Original Article



Record Books Do Not Capture Population Trends in Horn Length of Bighorn Sheep

MARCO FESTA-BIANCHET,¹ Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada SUSANNE SCHINDLER, Department of Zoology, University of Oxford, Oxford OX1 3PS, England, United Kingdom FANIE PELLETIER, Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

ABSTRACT Many agencies and researchers use data from harvested animals to study temporal trends in phenotype. For large mammals, complete harvest records are typically only available for the past few decades, but records of the largest trophies have been collected for over a century. To examine whether record books and data from male bighorn sheep (*Ovis canadensis*) harvested under a minimum-curl regulation could detect temporal trends in horn length, we simulated populations of trophy-harvested male bighorn sheep where horn length was modeled to increase, remain stable, and decrease over time. All populations experienced a simulated harvest based on a minimum horn length, but only horns in the longest 5% of the initial distribution were entered in a fictional record book. We then assessed whether monitoring of harvested and "record" males detected temporal trends. Data from selective harvest underestimated declines and initially underestimated increases, but qualitatively detected both trends. Record-book entries, however, severely underestimated increases and did not detect declines, suggesting that they should not be used to monitor population trends. When these biases are taken into account, complete trophy harvest records can provide useful biological information. © 2015 The Wildlife Society.

KEY WORDS biased sampling, bighorn sheep, horn size, *Ovis canadensis*, record books, temporal trends, trophy hunting.

Following the suggestion that intensive selective harvests may cause artificial selection and potentially lead to evolutionary change (Coltman et al. 2003, Darimont et al. 2009), there has been much interest from scientists, managers, and hunters on what circumstances may lead to artificial selection through trophy hunting (Mysterud and Bischof 2010). Tests of artificial selection require long-term data and ideally a comparison of what is available with what is harvested. Evidence for artificial selection remains limited (Mysterud 2011). Unfortunately, time series of horn or antler size for harvested animals tend to be relatively recent, spanning at most a few decades (Mysterud et al. 2006, Pérez et al. 2011, Crosmary et al. 2013).

Recent publications have examined an alternative to these short time series by analyzing entries in the Boone and Crockett record book (Monteith et al. 2013), other record books (Nuzzo and Traill 2014), or trophy shows (Rivrud et al. 2013), that span over a century. Record books and trophy shows, however, provide truncated samples because only large trophies are included, and may not detect declines over time. Record books may also not detect increases in horn size over time if they include only individuals near the biologically maximum potential size, especially if extremely large size is

Received: 8 December 2014; Accepted: 26 June 2015 Published: 17 October 2015

¹E-mail: m.festa@usherbrooke.ca

selected against by natural selection. It is difficult to establish the reliability and accuracy of these sources of information, because there are very few examples of known or estimated population-scale trends to which record books could be compared. In Alberta, Canada, records of harvested male bighorn sheep (*Ovis canadensis*) taken under minimum-curl legislation underestimated population-level declines in horn size by nearly half (Pelletier et al. 2012). Province-wide analyses of harvested males over nearly 4 decades showed a decline in horn size and an increase in age at harvest, suggesting reduced horn growth early in life, but several of the highestscoring bighorn males in North America were recorded in Alberta in the past decade (Festa-Bianchet et al. 2014).

When adequate data are unavailable, data-based modeling provides a useful alternative to explore the possible effects of sampling bias in monitoring known trends in a simulated population. Here, we assess the ability of record books to detect temporal trends in horn length. We do so by simulating fictional populations of trophy-harvested bighorn males where horn length changed by a known proportion each year, and where entries into a fictional record book were limited to horns in the longest 5% of the distribution in the unhunted population. Of 870 bighorn males harvested in Alberta in 2008–2012, 27 or 3.1% were listed in the Boone and Crockett record book (J. Spring, Boone & Crockett Club, personal communication). We used 5% because it is likely that more males from a previously unhunted population would meet the minimum score.

METHODS

Based on measured rates of age-specific horn growth and natural mortality from the long-term monitoring of the Ram Mountain bighorn sheep population (Jorgenson et al. 1998, Gaillard et al. 2004) in Alberta, we produced a simple model where the average horn length of 4-year-old males in fictitious populations was stable, declined by 1%/year, or increased by 1%/year over 50 years. This yearly change is realistic: the study population showed a decline in horn length of approximately 31% over 28 years (Coltman et al. 2003). Although changes in horn length of 4-year olds translated to changes at the population level, their magnitude varied. For example, when horns of 4-year olds were simulated to increase by 1% annually, the average population horn length only increased by approximately 36% over 50 years despite the 63% increase of horn length of 4-year olds. This is because the larger males are harvested in our simulated population, and annual horn increments after age 4 remained unchanged. We compared temporal trends in horn length for the entire population, harvested males, and record-book males. Initially, 4-year-old males had average horn length of 61 cm. The average for all males aged 4 years and older was 78 cm, with only 5% having horns >97 cm. We set the minimum length for entry in the record book at 97 cm. Harvest rate was 40% of males of "legal" size, defined as horns describing four-fifths of a curl. This harvest rate is comparable to that of "legal" bighorn males in Alberta (Festa-Bianchet et al. 2014). Harvest rates are likely lower in some U.S. jurisdictions; therefore, we provide results of a simulation with a 10% harvest rate of legal males in the Supporting Information (available online). The probability of being "legal" for harvest increases with horn length, following a logistic function based on observations of males at Ram Mountain (Festa-Bianchet et al. 2014). Bighorn males with horns of 70 cm had approximately a 20% chance

