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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 respectively by 12% and 45% 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; evolutionary change; harvest intensity; long-
term changes; Ovis dalli stonei; 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.

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 about 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 non-resident hunters (Mysterud et al. 2006,
Schmidt et al. 2007, Rivrud et al. 2013). For example, in Alaska 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 non-residents, who pay substantial fees to obtain large trophies. Surprisingly, however, in Alberta 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 non-resident 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 non-residents. We used measurements of approximately 10,000 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 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, non-resident hunters must engage a licensed guide. Guides try to satisfy their clients by providing an opportunity to harvest a large trophy.
Therefore, we expected non-residents 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).

MATERIAL AND METHODS

Study areas and hunting pressure

We studied Stone’s sheep in the Skeena Region, north-western British Columbia and the Peace Region, north-eastern 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 to 2011, provided by the British Columbia Fish, Wildlife and Habitat Management branch. To measure hunting pressure, we divided the average number of hunters by the area of Stone’s sheep range in each region.

Harvest regulations
Sport harvest of Stone’s sheep in British Columbia is restricted to males of either at least 8 years 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 August 1 and ended October 15. 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 about 250 permits.

Stone’s sheep data

All harvested Stone’s sheep must undergo compulsory inspection. We obtained measurements of 12,749 males (3,610 from Skeena and 9,139 from Peace) collected from 1975 to 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 non-resident). Horns grow from April to 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 about 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 dataset. 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 (9 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. d. 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, obtained from
http://jisao.washington.edu/pdo/PDO.latest, for two seasons that could affect horn growth. 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 average 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 2-level factor and the interaction between region and early growth. To investigate if there was a change in selection over time, we re-analyzed 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 non-resident hunters (H3), we used a $\chi^2$-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 non-resident 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\textsubscript{W} and PDO\textsubscript{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 average horn size is accounted for by each covariate. Auto-correlation 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 size metrics, we used generalized least square models (function ‘gls’ in R library ‘nlme’). We ran each model with a first order auto-regressive 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 2-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.

RESULTS

Contrasting hunting pressures

There were on average 2.3 times more hunters/year in the Peace than in the Skeena region (561 ± 23 vs. 246 ± 7). Stone’s sheep range was larger in the Skeena (23,360 km$^2$) than in the Peace (19,194 km$^2$). Therefore, hunting pressure was about 2.7 times higher in the Peace than in the Skeena (chi-square test for equality of two proportions: $\chi^2_1 = 6932$, $P < 0.001$) 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 area.

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 A). 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
about 9 years and appeared to decline for the oldest males ($\geq 13$ years), but increased
continuously with age at harvest in the ‘low’ hunting area. These results were similar when
excluding the first increment (Appendix B). 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
($F_{1,9340} = 0.36, P = 0.55$). 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 non-residents during the study period differed between regions ($\chi^2_1 = 131.30$, $P < 0.001$). In the ‘low’ hunting area, non-resident 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 non-residents (‘low’ hunting area: $\chi^2_8 = 53.50$, $P < 0.001$, ‘high’ hunting area: $\chi^2_8 = 212.41$, $P < 0.001$). The harvest by resident hunters included a greater proportion of males < 8 years of age and proportionately fewer older males than the non-resident harvest (Appendix C). Non-resident 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 non-residents 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 non-resident hunters harvested older males with longer horns at a given age than residents of British Columbia.

**Spatio-temporal trends**

There were strong regional differences in temporal trends for early horn growth (between-region difference in slope = $2.03 \pm 0.26$, $P < 0.001$). 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 average 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 $785.92 \pm 191.79$, $P < 0.001$) but not in the ‘low’ hunting area (slope of $265.17 \pm 903.37$, $P = 0.77$). Early horn growth in the ‘high’ hunting area declined by 10.4% also after accounting for temporal changes in hunting pressure in the region (slope of $-1.25 \pm 0.16$, $P < 0.001$).

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 = $1.34 \pm 0.53$, $P = 0.012$, Appendix D and E, Fig. 6A and Fig. 6D). 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 = $0.61 \pm 0.33$, $P = 0.06$, Appendix D and E, Fig. 6B and Fig. 6E). Horn length for males aged 11-13 years declined by 5% and 3.4% over time in the ‘low’ and ‘high’ hunting area, respectively (between-region difference in slope = $0.56 \pm 0.80$, $P = 0.53$, Appendix D and E, Fig. 6C and Fig. 6F). 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 (Appendix D and E).

