Lower}} = -0.01$, $\text{HPD}_{\text{Upper}} = 1.1$, $P = 0.054$) than males harvested under General permits.

Over the 28-yr time series total horn length of CBS harvested under Three-Quarter Curl regulation declined by 3.9% (31 mm) in young (3–5-yr-old) males, and 3.7% (31 mm) in older males (Table 1, Fig. 5A). Over the same period, early growth declined by 8.4% (36 mm) in males

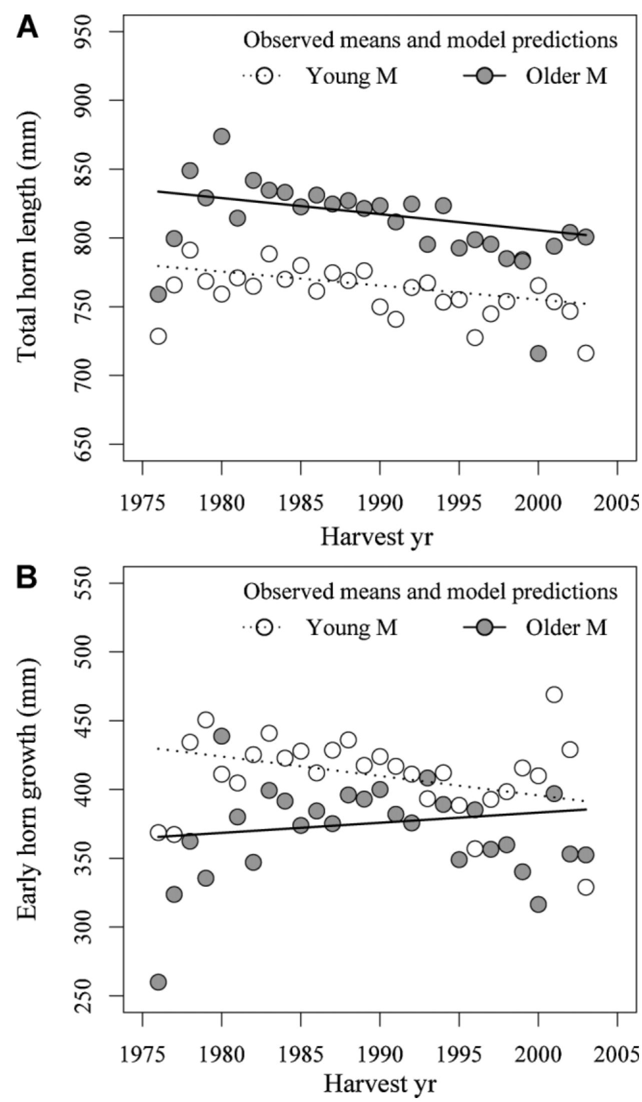

Figure 5. Linear mixed-effect models of [A] total horn length (mm) and [B] cumulative early horn growth during the second and third year of life (mm) of hunter-harvested California ecotype bighorn sheep males as a function of harvest year and harvest age group (young 3–5-yr-old M reference category and M $\geq$ 6 yr) in British Columbia, Canada, 1975–2003. We included Wildlife Management Unit (WMU) as a random effect. We limited analyses to males harvested at $\geq$3 yr of age under Three-Quarter Curl regulation ($n = 1{,}198$ M, 9 WMUs).

Table 2. Linear mixed-effects model of cumulative early horn growth (mm) in the second and third year of life of hunter-harvested California bighorn sheep males ($n = 1{,}123$) from 9 Wildlife Management Units (WMUs) in British Columbia, Canada, as a function of harvest year (1975–2003) and harvest age group (3–5-yr-old reference category, ≥6 yr). Males were harvested under a Three-Quarter Curl regulation.

