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2 Susanne Schindler

3 University of Bristol

4 24 Tyndall Avenue

5 BS8 1PQ Bristol

6 United Kingdom

7 Email: [Susanne.Schindler@bristol.ac.uk](mailto:Susanne.Schindler@bristol.ac.uk)

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## 11 **Hunting, Age Structure, and Horn Size Distribution in Bighorn Sheep**

12

13 SUSANNE SCHINDLER,<sup>1</sup> *University of Zurich, Department of Evolutionary Biology and*

14 *Environmental Studies, Winterthurer Str. 190, 8057 Zurich, Switzerland*

15 MARCO FESTA-BIANCHET, *Université de Sherbrooke, Département de biologie, 2500*

16 *boulevard de l'Université, Sherbrooke, J1K 2R1, Canada*

17 JOHN T. HOGG, *Montana Conservation Science Institute, 5200 Upper Miller Creek Road,*

18 *Missoula, MT 59803, USA*

19 FANIE PELLETIER, *Université de Sherbrooke, Département de biologie, 2500 boulevard de*

20 *l'Université, Sherbrooke, J1K 2R1, Canada*

21 **ABSTRACT** Trophy hunting, that is the selective removal of animal for human recreation, can

22 contribute to conservation when appropriately managed. Yet, little is known about how harvest

23 rates or different definitions of trophy affect age structure and trophy size in harvested animals

24 and in survivors because no controlled studies exist. To investigate the impacts of different

25 management regimes, we developed an individual-based model for bighorn sheep (*Ovis*

26 *canadensis*), based on empirical data on survival from a protected population and data on horn

27 growth from 2 populations which differed in their growth rates. One population showed slow

28 horn growth and the other population fast horn growth. We subjected these model populations to

29 varying harvest rates and 2 different hunting regulations: 4/5 curl and full-curl definitions of a

30 trophy male. We found that the effect of hunting regulations depends on horn growth rate. In

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<sup>1</sup> Current address: University of Bristol, School of Biological Sciences, 24 Tyndall Avenue, BS8 1QL, Bristol, UK

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31 populations with fast horn growth, the effects of trophy hunting on male age structure and horn  
32 size were greater and the effect of a change in the definition of legal male smaller than in  
33 populations with slow growth rates. High harvest rates led to a younger age structure and smaller  
34 horn size. Both effects were weakened by a more restrictive definition of trophy male. As  
35 harvest rates increased past 40% of legal males, the number of males harvested increased only  
36 marginally because an increasing proportion of the harvested males included those that had just  
37 become legal. Although our simulation focused on bighorn sheep, the link between horn growth  
38 rate and harvest effects may be applicable for any size-selective harvest regime.

39 **KEY WORDS** agent-based model, bighorn sheep, harvest management, horn growth, National  
40 Bison Range, *Ovis canadensis*, Ram Mountain, Sheep River, trophy hunting.

41 Trophy hunting is the killing of selected animals for human recreation. It is a widespread  
42 management practice for many ungulates, leading to the selective removal of males with large  
43 horns or antlers (Monteith et al. 2013). When properly managed, trophy hunting can be  
44 sustainable and provide a strong incentive for conservation (Leader-Williams et al. 2001). A high  
45 rate of selective removal of males with large horns or antlers, however, may lead to selection for  
46 smaller horns and reduce the availability of large trophies, as suggested for bighorn sheep (*Ovis*  
47 *canadensis*; Coltman et al. 2003, Traill et al. 2014, Pigeon et al. 2016). Empirical data to quantify  
48 the impact of harvest regulations on age structure and horn size of harvested males and of the  
49 overall population are scarce (Table 1) and usually rely on samples of harvested males, which can  
50 differ from the overall population (Pelletier et al. 2012, Festa-Bianchet et al. 2015). Most of these  
51 studies measured age and horn size of harvested males but had little or no information on the  
52 distribution of these traits in the population. Therefore, a modeling approach is needed to fill this  
53 gap.

54 We developed an individual-based model that allowed us to vary the definition of legal  
55 male and the harvest rate, 2 main tools used by managers to regulate trophy hunting of mountain

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56 sheep (*Ovis* spp.) in North America (Wild Sheep Foundation Professional Biologists 2008). Wild  
57 sheep exhibit strong sexual size-dimorphism and males bear large curved horns that are highly  
58 sought after by trophy hunters. Definitions of legal male in North American jurisdictions are  
59 usually based on a minimum degree of horn curl, which is related to horn length and shape  
60 (Festa-Bianchet et al. 2014). Consequently, the age at which males attain legal status is mostly a  
61 function of age-specific horn growth rate. Despite strong variation in horn growth rates  
62 (Jorgenson et al. 1998), no comparative or modeling study has investigated how the impact of  
63 hunting regulations varies with horn growth rate. We took advantage of detailed empirical data  
64 from 2 populations of bighorn sheep with markedly different rates of age-specific horn growth  
65 (Jorgenson et al. 1998) and modeled hunting effects on age structure and horn length of harvested  
66 and living males. We purposely modeled 2 populations with horn growth rates near the opposite  
67 extremes of the variability found within the species. We expected that a more restrictive  
68 definition of legal ram would increase the age and horn size of harvested males but decrease the  
69 harvest. We also expected that an increasing harvest rate would lead to a younger age structure  
70 of surviving males and a shorter life expectancy for legal males. These expectations are  
71 qualitatively obvious; however, their magnitude is unknown. Our primary goal was to assess how  
72 changes in hunting regulations affect the age and horn length of harvested males and the  
73 proportion of a cohort that would be harvested rather than dying of natural causes after reaching  
74 the minimum age at which horns could attain legal size. For example, although it seems  
75 inevitable that higher harvests will shorten male life expectancy, the extent of this effect given  
76 different horn growth rates and definitions of legal ram is unknown, yet it is important to inform  
77 management decisions.

## 78 **STUDY AREA**

79 To parameterize our model, we used data on males from 3 populations: 1 unharvested population in  
80 the National Bison Range (NBR), Montana, USA, and 2 hunted populations in Alberta, Canada:

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81 Ram Mountain and Sheep River. Hunting regulations specified a minimum legal horn size (Fig.  
82 S1, available online in Supporting Information) and an unlimited number of permits were  
83 available for Alberta residents (Coltman et al. 2003, Pelletier et al. 2012, Festa-Bianchet et al.  
84 2014). The NBR is an 80-km<sup>2</sup> National Wildlife Refuge located in northwestern Montana (47°  
85 N, 114° W). The terrain is Rocky Mountain foothill (800–1,500 m elevation) supporting  
86 vegetation composed of Palouse grasslands, patches of coniferous forest, and stringers of riparian  
87 shrub and woodland. The climate is seasonal with mild winters and warm summers subject to  
88 periodic drought (Köppen classification: humid continental; Köppen 1884). The bighorn study  
89 population was established by transplant from Banff National Park in 1922. Supplemental  
90 transplants occurred during 1985–1994. Detailed individual-based monitoring began in 1979 and  
91 has been continuous since with the exception of 1987. Resident predators of bighorn include  
92 cougars (*Puma concolor*), coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), and  
93 American black bears (*Ursus americanus*). Wolves (*Canis lupus*) and grizzly bears (*Ursus*  
94 *arctos*) are transients on the refuge. Hunting and domestic grazing are not permitted and public  
95 access to bighorn range is strictly regulated.

96 Ram Mountain, Alberta (52°N, 115°W) is an isolated mountain complex with about 38  
97 km<sup>2</sup> of alpine and subalpine habitat at 1,600–2,200 m elevation used by bighorn sheep. The  
98 climate is continental with cold winters and short summers (Douhard et al. 2017). Large  
99 predators include wolves, black bears, and cougars (Festa-Bianchet et al. 2006).

100 Sheep River, Alberta (50°N, 114°W) includes low-elevation (1,300–1,600 m) grasslands  
101 and high-elevation (1,800–2,600 m) alpine habitats, used by a metapopulation of bighorn sheep.  
102 The climate is similar to Ram Mountain but with more frequent warm Chinook winds in winter.  
103 The combination of lower elevation and milder climate leads to an earlier spring green-up, and  
104 the availability of an elevational gradient allows bighorn sheep to feed on nutritious growing  
105 vegetation over a long period (Festa-Bianchet 1988). Predators are the same as at Ram Mountain

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106 (Bourbeau-Lemieux et al. 2011). Both study areas are on public land, with seasonal cattle  
107 grazing at lower elevations in summer.

