Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure

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Abstract. Selective harvest may lead to rapid evolutionary change. For large herbivores, trophy hunting removes males with large horns. That artificial selection, operating in opposition to sexual selection, can lead to undesirable consequences for management and conservation. There have been no comparisons of long-term changes in trophy size under contrasting harvest pressures. We analyzed horn measurements of Stone's rams (*Ovis dalli stonei*) harvested over 37 years in two large regions of British Columbia, Canada, with marked differences in hunting pressure to identify when selective hunting may cause a long-term decrease in horn growth. Under strong selective harvest, horn growth early in life and the number of males harvested declined by 12% and 45%, respectively, over the study period. Horn shape also changed over time: horn length became shorter for a given base circumference, likely because horn base is not a direct target of hunter selection. In contrast, under relatively lower hunting pressure, there were no detectable temporal trends in early horn growth, number of males harvested, or horn length relative to base circumference. Trophy hunting is an important recreational activity and can generate substantial revenues for conservation. By providing a reproductive advantage to males with smaller horns and reducing the availability of desirable trophies, however, excessive harvest may have the undesirable long-term consequences of reducing both the harvest and the horn size of rams. These consequences can be avoided by limiting offtake.

Key words: artificial selection; British Columbia, Canada; evolutionary change; harvest intensity; long-term changes; Ovis dalli stonei; *Stone's sheep; wildlife management*

Introduction

Although conservation biologists have only recently begun to pay attention to how humans may affect evolution in wild species (Palumbi 2001, Smith and Bernatchez 2008), there is now convincing evidence that human harvest is a strong selective pressure (Allendorf and Hard 2009, Darimont et al. 2009). Harvest is usually selective for a certain size, morphology, or behavior (Allendorf and Hard 2009, Ciuti et al. 2012). Artificial selection is particularly obvious in trophy hunting of large herbivores, where hunters seek males with large horns, antlers, or tusks. These weapons evolved through sexual selection by conferring an advantage in male-male competition, female choice,

or both (Darwin 1871, Andersson 1994). Rapid growth in weapon size is associated with high reproductive success in adults of some species (Coltman et al. 2002, Kruuk et al. 2002). Trophy hunting, however, may remove males with rapidly growing horns, often at an age before those weapons improve reproductive success, as reported in bighorn sheep (*Ovis canadensis*) (Coltman et al. 2003). The heritability of horn size is substantial in this species (Coltman et al. 2003, Poissant et al. 2008), and selective harvest led to a rapid evolution of reduced horn growth in bighorn males, in opposition to sexual selection (Coltman et al. 2003). Recent studies have underlined the potential conservation value of tourist hunting (Leader-Williams et al. 2005), where much of the revenue generated depends on trophy size of harvested animals (Courchamp et al. 2006). Therefore, the ecological and evolutionary consequences of selective hunting are highly relevant to conservation.

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If horn traits are heritable, the evolutionary response to selection through trophy hunting depends on the strength of relationships between trophy size, age, and reproductive success (Festa-Bianchet and Lee 2009), which, in turn, can be influenced by hunting pressure. Evolutionary effects should increase with harvest intensity, particularly if traits that determine trophy quality only confer a fitness advantage at an advanced age. For instance, when hunting pressure is low, some bighorn males with fast-growing horns could survive to ~7 years, the age at which large horns improve reproductive success (Coltman et al. 2002), mitigating the potential impact of artificial selection. Among trophy-hunted African ungulates, the decline in horn length was more pronounced for sable antelope (*Hippotragus niger*) than for impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*), likely because hunting pressure and trophy value were higher for sable than for the other two species (Crosmary et al. 2013). Despite the important ecological, evolutionary, and conservation implications of harvest selection (Festa-Bianchet 2003), however, we know little about how its impacts may vary in relation to harvest intensity. Although two previous studies reported a decline in horn length of male bighorn sheep over time (Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014), neither examined the effects of regional changes in harvest pressure, leaving the possibility that some unknown temporal trends may have contributed to the results. From a wildlife management perspective, it is particularly important to identify what

harvest rate may limit the potential undesirable effects of artificial selection.

Variation in harvest selectivity has been studied in cervids by comparing hunting methods (Martinez et al. 2005) or resident and nonresident hunters (Mysterud et al. 2006, Schmidt et al. 2007, Rivrud et al. 2013). For example, in Alaska, USA, guided hunters harvested moose (*Alces alces*) with larger antlers compared to non-guided hunters because guides had a better knowledge of low-density areas producing large-antlered moose (Schmidt et al. 2007). Most guided hunters are nonresidents, who pay substantial fees to obtain large trophies. Surprisingly, however, in Alberta, Canada, guided hunters harvested slightly smaller-horned rams than residents, possibly because the high harvest intensity allowed very few rams to grow large horns (Festa-Bianchet et al. 2014). Replicated studies are needed to understand whether resident and nonresident trophy hunters exert different levels of selection on hunted species.

We explored how hunting pressure affects horn growth of Stone's sheep males in British Columbia, Canada, and compared age and horn length of individuals harvested by residents and by guided nonresidents. We used measurements of ~10000 males harvested over 37 years from two areas differing in hunting pressure to test six hypotheses (Table 1). The first three concerned hunter selection. First, we expected a negative association between early horn growth and age at harvest in both areas. That is because a ram with rapid horn growth will fit the legal definition of

TABLE 1. Hypotheses and predictions relating selective harvest and changes in horn development of Stone's sheep (*Ovis dalli stonei*) in British Columbia, Canada.

