Size-at-Age of Alberta's bighorn sheep (*Ovis canadensis*)

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ABSTRACT: As with many jurisdictions, the harvest and monitoring of bighorn sheep in Alberta relies on size-classes, which must be incorporated into a population-modelling framework for the results to be relevant to management. Using morphological measurements collected at registration from 193 male bighorn sheep, we developed a size-at-age relationship to describe the range of variability in how rams grow through these size classes to become available for harvest. Applying the size-at-age relationship within a population model allows wildlife managers to simulate size-restricted harvest, and compare the likely outcomes of a variety of alternative management scenarios.

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KEY WORDS: bighorn sheep; size-selective harvest; horn growth; population modelling

INTRODUCTION

Population models have many applications in wildlife management, including illustrating the likely results of changes to management. Alberta Environment and Parks (AEP) is currently using such a model for this purpose: to foster a common understanding of the trade-offs between alternative management regimes for bighorn sheep. Knowledge of these trade-offs is essential for stakeholders to provide informed opinions on their preferences, and to have confidence that the species is being managed in the best interest of Albertans.

Harvest of male bighorn sheep in Alberta is currently enabled by one of two minimum size restrictions defined under Alberta's *Wildlife Regulation*: either 'Trophy Sheep'- a ram having at least one horn tip crossing a line from the anterior edge of the horn base through the anterior edge of the eye (hereafter referred to as '4/5'); or 'Full Curl Trophy Sheep'- a ram having at least one horn tip crossing a line from the posterior edge of the horn base through the bottom edge of the eye socket (hereafter referred to as 'Full curl'). Prior to 1968, Alberta's bighorn sheep harvest was subject to a 3/4 curl restriction, which was defined under the regulation of the day as a ram having at least one horn tip crossing a line from the anterior edge of the horn base through the posterior edge of the eye. Size class definitions may vary in other jurisdictions, despite having similar naming conventions.

AEP's aerial survey program relies on a similar system for assigning sheep to classes based on maturation (adult; young of year), sex (male; female), and horn size for males over 1 year of age (1/4; 1/2; 3/4; 4/5; and Full curl). The larger ram classes (Full curl, 4/5 and 3/4) are defined according to Alberta's *Wildlife Regulation*, but the 1/2 curl class is only defined in the aerial ungulate survey protocol as a ram having at least one horn that has grown to point down and forward rather than down and backward when the head is held in a neutral anatomical position. The 1/4 curl class includes all rams >1 year of age that have not achieved 1/2 curl (Figure 1).

These size classes are defined by morphological landmarks so they can be applied in the field, but they are based on the proportion of a circle described by the horn (hence the naming convention). Therefore, while a ram's size class is primarily driven by horn length, it is also affected by how tightly the horn curls: A ram with tight curling horns could fall into a larger size class than one with wider curling horns even if there was no difference in horn length (*sensu* Wishart 1958; Heimer and Smith 1975; Wendling 2018). Describing bighorn sheep horn growth rates based on a two-dimensional approximation of their angular size class allows for a more explicit representation of how sheep grow to become available for harvest as compared to more simplistic linear models of horn growth that only consider horn length (e.g., Bonenfant *et al.* 2009; Douhard *et al.* 2016; Monteith *et al.* 2018).

Population models use survival rates reported from detailed demographic studies of bighorn sheep to determine which individuals advance to the next year (e.g., Loison *et al.* 1999; Portier, 2006). However, these survival rates are reported based on a sheep's age in years (rather than by the size of its horns), and population models are typically structured accordingly: allowing surviving individuals to advance to the next age class at each annual time step. To simulate size-restricted harvest of rams in an age-structured population model based on their size, we need to answer the following question: *Of rams that reach a given age, how many would belong to each size-class?*

In addition to deterministic patterns of horn growth rate, size-restricted harvest truncates the range of variability above the minimum size restriction. This is especially pronounced in the older age-classes, which are primarily represented by slower growing individuals who have experienced less cumulative exposure to harvest mortality than the faster growing members of their birth-year cohort. Lee (1912) was the first to describe the demographic effect of size-restricted harvest on population structure, which could conceivably contribute to an evolutionary effect depending on the heritability of the trait under selection. The Lee effect has been widely explored in fisheries management literature, but only recently has it been explicitly accounted for in predicting the outcomes of alternative management regimes (Kvamme and Frøysa 2004; Punt *et al.* 2013; Taylor and Methot 2013; Kraak *et al.* 2019). In this context, the survivor bias in the data is not