## 108 **METHODS**

### 109 **Species and Data**

110 Our model assumes no evolutionary changes from selective harvest (Pigeon et al. 2016) and  
111 therefore provides a useful comparison for time series of horn measurements in actual harvested  
112 populations of bighorn sheep. Furthermore, we did not model density dependence in either  
113 recruitment or horn growth, despite evidence to the contrary (Jorgenson et al. 1998), because we  
114 wanted to focus on how changes in harvest strategies affect the horn size and availability of  
115 trophy males in a stable population, such as what may be expected over a time frame of decades.  
116 Because we focused on a stable population, we assumed a near-constant yearly input of 4-year-  
117 old sheep, with a minor amount of stochastic variation in recruitment.

118 To obtain age-specific survival rates unbiased by harvest, we used data from the NBR  
119 (Table S1, available online in Supporting Information) where sport harvest is not permitted and  
120 poaching is rare. To obtain age-specific horn growth rates, we used data from Ram Mountain and  
121 Sheep River. The data from Ram Mountain are representative of slow horn growth, which means  
122 the typical age-specific annual increase in horn length of a male from the Ram Mountain  
123 population is small. In contrast, the data from Sheep River population are representative of fast  
124 horn growth, which means the typical age-specific annual increase in horn length of a male from  
125 the Sheep River population is large (Tables S2–S3). For example, the world record ram that has  
126 the largest horns ever measured stems from the Sheep River population (Platt 2015).

127 A combination of density-dependent and selective effects at Ram Mountain reduced horn  
128 growth rates (Jorgenson et al. 1998, Coltman et al. 2003, Festa-Bianchet et al. 2004, Pigeon et al.  
129 2016) so that after 1993 most males died before their horns fulfilled the 4/5 curl regulation.  
130 Consequently, we used only records from 1975 to 1992. Horn measurements could be taken only

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131 from males that survived the hunt, such that data of individuals >4 years old (the min. age at  
132 which they can attain legal status) were biased towards males with smaller horns (Pelletier et al.  
133 2012). This bias should be lower in the Sheep River dataset because this population is partly  
134 protected.

### 135 **Survival Analysis and Horn Growth**

136 To estimate age-specific survival rates unbiased by harvest, we used data collected during 1979–  
137 2015 from bighorn sheep in the NBR. All males in the population during this period were  
138 individually recognizable using photographically documented variation in horn and pelage  
139 characters and ear tags or notches applied at birth. We determined survival (0,1) to each age step  
140 by a capture-mark-recapture procedure in which individual identities were recorded in daily  
141 census of the population over a 4–6-week period during fall rut and defined 25 October as the  
142 first day of each male-year. We considered males seen anytime on or after 25 October during fall  
143 census as surviving the preceding age interval, whereas we considered males alive at the start of  
144 the previous age interval but last observed before 25 October as dying during the preceding  
145 interval. The rut was selected for this purpose because males are conspicuously associated with  
146 females at this time and all surviving males could be expected to participate. Conveniently, late  
147 October also corresponds to the end of the bighorn hunting season in many jurisdictions. The  
148 pool of at-risk males in each year divided into 1 of 2 re-sighting categories: those not recorded at  
149 all after 25 October and those seen on a majority of the approximately 28–42 census days. The  
150 probability of multiple re-sightings conditional on an initial sighting after 25 October was  
151 therefore 1.0. Some males in the former not-recorded category may have been undetected  
152 emigrants rather than mortalities. However, males missing in 1 year never reappeared in a  
153 subsequent year and the NBR is geographically isolated (Hogg et al. 2006).

154 We applied a Kaplan-Meier counting process to these field data to estimate the male  
155 survival function,  $S(t)$ , where we measured age,  $t$ , in years (Therneau and Grambsch 2000). We

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156 left-truncated survival data for adults alive at the start of the analysis period, whereas we right-  
157 censored survival data for adults alive at the end of the study, emigrant males of unknown fate ( $n$   
158 = 4), males poached ( $n = 2$ ), and males translocated to other populations ( $n = 10$ ). Natural  
159 immigrants ( $n = 3$ ) entered the analysis at the age at first arrival and males ( $n = 8$ ) translocated  
160 from other populations entered the analysis 1 year after their release to limit the influence of any  
161 adverse effects from transport or capture. We counted 6 males in extremely poor condition culled  
162 for veterinary necropsy as natural mortalities during the appropriate age interval. Finally, as in  
163 Hogg et al. (2006) and to control for effects of historical inbreeding (Hogg et al. 2006, Miller et  
164 al. 2012), we modeled age-specific male survival as a function of 2 measures of outbreeding (the  
165 source and hybridity indices; Lynch 1991) using Cox proportional hazards regression and the  
166 Efron approximation for estimating (partial) likelihoods in the Cox model (Therneau and  
167 Grambsch 2000). The NBR age-specific survival rates used in the simulations we report here are  
168 those predicted by the Cox model for the genetically rescued population at equilibrium with  
169 respect to individual levels of outbreeding (i.e., a population with median outbreeding indices  
170 equal to that calculated from the pedigree of the 2012 NBR population). We implemented the  
171 Kaplan-Meier and Cox model procedures using the R package survival version 2.38-1 (Therneau  
172 and Lumley 2014) running under R version 3.1.2. (R Core Team 2014). In the absence of  
173 hunting, bighorn sheep survival is independent of horn length (Bonenfant et al. 2009) and we  
174 applied these survival rates for the NBR (Table S1) to both hunted populations.

175         We measured horn length from tip to base along the top edge of keel. To obtain age-  
176 specific horn growth rates, we estimated the size of annual horn length increments, which are  
177 marked by annuli (Geist 1966). We estimated the annual increment length as the distance  
178 between 2 sequential annuli. We used measurements of annual increments to model horn growth  
179 instead of changes in total horn length to reduce the bias through premature death of hunted  
180 males. The sample sizes were sufficient to estimate the annual increments of males aged 4 to 8



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181 years at Ram Mountain (Table S2), and 4 to 7 years at Sheep River (Table S3). Horn tips often  
182 break when fighting with other males. Without accounting for breakage at the horn tips, we  
183 obtained unrealistically long horns. Consequently, we reduced the mean of increments for older  
184 ages (Ram Mountain, 6–8 yr; Sheep River, 6–7 yr) by 2 cm and set the mean increment to 0 cm  
185 for males >8 years at Ram Mountain and >7 years at Sheep River (Tables S2 and S3). For those  
186 ages with zero increments, we set the standard deviation (SD) to the mean value of SDs (Ram  
187 Mountain, 4–8 yr; Sheep River, 4–7 yr; Table S2 and S3, respectively). With this setting we  
188 achieved realistic age-specific horn lengths for both populations. We assumed that differences in  
189 horn circumference for a given horn length did not affect the probability of reaching legal status  
190 or the probability of being shot. All animal-handling procedures at Ram Mountain and Sheep  
191 River were approved by the Animal Care Committee of the Université de Sherbrooke, affiliated  
192 with the Canadian Council on Animal Care (protocol MFB2009-1). Field methods at NBR were  
193 subject to annual review and approval by refuge staff (U. S. Fish and Wildlife Service [USFWS])  
194 with additional optional oversight by the regional USFWS Wildlife Health Office (Bozeman,  
195 MT, USA).

### 196 **Definition of Legal Male**

197 We modeled 2 hunting regulations: 4/5 curl and full-curl (Fig. S1). Males that fulfill the  
198 regulation are called legal and can be harvested. These regulations are in general respected  
199 because, if harvested horns are >1 cm short, the trophy will be taken away and the hunter will  
200 usually be prosecuted. There are no data on males shot and left to avoid charges, but although this  
201 type of poaching may increase the mortality of sub-legal males, it will not affect the conclusions  
202 drawn from the model on how changes in hunting regulations and harvest rates affect age-  
203 structure and horn size distribution.