Hypothesis	Rationale	Prediction
Selective harvest		
Trophy hunter selection (H1)	Trophy hunting removes males with fast-growing horns but selection intensity varies with hunting pressure.	Rams with rapid early horn growth will be harvested at a younger age in both areas, but more markedly in high hunting area.
Filtering effect of hunting (H2)	Horn length does not increase continuously with harvest age at population level if males with slower horn growth survive to older ages.	Mean horn length for older males harvested in high hunting area will reach an asymptote or decline with age.
Hunter origin effect (H3)	Nonresident hunters must hire a guide. Guides deploy substantial effort to find larger trophies.	Nonresidents take older males with larger horns than residents.
Long-term changes in horn development		
Evolutionary consequences of trophy hunting for horn growth (H4)	Intense removal of large-horned males can lead to evolution of smaller horns.	Horn growth declines over time in high hunting area only.
Evolutionary effects of trophy hunting on horn shape (H5)	Trophy hunting removes males with longer horns at a given age rather than those with thicker bases.	Horn length at a given age will decrease over time for a given horn base in high hunting area only.
Intense trophy hunting reduces availability of trophy rams (H6)	Rams must have horns describing a complete curl to be harvested. Cohorts with slow-growing horns are exposed to a longer period of natural mortality before reaching legal harvest size.	Availability of trophy males will decrease over time in the high hunting area only.

Note: Peace region of British Columbia was considered the high hunting area, Skeena region was considered the low hunting area (Fig. 1).

harvestable ram at a younger age than a ram with slow horn growth early in life (Festa-Bianchet et al. 2014). This age-specific selection is important because it imposes an early negative selective pressure through hunting on rams that could develop into successful breeders if they survived a few more years (Coltman et al. 2003). For a given early growth, we expected, however, an older age at harvest under lower harvest pressure, particularly for males with rapidly growing horns (H1, Table 1). Although at an individual level, ram horns continue growing through life (Bonenfant et al. 2009), at the population level, horn length could reach an asymptote or decline for older males if males with slower horn growth survived to older ages. This filtering effect caused by selective hunting of males with rapid horn growth should be greater under high harvest pressure (H2, Table 1). Unlike residents of British Columbia, nonresident hunters must engage a licensed guide. Guides try to satisfy their clients by providing an opportunity to harvest a large trophy (Schmidt et al. 2007). Therefore, we expected nonresidents to harvest older males with larger horns (H3, Table 1).

We then examined temporal changes in horn size and shape to identify potential evolutionary responses to selective hunting (Coltman et al. 2003). We predicted a greater decrease in horn length at a given age over time under high harvest pressure (H4, Table 1). Unlike horn length, horn base circumference is not a direct target of hunter selection (Pelletier et al. 2012). The allometric relationship between horn length and horn base should thus change over time under high harvest pressure: for a given horn base, we expected horn length to decline in the high hunting area (H5, Table 1). Finally, a decrease in horn growth over time would reduce the availability of trophy males, by lengthening the time when males may die from natural causes before reaching legal harvest size. Therefore, we expected a decrease in harvest over time under high harvest pressure (H6, Table 1).

Materials and Methods

Study areas and hunting pressure

We studied Stone's sheep in the Skeena Region of northwestern British Columbia and the Peace Region of northeastern British Columbia (Fig. 1). Ideally, hunting pressure should be estimated by the proportion of a population that is harvested, but no reliable measure of population density was available. Therefore, we used the annual estimates of hunter numbers from 1976–2011, provided by the British Columbia Fish, Wildlife and Habitat Management branch. To measure hunting pressure, we divided the mean number of hunters by the area of Stone's sheep range in each region.

Fig. 1. Study area and distribution of Stone's sheep (*Ovis dalli stonei*) in British Columbia, Canada. We analyzed data from males harvested within the two polygons (Skeena and Peace). We excluded sheep in the Omineca Region (area between and to the south of Skeena and Peace) on the advice of provincial wildlife biologists, as very few sheep were harvested there.

Harvest regulations

Sport harvest of Stone's sheep in British Columbia is restricted to males of either at least 8 years old or whose horns describe a complete curl: these are referred to as legal males. Nevertheless, the hunter's decision to shoot likely rests on horn curl in most cases because it is difficult to count horn growth increments from a shooting distance to determine age. Hunting rules did not vary over time or between areas. Hunting started 1 August and ended 15 October. There is no quota on the number of licenses sold to residents of British Columbia, but each hunter may only harvest one legal male. Guides received a yearly allocation of ~250 permits.

Stone's sheep data

All harvested Stone's sheep must undergo compulsory inspection. We obtained measurements of 12749 males (3610 from Skeena and 9139 from Peace) collected from 1975–2012. Trophy hunting of Stone's sheep had been underway for several decades in both regions before compulsory registration and measurement of harvested rams were initiated in 1975.

Measurements usually included horn base circumference, total horn length, length of each annual growth increment, and age at death. Data also included the region of harvest and hunter origin (resident or nonresident). Horns grow from April–September (Bunnell 1978). Cessation of horn growth in winter creates a ring or annulus, allowing measurement of each annual growth increment, from which it is possible to estimate age (Geist 1966). Horns start to grow at ~10 weeks of age (Bowyer and Leslie 1992) and most lambs are born in late May or early June (Bunnell 1980). Hence, the first increment and part of the second increment develop before a male reaches 1 year of age. Unlike those of bighorn males, the horns of Stone's sheep are rarely "broomed" or broken at the tips (Krausman and Bowyer 2003, Bunnell 2005). Most males have some wear on the first increment but retain it until death. Because the first annulus is at times difficult to distinguish, however, a common error is to record the sum of growth increments 1 (lamb growth) and 2 (yearling growth) as a single first increment (Hengeveld and Festa-Bianchet 2011). This error produces an abnormally large first year growth measure, a smaller than average measure for subsequent increments, and an erroneous age estimate. We excluded biologically impossible growth increments (increment 1 > 160 mm and sum of increments 1 and 2 > 420 mm; Bunnell 1978, Hik and Carey 2000), eliminating 25% of the data set. Early horn growth was defined as the sum of increments 2 and 3, grown during the second and third years of life (Hengeveld and Festa-Bianchet 2011). Similarly to Bonenfant et al. (2009), we used the left horn measurement. Because our data set included few individuals >13 years (nine in Skeena and 13 in Peace), we pooled all males older than 12 into the same age class.

