



Testing the importance of harvest refuges for phenotypic rescue of trophy-hunted populations

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Handling Editor: Johan du Toit**Abstract**

1. Sustainable exploitation must minimize its impact on the ecology and evolution of exploited wildlife. Intense phenotype-based selective harvests can induce evolutionary change. Refuges could mitigate those evolutionary effects if individuals not subject to selective hunting in harvest refuges migrated and reproduced in hunted areas. The role of harvest refuges on phenotypic rescue of trophy-hunted species, however, has rarely been tested.
2. We investigated spatial and temporal variation in the effect of refuges on horn size and age at harvest in bighorn sheep *Ovis canadensis*. We analysed data on 5,826 males harvested over 39 years in Alberta, Canada.
3. Horn length, a trait targeted by hunters, and age at harvest increased with the amount of protected areas 5–40 km around each kill. Horn base circumference, however, was independent of proximity to refuges.
4. The number of males harvested increased during the last 10 days of the hunting season in late October, corresponding to the timing of bighorn male breeding migrations. Males shot during those 10 days were on average 17% closer to a refuge than males shot earlier in the season. Apparently, some large males exit refuges late in the hunting season, are shot, and cannot contribute to rescue. Uncertainty remains about the proportion of males exiting refuges after the hunting season and how many survive to reproduce.
5. *Synthesis and applications.* Harvest refuges are unlikely to rescue hunted populations of bighorn sheep in Alberta, because some males exiting refuges are at risk of harvest before they mate. For phenotypic rescue to be effective, unselected males must reproduce before they are shot. Closing the hunting season 10 days earlier would increase survival of unselected rams exiting refuges.

KEYWORDS

bighorn sheep, harvest refuge, horn size, phenotypic rescue, protected areas, size-selective harvest, source–sink dynamics, trophy hunting

1 | INTRODUCTION

Harvest of animals whose home ranges overlap protected areas is a major concern for the conservation of biological diversity,

especially when protected areas are small, and harvest rates high, as reported for lions *Panthera leo* (Loveridge, Searle, Murindagomo, & Macdonald, 2007). That is because edge effects, such as intense harvests along boundaries, can affect population and community

ecology inside protected areas. Alternatively, protected areas can be part of a large-scale management system to support harvested populations, particularly in marine environments (Baskett, Levin, Gaines, & Dushoff, 2005) by acting as a source of harvestable individuals. For trophy-hunted species, which can provide income to support conservation activities (Di Minin, Leader-Williams, & Bradshaw, 2016), protected areas may also be a source of individuals not subject to the selective pressure of intense trophy hunting, countering the potential evolutionary effects of selective harvest (Pigeon, Festa-Bianchet, Coltman, & Pelletier, 2016).

Selective harvesting can exert strong pressure on the phenotype of harvested species (Baskett et al., 2005; Ernande, Dieckmann, & Heino, 2004; Fenberg & Roy, 2008). High harvest rates of males with large secondary sexual characters such as horns, antlers or tusks can affect the mean and the variability of those traits, and reverse the relationship between male fitness and trait size from that seen in unharvested populations (Allendorf & Hard, 2009). Regulations enforcing size-selective harvests are frequently used to protect young males, but may favour individuals with slower growth (Tenhumberg, Tyre, Pople, & Possingham, 2004). For instance, modelling studies of moose *Alces alces* (Hundertmark, Thelen, & Schwartz, 1983) and elk *Cervus elaphus* (Thelen, 1991) suggested that size-selective harvests may change the frequency of alleles affecting antler growth. Selective harvesting may reduce population growth if alleles associated with trophy size also affect life-history traits (Coltman, O'Donoghue, Hogg, & Festa-Bianchet, 2005; Knell & Martínez-Ruiz, 2017). Rates of phenotypic change due to anthropogenic selective pressures are higher than those induced by natural selection (Darimont et al., 2009) because harvest-induced selective pressures are often stronger than natural selection (Conover, Munch, & Arnott, 2009). Selective harvest may thus have undesirable evolutionary consequences, such as shorter horns in wild sheep (Douhard, Festa-Bianchet, Pelletier, Gaillard, & Bonenfant, 2016; Garel et al., 2007; Hengeveld & Festa-Bianchet, 2011; Pigeon et al., 2016). Decreasing horn growth over time was also documented by Crosmarty et al. (2013) for trophy-hunted male impala *Aepyceros melampus* and sable antelope *Hippotragus niger* in Zimbabwe. For greater kudu *Tragelaphus strepsiceros*, however, horn growth increased over time (Crosmarty et al., 2013).