204 The probability that a male with a given horn length is legal under the 4/5 curl fits a  
205 logistic function (intercept = -19, slope = 0.25; Festa-Bianchet et al. 2014). With this probability

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206 function, males have a 50% probability of being legal at a horn length of about 75 cm. We  
207 modeled the full-curl regulation by shifting the probability function 10 cm to the right: horns  
208 must be 10 cm longer to classify a 4/5-legal male as legal under the full-curl regulation. The  
209 Draft Management Plan for Bighorn Sheep in Alberta (2015) reported that mean horn length of  
210 harvested males increased by 7.1 cm when regulation changed from 4/5 curl to full-curl. We  
211 chose 10 cm to cover a wider range of hunting regulations ranging from a liberal (4/5 curl) to a  
212 restrictive definition (full-curl) of legal ram. The probability function of the full-curl regulation  
213 gives a male a 50% probability of being legal at a horn length of about 85 cm.

#### 214 **The Model**

215 We implemented an individual-based model in the JAVA® programming language and compiled  
216 it with the javac-compiler, version 1.6.0\_24 (source code available at [http://github.com/s-](http://github.com/s-schindler/AgeAtHarvest)  
217 [schindler/AgeAtHarvest](http://github.com/s-schindler/AgeAtHarvest)). In our model, males are recruited to the population at age 4 and live for  
218 at most another 11 years; therefore, they are aged from 4 to 15 years. In addition to age, a male  
219 has 2 properties: horn length (without loss of generality we focus on 1 horn only), and legal  
220 status. One time step corresponded to 1 year and at each time step a cohort of 4-year-old males  
221 recruited to the population. We drew the number of recruits and their horn length randomly from  
222 a Gaussian distribution (Table S4). Males survived according to the estimated age-specific  
223 survival rates (Table S1). Age of surviving males increased by 1 year and their horns grew by  
224 age-specific increments randomly drawn from a Gaussian distribution (Tables S2 and S3).

225 After 12 initial time steps, all age classes were potentially present in the population and  
226 hunting commenced. We modeled harvest rates on legal males from 0% (no hunting) to 100%  
227 (all legal males were shot), in steps of 10%. For comparison, the estimated hunting pressure on  
228 legal males at Ram Mountain is 37.5% (Pelletier et al., 2012). By definition, sub-legal males  
229 cannot be shot and therefore we did not include them in the simulation of harvest rates.

230 The annual biological cycle in the 2 hunted populations was as follows. Males recruited to

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231 the population in May. Hunting season was from the end of August to the end of October and  
232 most natural deaths occurred during winter. The sequence of events in the model mirrored  
233 biological events: males entered the simulation with the randomly assigned horn lengths of 4-  
234 year-olds (Table S4). Male recruitment (May) was followed by updating the legal status of males  
235 (Jun) after which males were subjected to hunting (Aug–Oct). Following the hunting season,  
236 males were subjected to natural mortality (Nov–Mar), the age of survivors increased by 1 year,  
237 and horn size increased by annual increments (May–Aug).

238 We simulated population dynamics for each harvest rate (0–100%) for 100 time steps for  
239 slow and fast age-specific horn growth rates, and 2 hunting regulations (4/5 curl and full-curl).  
240 We simulated each combination of harvest rate, horn growth rate, and hunting regulation 10,000  
241 times, each time with a different seed for the random generator. To exclude autocorrelations  
242 within simulations and to remove bias from stochasticity, we averaged the age-specific horn  
243 length and age distribution over all 10,000 replicates at specific time points. We averaged horn  
244 and age distribution over the replicates in the first year of hunting, the first 19 time steps after  
245 hunting commenced (to monitor the transition period) and at the 99th time step to calculate  
246 measures after the population reached equilibrium. Because the results during the transition did  
247 not differ from those at equilibrium, we report the latter only.

248 To quantify the joint dynamics of hunting regulations, harvest rates, and horn growth  
249 rates, we monitored the number, age, and horn length of males alive before and after the hunt. We  
250 also monitored the number, age, and horn length of legal males and of those harvested. For  
251 harvested males, we monitored the number of years spent as legal males before they were shot.

## 252 **RESULTS**

253 Because we performed 10,000 simulations/harvest intensity, the statistical power of our estimates  
254 is large, even when effect sizes are small. For this reason, we report the variability in the  
255 simulation data, measured by their SD, rather than confidence intervals.

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256           Following the start of hunting of a previously unharvested population, average age at harvest  
257 initially declined but stabilized within 3–6 years (Fig. S2a). Similarly, the number of males and  
258 the number of harvested males stabilized within a few years (Fig. S2b,c). As expected, average  
259 age at harvest declined with increasing hunting pressure (Fig. 1). In populations with fast horn  
260 growth, age at harvest was consistently lower and declined more rapidly with increasing harvest  
261 rate (Fig. 1). For example, under the 4/5 curl regulation, the age at harvest in a population with  
262 fast horn growth dropped by 1.8 years, from 6.4 to 4.6 years as harvest rate increased from 10%  
263 to 100%, but it dropped by only 1.4 years, from 7.2 to 5.8 years in the population with slow  
264 growing horns. The smaller drop in age-at-harvest in populations with slow vs. fast horn growth  
265 is due to the smaller impact that changing the harvest rate has on the age distribution of harvested  
266 males in populations with slow horn growth (Fig. S3a,b). The proportion of harvested males aged  
267 4–5 years naturally increases under increased harvest pressure, whether horns grow rapidly or  
268 slowly, but this proportion increases faster in populations with rapid than with slow horn growth  
269 rate (Fig. S3a,b).

270           A few years after the onset of hunting, the average horn length stabilized among harvested  
271 and surviving males. The effects of hunting on age distribution of surviving males were stronger  
272 in the population with faster horn growth (Fig. 2, Fig. S4a,b). For example, the proportion of 4-  
273 year-olds among living males nearly doubled from no hunting to 100% hunting intensity in  
274 populations with slow horn growth (Fig. S4a), but it tripled in populations with fast-growing  
275 horns (Fig. S4b). The proportion of males aged 4 or 5 years increased from 40% to 70% with  
276 slow horn growth, and from 40% to 94% with fast horn growth (Fig. S4a,b).

277           As hunting intensity increased from 10% to 40%, mean horn length at the population level  
278 decreased the most for males aged  $\geq 7$ , especially in populations with slow horn growth (Fig. 4a).  
279 When hunting intensity exceeded 50%, <20% of surviving males were aged  $\geq 7$  (Fig. S4a), and  
280 they accounted for only 6–17% of legal males. As the harvest rate increased past 40%, the

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281 harvest removed a greater proportion of males in the year they became legal, so that the number  
282 of harvested males did not increase by much (Fig. S5a,b).

283 Switching from 4/5 curl to full-curl shifted the mode of age distribution of harvested  
284 males by about 1 year, from 6 to 7 years for slow horn growth at 10–60% harvest rate (Fig.  
285 S3a,c), and from 5 to 6 years for rapid horn growth at 10–30% harvest rate (Fig. S3b,d).  
286 Regardless of horn growth rate, the harvest included fewer males aged 4–5 years and more males  
287 aged  $\geq 7$  years under full-curl than 4/5 curl regulations. Life expectancy was less affected by  
288 regulation (4/5 curl or full-curl) in populations with fast growing horns (Fig. S6). With slow horn  
289 growth, 80% of males that had survived to age 4 became legal under 4/5 curl and 57% under full  
290 curl, the rest died of natural causes without attaining legal horn status. In a population with fast  
291 horn growth, 95% reached legality under 4/5 curl and 88% under full-curl. The decrease in the  
292 number of harvested males when switching from 4/5 to full-curl was greater in populations with  
293 slow-growing horns because more males died of natural causes without becoming legal (Fig. 4).  
294 In populations with fast growing horns, however,  $\geq 30\%$  of males that survived to age 4 died  
295 through hunting even when hunting pressure was only 10%, regardless of the curl regulation (Fig.  
296 4). Age-specific horn length declined with harvest pressure under both 4/5 curl and full-curl (Fig.  
297 3 and Fig. S7).