We restricted cohort analyses to cohorts that would have been included in our data from the youngest to the oldest age at harvest. Rams become legal at a minimum of 4 years of age and can live up to 14 years. Thus, some males born before 1972 may have been shot before 1975 when data recording started, while recent cohorts may not include old males not yet legal by 2012. We thus included only cohorts from 1972 to 2000 in our analyses.

Climate

High population density and harsh climate reduce antler size or horn growth (Jorgenson et al. 1998, Schmidt et al. 2001, Mysterud et al. 2005). Therefore, it is crucial to determine whether temporal changes in trophy size may be a consequence of changes in environmental conditions (Allendorf and Hard 2009). The Pacific Decadal Oscillation (PDO) in April–May has a positive effect on horn growth of conspecific Dall sheep (*O. dalli dalli*) in the Yukon (Loehr et al. 2010), just north of British Columbia (Fig. 1). We

controlled for possible confounding effects of climate on horn size by using monthly PDO, for two seasons that could affect horn growth (data *available online*).[4] April–September (spring-summer) PDO values reflect conditions during horn growth. During winter (November–March), horn growth stops, but climate in winter influences spring and summer plant phenology (Post and Stenseth 1999), which, in turn, may affect horn growth the following spring-summer (Giacometti et al. 2002). We tested the effects of mean PDO between birth and 2 years for each season (winter, PDO_W; spring-summer, PDO_S) on horn size metrics, as horn increment length decreases after 2 years (Bunnell 1978).

Statistical analyses

To test H1, we looked for a relationship between early horn growth and age at death using linear models, including region as a two-level factor and the interaction between region and early growth. To investigate if there was a change in selection over time, we reanalyzed the relationship between age at harvest and early horn growth in both regions by splitting the time series in the middle, comparing old (1972–1986) and recent (1987–2000) cohorts. We then compared age-specific total horn length between the two regions (H2) using linear models with horn length as a function of age, either as a linear or a quadratic term, region, and their first-order interactions. We replicated these analyses using horn base circumference as response variable.

To investigate whether age distribution of harvested males differed between resident and nonresident hunters (H3), we used a χ^2 test. We used linear models to test whether early horn growth, total horn length, and horn base circumference differed for rams harvested by resident or nonresident hunters.

To test our prediction of a greater decrease in horn size over time under higher harvest pressure (H4), early horn growth and total horn length were regressed against cohort (Garel et al. 2007). To quantify the amount of temporal variation in horn size accounted for by each covariate, seniority of the cohort (a continuous variable ordering cohorts from the oldest to the most recent), PDO_W, and PDO_S, we performed an analysis of deviance (ANODEV; Skalski et al. 1993). The ANODEV compares the deviance of three nested models: a basic model, a basic model including a time-specific covariate, and a basic model with cohort as a discrete factor. The R^2 of the ANODEV quantifies how much of the temporal variation in mean horn size is accounted for by each covariate. Autocorrelation must be taken into account in time-series analyses to avoid inflated probabilities of Type I error (Legendre 1993). To account for temporal autocorrelation in horn

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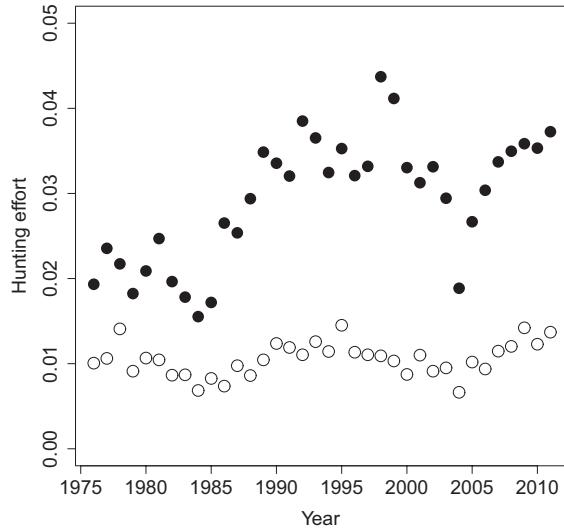[4] http://jisao.washington.edu/pdo/PDO.latest

Fig. 2. Yearly variations in hunting effort, defined as number of hunters divided by the area of Stone's sheep range in two regions of British Columbia (solid circles, Peace region, high hunting area; open circles, Skeena region, low hunting area).

size metrics, we used generalized least square models (function gls in R library nlme). We ran each model with a first-order autoregressive structure, specifying the corAR1 correlation option with respect to cohort (Pinheiro and Bates 2000). To test whether horn shape changed over time (H5), we assessed the relationship between horn length and base (on a log scale to account for the allometric link; Houle et al. 2011) using linear models, including cohort seniority as a two-level factor (old cohorts, 1972–1986; recent cohorts, 1987–2000) and the interaction between cohort seniority and horn base. Finally, we regressed the number of harvested males from each cohort on the seniority of the cohort in each region (H6). All analyses were run in R 2.11 (R Development Core Team 2011). Estimates are given as mean ± SE and statistical significance was set at $P = 0.05$.

Results

Contrasting hunting pressures

There were on average 2.3 times more hunters per year in the Peace than in the Skeena region (561 ± 23 vs. 246 ± 7). Stone's sheep range was larger in the Skeena (23360 km²) than in the Peace (19194 km²). Therefore, hunting pressure was ~2.7 times higher in the Peace than in the Skeena (chi-square test for equality of two proportions: $\chi_1^2 = 6932$, $P < 0.001$) and this difference increased over time (Fig. 2). Overall, 72% of males were harvested in the Peace and only 28% in the Skeena. Henceforth, we refer to the Peace as high and the Skeena as low hunting areas.