The evolutionary consequences of intense selective hunting may be alleviated if individuals from harvest refuges reproduce in hunted areas (Baskett et al., 2005; Carr & Reed, 1993; Dunlop, Baskett, Heino, & Dieckmann, 2009; Quinn, Wing, & Botsford, 1993; Tenhumberg et al., 2004). A phenotypic rescue from harvest refuges can be assessed by examining the traits of harvested individuals, with the expectation that larger individuals will be found near refuges. Those phenotypic measurements, however, cannot distinguish between a genetic rescue, stimulated by males exiting refuges and breeding in hunted areas, and a phenotypic effect of larger, unselected males exiting refuges and being shot. Emigrants from protected areas may also increase the overall harvest in hunted areas.

Most research on harvest refuges has focused on marine ecosystems, where size-selective fishing can lead to phenotypic and

evolutionary changes over a few generations (reviewed in Hutchings & Fraser, 2008). Intense selective fishing can affect growth rate and timing of maturation (reviewed by Heino & Godø, 2002). Marine protected areas (Pauly et al., 2002) may help population recovery, increase population persistence and protect source populations that may sustain fished populations (Baskett et al., 2005; Murray et al., 1999). A large marine harvest refuge may increase average age and size at maturation in exploited areas, if protected areas provide individuals not subjected to heavy pre-breeding harvest (Trexler & Travis, 2000).

The potential for harvest refuges to mitigate the selective effects of trophy hunting on secondary sexual traits in terrestrial mammals has rarely been tested. Crosmarty et al. (2013) showed that horn size decreased with distance from a harvest refuge in Zimbabwe for only 1 of 3 ungulate species. Pelletier, Festa-Bianchet, Jorgenson, Feder, and Hubbs (2014) found that the horns of bighorn sheep *Ovis canadensis* males harvested near refuges were 3% longer than those of males harvested far from refuges in Alberta, Canada. They suggested that migration of rams from refuges was insufficient to provide a phenotypic rescue for hunted areas, as horn size declined over time at the same rate in areas near and far from refuges. With effective phenotypic rescue, the decline in horn size over time was expected to be weaker near refuges (Pelletier et al., 2014). That analysis, however, compared Wildlife Management Units that did and did not border protected areas, and could not quantify the spatial extent of a possible effect of harvest refuges on male horn size. Here, we analysed a larger dataset at a finer spatial scale to test whether proximity to refuges affects horn size and age structure of harvested males.

The efficiency of refuges as a source of unselected individuals can vary over time and space, depending on animal behaviour. Phenotypic rescue would be less efficient if males which emigrated were at risk of harvest before they bred. Also, if males prefer to move to areas with reduced competition, such as hunted areas where potential competitors have been shot (Hogg, 2000), protected areas may suffer a decrease in genetic variability over time, as migration may be mostly unidirectional. There is limited information on the breeding migrations of male ungulates, including mountain sheep (Hogg, 2000). Festa-Bianchet (1986, 1991) found that 20%–50% of males from Sheep River, Alberta, left their natal population to rut elsewhere. For the same population, Hogg (2000) found that most males which left rutted 20–25 km away. The breeding migration begins in mid-to late October (Pelletier & Festa-Bianchet, 2006). Thus, males which exit refuges may be at risk of harvest as hunting lasts until the end of October.

Here, we quantify the effects of harvest refuges on horn size and age at harvest for bighorn sheep in Alberta (1975–2013) at a fine spatial scale. Trophy hunting selectively removes bighorn males with rapid horn growth at the age of 4–5 years, before the age when large horns provide high reproductive success (Coltman, Festa-Bianchet, Jorgenson, & Strobeck, 2002). Because the reproductive success of young males is mostly independent of horn size (Martin, Festa-Bianchet, Coltman, & Pelletier, 2016), that management

scheme favours slow horn growth (Coltman et al., 2003; Festa-Bianchet, Coltman, Turelli, & Jorgenson, 2004). Proximity to harvest refuges could influence horn size, but this effect should decline with distance. We also investigated how horn size and ram age varied over the hunting season in respect to proximity to refuges. We expected that in late October males would begin their pre-rut migration (Pelletier, Hogg, & Festa-Bianchet, 2006). We therefore hypothesized that an influx of males with longer horns exiting refuges (Demarchi, 2004; Geist, 1971) would increase the size and age of males harvested near refuges in late October. To test these hypotheses, we analysed horn measurements and age of 5,826 males harvested over 39 years.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

In Alberta, there are about 4,500 bighorn sheep in national parks and 7,000 in provincial lands (Government of Alberta, 2015). A map of hunted and protected areas is provided in Festa-Bianchet, Pelletier, Jorgenson, Feder, and Hubbs (2014). Outside protected areas, bighorn males are hunted based on a definition of minimum horn curl. Since 1971, in most of the province males can be harvested if their horns describe 4/5 of a curl (see Pelletier, Festa-Bianchet, & Jorgenson, 2012 for an illustration of the curl regulation). Sheep in Alberta are more vulnerable to harvest-induced evolutionary change than in other jurisdictions, because the definition of 'legal' male is more permissive (Wild Sheep Foundation Professional Biologist Meeting Attendees, 2008). There is no harvest quota for resident hunters, and the harvest rate of trophy males is likely about 40% higher than in other jurisdictions (Government of Alberta, 2015).