## 298 **DISCUSSION**

299 The most important result of our simulations is that the effects of trophy hunting regulations are  
300 strongly dependent on horn growth rate. That is because as horn growth rate increases, more  
301 males become legal at a younger age, and more survive to reach the definition of legal male,  
302 regardless of whether it is set to 4/5 curl or full-curl. Therefore, harvest rates  $>30\text{--}40\%$  have a  
303 more drastic effect on the age and horn size of legal males in populations with rapid horn growth  
304 rate. In these populations, many males become legal at 4–5 years of age, well before their  
305 maximum potential horn size. If harvests exceed about 30% of legal males, then  $<20\%$  of adults

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306 will reach  $\geq 7$  years and hunters would most likely encounter young legal males. Our model  
307 predicts that in populations with slow-growing horns, a switch from 4/5 curl to full-curl  
308 regulations would reduce the number of harvested males by 10–25% depending on harvest  
309 pressure, because males would become legal at older ages, when natural mortality increases  
310 (Loison et al. 1999). More males would die of natural causes before reaching legal status,  
311 compared to populations with rapid horn growth rate, where our model predicts a decline in  
312 harvest of only 2–8%.

313 Our simulations revealed that as harvest rates increase past 40–50%, the number of males  
314 harvested increases very little; at these very high levels of harvest most males are taken the year  
315 they become legal, and there are very few males  $> 7$  years. High harvest rates also increase the  
316 selective effects of trophy hunting; older age classes would be made up mostly of small-horned  
317 males that are illegal to harvest (Bonenfant et al. 2009). At Ram Mountain, harvest rate was  
318 approximately 37.5% (Pelletier et al. 2012). At this level of harvest, our simulation predicts a  
319 median age of harvested males of 5 years and the average life expectancy of a legal male is about  
320 10 months; most legal males are taken the year they become legal or the following year. That  
321 compares favorably with the results from Ram Mountain, where between 1975 and 1996, 92  
322 males that attained legal status survived on average 0.86 years after their first hunting season as  
323 legal males (SD = 1.29, range = 0–6 yr; 80% survived 0 or 1 yr). The median age at harvest was 6  
324 years ( $\bar{x} = 6.1$  yr), but 40% were shot at 4 or 5 years of age.

325 As harvest rates increase, the average horn size of males decreases in the total population  
326 and among those harvested. That decline is caused by 2 factors: when harvest rates are high,  
327 males are shot at a younger age and males of any age tend to be shot as soon as their horns meet  
328 the legal definition.

329 A clear prediction of our model is that the average age at harvest should decrease as  
330 harvest intensity increases. Although this result appears intuitive, some empirical studies report

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331 the opposite pattern, with age-at-harvest increasing with higher hunting pressure (Table 1). In the  
332 simulations, age-at-harvest stabilized after only 7–8 years of hunting. In all simulations, hunting  
333 initially led to a rapid decline in the average age of harvested males because unharvested  
334 populations include several legal males in many age classes, but as those are harvested, the  
335 population quickly reaches an equilibrium where most legal males are those that just became  
336 legal that year or the year before. The younger but stable age distribution predicted by our model  
337 does not match several recent observations of trophy-hunted ungulates, where the average age at  
338 harvest increased over time, particularly because of a diminishing proportion of young males  
339 (Garel et al. 2007, Festa-Bianchet et al. 2014). The increase in age of harvested males reported by  
340 recent studies may therefore suggest a decrease in horn growth rate (Garel et al. 2007, Hengeveld  
341 and Festa-Bianchet 2011, Festa-Bianchet et al. 2014, Pelletier et al. 2014), consistent with a  
342 possible evolutionary effect of selective hunting (Coltman et al. 2003, Festa-Bianchet et al. 2014,  
343 Gabriel et al. 2016, Pigeon et al. 2016).

344 Our model is based on data on natural survival of bighorn males from the NBR  
345 population, the only available source of this detailed age-specific information. Survival of males  
346 aged 4–8 at the NBR (Table S1) is very similar to the age-specific natural survival (excluding  
347 hunting mortality) of adult males in 2 hunted populations in Alberta (Loison et al. 1999). For  
348 example, natural survival from 4 to 9 years of age would be 0.37, 0.38, and 0.39 at NBR, Ram  
349 Mountain, and Sheep River, respectively, all populations with long-term data on age-specific  
350 survival. The precision of our estimates of survival of males >9 years is limited by the small  
351 sample size, but in most hunted populations very few males survive to that age (Festa-Bianchet et  
352 al. 2014). In very lightly hunted populations, a higher survival of older males would clearly  
353 increase the availability of trophies compared to our model's predictions.

354 Our simulations are relevant for other trophy-hunted species where harvest regulations are  
355 based on horn size or shape, such as other wild sheep, including Stone's (*O. dalli*; Douhard et al.

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356 2016), and wild goats such as ibex (*Capra ibex*; Büntgen et al. 2014). For other bovids that reach  
357 near-asymptotic horn size by 2–3 years of age, such as mountain goat (*Oreamnos americanus*) or  
358 pronghorn (*Antilocapra americana*; Festa-Bianchet 2012), we expect a much weaker interplay  
359 between horn size and age. For cervids, hunting regulations are often based on number of tines  
360 rather than on antler size or shape (Strickland et al. 2001) and the relationship between number of  
361 tines and age often reaches an asymptote at 3–6 years of age, depending on the species (Myserud  
362 et al. 2005). In those species, regulations imposing hunter selectivity and changes in harvest rate  
363 may affect antler branching pattern more than antler size, and considerable attention has been  
364 devoted, for example, to how restrictions on tine numbers may affect the harvest of young male  
365 white-tailed deer (*Odocoileus virginianus*; Strickland et al. 2001).

#### 366 **MANAGEMENT IMPLICATIONS**

367 Our simulations provide managers with guidelines to the possible consequences of varying  
368 harvest rates in bighorn sheep populations with different horn growth characteristics. Our model  
369 suggests that harvest rates above 30–40% of legal males will lead to a marginal increase in the  
370 harvest while reducing the average horn size and shifting the age distribution of males towards  
371 those aged 4–6 years. The determination of harvest rates of legal males, however, remains a  
372 major challenge. Our simulations imply that a young age structure indicates a high harvest rate,  
373 especially under the slow versus fast growth scenario. Accurate measurements of the first 4  
374 growth increments would allow managers to estimate population-specific horn growth rates at  
375 ages before males become vulnerable to hunting. This information can be used to assess the  
376 likely impacts of different hunting regulations, limit the effect of trophy hunting on male age  
377 structure, reduce the risk of artificial selection, and increase the average age and horn size of  
378 harvested males. The optimal regulation will differ between herds of different horn growth rates.  
379 A combination of full-curl definition of legal male and quotas may be required in populations  
380 with rapid horn growth. In populations with slow horn growth, a full-curl regulation may reduce



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381 the harvest sufficiently without the imposition of quotas.

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## **LITERATURE CITED**

- 394 Alberta Government. 2015. Draft Management Plan for Bighorn Sheep in Alberta. Alberta  
395 Wildlife Management Branch, Edmonton, Canada.
- 396 Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009. Age-dependent relationship  
397 between horn growth and survival in wild sheep. *Journal of Animal Ecology* 78:161–171.
- 398 Bourbeau-Lemieux, A., M. Festa-Bianchet, J.-M. Gaillard, and F. Pelletier. 2011. Predator-driven  
399 component Allee effects in a wild ungulate. *Ecology Letters* 14:358–386.
- 400 Büntgen, U., A. M. Liebhold, H. Jenny, A. Mysterud, S. Egli, D. Nievergelt, N. C. Stenseth, and  
401 K. Bollmann. 2014. European springtime temperature synchronises ibex horn growth across  
402 the eastern Swiss Alps. *Ecology Letters* 17:303–313.
- 403 Coltman, D.W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet.