Selective pressure of harvesting

A decline in harvest age with rapid early horn growth was more marked in the high than in the low hunting area (interaction of early growth and region, $F_{1,9493} = 10.57$, $P = 0.001$, $R^2 = 0.10$, Fig. 3). For an increase in early horn growth of 100 mm, harvest age decreased by 0.64 yr and 0.82 yr in the low and high hunting areas, respectively. Supporting H1, males with rapidly growing horns were consistently harvested at an older age in the low than in the high hunting area, and this relationship did not vary over time (Appendix S1). We found an interactive effect of age and region on total horn length ($F_{1,9370} = 42.47$, $P < 0.001$, $R^2 = 0.09$). Males harvested between the ages of 5 and 8 in the high hunting area had longer horns than in the low hunting area, while the reverse was true between the ages of 9 and 13 (Fig. 4A). Supporting H2, in the high hunting area, horn length stopped increasing with harvest age at ~9 years and appeared to decline for the oldest males (≥13 years), but increased continuously with age at harvest in the low hunting area. These results were similar when excluding the first increment (Appendix S2). Correcting for age, males harvested in the high hunting area had horn bases 2.1% thicker than those in the low hunting area ($\beta = 6.64 \pm 0.59$, $P < 0.001$, Fig. 4B). There was no interaction between age and region on base circumference ($F_{1,9340} = 0.36$,
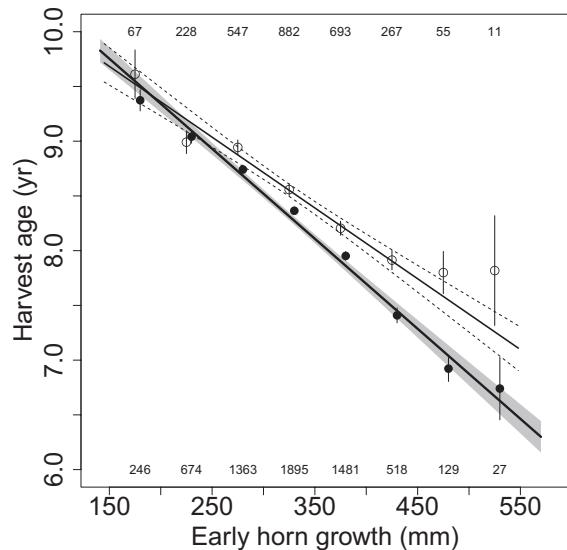

Fig. 3. Length of horn increments grown during the second and third years of life and age at harvest for Stone's rams in the low (open circles and solid line, 95% confidence intervals shown by dotted lines) and high (solid circles and solid line, 95% confidence intervals shown by shaded area) hunting areas of British Columbia. Points are mean (± standard error [SE]) harvest age for each class, defined as 50 mm of horn growth. Sample size for each point in the low and high hunting areas is shown at the top and bottom of the figure, respectively.

$P = 0.55$). Variation in circumference between 5 and 13 years of age was best captured by a quadratic relationship with age that did not differ between regions (age: $\beta = 5.06 \pm 1.28$, age^2: $\beta = -0.27 \pm 0.07$, $P < 0.001$, Fig. 4B).

Hunter residency and horn characteristics

The proportion of males harvested by residents and nonresidents during the study period differed between regions ($\chi^2_1 = 131.30$, $P < 0.001$). In the low hunting area, nonresident hunters took 62.6% of males (95% CI = 61.1%, 64.2%), while they took 51.6% (95% CI = 50.5%, 52.6%) in the high hunting area. The age distribution of males differed between resident and nonresidents (low hunting area: $\chi^2_8 = 53.50$, $P < 0.001$, high hunting area: $\chi^2_8 = 212.4l$, $P < 0.001$). The harvest by resident hunters included a greater proportion of males <8 years of age and proportionately fewer older males than the nonresident harvest (Appendix S3). Nonresident hunters shot males with horns 2.4% and 3.6% longer after accounting for age than resident hunters in the low ($F_{1,2256} = 34.04$, $P < 0.001$) and high hunting area ($F_{1,4939} = 164.71$, $P < 0.001$), respectively, independently of male age (interactions between age and hunter origin, $P > 0.40$). Early horn growth differed by hunter origin in the high hunting area, being 2.1% faster for males taken by residents ($F_{1,5027} = 11.75$, $P < 0.001$). The relationships between early growth, age at harvest, and hunter origin probably accounted for this difference because the effect of hunter origin on early horn growth was not retained when age at harvest was included in the model ($F_{1,5026} = 0.44$, $P = 0.50$). Early horn growth in the low hunting area did not vary with hunter origin ($F_{1,2282} = 0.38$, $P = 0.53$). Horn base of males harvested by nonresidents was slightly thicker than for males taken by residents (1.6% in the low hunting area, $F_{1,2237} = 13.47$, $P < 0.001$, and 0.7% in the high hunting area, $F_{1,4936} = 11.72$, $P < 0.001$). These results support H3, that nonresident hunters harvested older males with longer horns at a given age than residents of British Columbia.