We analysed data collected by Alberta Fish & Wildlife on males harvested by sport hunters from 1975 to 2013. The hunting season begins in late August or early September and usually ends the last day of October. We did not consider males that were poached, found dead or harvested by indigenous people who do not require a license. We also removed 16 individuals with a horn base circumference greater than 50 cm, which is biologically unlikely, 14 with aberrant horn base circumference given the estimated age, and 11 with horn length less than 60 cm. It is nearly impossible for a male to be legally harvested with such short horns (Festa-Bianchet et al., 2014). We retained data from 5,826 males for analyses of total length and base circumference (cm) of both horns, age at harvest (estimated by counting horn annuli; Geist, 1966), kill date and location on the 'Township' scale, an administrative 9.7×9.7 km grid of the province. Hunters must register harvested males with Alberta Fish & Wildlife. Any Alberta resident can purchase one trophy sheep license per year, but cannot buy a license the year after harvesting a trophy ram. Given a hunting success rate of about 7% (Festa-Bianchet et al., 2014), this restriction has little impact on harvest. About 80 additional licenses are available to non-residents,

who must engage a guide. We considered only males killed by rifle under the 4/5 curl regulation and excluded those harvested under a full-curl regulation which applied to a few areas of the province after 1995.

2.2 | Data handling and variable description

We analysed variation in horn length, base circumference and shape. For length, we used the longest horn because horns often break during fights. We used the mean base circumference in analyses. To test for horn shape changes over time, we set horn length as response variable and horn base circumference as a fixed effect. That analysis examined how length varied as a function of circumference. In Stone's sheep *Ovis dalli stonei*, intense selective harvest led to a decrease in the horn length to circumference ratio, likely because thicker horns are effective in male-male combat but longer horns increase the chance that a male would be 'legal' (Douhard et al., 2016). Indeed, base circumference is not directly targeted by hunters (Pelletier et al., 2012). To assess how distance from refuges affected horn size and age at harvest, we estimated the shortest Euclidean distance (km) from the nearest refuge boundary and the proportion of circular buffer zones around each kill site which were inside refuges. We used buffers of 5, 15, 25 and 40-km radii to assess at what distance we could detect an effect. These buffers range from the approximate minimum size of a bighorn sheep winter range (Festa-Bianchet, 1986) to the maximal straight line distance between locations observed for males undergoing breeding commutes before and during the rut (Hogg, 2000). All National and Provincial Parks with no sheep hunting season were considered as harvest refuges. For spatial analyses, we calculated the centroid, in decimal degrees, for each Alberta Township Survey (ATS) square where at least one male had been shot. We used the ATS centroid as the kill location, as this was the smallest scale for which locations were reported. We examined kill locations at both the ATS level and the Sheep Management Area level, a much larger spatial scale. Sheep Management Areas were established by Alberta Fish and Wildlife biologists based on genetic information and major breaks between subpopulations, such as wide river valleys (see Festa-Bianchet et al., 2014 for a map of the eight Areas).

2.3 | Statistical analyses

To determine which spatial scale best explained horn size, horn shape and age at harvest, we developed candidate models including different measures of refuge proximity: shortest Euclidean distance and proportion of harvest refuges at four spatial scales (see Tables S2-S4 and S6 for model details). Euclidean distance tested if the effect of refuges on horn size weakened with distance. Because age-specific horn size declined over time (Festa-Bianchet et al., 2014), in all models, we included harvest year as a continuous variable. We included latitude, that is the ATS centroid in decimal