- Schindler et al.  
404 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- 405 Crosmary, W. G., A. J. Loveridge, H. Ndaimani, S. Lebel, V. Booth, S. D. Côté, and H. Fritz.  
406 2013. Trophy hunting in Africa: long-term trends in antelope horn size. *Animal Conservation*  
407 16:648–660.
- 408 Douhard, M., M. Festa-Bianchet, F. Pelletier, J.-M. Gaillard, and C. Bonenfant. 2016. Changes in  
409 horn size of Stone's sheep over four decades correlate with trophy hunting pressure.  
410 *Ecological Applications* 26:309–321.
- 411 Douhard, M., G. Pigeon, M. Festa-Bianchet, D. W. Coltman, S. Guillemette, and F. Pelletier.  
412 2017. Environmental and evolutionary effects on horn growth of male bighorn sheep. *Oikos* in  
413 press. doi:10.1111/oik.03799
- 414 Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage  
415 quality, forage quantity and predator avoidance. *Oecologia* 75:580–586.
- 416 Festa-Bianchet, M. 2012. The cost of trying: weak interspecific correlations among life-history  
417 components in male ungulates. *Canadian Journal of Zoology* 90:1072–1085.
- 418 Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to  
419 horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology*  
420 15:305–312.
- 421 Festa-Bianchet, M., T. Coulson, J. M. Gaillard, J. T. Hogg and F. Pelletier. 2006. Stochastic  
422 predation and population persistence in bighorn sheep. *Proceedings of the Royal Society B-*  
423 *Biological Sciences* 273:1537–1543.
- 424 Festa-Bianchet, M., F. Pelletier, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Decrease in horn  
425 size and increase in age of trophy sheep in Alberta over 37 years. *Journal of Wildlife*  
426 *Management* 78:133–141.
- 427 Festa-Bianchet, M., S. Schindler, and F. Pelletier. 2015. Record books do not capture population  
428 trends in horn length of bighorn sheep. *Wildlife Society Bulletin* 39:746–750.

Schindler et al.

- 429 Gabriel P., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting  
430 leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- 431 Garel, M., J. M. Cugnasse, D. Maillard, J. M. Gaillard, A. J. Hewison, A. J. M., and D. Dubray.  
432 2007. Selective harvesting and habitat loss produce long-term life history changes in a  
433 mouflon population. *Ecological Applications* 17:1607–1618.
- 434 Geist, V. 1966. Validity of horn segment counts in aging bighorn sheep. *Journal of Wildlife*  
435 *Management* 30:634–646.
- 436 Hengeveld, P. E., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on  
437 horn size in male bighorn sheep. *Journal of Wildlife Management* 75:189–197.
- 438 Hogg, J. T., S. H. Forbes, B. M. Steele, and G. Luikart. 2006. Genetic rescue of an insular  
439 population of large mammals. *Proceedings of the Royal Society of London B: Biological*  
440 *Sciences* 273:1491–1499.
- 441 Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on  
442 horn development in bighorn rams. *Journal of Wildlife Management* 62:1011–1020.
- 443 Köppen, W. 1884. Die Wärmezonen der Erde, nach der Dauer der heissen, gemässigten und  
444 kalten Zeit und nach der Wirkung der Wärme auf die organische Welt betrachtet (The thermal  
445 zones of the earth according to the duration of hot, moderate and cold periods and to the  
446 impact of heat on the organic world). – *Meteorol. Z.* 1, 215–226. (translated and edited by  
447 Volken, E. and S. Brönnemann – *Meteorol. Z.* 20 (2011), 351–360).
- 448 Leader-Williams, N., R. J. Smith, and M. J. Walpole. 2001. Elephant hunting and conservation.  
449 *Science* 293:2203.
- 450 Leclerc, M. J. Van de Walle, A. Zedrosser, J. E. Swenson, and F. Pelletier. 2016. Can hunting  
451 data be used to estimate unbiased population parameters? A case study on brown bears.  
452 *Biology Letters* 12(6). Doi: 10.1098/rsbl.2016.0197.
- 453 Loehr, J., J. Carey, J., R. B. O'Hara, and D. S. Hik. 2010. The role of phenotypic plasticity in

Schindler et al.

- 454 responses of hunted thinhorn sheep ram horn growth to changing climate conditions. *Journal*  
455 *of Evolutionary Biology* 23:783–790.
- 456 Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999. Age-  
457 specific survival in five populations of ungulates: Evidence of senescence. *Ecology* 80:2539–  
458 2554.
- 459 Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression.  
460 *Evolution* 45:622–629.
- 461 Miller, J. M., J. Poissant, J. T. Hogg, and D. W. Coltman. 2012. Genomic consequences of  
462 genetic rescue in an insular population of bighorn sheep (*Ovis canadensis*). *Molecular*  
463 *Ecology* 21:1583–1596.
- 464 Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective  
465 hunting in ungulates and carnivores. *Conservation Biology* 21:36–47.
- 466 Monteith, K. L., R. A. Long, V. C. Bleich, J. R. Heffelfinger, P. R. Krausman, and R. T. Bowyer.  
467 2013. Effects of harvest, culture, and climate on trends in size of horn-like structures in  
468 trophy ungulates. *Wildlife Monographs* 183:1–28.
- 469 Mysterud, A., E. Meisingset, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2005. Climate-  
470 dependent allocation of resources to secondary sexual traits in red deer. *Oikos* 111:245–252.
- 471 Pelletier, F., M. Festa-Bianchet, and J. T. Jorgenson. 2012. Data from selective harvests  
472 underestimate temporal trends in quantitative traits. *Biology Letters* 8:878–881.
- 473 Pelletier, F., M. Festa-Bianchet, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Can phenotypic  
474 rescue from harvest refuges buffer wild sheep from selective hunting? *Ecology and*  
475 *Evolution* 4:3375–3382.
- 476 Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting  
477 leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- 478 Platt, M. 2015. Alberta bighorn sheep killed near Longview sets worldrecord. *Calgary Sun*. 09

Schindler et al.

- 479 March 2015; [http://www.calgarysun.com/2015/03/09/alberta-bighorn-sheep-killed-near-](http://www.calgarysun.com/2015/03/09/alberta-bighorn-sheep-killed-near-longview-sets-world-record)  
480 [longview-sets-world-record](http://www.calgarysun.com/2015/03/09/alberta-bighorn-sheep-killed-near-longview-sets-world-record). Accessed 08 Mar 2017.
- 481 R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for  
482 Statistical Computing, Vienna, Austria.
- 483 Rivrud, I. M., K. Sonkoly, R. Lehoczki, S. Csányi, G. O. Storvik, and A. Mysterud. 2013. Hunter  
484 selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. *Journal of*  
485 *Applied Ecology* 50:168–180.
- 486 Strickland, B. K., S. Demarais, L. E. Castle, J. W. Lipe, W. H. Lunceford, H. A. Jacobson, D.  
487 Frels, and K. V. Miller. 2001. Effects of selective-harvest strategies on white-tailed deer antler  
488 size. *Wildlife Society Bulletin* 29:509–520.
- 489 Therneau, T., and P. Grambsch. 2000. *Modeling survival data*. Springer, New York, New York,  
490 USA.
- 491 Therneau, T., and T. Lumley. 2014. *Survival*. R package version 3.8-1 [http://CRAN.R-](http://CRAN.R-project.org/package=survival)  
492 [project.org/package=survival](http://CRAN.R-project.org/package=survival). Accessed 08 Mar 2017.
- 493 Traill, L. W., S. Schindler, and T. Coulson. 2014. Demography, not inheritance, drives  
494 phenotypic change in hunted bighorn sheep. *Proceedings of the National Academy of*  
495 *Sciences of the United States of America* 111:13223–13228.
- 496 Wild Sheep Foundation Professional Biologist Meeting Attendees. 2008. Ram harvest strategies  
497 for western states and provinces—2007. *Proceedings of the Biennial Symposium of the*  
498 *Northern Wild Sheep and Goat Council* 16:92–98.

499

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500 **FIGURE CAPTIONS**

501 **Figure 1** Age at death [yr] of harvested bighorn males under varying hunting pressure [%  
502 harvested] and 4/5 curl regulation for slow-growing (circles) and fast-growing (squares) horns.  
503 Error bars indicate standard deviations.

504  
505 **Figure 2** Age distribution of harvested bighorn males under high hunting pressure (solid lines,  
506 40% harvested) and low hunting pressure (dashed lines, 10% harvested) when horns grow slowly  
507 (black lines) or grow fast (red lines). Hunting is modeled according to the 4/5 curl regulation.

508  
509 **Figure 3** Age-specific [yr] horn length [cm] of all bighorn males at the start of the hunting season  
510 for low hunting pressure (10% harvested, circles) and high hunting pressure (40% harvested,  
511 squares) under the 4/5 curl regulation for populations with A) slow growth or B) fast growth. If  
512 hunting pressure is high in the population with fast-growing horns, no male survives until age 15.  
513 Error bars indicate standard deviation.