In the ‘low’ hunting area, the allometric coefficients between horn length and base were similar between the older and more recent cohorts (difference of $-0.017 \pm 0.053$, $P = 0.75$). For a given horn base, horns were slightly longer for recent cohorts (difference in intercept of $0.0068 \pm 0.0030$, $P = 0.02$). These results did not change when we only considered males older than 7 years (interaction between cohort seniority and horn base = $-0.017 \pm 0.054$, $P = 0.75$, additive effect of cohort seniority = $0.0057 \pm 0.0034$, $P = 0.09$). 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 F). For the average 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.

The number of harvested males from each cohort tended to be positively related to the cohort’s early horn growth in the ‘high’ hunting area ($\beta = 1.12 \pm 0.60$, $P = 0.07$, $R^2 = 0.12$). The number of males harvested from each cohort in the ‘high’ hunting area increased for cohorts born through the 1970’s and then decreased by 45% (from 285 born in 1980 to 156 born in 2000; $\beta = 2015.2 \pm 643.2$, $\beta^2 = -0.5 \pm 0.01$, $P = 0.004$, $R^2 = 0.33$). In contrast, the number of harvested males from each cohort was rather stable in the ‘low’ hunting area ($\beta = 0.03 \pm 0.21$, $P = 0.88$, $R^2 < 1\%$). 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.
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 non-residents in the ‘low’ hunting area compared to the ‘high’ hunting area is consistent with greater access in the latter. Non-residents must be accompanied by a licensed guide and guiding services are costly (currently about $34,000 CAD). Guides deploy substantial efforts to access remote areas and find the largest trophies. Hence, non-residents 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 non-residents 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
eyearly growth to survive to old age, decreasing the average 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.
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 co-exists 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 1980’s, while it changed little in the ‘low’ hunting area (Fig. 2). Greater hunting pressure led to a decrease in average 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 about 1977 would have been harvested when hunting pressure was relatively lower in 1976-1985. Between about 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 inter-annual 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 in press).

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 to 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 millions 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.

ACKNOWLEDGEMENTS

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LITERATURE CITED


Mysterud, A., P. Tryjanowski, and M. Panek. 2006. Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. Biology Letters 2:632-635.


Appendix A

A figure showing the relationships between early horn growth and age at harvest for Stone’s rams in both hunting areas of British Columbia during two periods of study.

Appendix B

A figure showing relationship between harvest age and horn length excluding the first annual increment for Stone’s rams.

Appendix C

A figure showing age distribution of Stone’s rams harvested by resident and non-resident hunters.

Appendix D

A table showing effects of time on total horn length of Stone’s rams harvested in the ‘low’ hunting area.

Appendix E

A table showing effects of time on total horn length of Stone’s rams harvested in the ‘high’ hunting area.

Appendix F

A figure showing allometric relationships between horn length and horn base of males aged 8-13 years during two periods of study in the ‘high’ hunting area.

Appendix G

A figure showing proportion of harvested males aged 5 to 7 years as a function of year of birth in the ‘high’ hunting area.
Table 1: Hypotheses and predictions relating selective harvest and changes in horn development of Stone’s sheep in British Columbia.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Rationale</th>
<th>Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Selective harvest</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H1. Trophy hunter</td>
<td>Trophy hunting removes males with fast-growing horns but selection intensity varies with hunting pressure</td>
<td>Rams with rapid early horn growth will be harvested at a younger age in both areas, but more markedly in the ‘high’ hunting area</td>
</tr>
<tr>
<td>H2. Filtering effect</td>
<td>Horn length does not increase continuously with harvest age at the population level if males with slower horn growth survive to older ages</td>
<td>The average horn length for older males harvested in the ‘high’ hunting area will reach an asymptote or even decline with age</td>
</tr>
<tr>
<td>H3. ‘Hunter origin’</td>
<td>Non-resident hunters must hire a guide. Guides deploy substantial effort to find larger trophies</td>
<td>Non-residents take older males with larger horns than residents</td>
</tr>
<tr>
<td><strong>Long-term changes in horn development</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H4. Evolutionary</td>
<td>The intense removal of large-horned males can lead to Horn growth declines over time in the ‘high’ hunting area only</td>
<td></td>
</tr>
</tbody>
</table>


trophy hunting for horn growth

H5. Evolutionary effects of trophy hunting on horn shape

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 the ‘high’ hunting area only.

H6. Intense trophy hunting reduces availability of trophy rams

Rams must have horns describing a complete curl to be harvested. Cohorts with slow-growing horns are thus 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.
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. These effects were tested with an analysis of deviance (ANODEV, see main text for details). \( P_{\text{ANODEV}} \) is the P-value of the ANODEV test on covariates while \( R^2_{\text{dev}} \) quantifies how much of the temporal variation in average horn growth is accounted for by each covariate. \( k \) stands for the number of parameters in the model. PDO\(_W\) and PDO\(_S\) are average 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 (non-residents vs. residents of British Columbia).