Spatiotemporal trends

There were strong regional differences in temporal trends for early horn growth (between-region difference in slope = 2.03 ± 0.26, $P < 0.001$). Supporting H4, early growth declined by 12.5% for males born between 1972 and 2000 in the high hunting area, but remained relatively stable in the low hunting area (Table 2, Fig. 5). The temporal trend accounted for 40% of cohort variation in mean early horn growth in the high hunting area, independently of male age (interaction between age class and seniority of cohort, $F_{2,5022} = 0.11$, $P = 0.89$). Hunting pressure has a negative effect on early horn growth in the high (slope of 785.92 ± 191.79, $P < 0.001$) but not in the low hunting area (slope of 265.17 ± 903.37, $P = 0.77$). Early horn growth in the high hunting area declined by 10.4% after also
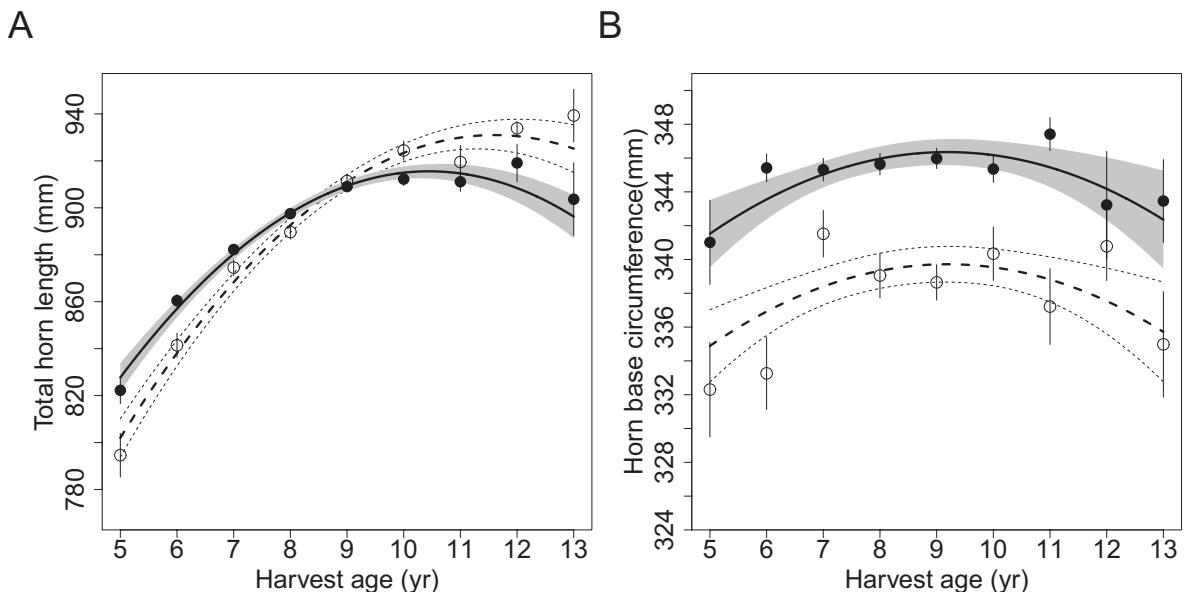

FIG. 4. Relationship between harvest age and (A) total horn length or (B) horn base circumference of Stone's rams harvested in the low (open circles and dashed line, 95% confidence intervals are shown by dotted lines) and high (solid circles and solid line, 95% confidence intervals are shown by shaded area) hunting areas of British Columbia; vertical lines indicate SE.

TABLE 2. Effects of time T (i.e., seniority of the cohort) after accounting for effects of climate on cumulative horn growth during the second and third years of life of harvested Stone's sheep males from two regions of British Columbia, Canada.

Model, by region	k	Deviance	P_{ANODEV}	R^2_{dev}	Slope ($\pm$ SE)
Skeena (low hunting area)					
Constant	3	25403.17			
Cohort dependent	31	25282.69			
Covariate models					
PDO_W	4	25400.17	0.41	0.02	4.38 ± 2.52
PDO_S	4	25401.39	0.53	0.01	-3.67 ± 2.74
T	4	25397.30	0.25	0.05	0.50 ± 0.21
Peace (high hunting area)					
Base	4	56831.26			
Cohort dependent	32	56589.26			
Covariate models					
PDO_W	5	56824.90	0.40	0.03	4.76 ± 1.89
PDO_S	5	56825.20	0.41	0.03	-5.04 ± 2.05
T	5	56733.45	<0.001	0.40	-1.53 ± 0.15

Notes: These effects were tested with an analysis of deviance (ANODEV, see *Materials and Methods: Statistical analyses* for details). P_{ANODEV} is the P value of the ANODEV test on covariates, while R^2_{dev} quantifies how much of the temporal variation in mean horn growth is accounted for by each covariate, and k stands for the number of parameters in the model. PDO_W and PDO_S are mean winter and spring-summer Pacific Decadal Oscillation between birth and 2 years, respectively. In the Peace region, the baseline model (base) included hunter origin as a two-level factor (nonresidents vs. residents of British Columbia).
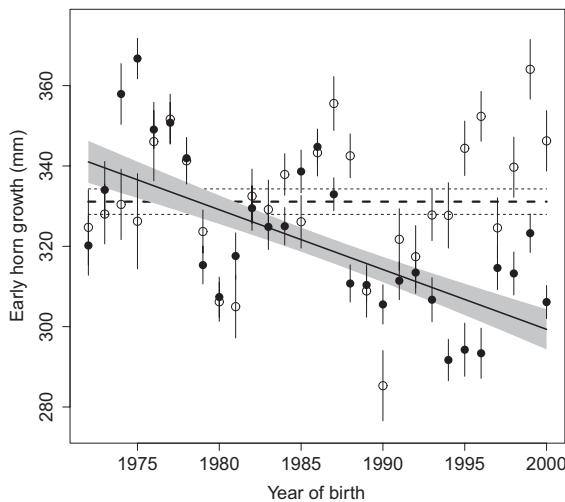

FIG. 5. Early horn growth (adjusted for winter Pacific Decadal Oscillation [PDO_W] and hunter origin; Table 2) of Stone's rams as a function of year of birth for cohorts born between 1972 and 2000 in the low (open circles and dashed line, 95% confidence intervals are shown by dotted lines) and high (solid circles and solid line, 95% confidence intervals are shown by shaded area) hunting areas of British Columbia; vertical lines indicate SE.

accounting for temporal changes in hunting pressure in the region (slope of -1.25 ± 0.16, $P < 0.001$).