	Estimate	SE	HPD[a] lower	HPD upper	*P*-value
Fixed effects					
Intercept	431.1	10.3	409.5	455.1	≤0.001
Yr	−1.4	0.5	−2.4	−0.4	0.007
Age ≥6 yr	−66.2	10.3	−86.6	−46.2	≤0.001
Yr × age ≥6 yr	2.1	0.7	0.8	3.5	0.004
			Variance		SD
Random effects					
WMU			363.6		19.1
Residual			4,835.4		69.5

[a] HPD = 95% highest posterior density intervals derived from Markov chain Monte Carlo sampling of the estimated model coefficients.

harvested as 3–5-yr-olds, but there was no temporal trend in older males (Table 2, Fig. 5B). Model results were similar when we excluded the highest 5% of first growth increment measures. There was no temporal trend in harvest age of CBS ($n = 1{,}175$ M, 9 WMUs, $P = 0.382$). In RMBS harvested under a Full Curl regulation, neither total horn length ($n = 901$ M, 8 WMUs, $P = 0.822$) nor early horn growth ($n = 643$ M, 8 WMUs, $P = 0.952$) changed over time, also when we excluded the highest 5% of first increment measures. Rocky Mountain bighorn sheep harvest age increased by 0.7 yr between 1975 and 2003 (+0.025 mm/yr, SE = 0.006, $HPD_{Lower} = 0.01$, $HPD_{Upper} = 0.04$, $P \leq 0.001$).

DISCUSSION

Independent of harvest regulations and bighorn ecotype, males with greater early horn growth were harvested at younger ages than males with less early growth. Without compensatory growth, males with less early horn growth are likely to have small horns throughout their lives whereas greater early growth imparts a lifelong advantage in horn size. Differences in harvest age of CBS males among the 3 regulations were small and >65% of harvested males were <8 yr old, suggesting that many large-horned males in hunted populations in British Columbia were harvested before reaching ages typically associated with high dominance rank and breeding success (Coltman et al. 2002). Males with exceptional early horn growth reached Three-Quarter Curl before age 5 yr and Full Curl before age 6 yr. Consequently, we observed the greatest effect of harvest regulation on both mean horn length and early horn growth for CBS males harvested at <7 yr of age. For older males the difference in horn length of CBS males harvested under Full Curl and Three-Quarter Curl regulations became negligible, suggesting that as harvest age increased the relationship between horn length and horn shape, which partly determines legality, weakens. In addition to horn length, selective harvest could affect horn shape by favoring males that, for a given horn length, took longer to reach legal harvest definitions.

Estimated effects suggested a stronger decline under Full Curl regulation than expected from the observed mean values for each harvest age (Fig. 2B) because of the influence of persistent differences in early growth among WMUs and imbalance in sample sizes among groups. The model fit line for males harvested under Full Curl regulation reflected the strong decline in early growth with increasing harvest age ($n = 126$ M) compared with more moderate declines under Three-Quarter Curl ($n = 1{,}125$ M) and Any Male harvests ($n = 164$ M; Fig. 2B). When we analyzed Full Curl harvest separately for the 2 ecotypes, the model fit line for young RMBS appeared lower than the plotted age-specific average (Fig. 3) because of the predominance of 4- and 5-yr-old males harvested from 1 WMU with greater than average early growth. We accounted for this bias in the statistical analysis by including WMU as a random factor. The fit line for Full Curl CBS males reflected observed means because we modeled the data independently of trends observed under Three-Quarter Curl and Any Male regulations and random effects were no longer significant (Fig. 3). Mixed-effects models are advantageous for this type of study design because they improve model fit for data sets with unequal sample sizes, even without any grouped correlation structures in hierarchical data (Gillies et al. 2006). Where correlation structures exist, such as persistent differences in mean early growth among WMUs and cohorts, the estimates for mixed model parameters are independent of the sampling intensity for each group; variability among groups is accounted for and contributes to explained variance; and statistical inferences can be extrapolated to the population level rather than being limited to sampled individuals (Steele and Hogg 2003, Gelman and Hill 2007). Estimates of fixed and random effects in mixed models reveal average effect sizes across the population and thereby help to evaluate the biological implications of harvest regulations at a broad scale.

Permit type and hunter origin had little influence on the horn size and age of harvested males. The apparent negative effect of LEH permits on horn size was likely the result of LEH harvest being predominantly from 3 WMUs with high-density populations where Three-Quarter Curl LEH harvest was implemented concurrent with Full Curl General permit hunts. While reductions in early horn growth and total horn length may be due to limited resource availability in high-density populations they also may indicate high harvest pressure in these populations (Jorgenson et al. 1993, 1998). If harvest pressure is high, many males will be harvested the year they reach the legal horn curl definition.