degrees, as a control variable because bighorn sheep horn size in Alberta decreases from South to North (Gorrell, Kneteman, Hik, & Coltman, 2016). As the beginning and the end of the hunting period changed over years and between Sheep Management Areas, we considered kill date as a three-level period during the hunting season: beginning (first 10 days), middle (from 11 days after opening day to 11 days before closing) and end (last 10 days). We chose these dates because harvest typically peaks in the first few and last few days of the season (Government of Alberta, 2015). The duration of the middle period varied from year to year, with a mean of 60 days, mostly because of differences in start date (range 19 August–9 September). The last day of hunting varied from October 27 to November 1. In addition, we tested the hypothesis that males shot late in the season near refuges had larger horns after accounting for age, expecting that some of those rams were exiting refuges (Hogg, 2000) and therefore came from areas without selective hunting. Age at harvest was entered as a quadratic fixed effect, to account for decreasing horn growth with age (Jorgenson, Festa-Bianchet, & Wishart, 1998). We fitted linear mixed models (Pinheiro & Bates, 2000) with the lmer function of the lme4 R package (Bates, Mächler, Bolker, & Walker, 2015). We used the full model fitted by restricted maximum likelihood and tested the best random effect structure with the likelihood ratio test. Sheep Management Area was included as a random intercept to account for regional differences in horn size and changes in the distribution of harvest over years. Once the best random effect structure was selected, AIC was used to determine the most parsimonious model fitted by maximum likelihood (Burnham & Anderson, 2002). When more than one model was within $\Delta AIC < 2$, we calculated model-averaged estimates and unconditional 95% confidence intervals with multimodel inference (Burnham & Anderson, 2002) with the package AICcmodavg (Mazerolle, 2010). All continuous variables were scaled (mean = 0, variance = 1) and were not multicollinear ($VIF < 2$; Graham, 2003). We considered results significant when the 95% confidence intervals of parameter estimates did not overlap zero. Significant results obtained for horn size and age at harvest were further examined using Tukey's post hoc comparisons with the emmeans R package. All statistical analyses were performed in R 3.3.1 (R Core Team, 2016) and spatial analyses in ArcMap 10.2.2 (ESRI, 2016).

3 | RESULTS

3.1 | Effect of refuges on horn size and age at harvest

Horn length increased with the proportion of harvest refuges within any buffer (Figure 1a, Table 1) and with age (Figure 1c, Table 1). Variation in horn length was best explained by a model with a 15-km buffer, with an AIC weight of 0.50 (model 1, Table S2). Because two models with buffers of 15 or 25 km had $\Delta AIC < 2$, we calculated model-averaged estimates of all variables included in those models