<table>
<thead>
<tr>
<th>Region</th>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>( P_{\text{ANODEV}} )</th>
<th>( R^2_{\text{dev}} )</th>
<th>Slope (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Skeena</strong> (‘low’ hunting area)</td>
<td>Constant</td>
<td>3</td>
<td>25403.17</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cohort dependent</td>
<td>31</td>
<td>25282.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Covariate models</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PDO(_W)</td>
<td>4</td>
<td>25400.17</td>
<td>0.41</td>
<td>0.02</td>
<td>4.38 ± 2.52</td>
</tr>
<tr>
<td></td>
<td>PDO(_S)</td>
<td>4</td>
<td>25401.39</td>
<td>0.53</td>
<td>0.01</td>
<td>-3.67 ± 2.74</td>
</tr>
<tr>
<td></td>
<td>T</td>
<td>4</td>
<td>25397.30</td>
<td>0.25</td>
<td>0.05</td>
<td>0.50 ± 0.21</td>
</tr>
<tr>
<td><strong>Peace</strong> (‘high’ hunting area)</td>
<td>Base</td>
<td>4</td>
<td>56831.26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cohort dependent</td>
<td>32</td>
<td>56589.26</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Covariate models</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PDO(_W)</td>
<td>5</td>
<td>56824.90</td>
<td>0.40</td>
<td>0.03</td>
<td>4.76 ± 1.89</td>
</tr>
<tr>
<td>Variable</td>
<td>Value 1</td>
<td>Value 2</td>
<td>Value 3</td>
<td>Value 4</td>
<td></td>
<td></td>
</tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>PDOS</td>
<td>5</td>
<td>56825.20</td>
<td>0.41</td>
<td>0.03</td>
<td>-5.04 ± 2.05</td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>5</td>
<td>56733.45</td>
<td>&lt; 0.001</td>
<td>0.40</td>
<td>-1.53 ± 0.15</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1. Study area and distribution of Stone’s sheep in British Columbia. We analyzed data from males harvested within the two polygons. We excluded the Omineca Region on the advice of provincial wildlife biologists as very few sheep were harvested there.

Fig. 2. Yearly variations in number of hunters, divided by the area of Stone’s sheep range in two regions of British Columbia (black circles, Peace region or ‘high’ hunting area; white circles, Skeena region or ‘low’ hunting area).

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’ (white circles, solid line and 95% confidence intervals shown by dotted lines) and ‘high’ (black circles, solid line and shaded area for 95% confidence intervals) hunting areas of British Columbia. Points are average (± SE) harvest age for each class of 50-mm/2 years 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.

Fig. 4. Relationship between harvest age and A) total horn length, B) horn base circumference of Stone’s rams harvested in the ‘low’ (white circles, dashed line and 95% confidence intervals are shown by dotted lines) and ‘high’ (black circles, solid line and a shaded area for 95% confidence intervals) hunting areas of British Columbia.

Fig. 5. Early horn growth (adjusted for PDO 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’ (white circles, dashed line and 95% confidence intervals are shown by dotted lines) and ‘high’ (black circles, solid line and a shaded area for 95% confidence intervals) hunting areas of British Columbia.
Fig. 6. Age-specific total horn length of Stone’s rams harvested in the ‘low’ (A, B and C) and
‘high’ (D, E, and F) hunting areas of British Columbia as a function of year of birth for cohorts
born between 1972 and 2000. Points are average (± SE) observed values, solid lines are
predicted age-specific temporal trends and dotted lines indicate the 95% confidence intervals.
Total horn length (mm)

Harvest age (yr)
8–10 years

B)
C) 11–13 years

The graph shows the total horn length (mm) over different cohorts from 1975 to 2000. The x-axis represents the cohort year, while the y-axis indicates the total horn length in millimeters. The data points are scattered with error bars indicating variability.
D) 5–7 years

![Graph showing total horn length (mm) across different cohorts from 1975 to 2000. The x-axis represents the cohort, and the y-axis represents total horn length in millimeters. The data points are marked with circles, and error bars indicate variability. The graph shows a range of total horn lengths with a peak around the 5–7 year mark.]
E) **8–10 years**

![Graph showing total horn length (mm) over various cohorts from 1975 to 2000.](image)
F) 11–13 years

- Total horn length (mm)
- Cohort

- Bars represent the range of total horn length for each cohort.