In both regions, seniority of the cohort interacted with harvest age to affect total horn length (all $P < 0.001$). Horn length for males aged 5–7 years increased over time in the low hunting area and was stable in the high hunting area (between-region difference in slope = 1.34 ± 0.53, $P = 0.012$, Appendices S4 and S5, Fig. 6A, D). Horn length for males aged 8–10 years varied between cohorts but showed no linear temporal trend in the low hunting area. It declined by 3.4% over time in the high hunting area (between-region difference in slope = 0.61 ± 0.33, $P = 0.06$, Appendices S4 and S5, Fig. 6B, E). Horn length for males aged 11–13 years declined by 5% and 3.4% over time in the low and high hunting areas, respectively (between-region difference in slope = 0.56 ± 0.80, $P = 0.53$, Appendices S4 and S5, Fig. 6C, F). While PDO_W had a positive influence on horn length in some age groups, there were no detectable effects of PDO_S on horn length at a given age (Appendices S4 and S5).

In the low hunting area, the allometric coefficients between horn length and base were similar between the older and more recent cohorts (difference of -0.017 ± 0.053, $P = 0.75$). For a given horn base, horns were slightly longer for recent cohorts (difference in intercept of 0.0068 ± 0.0030, $P = 0.02$). These results did not change when we only considered males older than 7 years (interaction between cohort seniority and horn base = -0.017 ± 0.054, $P = 0.75$, additive effect of cohort seniority = 0.0057 ± 0.0034, $P = 0.09$). In the high hunting area, there was no interaction between cohort seniority and horn base (difference in allometric coefficient of -0.001 ± 0.036, $P = 0.97$). In support of H5, the intercept was higher for older than for more recent cohorts (difference of -0.0064 ± 0.0020, $P = 0.001$), especially for males aged 8–13 years (difference of -0.014 ± 0.002, $P < 0.001$, Appendix S6). For the mean horn base circumference, males aged 8–13 years born in 1987–2000 had horns 1.33 cm (95% CI = 1.06, 1.61 cm) shorter than males born in 1972–1986.
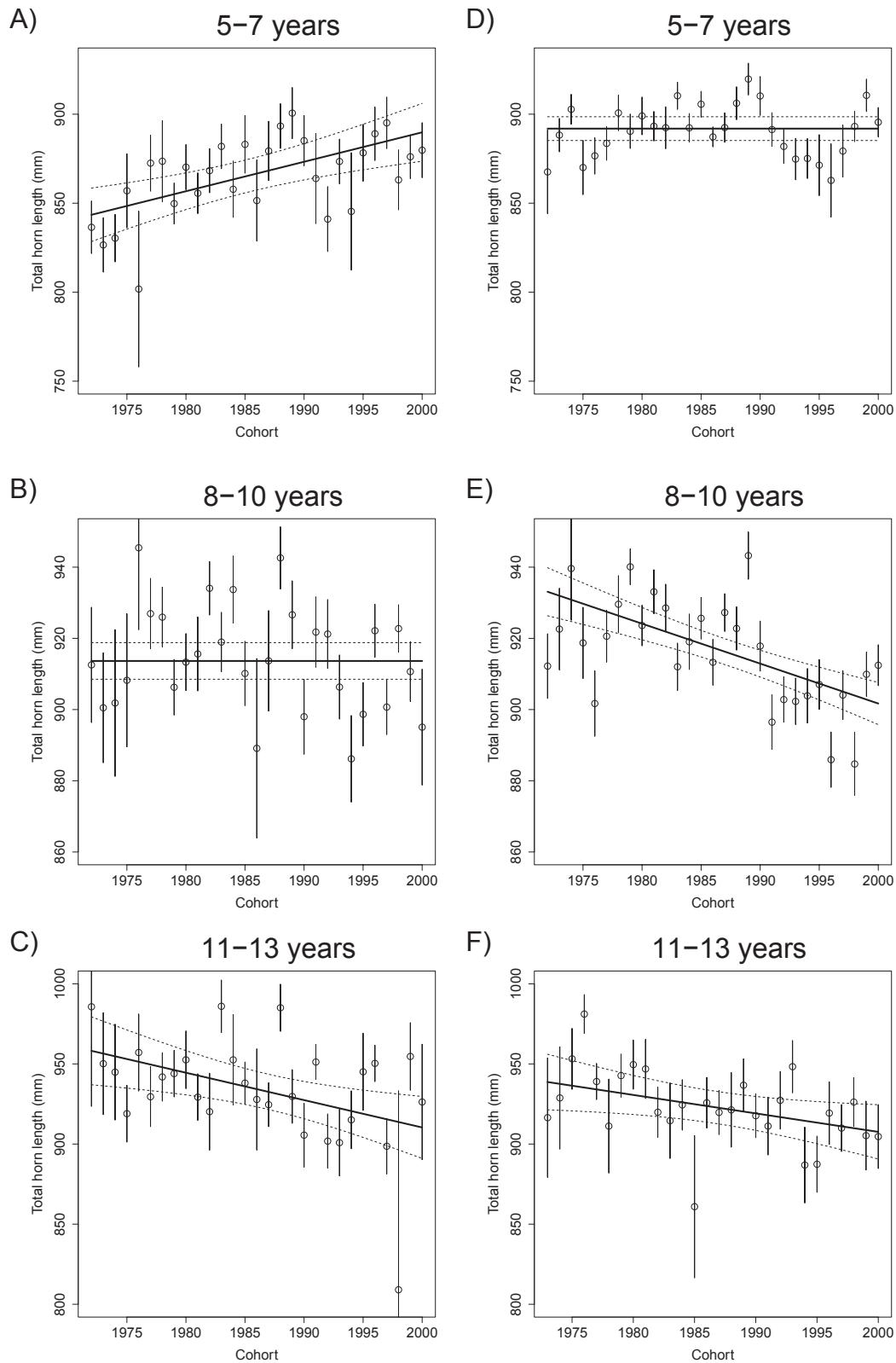
FIG. 6. Age-specific total horn length of Stone's rams harvested in the low (A–C) and high (D–F) hunting areas of British Columbia as a function of year of birth for cohorts born between 1972 and 2000. Points are mean (± SE) observed values, solid lines are predicted age-specific temporal trends, and dotted lines indicate the 95% confidence intervals.

