MS YOANNA POISSON (Orcid ID : 0000-0001-7884-4818)

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

Yoanna Poisson¹, Marco Festa-Bianchet¹ and Fanie Pelletier¹.

¹ Département de biologie, Université de Sherbrooke, Québec, Canada, J1K 2R1

Corresponding author: Yoanna.Poisson@usherbrooke.ca

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.

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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 analyzed 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 with 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.

Key-words: Bighorn sheep, harvest refuge, horn size, phenotypic rescue, protected areas, size-selective harvest, source-sink dynamics, trophy hunting.

Résumé

1. L'exploitation durable doit minimiser ses impacts sur l'écologie et l'évolution des espèces exploitées. Une intense récolte sélective peut induire des conséquences évolutives. Les refuges peuvent atténuer ces effets évolutifs si des individus non sujets à cette récolte, provenant de ces refuges, migrent et se reproduisent dans les zones chassées. Cependant, le rôle des refuges sur la rescousse phénotypique des espèces chassées pour le trophée a rarement été évalué.

2. Nous avons étudié les variations spatiales et temporelles dans l'effet des refuges sur la taille des cornes et l'âge à la récolte chez le mouflon d'Amérique (*Ovis canadensis*). Nous avons analysé les données sur 5 826 béliers récoltés sur 39 ans en Alberta, Canada.
3. La longueur des cornes, un trait ciblé par les chasseurs, et l'âge à la récolte augmentaient avec la proportion d'aires protégées dans des zones tampons de 5-40 km autour de chaque localisation de bélier tué. Toutefois, la circonférence à la base des cornes était indépendante de la proximité aux refuges.
4. Le nombre de béliers récoltés augmentait pendant les 10 derniers jours de la saison de chasse à la fin octobre, correspondant avec la période de migration des béliers pour le rut. Les mâles tués pendant ces 10 jours étaient en moyenne 17% plus près d'un refuge que ceux récoltés plus tôt pendant la saison de chasse. Nos résultats suggèrent que certains mâles pourvus de grandes cornes sortant des refuges vers la fin de la saison de chasse sont récoltés et ne peuvent donc pas contribuer à la rescousse. Cependant, de l'incertitude demeure quant à la proportion de mâles qui sortent des refuges après la saison de chasse et qui survivent pour se reproduire.
5. *Synthèse et applications.* Il est peu probable que les refuges assurent une rescousse aux populations chassées de mouflon d'Amérique en Alberta puisque certains mâles qui sortent des refuges sont à risque d'être récoltés avant de s'être reproduits. Pour qu'une rescousse phénotypique soit efficace, les mâles doivent se reproduire avant d'être récoltés. Une fermeture de la saison de chasse 10 jours plus tôt permettrait une meilleure survie des mâles provenant des zones protégées.

Mots-clés : Aires protégées, chasse au trophée, dynamique source-puits, mouflon, récolte sélective, refuges, rescousse phénotypique, taille des cornes.

74 Introduction

75 Harvest of animals whose home ranges overlap protected areas is a major concern for the
76 conservation of biological diversity, especially when protected areas are small, and harvest rates
77 high, as reported for lions (*Panthera leo*) (Loveridge *et al.* 2007). That is because edge effects,
78 such as intense harvests along boundaries, can affect population and community ecology inside
79 protected areas. Alternatively, protected areas can be part of a large-scale management system to
80 support harvested populations, particularly in marine environments (Baskett *et al.* 2005) by
81 acting as a source of harvestable individuals. For trophy-hunted species, which can provide
82 income to support conservation activities (Di Minin, Leader-Williams & Bradshaw 2016),
83 protected areas may also be a source of individuals not subject to the selective pressure of intense
84 trophy hunting, countering the potential evolutionary effects of selective harvest (Pigeon *et al.*
85 2016).