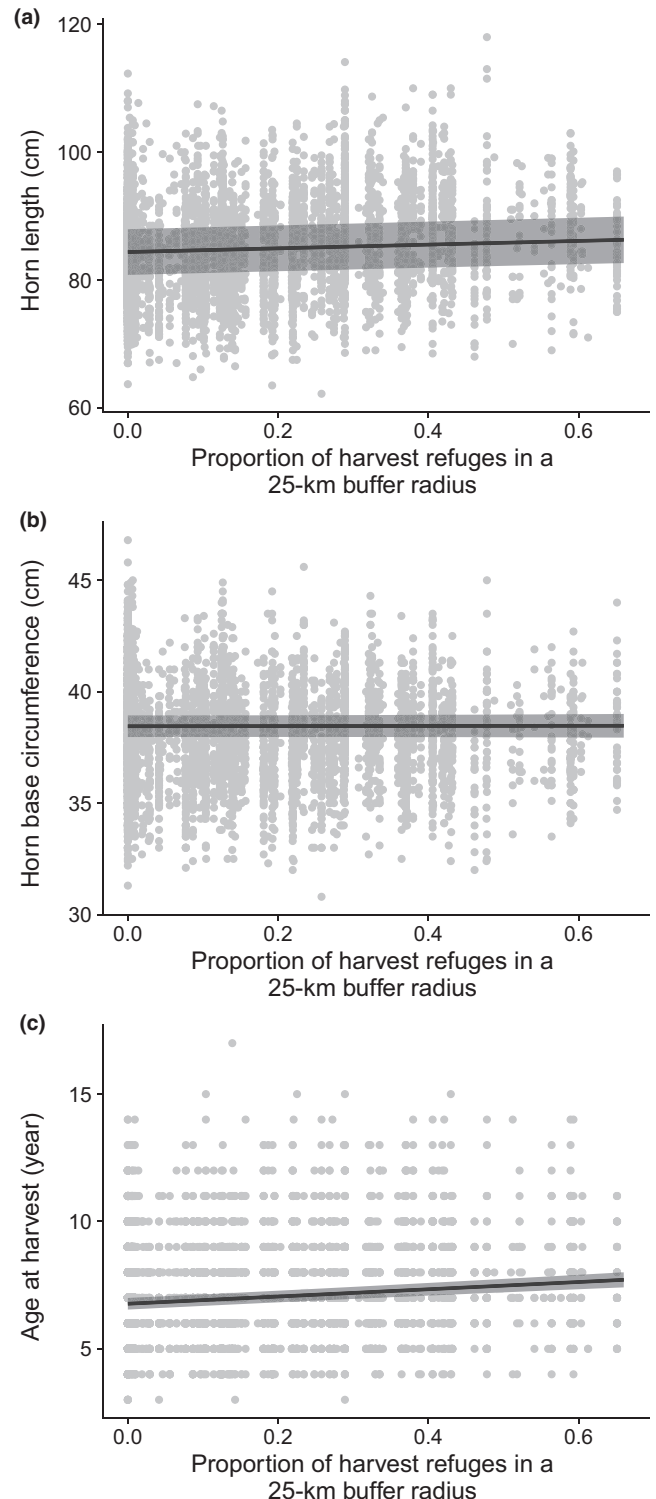


FIGURE 1 Relationship between (a) horn length (cm), (b) horn base circumference (cm), (c) age and the proportion of harvest refuges in a 25 km of 5 826 bighorn sheep males harvested in Alberta, Canada, 1975–2013. 95% confidence intervals are shown by the shaded area

and of the interaction of refuge area with period within the hunting season (Table 1). Horn base circumference was independent of refuge area within any buffer (Figure 1b, Table 2). The significant interaction

TABLE 1 Model-averaged estimates (β) of explanatory variables with unconditional \pm SE and 95% unconditional confidence intervals for models explaining horn length of harvested bighorn sheep males in Alberta, Canada, 1975–2013 (see Table S2)

Variable	β	SE	95% confidence interval	
			Lower limit	Upper limit
Intercept	84.20	1.99	80.30	88.10
Age	8.22	0.43	7.37	9.06
Age ²	-4.42	0.43	-5.26	-3.58
Period-middle	-0.11	0.17	-0.44	0.22
Period-end	0.37	0.19	0.00	0.75
Latitude	-4.04	0.40	-4.81	-3.26
Harvest year	-0.35	0.07	-0.50	-0.21
Refuges within 15 km	0.44	0.08	0.28	0.61
Refuges within 15 km \times period-middle	0.32	0.17	-0.02	0.66
Refuges within 15 km \times period-end	0.26	0.18	-0.10	0.61
Refuges within 25 km	0.47	0.09	0.29	0.65
Refuges within 25 km \times period-middle	0.31	0.17	-0.03	0.64
Refuges within 25 km \times period-end	0.40	0.18	0.04	0.76
Refuges within 5 km	0.30	0.08	0.15	0.45
Refuges within 5 km \times period-middle	0.42	0.17	0.09	0.76
Refuges within 5 km \times period-end	0.15	0.18	-0.20	0.51
Euclidean distance	-0.53	0.12	-0.76	-0.30
Euclidean distance \times period-middle	-0.11	0.17	-0.44	0.22
Euclidean distance \times period-end	-0.47	0.20	-0.85	-0.08
Refuges within 40 km	0.31	0.10	0.10	0.51
Refuges within 40 km \times period-middle	0.29	0.17	-0.04	0.62
Refuges within 40 km \times period-end	0.53	0.19	0.16	0.90

Note: The effects of the proportion of refuges in various buffers were estimated using different models (see methods). Estimates whose 95% unconditional confidence intervals exclude 0 are in bold. The best model, with a 15-km buffer, is presented first. Period refers to the timing of harvest during the hunting season with beginning as reference, then middle and end. 'Refuges' refers to the proportion of buffer area within refuges at different buffers from a kill site. All numerical variables were scaled.

between hunting season period and refuge area in the 25- and 40-km buffers suggested that age-specific horn length increased for rams shot in the last 10 days of the season only near refuges (Table 1). Horn length decreased from south to north. The model with no effect of refuges best explained variation in horn base circumference (model 1, Table S3). Hunting season period had no effect on horn circumference (Table 2). Latitude had weak but significant negative effects on horn circumference.

The model with a 15-km radius buffer best explained variability in horn shape, with an AIC weight of 0.87 (model 1, Table S4). Length increased for a given base circumference with refuge area within a 15-km buffer (Table S5). On average, a male with 38-cm horn base circumference had horns 85.5 cm long in areas with no refuges within 15 km, and 87.7 cm if it was shot in an area with 75% protected areas (i.e. maximum of refuges within the 15-km buffer; Table S1). Harvest year and latitude had significant negative effects on horn shape, with length for a given circumference decreasing over time and from South to North. The 25-km buffer best explained variability in age at harvest, with an AIC weight of 0.60 (model 1,

Table S6). Proportion of refuges in the 25-km buffer and year had significant positive effects on age at harvest (Table 3).

3.2 | Temporal dynamics of horn size, age at harvest and spatial distribution of harvest

After the first 10 days of the season, the number of males harvested declined independently of refuges (Figure 2). A second peak in harvest at the end of the season was only significant in areas with at least some refuges within 25 km (Figure 2). On average, males killed during the last 10 days were 17% closer to refuges (4.2 km) than males shot earlier in the season.