cohort's early horn growth in the high hunting area (β = 1.12 ± 0.60, P = 0.07, R^2 = 0.12). The number of males harvested from each cohort in the high hunting area increased for cohorts born through the 1970s and then decreased by 45% (from 285 born in 1980 to 156 born in 2000; β = 2015.2 ± 643.2, β^2 = −0.5 ± 0.01, P = 0.004, R^2 = 0.33). In contrast, the number of harvested males from each cohort was rather stable in the low hunting area (β = 0.03 ± 0.21, P = 0.88, R^2 < 1%). These results support H6: the number of legal males decreased over time only in the high hunting area.

DISCUSSION

Horn growth and availability of trophy Stone's males decreased over time in the high hunting area, where selective harvest was strongest. Early horn growth declined by 12% over 37 years, age-specific horn length declined for males aged 8 years and older, horn length became shorter for a given horn base, and the number of harvested males declined over time. In contrast, in the low hunting area, early horn growth, age-specific horn length, horn length for a given base, and yearly harvests did not decline over time. The only exception was a decline for the oldest males (>10 years) that represented only 12% of the harvest. These results provide important insights on the conditions under which selective hunting can impact horn growth in harvested populations.

Regional differences in selective harvest effects

Over time, harvest pressure became increasingly higher in Peace (high hunting area) than in Skeena (low hunting area), likely because of easier access to hunting areas. Road density nearly doubled from 1988 to 1999 in British Columbia, but is much greater in the high hunting area (Gayton 2007). Roads increase vulnerability of wildlife to hunting (Brody and Pelton 1989). Although all Stone's sheep populations are now accessible to some degree either by road, all-terrain vehicle, horse, float plane, or riverboat (B. Jex and C. Thiessen, *personal communication*), those closer to roads experience greater hunting pressure than those further away (Paquet and Demarchi 1999). The higher proportion of males harvested by nonresidents in the low hunting area compared to the high hunting area is consistent with greater access in the latter. Nonresidents must be accompanied by a licensed guide and guiding services are costly (currently about $34000 Canadian dollars; CAD). Guides deploy substantial efforts to access remote areas and find the largest trophies. Hence, nonresidents shot older males with greater age-specific horn length than those taken by resident hunters. In addition, guides are rewarded for harvesting old males and penalized for taking young males in their subsequent quota allocation (B. Jex,

personal communication), creating an incentive to harvest older males. The difference in harvest age and horn length at a given age of males according to hunter residency underlines that large males remain available to be harvested, likely in more inaccessible sites. This result also suggests that harvest by nonresidents has lower selective effects than harvest by residents, as the latter tend to remove more young males with fast-growing horns before those males have an opportunity to become dominant. In contrast, a recent study of a related species in Alberta, the bighorn sheep, found no effect of hunter residency on horn size of harvested males, suggesting that few survive to grow long horns (Festa-Bianchet et al. 2014).

As a possible consequence of the difference in harvest pressure between the two regions, males were harvested at a younger age for a given early horn growth in the high than in the low hunting area. Males harvested before 8 years had also longer horns at a given age in the high compared to the low hunting area, while the reverse was true for individuals harvested at older ages (Fig. 4). Differences in horn shape may partly account for the difference in horn length among rams aged 5–7 years: if rams in the high hunting area had horns describing wider curls, they would need a greater horn length to reach legal status. Among males older than 10 years at the population level, horn length seemed to reach an asymptote in relation to age at harvest in the high hunting area, but continued to increase with age in the low hunting area. This was consistent with regional differences in hunting pressure: intense removal of males with rapid early horn growth at an early age left mostly males with slow early growth to survive to old age, decreasing the mean horn length.

Strong selection against fast horn growth in young adults increases the proportion of males with small horns at older ages, especially in the region with higher harvest intensity. This age- and phenotypic-specific mortality is particularly important for the possible evolutionary effects of selective hunting, because large horns do not confer a fitness advantage to young males (Coltman et al. 2002). On the other hand, males harvested in the high hunting area had thicker horn bases than those in the low hunting area. Because the definition of legal male is based on age and horn length, base circumference is not a direct target of artificial selection (Pelletier et al. 2012). Thicker bases in the high than in the low hunting area suggest that overall the high hunting area produces larger-horned males, and argue against a possible effect of an increase in population density over time in reducing both the number and the horn length of males harvested in the high hunting area. We speculate that without selective hunting, males in the high hunting area should have longer horns at any age than males in the low hunting area. That is because males in the high hunting area have thicker horn bases and longer horns at ages 5–8. Instead,

most males that may have developed large horns in the high hunting area were apparently shot at young ages.

Spatiotemporal changes in horn characteristics

Although it is often suggested that larger horns may lower survival (Loehr et al. 2010), there is little empirical evidence of such costs in large herbivores (Bonenfant et al. 2009). For instance, early horn growth had no impact on longevity (Bergeron et al. 2008) or future survival (Toïgo et al. 2013) in Alpine ibex (*Capra ibex*). Natural selection coexists with artificial selection that generates a negative association between early horn growth and survival. The relative strength of these two opposing evolutionary forces shapes horn growth. The decreasing trend in early horn growth limited to the high hunting area (Fig. 5) is consistent with a phenotypic response to selective harvest. Hunting pressure increased over time in the high hunting area, particularly in the late 1980s, while it changed little in the low hunting area (Fig. 2). Greater hunting pressure led to a decrease in mean horn growth of harvested rams in the high hunting area, likely because as harvest pressure increases some hunters will take smaller rams that may otherwise have survived. The analysis by cohort reported in Fig. 5, however, is mainly unaffected by this change because only males from cohorts between 1972 and ca. 1977 would have been harvested when hunting pressure was relatively lower in 1976–1985. Between ca. 1989 and 2012 there was no obvious temporal trend in hunting pressure in the high hunting area. As expected if early horn growth decreased over time, for successive cohorts a smaller proportion of the harvest was made up of rams aged 5–7 in the high hunting area, although much of that decline took place over the first few years of the time series (Appendix G). Total horn length also declined in the high hunting area but only for males >7 years. The probability to reach legal status increases with age (Festa-Bianchet et al. 2014), therefore the difference in horn size between the harvested sample and the overall population (Pelletier et al. 2012) likely decreased with age.