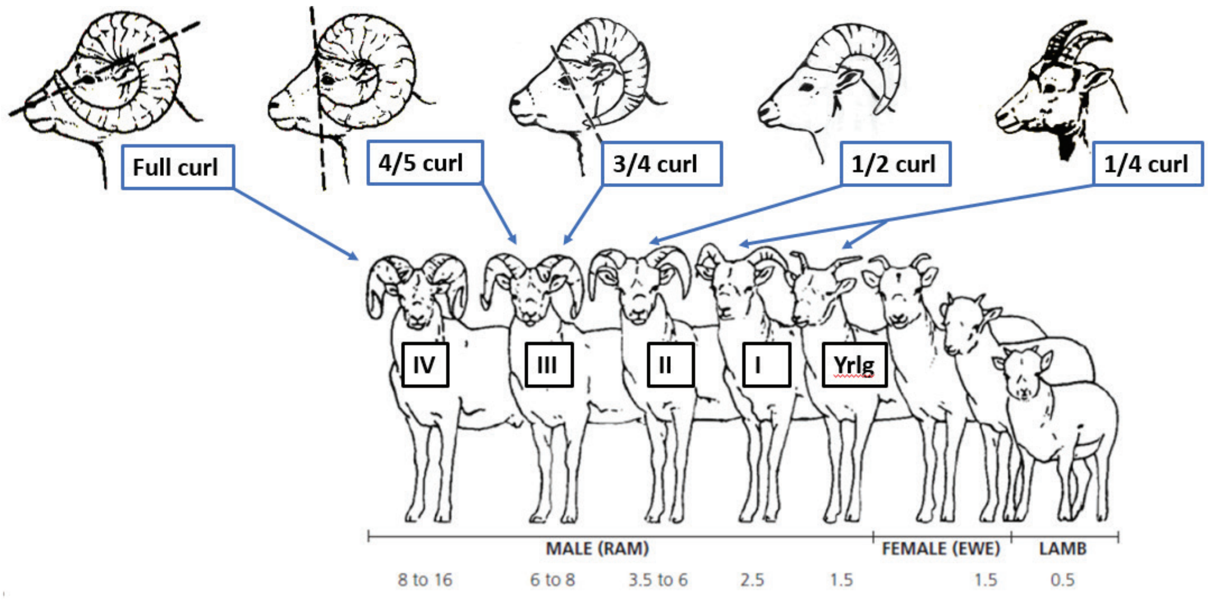

Figure 1. Size classes used by Alberta for harvest and monitoring of bighorn sheep rams (top), and how this system compares to the classification system developed by Geist (1966): Alberta divides Class III rams into separate 4/5 and 3/4 classes, but lumps yearlings and Class I rams together as 1/4 curls. Note that Alberta's *Wildlife Regulation* does not provide a legal definition for 1/2 curl, as this has never been used as a minimum size restriction. Likewise, Geist (1966) only defines class II rams as having horns that "form about ½ circle." On surveys, the 1/2 curl class has been defined by having a horn that has grown to point down and forward rather than down and backward, and serves as an approximate separation between 2 and 3 year old rams (though these age-classes have considerable overlap in size).

necessarily a problem because it is an accurate representation of the individuals that have survived to remain part of the population under the current management regime. However, the nature of the bias is dependent on both the minimum size restriction and the harvest rate of individuals above that minimum size, so survivor bias in the size-at-age relationship must be adjusted appropriately for the scenario to which that relationship is applied- especially those with alternative size restrictions (Kraak *et al.* 2019).

Any model requires a starting point, and a realistic initial population structure can improve the reliability of model projections, especially in the short term. To convert size-structured survey results to an age-structured initial population, we need to answer the following question: *How old are the sheep in a given size class?*

Non-hunting mortality is presumed to be dependent on age rather than size (Bonenfant *et al.*, 2009). Therefore, accounting for such mortality was not necessary to convert from age to size class. However, non-hunting mortality must be considered to convert from size to age because older sheep have been exposed to more years of mortality from all sources and thus will be less common relative to the younger members of the same size class. Therefore, the cumulative effects of both size-restricted harvest mortality and age-specific non-hunting mortality must be accounted for to determine the age distribution of sheep within a given size class.

To illustrate how AEP has addressed the challenge of simulating size restricted harvest in recent population modelling exercises, this paper examines the development of a preliminary size-at-age relationship to describe the realized results of the current management regime in Sheep Management Areas 7 and 8 (north of the Athabasca River to the border with British Columbia) from 2009-19: a 4/5 minimum size restriction with 32% of legal rams being harvested annually; 0.6% of ewes and lambs being harvested annually; and age-specific non-hunting mortality rates reported from Alberta's Ram Mountain study area (Loison *et al.* 1999; Portier 2006). The size-at-age relationship presented in this paper should be considered preliminary, with a more robust analysis of a larger dataset expected in the near future.

METHODS

Of rams that reach a given age, how many would belong to each size-class?

Measurements of annuli and curl diameter (Figure 2) from 193 of the rams harvested in Alberta between 2015 and 2019 were used to develop a relationship between a ram's age and the angular size class of his largest horn. Age-specific cumulative horn length for each year of a ram's life was used to maximize the information available from each sheep, providing a total of 1331 sheep-years (though sample size declines in the older age classes, and no sheep over 11 years of age were available in the dataset). Only complete years of growth were included in this dataset (the incomplete year of growth in the ram's final year of life was not included), thus the size-at-age relationship reflects individuals at the end of the growing year. The size of a ram at the end of the growing season is a reasonable representation of how large that individual would grow by the end of the hunting season (typically October 31st across most of Alberta), and therefore whether that individual should be considered to have been available for harvest. This relationship would also be representative of the sizes observed on late winter surveys (typically conducted in February, before horn growth has resumed in spring).