of being legal, whereas nearly all males with horns of \geq 90 cm were legal for harvest. Additional details about the model are in the Supporting Information.

RESULTS

When the average horn length of 4-year-old males increased by 1%/year (Fig. 1A), record-book entries suggested a 9.7% increase in length over 50 years, which was a fourth of the actual increase of 36% for males aged \geq 4 years. Horn length of harvested males increased by 25%. When the population trend was a decrease in horn length, however, record-book entries showed a 1% decrease over the first 20 years, whereas the population horn length decreased by 26% and horn length for all harvested males declined by 16%. Record-book entries then disappeared after approximately 25-30 years because no male had horns longer than 97 cm. Over the entire 50-year time series of simulated decline, horn length of harvested males decreased by about half as much as the population horn length (Fig. 1B). With no change in horn length of 4-year olds over time, there were no temporal changes in "record-book" males, but the average horn length of the population and of harvested males declined by 7.6% over the first 5-6 years as the largest males were quickly removed (Fig. 1C). Results for a simulated harvest of 10% of "legal" males (Supporting Information) were similar, except for a smaller initial dip in horn length and larger average horn length of harvested males.

The standard deviations obtained by our simulation provide additional insights into the consequences of selective hunting, and into what may be detected by monitoring harvest data or record books. Variability in horn length of harvested males was always lower than in the total population, and variability in record-book males was always lower than for harvested males (Fig. 2), as expected under severe (harvest) and extreme (record book) truncation. With

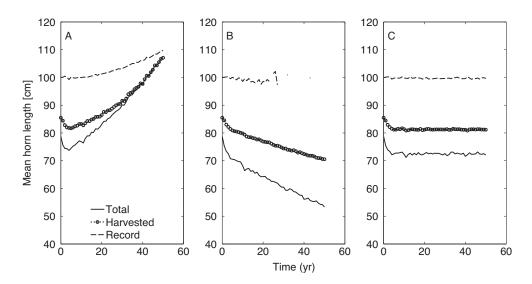


Figure 1. Simulated changes in the average horn length of harvested male bighorn sheep with horns of \geq 97 cm (Record), all harvested males with horns describing at least four-fifths of a curl (Harvested), and all males aged \geq 4 years (Total). We compared 3 bighorn populations with a starting average length of 61 cm for 4-year-old males, then simulated (A) an increase of horn length of 4-year olds by 1%/year, (B) a decrease by 1%/year, and (C) no temporal change in horn length of 4-year olds.

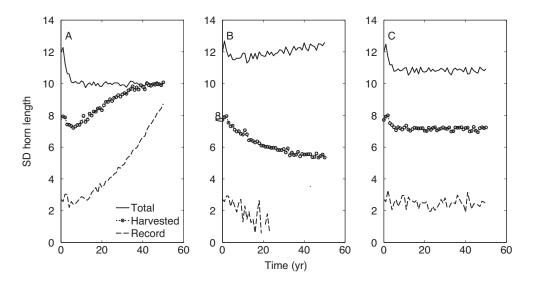


Figure 2. Simulated changes in the standard deviation of horn length of harvested male bighorn sheep with horns \geq 97 cm (Record), all harvested males with horns describing at least four-fifths of a curl (Harvested), and all males aged \geq 4 years (Total) in a bighorn population with a starting standard deviation of 5.94 and average length of 61 cm for 4-year-old males, then (A) average horn length of 4-year olds increasing by 1%/year, (B) declining by 1%/year, and (C) stable.

declining population horn length, the standard deviation of harvested and record-book males declined, because fewer large males remained and an increasing proportion of those harvested or entered in the record book barely met the minimum criteria. In Alberta, harvested males aged 4 or 5 years showed limited variability in horn length, because only exceptionally well-developed males can be "legal" at such a young age (Festa-Bianchet et al. 2014). With increasing horn length, eventually the standard deviation of the population and harvested males overlapped, because nearly all males were already legal at 4 years of age. The standard deviation of record-book males also increased, but remained lower than for the overall population.