514  
515 **Figure 4** Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural  
516 causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty  
517 symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn  
518 growth.

519

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520 Table 1. Empirical studies assessing the effects of hunting on demography, trophy measures, and  
 521 life-history of ungulates and carnivores.

Species	Traits studied	Trait trends	Methods	Reference
Ungulates and carnivores	M age	Reduction of mean M age.	Population census.	Milner et al. 2007
Mouflon ( <i>Ovis gmelini musimon</i> )	Age and horn size	Age of desirable trophies increased by ~4 yrs. Proportion of young M in the harvest decreased. Horn size decreased under harvesting.	Compared harvested M of populations under hunting with a protected population.	Garel et al. 2007
Thinhorn ( <i>Ovis dalli</i> )	M age	M with rapid horn growth are shot earlier in life than slow-growers.	Horn size of harvested M.	Loehr et al. 2010
Bighorn	Horn length and circumference	Lower decrease in length for harvested M (-11%) than	Compared horn trends between shot M and all M.	Pelletier et al. 2012

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overall (−20%).

Decline in

circumference not

different.

Bighorn	Horn length, age, counts	No. harvested M and horn size decreased. Age-at-harvest increased.	Size measurements on harvested M.	Festa-Bianchet et al. 2014
Red deer ( <i>Cervus elaphus</i> )	Antler size	No consistent temporal pattern.	Measurements of harvested M and entries in trophy shows.	Rivrud et al. 2013
Impala ( <i>Aepyceros melampus</i> )	Horn length and age-at-harvest	Horn length decreased (−4%) and age-at-harvest decreased.	Size of harvested trophies.	Crosmary et al. 2013
Greater kudu ( <i>Tragelaphus strepsiceros</i> )	Horn length and age-at-harvest	Horn length increased (14%) and age-at-harvest increased, possibly because of decreasing harvest pressure.	Size of harvested trophies.	Crosmary et al. 2013



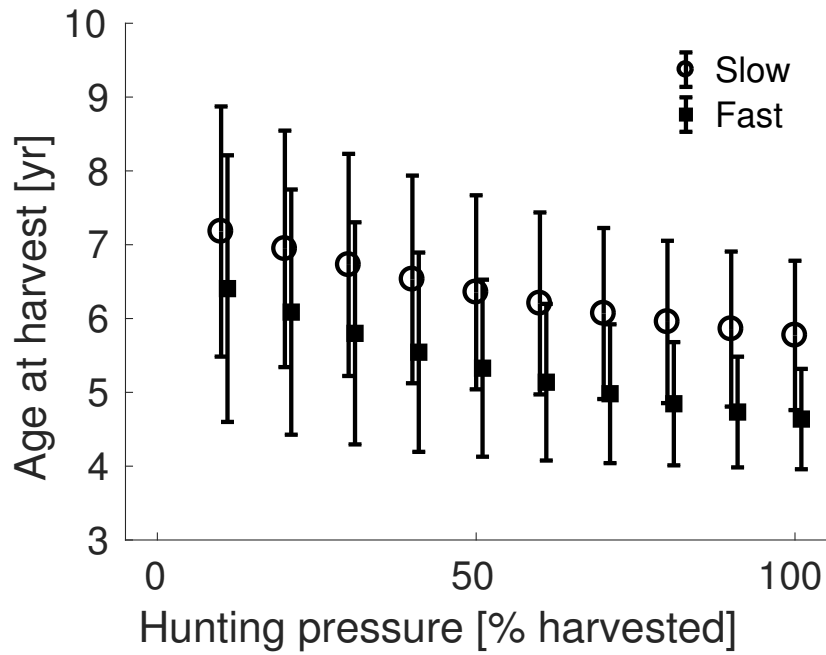
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Sable antelope ( <i>Hippotragus niger</i> )	Horn length and age-at-harvest	Horn length decreased (−6%), no change in age-at-harvest.	Size of harvested trophies.	Crosmary et al. 2013
Trophy ungulates	Trophy size	Decline in trophy size for most species.	Record book entries.	Monteith et al. 2013
Brown bear ( <i>Ursus arctos</i> )	Age structure and body mass	Ratio of yearlings to adult F and yearling body mass declined over time. Mass of shot F showed no trend, whereas mass of monitored F decreased.	Compared data from monitoring project with hunting records.	Leclerc et al. 2016

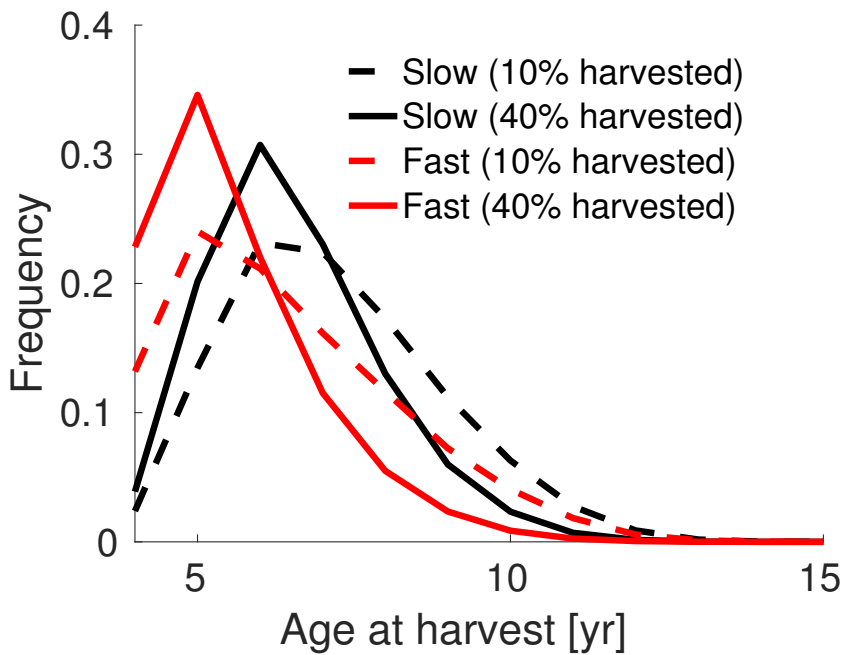
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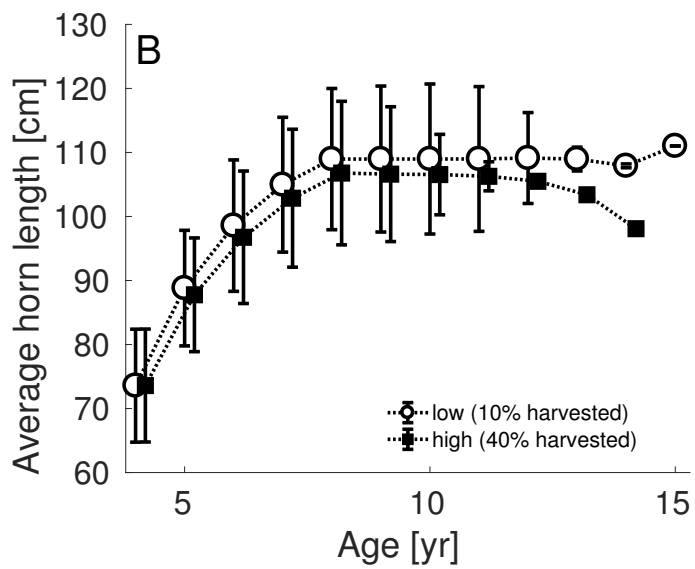
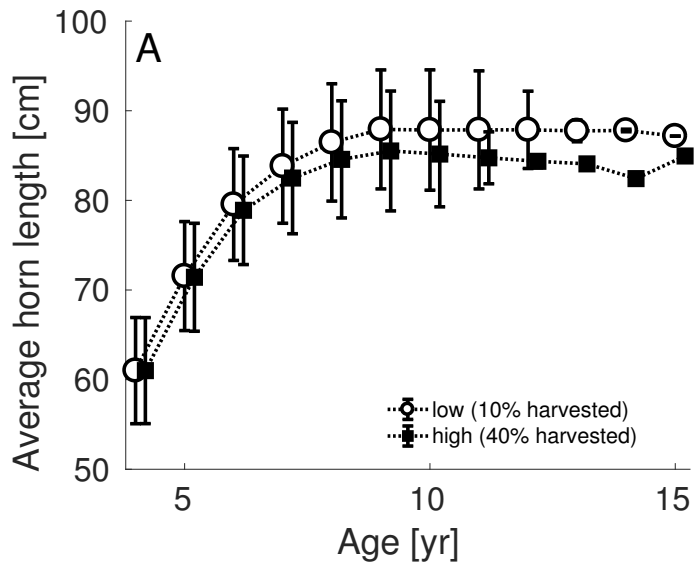
524 Article Summary: We show that the effect of hunting regulations on age structure and trophy size  
525 depends strongly on the rate of trophy growth, which naturally varies between populations of the  
526 same species. This implies that the optimal hunting regulation differs between herds of different  
527 trophy growth rates.