86 Selective harvesting can exert strong pressure on the phenotype of harvested species (Ernande,
87 Dieckmann & Heino 2004; Baskett *et al.* 2005; Fenberg & Roy 2008). High harvest rates of
88 males with large secondary sexual characters such as horns, antlers or tusks can affect the mean
89 and the variability of those traits, and reverse the relationship between male fitness and trait size
90 from that seen in unharvested populations (Allendorf & Hard 2009). Regulations enforcing size-
91 selective harvests are frequently used to protect young males, but may favor individuals with
92 slower growth (Tenhumberg *et al.* 2004). For instance, modelling studies of moose (*Alces alces*;
93 Hundertmark, Thelen & Schwartz 1983) and elk (*Cervus elaphus*; Thelen 1991) suggested that
94 size-selective harvests may change the frequency of alleles affecting antler growth. Selective
95 harvesting may reduce population growth if alleles associated with trophy size also affect life
96 history traits (Coltman *et al.* 2005; Knell & Martínez-Ruiz 2017). Rates of phenotypic change
97 due to anthropogenic selective pressures are higher than those induced by natural selection
98 (Darimont *et al.* 2009) because harvest-induced selective pressures are often stronger than
99 natural selection (Conover, Munch & Arnott 2009). Selective harvest may thus have undesirable
100 evolutionary consequences, such as shorter horns in wild sheep (Garel *et al.* 2007; Hengeveld &
101 Festa-Bianchet 2011; Douhard *et al.* 2016; Pigeon *et al.* 2016). Decreasing horn growth over
102 time was also documented by Crosmar *et al.* (2013) for trophy-hunted male impala (*Aepyceros*

103 *melampus*) and sable antelope (*Hippotragus niger*) in Zimbabwe. For greater kudu (*Tragelaphus*
104 *strepsiceros*), however, horn growth increased over time (Crosmar *et al.* 2013).

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

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

122 The potential for harvest refuges to mitigate the selective effects of trophy hunting on secondary
123 sexual traits in terrestrial mammals has rarely been tested. Crosmar *et al.* (2013) showed that
124 horn size decreased with distance from a harvest refuge in Zimbabwe for only 1 of 3 ungulate
125 species. Pelletier *et al.* (2014) found that the horns of bighorn sheep (*Ovis canadensis*) males
126 harvested near refuges were 3% longer than those of males harvested far from refuges in Alberta,
127 Canada. They suggested that migration of rams from refuges was insufficient to provide a
128 phenotypic rescue for hunted areas, as horn size declined over time at the same rate in areas near
129 and far from refuges. With effective phenotypic rescue, the decline in horn size over time was
130 expected to be weaker near refuges (Pelletier *et al.* 2014). That analysis, however, compared
131 *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 analyze a larger data set 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 behavior. 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 *et al.* 2002). Because the reproductive success of young males is mostly independent of horn size (Martin *et al.* 2016), that management scheme favors slow horn growth (Coltman *et al.* 2003; Festa-Bianchet *et al.* 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 (Geist 1971; Demarchi 2004) would increase the size and age of males harvested near refuges in late October. To test these hypotheses, we analyzed horn measurements and age of 5 826 males harvested over 39 years.

Materials and methods

Study area and data collection

In Alberta, there are about 4500 bighorn sheep in national parks and 7000 in provincial lands (Government of Alberta 2015). A map of hunted and protected areas is provided in Festa-Bianchet *et al.* (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 analyzed 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 x 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 nonresidents, 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.

189 We analyzed variation in horn length, base circumference and shape. For length, we used the
190 longest horn because horns often break during fights. We used the mean base circumference in
191 analyses. To test for horn shape changes over time, we set horn length as response variable and
192 horn base circumference as a fixed effect. That analysis examined how length varied as a
193 function of circumference. In Stone's sheep (*Ovis dalli stonei*), intense selective harvest led to a
194 decrease in the horn length to circumference ratio, likely because thicker horns are effective in
195 male-male combat but longer horns increase the chance that a male would be 'legal' (Douhard *et*
196 *al.* 2016). Indeed, base circumference is not directly targeted by hunters (Pelletier, Festa-
197 Bianchet & Jorgenson 2012). To assess how distance from refuges affected horn size and age at
198 harvest, we estimated the shortest Euclidean distance (km) from the nearest refuge boundary and
199 the proportion of circular buffer zones around each kill site which were inside refuges. We used
200 buffers of 5, 15, 25, and 40-km radii to assess at what distance we could detect an effect. These
201 buffers range from the approximate minimum size of a bighorn sheep winter range (Festa-
202 Bianchet 1986) to the maximal straight-line distance between locations observed for males
203 undergoing breeding commutes before and during the rut (Hogg 2000). All National and
204 Provincial Parks with no sheep hunting season were considered as harvest refuges. For spatial
205 analyses, we calculated the centroid, in decimal degrees, for each Alberta Township Survey
206 (ATS) square where at least one male had been shot. We used the ATS centroid as the kill
207 location, as this was the smallest scale for which locations were reported. We examined kill
208 locations at both the ATS level and the Sheep Management Area level, a much larger spatial
209 scale. Sheep Management Areas were established by Alberta Fish & Wildlife biologists based on
210 genetic information and major breaks between subpopulations, such as wide river valleys (see
211 Festa-Bianchet *et al.* 2014 for a map of the 8 Areas).