DISCUSSION

Our results suggest that entries in record books cannot reliably detect temporal trends in horn length, especially declining trends, because they must attain a minimum score, determined by the size of the horns of the animal killed. If the minimum score is not attained, the trophy is not listed. Therefore, a population- or species-level decrease in horn length may result in fewer entries, but will not produce a temporal trend in average scores. A similar, but weaker, bias was quantified using actual data for harvested bighorn males from one population in Alberta (Pelletier et al. 2012). Because hunting regulations set a minimum horn curl, small-horned males cannot be harvested. Over 17 years, horn length in the population declined by 14 cm, but horn length of harvested males decreased by just 7.7 cm, underestimating the decline by nearly 50%. Accordingly, in the simulation we present here, a decline in horn length of 26% over 50 years was accompanied by a decline of only 16% in horn length of harvested males. The reporting bias in simulated record books was much stronger, because it recorded only exceptional trophies, corresponding to the top 5% of the distribution of horn length of the unharvested

population. The horn length of record-book entries under a simulated decline remained nearly stable, then entries disappeared because none of the males in the simulated population met the minimum threshold for horn length. A similar approach to monitoring changes in a country's wealth could involve only noting the income of billionaires, whereas a comparable approach to human speed may involve statistics on Olympic runners. For sports records, mathematical approaches can reduce this bias and detect real improvements from random (Gembris et al. 2007), but these techniques have so far been ignored in published analyses of trophy scores from record books.

Our study illustrated how the degree of bias increases with the degree of selectivity. If record books set a lower minimum threshold for entry, their ability to detect changes would increase, and likely would approach the level of bias of harvest records. Therefore, it would be useful to know, for a given region and species, what is the proportion of harvested animals likely to be listed in a record book or harvested and measured, because the lower the proportion the greater the bias. Our study clearly showed, however, that both harvest records and record-book entries are more likely to detect increasing trends than to detect decreasing trends, as one may expect from distributions that are left truncated.

Ân additional shortcoming of the Boone and Crockett records is that age of harvested animals is unknown (Monteith et al. 2013). Monteith et al. (2013) suggest that harvest at a younger age may be responsible for the declines they detected for most trophy categories. In bighorn sheep, the opposite appears to be the case. A decline in horn size of trophy males harvested in Alberta over 37 years was accompanied by increased age at harvest: the age at which horns attained legal size increased over time, presumably because of slower horn growth rate (Festa-Bianchet et al. 2014). Over that same period, a new "world record" male was shot in Alberta in 2002 and an even higher scoring male was found dead in 2010. Scores for bighorn sheep in the Boone and Crockett records have increased since 1950 (Monteith et al. 2013), but despite the biases reported by Pelletier et al. (2012), harvested males in Alberta and central British Columbia (Canada) showed temporal declines in horn length (Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014, Pelletier et al. 2014). Analyses of record-book entries offer insights into what hunting trophies are listed but cannot assess whether or not selective hunting leads to artificial selection. The bias involved in analyses of trophy shows (Rivrud et al. 2013) is unclear, because the criteria for inclusion are not specified, and may be affected over time by hunters' perception of what constitutes a large trophy, leading to a problem of shifting baselines similar to that encountered in fisheries and in other fields of conservation biology (Papworth et al. 2009).

We used a realistic but high cutoff for inclusion in our simulated record book, corresponding to the top 5% of horn lengths of an unhunted population. We also based our models on measurements from the Ram Mountain population of bighorn sheep, which is not known to produce record-book males and where males generally have smaller horns than in many other populations in Alberta. Because we set our initial criterion for entry in the record book based on the simulated horn-length distribution, however, we generated a system comparable to any wild sheep population where only the largest horns within a natural distribution qualify for entry in the record book. Therefore, our conclusions are independent of the source of the data at the base of our model. We based our simulation on horn length only, while listing in record books also depends on horn circumference and symmetry in circumference at each quarter. The definition of "legal" male, however, is mostly affected by horn length (Festa-Bianchet et al. 2014), and although the correlation between horn length and horn circumference is weak in mature males (Festa-Bianchet et al. 2014), we see no reason to suspect that the difference between horn length and the scoring formula used by the Boone and Crockett Club should strongly affect our conclusions. It is less clear how our results may apply to cervids. Scoring of antlers tends to be more complex and the age-related patterns of antler growth may differ widely among species. Although we encourage further investigation of this topic in other species, we suggest that the basic message of our analysis should apply to most species, because entry in record books depends on attaining a minimum score, generating a truncated distribution. Almost by definition, truncated distributions should be unable to detect a declining trend. A less selective record-book threshold would produce a trend curve somewhere between the ones for harvest based on a minimum four-fifths curl and record books with a 5% threshold for inclusion. Finally, our conclusions were robust to changes in harvest rate of "legal" males, suggesting that they were not affected by the harvest rate of 40% that we simulated for "legal" males.