Accounting for age, horn length increased during the last 10 days of the season, but this increase was significant only near refuges (Figure 3a,d), where horn length increased by 1.6 cm compared to earlier in the hunting season. Mean horn circumference did not change during the season (Figure 3b,e). The average age at harvest showed a slight but significant decrease during the middle of the

TABLE 2 Estimates (β), SE and 95% confidence interval of fixed effects included in the best model explaining horn base circumference of harvested bighorn sheep males in Alberta, Canada, 1975–2013 (see Table S3)

Fixed effects	β	SE	95% Confidence interval	
			Lower limit	Upper limit
Intercept	38.47	0.27	37.92	39.01
Period-middle	-0.05	0.06	-0.16	-0.06
Period-end	-0.04	0.07	-0.17	0.09
Latitude	-0.31	0.11	-0.52	-0.10
Age	-0.01	0.15	-0.30	0.28
Age ²	-0.12	0.15	-0.40	0.17
Year	-0.05	0.03	-0.10	0.00
Random effect	Variance	SD		
Sheep management area	0.55	0.74		
Residuals	3.54	1.88		

Note: Estimates whose 95% unconditional confidence intervals exclude 0 are in bold. Period refers to the timing of harvest during the hunting season with beginning as reference, then middle and end. 'Refuges' refers to the proportion of buffer area within refuges at different buffers from a kill site. All numerical variables were scaled.

TABLE 3 Estimates (β), SE, and 95% confidence interval of fixed effects included in the best model explaining age at harvest of bighorn males in Alberta, Canada, 1975–2013 (see Table S6)

Fixed effects	β	SE	95% Confidence interval	
			Lower limit	Upper limit
Intercept	7.03	0.14	6.75	7.29
Refuges within 25 km	0.23	0.03	0.18	0.29
Period-middle	-0.22	0.05	-0.32	-0.11
Period-end	0.08	0.06	-0.04	0.20
Latitude	0.13	0.08	-0.03	0.29
Year	0.11	0.02	0.06	0.15
Random effect	Variance	SD		
Sheep management area	0.13	0.36		
Residuals	3.19	1.79		

Note: Estimates whose 95% confidence intervals exclude 0 are in bold. Period refers to the timing of harvest during the hunting season with beginning as reference, then middle and end. 'Refuges' refers to the proportion of buffer area within refuges at different buffers from a kill site. All numerical variables were scaled.

season and then increased at the end (Figure 3c,f). On average, males harvested in the middle of the season were about 0.40 years younger than those shot at its end. Overall, males shot near protected areas

were about 0.54 years older than those killed in areas with no refuges within 25 km.

4 | DISCUSSION

Our analyses revealed that horn size and age at harvest of bighorn males increased near refuges, in a pattern consistent with the hypothesis that some males exiting refuges are shot, especially in late October. Kill locations were closer to protected areas in late October, and a late-season peak in harvest occurred only near refuges. In addition, males harvested near refuges late in the season were slightly older and had longer horns for their age, again supporting the hypothesis that mature males exit harvest refuges in late October to prospect for mating opportunities (Hogg, 2000). The longer age-adjusted horns of these males may indicate that they originate from populations where the selective pressure of the trophy hunt is weaker. Comparing kill locations with no protected areas within a 25-km buffer and locations with 66% protected areas (i.e. maximum of refuges within the 25-km buffer; Table S1), horn length and age at harvest increased by 2.7 cm and 0.9 years respectively. Although males shot late in the season near refuges had longer horns, they showed a decline in horn length over time. As our analysis is restricted to rams shot by hunters, it likely underestimates the declining trend, as small-horned rams cannot be shot (Pelletier et al., 2012).

The overall slight positive effect of harvest refuges on horn length, independently of period within the hunting season, supports the hypothesis that migration from inside refuges may partly weaken the artificial selective effect of the trophy hunt. Although migration from refuges may prevent evolutionary change induced by size-selective harvesting (Tenhumberg et al., 2004), genetic rescue can only occur if unselected individuals survive the hunting season and reproduce (Pelletier et al., 2014). Winter aerial surveys in Alberta between 2011 and 2013 reported that 13% more males were 'legal' inside national parks than in hunted areas (Government of Alberta, 2015). Therefore, intrasexual competition for breeding opportunities is likely stronger inside refuges. Hogg (2000) reported that middle-ranking males in a small protected area were likely to leave before the rut, and suggested that by entering hunted areas, where many of their competitors would have been shot, these males may improve their mating success. Consequently, it is reasonable to expect gene flow from harvest refuges to protected areas, but only for males that survive the hunting season. Our results underline the need for research on the amount and timing of genetic exchange among protected and hunted areas in terrestrial environments, not only for mountain sheep but also for other species that face similar landscapes with varying degrees of selective harvest (Crosmary et al., 2013; Loveridge et al., 2007).