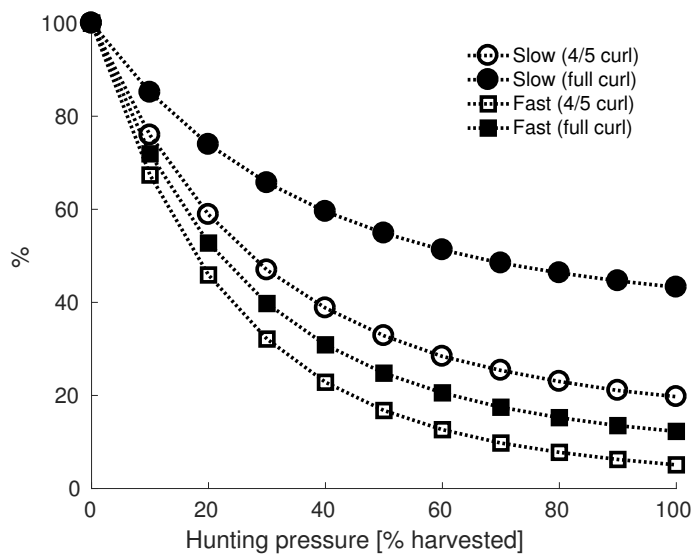
Figures for  
Hunting effects on age-structure and  
horn size distribution in bighorn sheep.

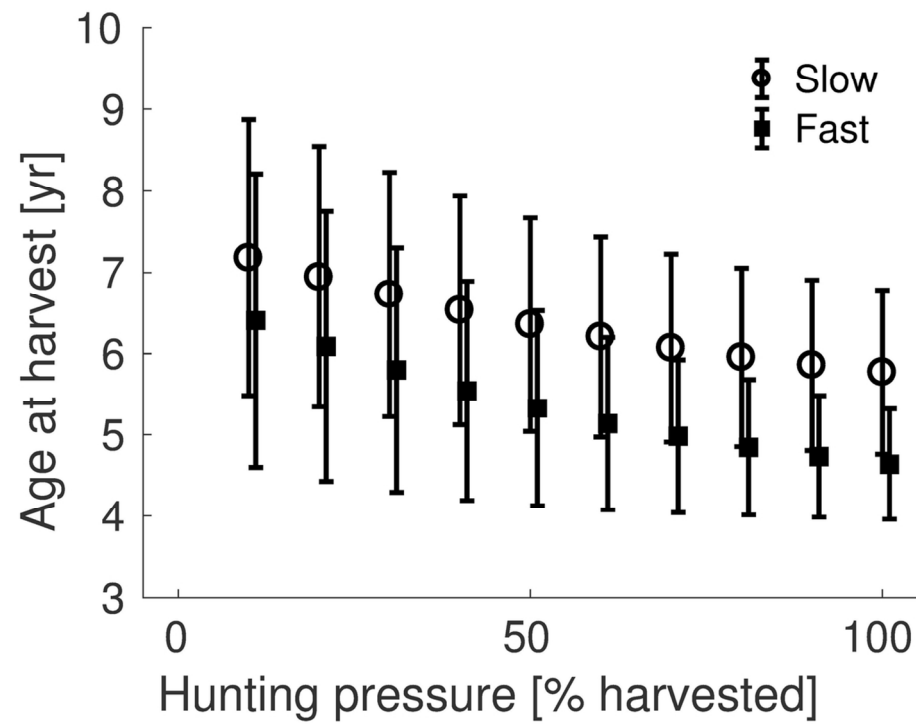
Susanne Schindler, Marco Festa-Bianchet, John T. Hogg & Fanie Pelletier





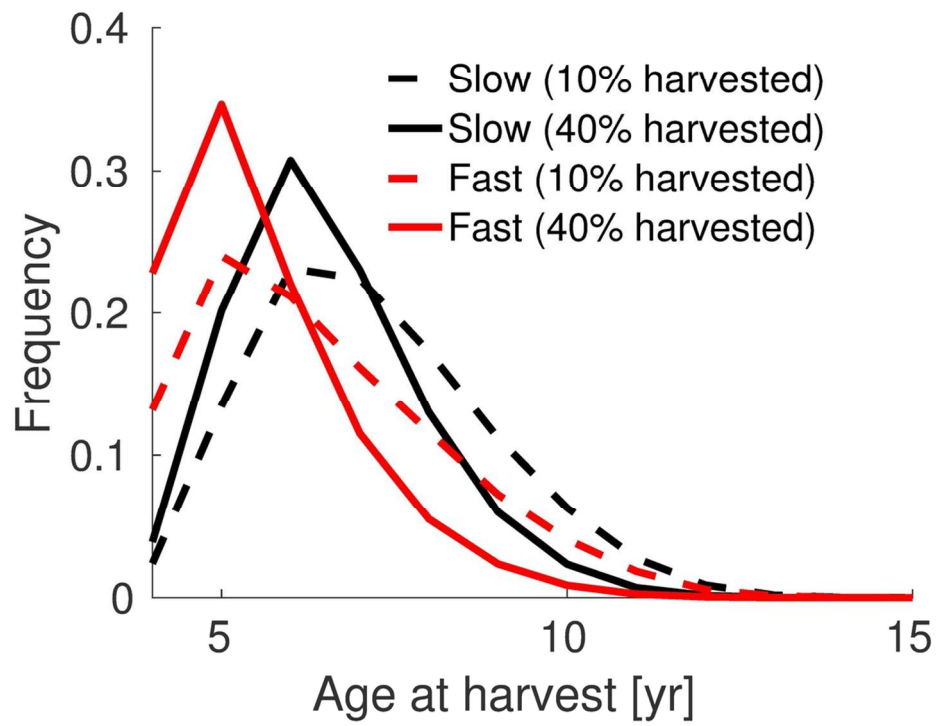






Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn growth.

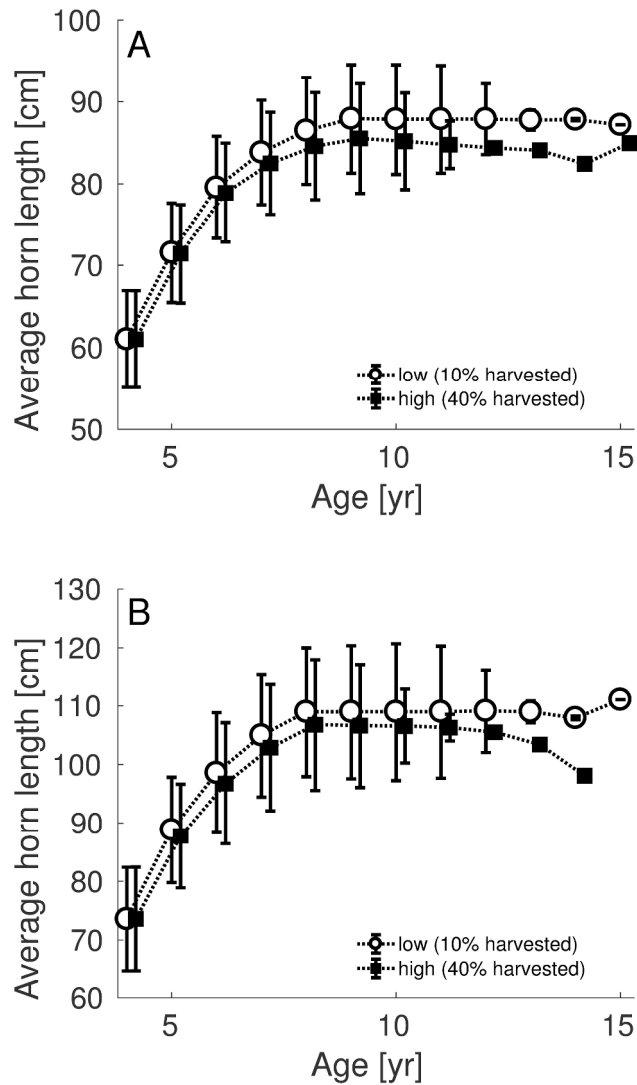
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Age distribution of harvested bighorn males under high hunting pressure (solid lines, 40% harvested) and low hunting pressure (dashed lines, 10% harvested) when horns grow slowly (black lines) or grow fast (red lines). Hunting is modeled according to the 4/5 curl regulation.