212 *Statistical analyses*

213 To determine which spatial scale best explained horn size, horn shape and age at harvest, we
214 developed candidate models including different measures of refuge proximity: shortest Euclidean
215 distance and proportion of harvest refuges at four spatial scales (see Tables S2-4 and S6 in
216 Supporting Information for model details). Euclidean distance tested if the effect of refuges on

217 horn size weakened with distance. Because age-specific horn size declined over time (Festa-
 218 Bianchet *et al.* 2014), in all models, we included harvest year as a continuous variable. We
 219 included latitude, *i.e.* the ATS centroid in decimal degrees, as a control variable because bighorn
 220 sheep horn size in Alberta decreases from South to North (Gorrell *et al.* 2016). As the beginning
 221 and the end of the hunting period changed over years and between Sheep Management Areas, we
 222 considered kill date as a 3-level period during the hunting season: beginning (first 10 days),
 223 middle (from 11 days after opening day to 11 days before closing) and end (last 10 days). We
 224 chose these dates because harvest typically peaks in the first few and last few days of the season
 225 (Government of Alberta 2015). The duration of the middle period varied from year to year, with
 226 a mean of 60 days, mostly because of differences in start date (range 19 August - 9 September).
 227 The last day of hunting varied from October 27 to November 1. In addition, we tested the
 228 hypothesis that males shot late in the season near refuges had larger horns after accounting for
 229 age, expecting that some of those rams were exiting refuges (Hogg 2000) and therefore came
 230 from areas without selective hunting. Age at harvest was entered as a quadratic fixed effect, to
 231 account for decreasing horn growth with age (Jorgenson, Festa-Bianchet & Wishart 1998). We
 232 fitted linear mixed models (Pinheiro & Bates 2000) with the lmer function of the lme4 R package
 233 (Bates *et al.* 2015). We used the full model fitted by restricted maximum likelihood and tested
 234 the best random effect structure with the likelihood ratio test. Sheep Management Area was
 235 included as a random intercept to account for regional differences in horn size and changes in the
 236 distribution of harvest over years. Once the best random effect structure was selected, AIC was
 237 used to determine the most parsimonious model fitted by maximum likelihood (Burnham &
 238 Anderson 2002). When more than one model was within $\Delta AIC < 2$, we calculated model-
 239 averaged estimates and unconditional 95% confidence intervals with multimodel inference
 240 (Burnham & Anderson 2002) with the package AICcmodavg (Mazerolle 2010). All continuous
 241 variables were scaled (mean = 0, variance = 1) and were not multicollinear ($VIF < 2$; Graham
 242 2003). We considered results significant when the 95% confidence intervals of parameter
 243 estimates did not overlap zero. Significant results obtained for horn size and age at harvest were
 244 further examined using Tukey's post hoc comparisons with the emmeans R package. All
 245 statistical analyses were performed in R 3.3.1 (R Core Team 2016) and spatial analyses in
 246 ArcMap 10.2.2 (ESRI 2016).

Results

Effect of refuges on horn size and age at harvest

Horn length increased with the proportion of harvest refuges within any buffer (Fig. 1A; Table 1) and with age (Fig. 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 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 (Fig. 1B; Table 2). The significant interaction between hunting season period and refuge area in the 25-km 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).

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 (Fig. 2). A second peak in harvest at the end of the season was only significant in areas

274 with at least some refuges within 25 km (Fig. 2). On average, males killed during the last 10 days
275 were 17% closer to refuges (4.2 km) than males shot earlier in the season.

276 Accounting for age, horn length increased during the last 10 days of the season, but this increase
277 was significant only near refuges (Figs 3A; 3D), where horn length increased by 1.6 cm
278 compared to earlier in the hunting season. Mean horn circumference did not change during the
279 season (Figs 3B; 3E). The average age at harvest showed a slight but significant decrease during
280 the middle of the season, then increased at the end (Figs 3C; 3F). On average, males harvested in
281 the middle of the season were about 0.40 years younger than those shot at its end. Overall, males
282 shot near protected areas were about 0.54 years older than those killed in areas with no refuges
283 within 25 km.