We found no evidence that horn base circumference varied with refuge proximity. Hunting regulations specify a minimum horn curl, which is more affected by length than by circumference (Pelletier et al., 2012). While horn length increases with age, base circumference nearly stops growing after 6 years (Jorgenson et al., 1998). We found

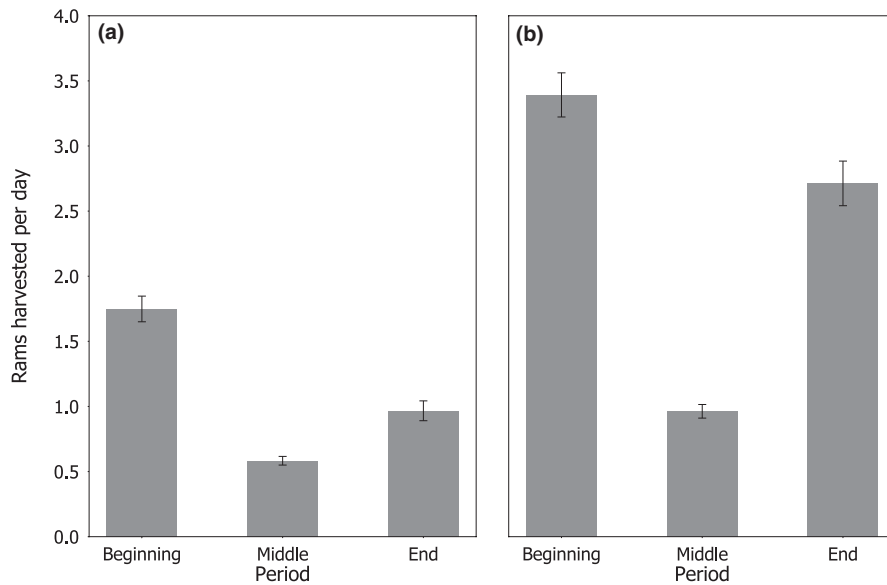


FIGURE 2 Mean number of bighorn males harvested per day in (a) areas with no protected areas within a 25-km radius ($N = 1,911$) and (b) areas with some protected areas within 25 km ($N = 3,915$), according to the timing of the hunting season (beginning, middle or end, see text) in Alberta, Canada, 1975–2013. Vertical lines indicate SE

