



Letter to the Editor

Mountain Sheep Management Using Data Versus Opinions: A Comment on Boyce and Krausman (2018)

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Sustainable wildlife management must consider the possible evolutionary effects of harvest schemes (Festa-Bianchet 2017). A recent Editor's Message in the *Journal of Wildlife Management* (Boyce and Krausman 2018) about the Special Section on mountain sheep management and 2 invited papers (Coulson et al. 2018, Heffelfinger 2018) question whether quota-free, phenotype-based selective hunting of bighorn (*Ovis canadensis*) males can lead to a measurable evolutionary change in horn size over a few generations. Responding to the Editor's Message, I argue that evidence of harvest-caused evolutionary changes in mountain sheep horns is strong, and worthy of consideration in management plans. Those evolutionary changes are brought about by very intense artificial selection against males with rapidly growing horns, a trait with a strong genetic component (Poissant et al. 2008).

Bighorn sheep management in the United States and Canada differs. Although Heffelfinger (2018) refers to regulations at Ram Mountain, Alberta, as atypical, those regulations up to 2011 were typical of most of Canada: phenotype-based definition of legal male, long hunting season (late Aug to 31 Oct) and no quota for provincial residents (Festa-Bianchet et al. 2014). Although successful hunters cannot purchase a license the following year, given their success rate of 7% (Festa-Bianchet et al. 2014), that restriction has little impact. In contrast, most U.S. states have more restrictive regulations, typically including harvest quotas.

Boyce and Krausman (2018:5) assert that Coltman et al. (2003) "failed to eliminate the possible influence of change in environment as an alternative explanation for phenotypic change." Coltman et al. (2003) accounted for the strong effects of population density on horn growth (Jorgenson et al. 1998) by including annual yearling female mass as a covariate. That is likely why their results were corroborated by a reanalysis (Pigeon et al. 2016) that accounted for possible environmental changes and other statistical criticisms (Postma 2006, Hadfield et al. 2009) and revealed that the genetic decline in horn size stopped when the intense selective hunt stopped.

Boyce and Krausman (2018) question the magnitude of evolutionary change caused by trophy hunting and our ability to detect it. They cite van Benthem et al. (2016) to claim that "the animal model from quantitative genetics estimates evolution with a negative bias." Van Benthem et al. (2016) report a negative bias only when simulated maternal effects decrease but are not correctly modeled. More relevant to this discussion, van Benthem et al. (2016), like several others (Hedrick et al. 2014, Chevin 2015, Janeiro et al. 2017) demonstrate that the Integral Projection Model in Traill et al. (2014), claiming that changes in horn size at Ram Mountain were demographic, cannot detect even strong evolutionary changes. Despite having been refuted by multiple publications, Traill et al. (2014) is frequently cited in this Special Section as evidence against evolutionary change in bighorn sheep horn size.

Boyce and Krausman (2018) imply that Pigeon et al. (2016) reported that evolutionary change accounted for only 9% of the total phenotypic decline in male horn length at Ram Mountain. This is incorrect. The 9% effect is for the proportion of variance in horn length of 3-year-old males in another analysis (Douhard et al. 2017) that included nearly 20 years of data when horn size was not affected by hunting-induced selection. The proportional decline in horn length while legal males were intensively harvested was about 15% (Pelletier and Coltman 2018). Considerations of the proportional decline, however, distract from the real issue of the absolute effect of evolutionary change. The definition of legal male is based on degree of horn curl; the 2.6-cm evolutionary decline in horn length over 2 generations, estimated by Pigeon et al. (2016), can make the difference between being shot or not. That is likely why Pigeon et al. (2016) found a direct link between the predicted fitness decline caused by evolutionary change and fitness measured as male survival. The large overall phenotypic decline in horn size at Ram Mountain was partly due to a doubling of population size (Jorgenson et al. 1998). Several hunted populations of mountain sheep have shown similar declines in male horn size, consistent with an evolutionary effect, without major increases in density (Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014, Douhard et al. 2016).

Boyce and Krausman (2018) praise the model in the invited contribution by Coulson et al. (2018:52), whose conclusion is that "it is expected to take tens of generations before the

Received: 28 February 2018; Accepted: 12 June 2018

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mean trophy size has evolved to be significantly smaller than it was prior to the onset of selective harvesting.” Coulson et al. (2018) claim that about 70% of the phenotypic decline recorded at Ram Mountain was attributed to evolution by Coltman et al. (2003), contradicting 3 papers in this Special Section, including the Editor’s Message (Boyce and Krausman 2018, Heffelfinger 2018, Monteith et al. 2018). Coltman et al. (2003) reported a decline in horn length breeding value but did not explicitly provide an estimate of what part of the phenotypic decline could be attributed to evolution. Apparently, Boyce and Krausman (2018) did not notice that Coulson et al. (2018:53) admit that the evolutionary change estimated by Pigeon et al. (2016) is consistent with their model. The 1-cm/generation decline in horn length mentioned by Coulson et al. (2018), extrapolated over the 7 generations that liberal bighorn hunting regulations have been in place in Alberta, predicts a substantial evolutionary change. Selection against males with rapidly growing horns in Canada is intense and has been intense for several generations. It should not surprise anyone that it led to an evolutionary change in horn phenotype.

Boyce and Krausman (2018:5–6) cite Heffelfinger (2018) to claim that “the intensity of selection by trophy hunters is seldom high.” Heffelfinger (2018) reports no measurements of the intensity of selection. In Canada, selection through unlimited phenotype-based hunting is intense: at Ram Mountain, a male with fast-growing horns that became legal at age 4 had an 8% chance of surviving to rut at age 7, when horn size plays a strong role in mating success (Coltman et al. 2002, Martin et al. 2016). In contrast, a male exposed to only natural mortality had a 60% chance of surviving over the same period. A 92% mortality rate represents a selective pressure comparable to those applied to domestic animals. Data on the harvest rate of legal males under different regulatory schemes are required to quantify selective pressures and advance this debate.

Finally, Boyce and Krausman (2018) argue that genetic rescue from protected areas will swamp any evolutionary effect of selective hunting. Indeed, males range widely in autumn looking for breeding opportunities (Hogg 2000). Unselected males exiting protected areas would be advantaged in areas where their potential competitors have been shot. Genetic rescue, however, requires males from refuge areas to survive to the rut. In Alberta, the hunting season lasts until the end of October, ensuring that at least some of those males are shot. Indeed, for a given age at harvest, the largest males are taken in late October near national parks (Pelletier et al. 2014). Effective breeding immigration from protected areas could counter the exceptionally strong selective effect of the hunt. Currently, that immigration is not quantified.

I welcome constructive criticism of results indicating an effect of intense selective hunting on mountain sheep horn size. I encourage wildlife managers to better document selective pressures in trophy-hunted species. Critiques that simply discredit results based on opinions, however, do not advance our knowledge of mountain sheep or our ability to manage them sustainably.

ACKNOWLEDGMENTS

I thank T. Bonnet, D. W. Coltman, R. M. Malenfant, M. B. Morrissey, and F. Pelletier for comments on an earlier draft of this paper. My long-term research on bighorn sheep is supported by Discovery Grants from the Natural Sciences and Engineering Research Council of Canada.

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