MANAGEMENT IMPLICATIONS

Our simulations suggest that managers should not rely on record books to draw biological inferences. Even when harvests are selective with respect to horn length, however, managers would obtain useful information by monitoring variability in trophy size over time. In heavily exploited populations, most animals are taken as soon as they reach trophy size, which reduces variability in the harvested sample. An increase in variability in trophy size may suggest a decrease in harvest rate, allowing more individuals to survive one or more hunting seasons before being shot. Perhaps inclusion of as many "found dead" males in analyses of temporal trends may help reduce the bias inherent in harvest data, assuming that registration of males dead of natural causes was independent of their horn size. Finally, we suggest that to better understand the relationships between horn size in the population and in the harvested sample, it would be useful for managers to quantify harvest as a proportion of "legal" males rather than of all males, as by definition sublegal males are not part of the harvestable pool.

ACKNOWLEDGMENTS

We acknowledge the use of the University of Oxford Advanced Research Computing facility. S. Schindler is funded by an Advanced European Research Council grant awarded to T. Coulson. Our long-term research on bighorn sheep is supported by the Natural Sciences and Engineering Research Council of Canada, the Canada Research Chairs program, and the Alberta Conservation Association. We are grateful to J.-M. Gaillard and an anonymous reader for constructive comments on an earlier draft of the manuscript. Comments by the Associate Editor and two anonymous reviewers also improved the manuscript.

LITERATURE CITED

- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658.
- Crosmary, W.-G., A. J. Loveridge, H. Ndaimani, S. Lebel, V. Booth, S. D. Côté, and H. Fritz. 2013. Trophy hunting in Africa: long-term trends in antelope horn size. Animal Conservation 16:648–660.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. Proceedings of the National Academy of Sciences 106:952–954.
- Festa-Bianchet, M., F. Pelletier, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Decrease in horn size and increase in age of trophy sheep in Alberta over 37 years. Journal of Wildlife Management 78:133–141.
- Gaillard, J. M., A. Viallefont, A. Loison, and M. Festa-Bianchet. 2004. Assessing senescence patterns in populations of large mammals. Animal Biodiversity and Conservation 27:47–58
- Gembris, D., J. G. Taylo, and D. Suter. 2007. Evolution of athletic records: statistical effects versus real improvements. Journal of Applied Statistics 34:529–545.
- Hengeveld, P. E., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. Journal of Wildlife Management 75:189–197.
- Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on horn development in bighorn rams. Journal of Wildlife Management 62:1011–1020.
- Monteith, K. L., R. A. Long, V. C. Bleich, J. R. Heffelfinger, P. R. Krausman, and R. T. Bowyer. 2013. Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. Wildlife Monographs 183.
- Mysterud, Å. 2011. Selective harvesting of large mammals: how often does it result in directional selection? Journal of Applied Ecology 48:827–834.
- Mysterud, A., and R. Bischof. 2010. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? Journal of Animal Ecology 79:148–160.

- Mysterud, A., P. Trjanowski, and M. Panek. 2006. Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right time. Biology Letters 2:632–635.
- Nuzzo, M., and L. W. Traill. 2014. What 50 years of trophy records illustrate for hunted African elephant and bovid populations. African Journal of Ecology 52:250–253. doi:10.1111/aje.12104
- Papworth, S. K., J. Rist, L. Coad, and E. J. Milner-Gulland. 2009. Evidence for shifting baseline syndrome in conservation. Conservation Letters 2:93–100.
- Pelletier, F., M. Festa-Bianchet, and J. T. Jorgenson. 2012. Data from selective harvests underestimate temporal trends in quantitative traits. Biology Letters 8:878–881.
- Pelletier, F., M. Festa-Bianchet, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Can phenotypic rescue from harvest refuges buffer wild sheep from selective hunting? Ecology and Evolution 4:3375–3382.
- Pérez, J. M., E. Serrano, M. Gonzaléz-Candela, L. Léon-Vizcaino, G. G. Barbera, M. A. de Simon, P. Fandos, J. E. Granados, R. C. Soriguer, and

M. Festa-Bianchet. 2011. Reduced horn size in two wild trophy-hunted species of Caprinae. Wildlife Biology 17:102–112.

Rivrud, I. M., C. Sonkoly, R. Lehoczki, S. Csanyi, G. O. Storvik, and A. Mysterud. 2013. Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. Journal of Applied Ecology 50:168–180.

Associate Editor: Millspaugh.

SUPPORTING INFORMATION

Additional supporting information, including the model description, the data used to parameterize the model, and a simulation of a 10% harvest rate, may be found in the online version of this article at the publisher's website.