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, Festa-Bianchet & Jorgenson 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

314 only for mountain sheep but also for other species that face similar landscapes with varying
315 degrees of selective harvest (Loveridge *et al.* 2007; Crosmar *et al.* 2013).

316 We found no evidence that horn base circumference varied with refuge proximity. Hunting
317 regulations specify a minimum horn curl, which is more affected by length than by
318 circumference (Pelletier, Festa-Bianchet & Jorgenson 2012). While horn length increases with
319 age, base circumference nearly stops growing after 6 years (Jorgenson, Festa-Bianchet &
320 Wishart 1998). We found changes in horn shape, suggesting that intense selective hunting may
321 favor shorter horns for a given base circumference (Table S5) and that selective hunting affects
322 horn shape and length. Whether or not horns attain the definition of 'legal' male depends mostly
323 upon length and curl shape, rather than base circumference (Tables S4 and S5). At the same
324 time, horn length and base circumference are correlated, both phenotypically and genetically
325 (Poissant *et al.* 2008). Horn base circumference may be important in male-male contests because
326 when rams clash the horns collide near the base, often smashing the tips. Garel *et al.* (2007)
327 found changes in horn shape over 28 years in mouflon (*Ovis gmelini musimon*) males subjected
328 to selective hunting: horn spread decreased for a given horn length. The change in horn shape
329 was attributed to selective harvest, as hunters prefer widely flaring horns (Garel *et al.* 2007). The
330 small effect of proximity to refuges on horn length may have important fitness consequences by
331 determining whether or not a male is at risk of harvest. The difference of 2.7 centimeters is
332 similar to that reported by a pedigree-based study of evolutionary changes in horn size (Pigeon *et*
333 *al.* 2016).

334 Crosmar *et al.* (2013) found that impala shot near national parks had longer horns than those
335 shot far from refuges, the opposite trend for greater kudu, and no effect for sable antelope. They
336 attributed this interspecific variability to differences in home range size, which increases with
337 body mass (du Toit 1990). Greater kudu and sable antelope may disperse farther from refuges
338 than the smaller impalas. For greater kudu, hunting pressure was higher at the edge of refuges,
339 possibly acting as a barrier to male dispersal into hunting areas (Crosmar *et al.* 2013). They
340 concluded that phenotypic rescue was unlikely, since refuges were not an effective source of
341 immigrants to hunting areas. As regards bighorn sheep in Alberta, the peak in harvest near
342 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 behavior 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.

Data availability statement

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

Authors' contributions

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

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Tables

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

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
Age²	-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 x period-middle	0.32	0.17	-0.02	0.66
Refuges within 15 km x 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 x period-middle	0.31	0.17	-0.03	0.64
Refuges within 25 km x 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 x period-middle	0.42	0.17	0.09	0.76
Refuges within 5 km x period-end	0.15	0.18	-0.20	0.51
Euclidean distance	-0.53	0.12	-0.76	-0.30
Euclidean distance x period-middle	-0.11	0.17	-0.44	0.22
Euclidean distance x 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 x period-middle	0.29	0.17	-0.04	0.62
Refuges within 40 km x period-end	0.53	0.19	0.16	0.90

Table 2. Estimates (β), standard error (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). 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.

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	Std. deviation		
Sheep Management Area	0.55	0.74		
Residuals	3.54	1.88		

Table 3. Estimates (β), standard error (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). 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.

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	Std. deviation		
Sheep Management Area	0.13	0.36		
Residuals	3.19	1.79		

Figure legends

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.

Figure 2. Mean number of bighorn males harvested per day in A) areas with no protected areas within a 25-km radius (N = 1911) and B) areas with some protected areas within 25 km (N = 3915), according to the timing of the hunting season (beginning, middle or end, see text) in Alberta, Canada, 1975 to 2013. Vertical lines indicate standard error.

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 25km (A, B, C; N = 1911) and (D, E, F) shot in areas with at least some refuges within 25km (N = 3915) 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 multiple range test differences in horn size and age at harvest for hunting season periods are indicated by different letters.

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Author/s:

Poisson, Y; Festa-Bianchet, M; Pelletier, F

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