Both CBS and RMBS were primarily harvested under General (unlimited) permits. The difference in mean early horn growth of CBS males taken under each harvest regulation and the young age structure of the harvest suggest high harvest intensity. High harvest combined with a less restrictive Three-Quarter Curl regulation could explain the temporal decline in CBS horn measures that we did not observe in RMBS males. The increasing trend in RMBS harvest age, however, may suggest that males harvested over the later part of the time series required more years to reach legal horn size, possibly because of slower horn growth. If harvest rates are low and several rapidly growing males survive to older ages and sizes associated with high reproductive success, then genetic variability for large horn size should be conserved. Harvest refuges may buffer artificial selective pressures and could maintain genetic diversity of horn size in bighorn populations (Jachmann et al. 1995, Tenhumberg et al. 2004, Hogg et al. 2006). Immigration of high-quality males from areas protected from harvest should buffer artificial selection. Many British Columbia RMBS populations likely benefit from gene flow from National Parks, where hunting is not permitted, but few CBS in British Columbia are in protected areas (Shackleton 1999). Genetic rescue may therefore be more likely for RMBS than for CBS.

Our analysis showed evidence of differential responses to selective harvesting under 3 management strategies in 2 bighorn ecotypes. However, without data on harvest intensity it is difficult to establish how different definitions of legal horn size may affect the selective pressure of trophy hunting. Under Full Curl regulations only the fastest-growing males can be harvested at young ages whereas under Three-Quarter Curl regulation a greater proportion of males will meet the minimum horn curl criteria before 7 yr of age. Therefore, Full Curl regulations may allow some males with rapidly growing horns to participate in 1 or 2 additional breeding seasons before being harvested. The small difference in age at harvest between Three-Quarter Curl and Full Curl regulations suggests that this effect may be minimal. Any Male harvest regulations, intended to distribute harvest over all age classes, appeared to be least selective for young, large-horned males, but this interpretation may be confounded because all Any Male harvests were under LEH permits and therefore harvest pressure was limited. If Any Male hunts led to the harvest of small-horned males simply because all large males had already been harvested, then Any Male hunts clearly would not achieve their purpose. Male bighorn sheep are gregarious and most hunters will likely select the largest male in a group, provided that male meets whatever horn regulations are in place.

Our results are consistent with previous studies which suggested that selective removal of high-quality males through trophy hunting can produce an undesirable response in horn size (Fitzsimmons et al. 1995, Coltman et al. 2003, Festa-Bianchet et al. 2004, Garel et al. 2007). We suggest that minimum horn curl regulations without severe restrictions on harvest intensity do not protect bighorn sheep populations from negative effects of selective harvests. Harvest intensity, regardless of curl restriction, may be the most critical factor driving artificial selection.

MANAGEMENT IMPLICATIONS

In bighorn sheep populations management strategies that protect some fast-growing males, or provide harvest refuges to maintain genetic diversity, may reduce negative evolutionary consequences of trophy hunting. The key to sustainable management of bighorn sheep is to ensure that high-quality males have sufficient opportunity to breed before being harvested. Lower evolutionary impacts could be achieved by reducing emphasis on trophy size in favor of hunt quality. Any Male LEH seasons might be an alternative to minimum curl regulations, because they do not force hunters to select high-quality males. Because success rate is likely high under Any Male regulations and because most hunters will likely continue to harvest the largest male they find, however, permit numbers may have to be much lower than those issued for LEH seasons in British Columbia. We recommend that future research investigates how hunter success rate varies with changes in harvest regulations and in the number of permits issued. Further study should also quantify harvest pressure on legal males over time, to identify which horn curl restriction and level of harvest could reduce unwanted selective effects. Evaluating potential selective effects of harvest regulations would require data on the number of males per cohort, the proportion of legal males harvested each year, and the proportion of males that do not meet minimum horn curl criteria at each age. Periodic harvest closures in some WMUs or establishment of protected areas in strategic locations relative to the metapopulation could facilitate genetic rescue while serving as an experimental test of harvest-induced selection. If genes for greater horn growth still exist in the population, protection from harvest should counter artificial selection and restore large horn growth over time. Compulsory inspection records of male horn growth may provide an effective monitoring tool for management, particularly when annual horn growth increment measures and harvest age are recorded. Horn collections from unhunted populations would enable further comparative assessment of population age structures, male social dynamics, and natural mortality rates in hunted and protected populations.

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