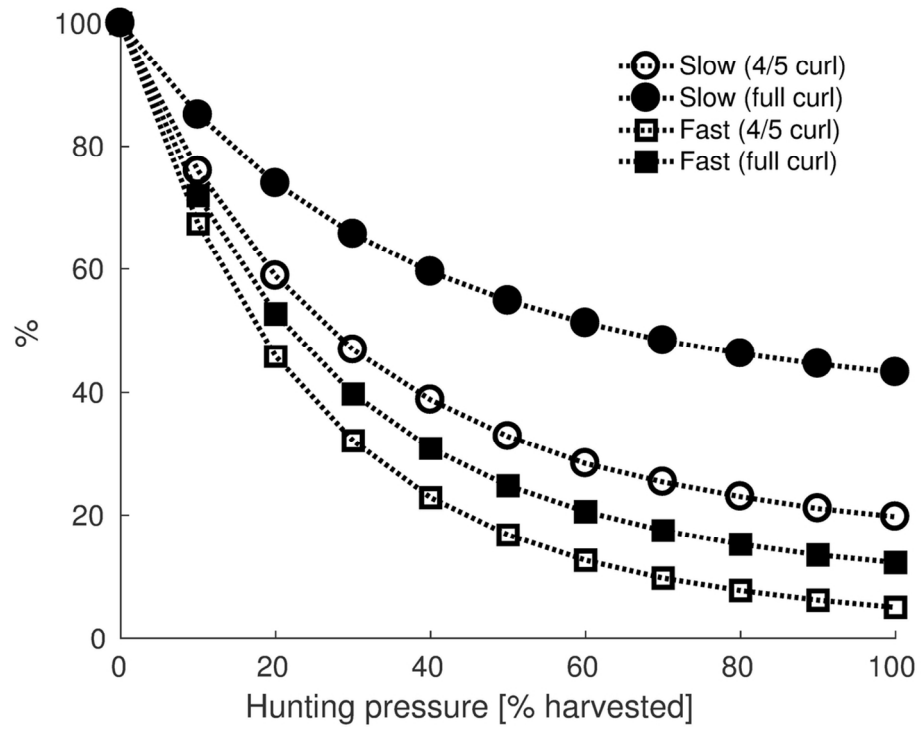
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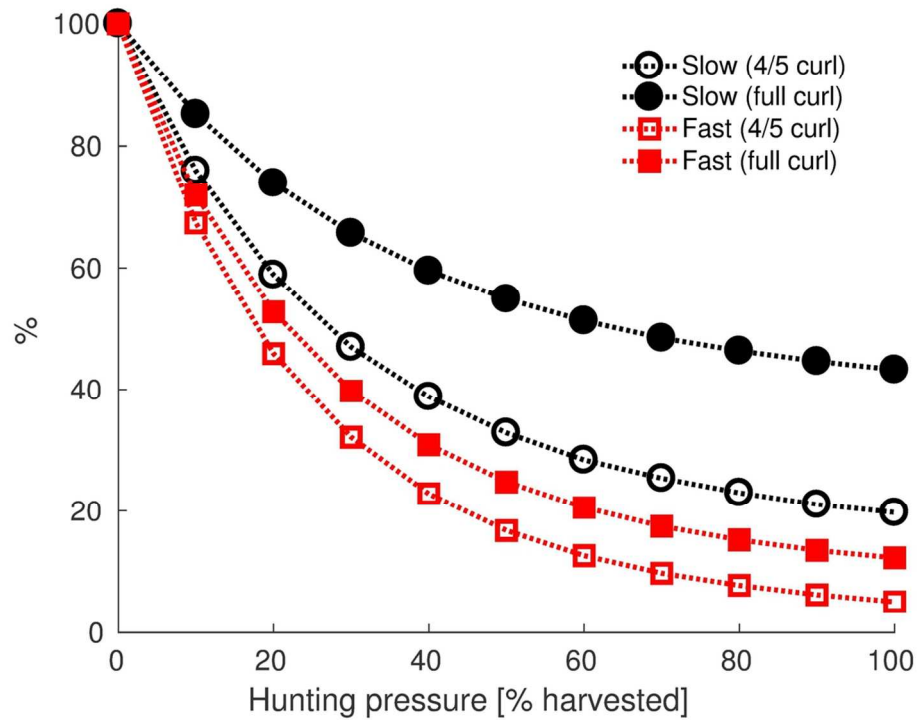
Age-specific [yr] horn length [cm] of all bighorn males at the start of the hunting season for low hunting pressure (10% harvested, circles) and high hunting pressure (40% harvested, squares) under the 4/5 curl regulation for populations with A) slow growth or B) fast growth. If hunting pressure is high in the population with fast-growing horns, no male survives until age 15. Error bars indicate standard deviation.

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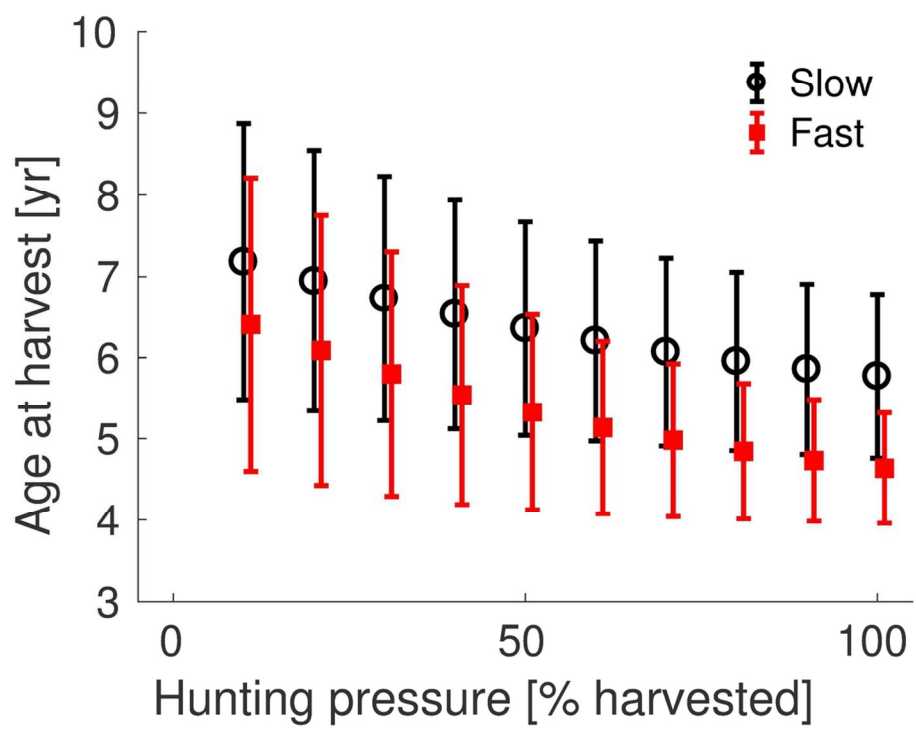
Fraction of a cohort of bighorn males that survived to 4 years of age and died of natural causes for varying hunting pressures [% harvested] and hunting regulations (4/5 curl = empty symbols, full-curl = filled symbols). Circles refer to slow horn growth, squares to fast horn growth.

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Online color version of fig 4

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Online color version of fig 1

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