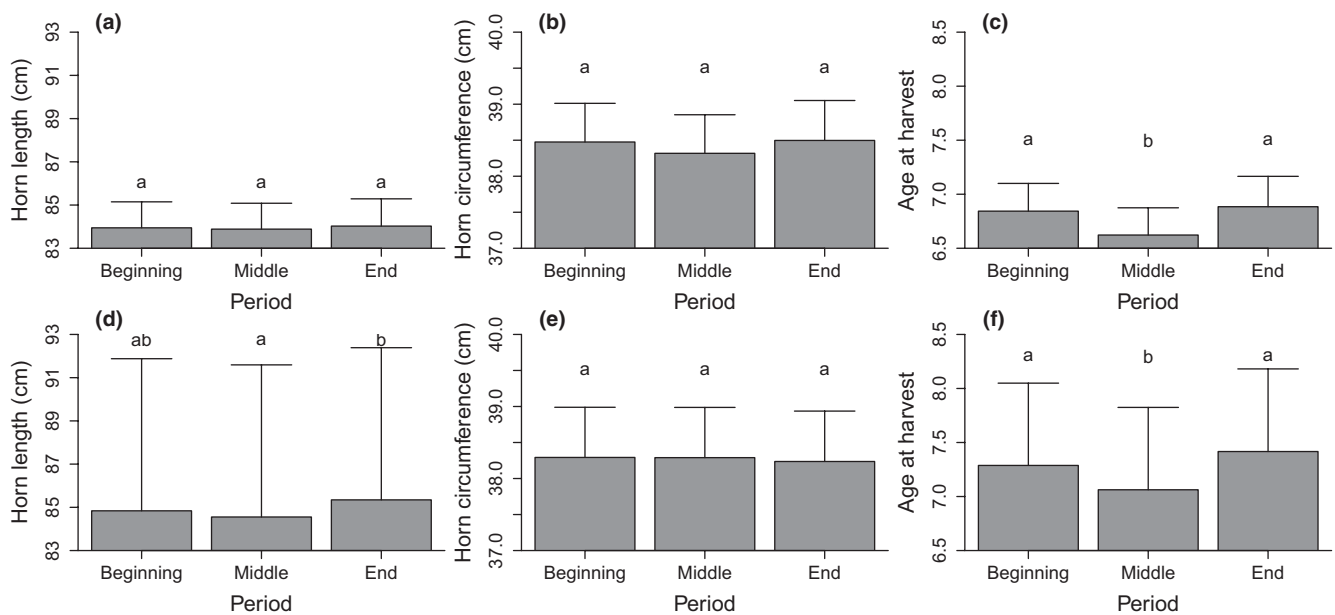


FIGURE 3 Predicted effect of period within the hunting season on horn length (cm), horn base circumference (cm) and age at harvest for bighorn males shot in areas with no refuges within 25 km (a, b, c; $N = 1,911$) and (d, e, f) shot in areas with at least some refuges within 25 km ($N = 3,915$) at different times during the hunting season (beginning, middle or end, see text) in Alberta, Canada between 1975 and 2013. Vertical lines indicate 95% confidence intervals. Tukey's multiple range test differences in horn size and age at harvest for hunting season periods are indicated by different letters

changes in horn shape, suggesting that intense selective hunting may favour shorter horns for a given base circumference (Table S5) and that selective hunting affects horn shape and length. Whether horns attain the definition of 'legal' male depends mostly upon length and curl shape, rather than base circumference (Tables S4 and S5). At the same time, horn length and base circumference are correlated, both phenotypically and genetically (Poissant, Wilson, Festa-Bianchet, Hogg, & Coltman, 2008). Horn base circumference may be important in male–male contests because when rams clash the horns collide near the base, often smashing the tips. Garel et al. (2007) found changes in horn shape over 28 years in mouflon *Ovis gmelini musimon* males

subjected to selective hunting: horn spread decreased for a given horn length. The change in horn shape was attributed to selective harvest, as hunters prefer widely flaring horns (Garel et al., 2007). The small effect of proximity to refuges on horn length may have important fitness consequences by determining whether a male is at risk of harvest. The difference of 2.7 cm is similar to that reported by a pedigree-based study of evolutionary changes in horn size (Pigeon et al., 2016).

Crosmary et al. (2013) found that impala shot near national parks had longer horns than those shot far from refuges, the opposite trend for greater kudu, and no effect for sable antelope. They attributed this interspecific variability to differences in home range size, which

increases with body mass (du Toit, 1990). Greater kudu and sable antelope may disperse farther from refuges than the smaller impalas. For greater kudu, hunting pressure was higher at the edge of refuges, possibly acting as a barrier to male dispersal into hunting areas (Crosmary et al., 2013). They concluded that phenotypic rescue was unlikely, since refuges were not an effective source of immigrants to hunting areas. With regard to bighorn sheep in Alberta, the peak in harvest near refuges in late October suggests that an unknown but possibly substantial part of the provincial harvest takes males originating from protected areas. The large Canadian national parks, combined with the long-distance prospecting behaviour of bighorn males (Hogg, 2000), could weaken the artificial selective pressure of the intense trophy hunt (Pigeon et al., 2016). If the hunting season ended about 10 days earlier, would-be rescuer males exiting protected areas may survive to rut. In order to facilitate rescue, wildlife managers should account for the timing of possible migrations of animals from protected areas.

As Tenhumberg et al. (2004) pointed out, a better understanding of dispersal and breeding migrations of harvested species is essential to assess if harvest refuges can buffer the evolutionary effects of size-selective harvests. Bighorn sheep populations in protected areas may be affected by hunting, if many adult males exit those areas before the rut and are shot. Researchers should test for a possible hunting-induced decline in genetic diversity inside protected areas. If gene flow is mostly from protected areas to outside, and if most males which leave are shot, effective population size inside protected areas may decrease.

The impacts of protected areas on harvest outside their boundaries appear very different in marine and terrestrial environments. Moland et al. (2013) found that marine refuges increased both the density and size of European lobster *Homarus gammarus* and Atlantic cod *Gadus morhua*. Protected areas led to both demographic and phenotypic rescue in harvested areas (Moland et al., 2013). Since dispersal is greater in marine environments, demographic rescue is more likely than in terrestrial environments (Carr et al., 2003). The size of a marine protected areas may influence its effectiveness in protecting targeted species against fisheries, especially for species with long dispersal distance (Baskett et al., 2005). Although harvest refuges in Alberta are large and hold thousands of bighorn sheep (Government of Alberta, 2015), we found limited evidence of phenotypic rescue, consistent with Pelletier et al. (2014). There was likely some demographic rescue as 'park' males may contribute a substantial part of the provincial harvest.

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AUTHORS' CONTRIBUTIONS

Y.P., M.F.-B. and F.P. conceived the ideas and designed methodology; Alberta Fish and Wildlife collected the data; Y.P. analysed the data and wrote the first draft of the manuscript. All authors contributed critically to the final draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.547d7wm49> (Poisson, Festa-Bianchet, & Pelletier, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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