Analyses of Dall sheep in the Yukon show a slight increase in horn growth over time, suggesting a moderate hunting intensity in that territory (Loehr et al. 2010). When hunting pressure remains low, some males with fast-growing horns likely reach the age at which large horns improve reproductive success, mitigating the impact of artificial selection (Festa-Bianchet and Lee 2009). Refugia from hunting such as the Spatsizi wilderness park in the low hunting area could also counter artificial selection by providing a source of non-selected immigrants (Tenhumberg et al. 2004, but see Pelletier et al. 2014). A recent study in Hungary reported no long-term negative trend in red deer antler size despite more than a century of trophy hunting

(Rivrud et al. 2013). Unlike horns, however, antlers are regrown each year and are strongly influenced by interannual variation in environmental conditions (Schmidt et al. 2001, Kruuk et al. 2002). The strength of relationships between trophy size, age, and reproductive success also modulates the response to artificial selection. In chamois (*Rupicapra rupicapra*), for instance, males with rapid early growth do not develop into the largest adults and sexual selection appears relatively weak, likely limiting the potential evolutionary effects of selective removals of large-horned males (Rughetti and Festa-Bianchet 2010). On the other hand, selective hunting induced evolutionary responses in bighorn sheep because horn size is a heritable trait in this species (Coltman et al. 2003, Poissant et al. 2008) and males with fast-growing horns are harvested before the age at which large horns influence reproductive success (Coltman et al. 2002, 2003). A recent study questioned this result (Traill et al. 2014), but their model examined a fictitious harvest based on ram mass, which is not the direct target of hunter selection, and ignored the heritability of adult mass (Hedrick et al. 2014, Chevin 2015). Although there are no data on heritability of horn size or on the relationships between horn length and age-specific reproductive success in Stone's sheep, similarities in sexual size dimorphism, mating system, and age-specific horn growth among species of mountain sheep in North America (Krausman and Bowyer 2003) suggest that evolutionary responses to selective hunting in Stone's sheep should be similar to those reported for bighorns.

Changes in environmental conditions should be accounted for in analyses of temporal trends in horn or antler size. Development of horns and antlers is affected by factors influencing food quantity or quality, such as population density and climate (Jorgenson et al. 1998, Schmidt et al. 2001, Festa-Bianchet et al. 2004, Mysterud et al. 2005). We controlled for climate, but unfortunately, no reliable measure of density was available, a problem often encountered in studies examining the effects of trophy hunting at large spatial scales (e.g., Rivrud et al. 2013). Local wildlife managers' opinions and aerial counts conducted every 3 or 4 years between 1987 and 2011, however, suggest that density of Stone's sheep was relatively stable over time in both regions (Demarchi and Hartwig 2004, Kuzyk et al. 2014). It is unlikely that the changes in horn shape suggested by the decrease in length for a given horn base were due to changes in environmental conditions (Garel et al. 2007). Selection on a heritable trait does not always lead to evolutionary change (Kruuk et al. 2002, Ozgul et al. 2009). Thus, we cannot affirm that evolution of smaller growing horns is responsible for the observed decline in horn growth under high hunting pressure. Our results, however, suggest that hunter selection has likely played a role in this decline.

Management implications

We suggest that the decline in male harvest in the high hunting area was partly a consequence of decreasing horn growth. Slow-growing horns require more time to reach legal status, so that more males will die from natural causes before they can be harvested. Monitoring of marked bighorn rams in two populations revealed that 19–27% of 4-year-olds die of natural causes before reaching age 6 (Loison et al. 1999), and age-specific mortality rates of Stone's rams are likely similar. The decline over time in the proportion of harvested males aged 5–7 years also supports our contention of decreasing horn growth rate (Appendix G). Although aerial counts suggested no decrease in density of sheep in this region, we cannot completely rule out a decrease in population abundance or in the number of males, since no reliable measures of density or population sex–age structure were available. Even if other causes contributed to the decline in harvest rate, however, selection favoring the survival of males with smaller growing horns would also reduce the availability of legal males. In the low hunting area, where horn growth did not show any clear temporal trend, harvest remained stable.

Trophy hunting is an important economic activity in British Columbia, where hunters generated $48 million CAD in 2003 (Demarchi and Hartwig 2004), and elsewhere (Leader-Williams et al. 2001, Lewis and Alpert 1997), potentially contributing to conservation and management (Lewis and Alpert 1997, Lindsey et al. 2007). For instance, a portion of hunting revenues in British Columbia finances sheep range improvements (Demarchi and Hartwig 2004). Sustainable harvest, however, must consider trade-offs between economic benefits and evolutionary, not just ecological, consequences (Garel et al. 2007). By favoring males with small horns, excessive hunting may reduce the availability of desirable phenotypes. Our analyses reveal that low harvest intensity, for instance by limiting the number of permits, is an effective way to limit the undesirable effects of hunter selection. What remains uncertain is the actual rate of harvest that may avoid evolutionary effects: to estimate that rate one needs information on the availability of legal males.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/14-1461.1/suppinfo

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.df81n