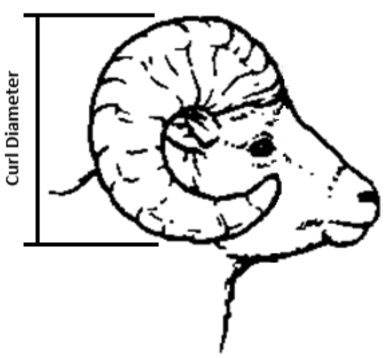

Figure 2. Diameter of curl. This measurement is used to convert linear annuli measurements into a 2-dimensional approximation of size class for male bighorn sheep based on the proportion of a complete circle described by the horn.

The cumulative length of the horn in each year of a ram's life was divided by the circumference of the circle described by the horn (*pi* x curl diameter) to convert length into proportion of a circle (*sensu* Wishart 1958; Heimer and Smith 1975; Wendling *et al.* 2018). Curl diameter was measured either in hand, or from photos taken at the time of registration, and the availability of this metric was the main constraint on sample size. From a subset of these sheep where the data were available, morphological landmarks were used to establish the average threshold for each size class (1/4 < 0.454; 1/2 > 0.454 and < 0.635; 3/4 > 0.635 and < 0.795; 4/5 > 0.795 and < 0.901; and Full curl > 0.901). These values are likely to be refined and updated as sample size increases, but are adequate to illustrate the concept. Note that the half curl threshold is not precisely defined in regulation- the value of 0.454 was chosen based on the less precise definition used on aerial surveys (i.e., horns that have grown to point down and forward rather than down and backward when the head is held in a neutral anatomical position) and the size at which a ram is equally likely to be either 2 or 3 years old.

Non-hunting mortality of adult sheep varies by age-class, but is not strongly correlated with horn size within an age class (Bonenfant *et al.,* 2009). As a result, there is no need to account for non-hunting mortality to address the size of rams within a given age-class, but the bias introduced by size-restricted hunting mortality must be addressed. First, the expected size of each individual was projected for the years after its death based on the consistent pattern of declining growth as a ram ages (made relative to the combined length of the 2nd, 3rd and 4th growth increments, Table I). This effectively erases the survivor bias, and provides an approximation of the size-at-age relationship in the absence of size restricted harvest. Next, an appropriate bias is reintroduced by weighting each sheep-year above the minimum size restriction according to the cumulative probability of that individual escaping harvest to that point (i.e., multiplied by $[1\text{- harvest rate}]^{[\text{years legal}]}$, or in this example: $0.68^{[\text{years legal}]}$).

The population model developed by Alberta Environment and Parks reports the population before harvest mortality has been applied (i.e., a preseason population representing the animals available to be harvested in that year). Therefore, sub-legal and first year legal sheep have not been exposed to harvest, and so these sheep-years are weighted as $0.68^0 = 1.00$. In this example, a second year legal sheep has been exposed to harvest for one year and is weighted as $0.68^1 = 0.68$; a third year legal sheep has been legal for two years and is weighted as $0.68^2 = 0.46$; and so on. The weighted sheep-years are then summed for each combination of age- and size-class (e.g., 4 year old 3/4 curls), and converted to proportion of the total for that age-class. This approach to weighting sheep-years should yield equivalent frequencies for age-and size-class combinations, as would be achieved on average by repeatedly removing individual rams,

Table I. Summary of the simplistic horn growth model used to project the hypothetical horn size of a ram after death. Average length of each annual increment is expressed relative to the combined length of the 2nd, 3rd, and 4th increments (which were present and complete in all individuals) so that the projected growth accounts for that individual's growth trajectory. Estimates of variance are not presented here, because this growth projection model was applied deterministically without any inclusion of stochastic variance. Sample sizes are included to give some indication of the relative reliability of the projection model across age-classes.

Increment	Average Length	Average of Prop_234	Sample Size
1	6.1	0.136	193
2	16.0	0.348	193
3	15.8	0.347	193
4	13.8	0.305	193
5	11.8	0.266	185
6	9.5	0.219	152
7	7.1	0.165	113
8	5.8	0.138	67
9	4.5	0.104	25
10	3.3	0.082	11
11	3.2	0.087	5
12	2.5	0.071	1

but allows for somewhat more straightforward computation.

How old are the sheep in a given size class?

To address the second question, both hunting and non-hunting mortality must be accounted for, because older sheep within a size class will have experienced more cumulative mortality from all sources and will therefore be less common than the younger age classes. The weighted frequencies calculated previously already account for the size specific hunting mortality, and only need to be multiplied by the cumulative probability of escaping non-hunting mortality up to that age to allow for conversion from size to age. Rows and columns are transposed, and the proportions are calculated relative to the size-class totals rather than the age-class totals. There is only one size class for female sheep (adult ewes), but observed individuals still need to be distributed amongst the many age-classes. The proportion of adult ewes belonging to each age class is derived the same way as for rams, by weighting according to hunting and non-hunting mortality.

RESULTS

The truncating effect of size-restricted harvest is evident in the raw data (Figure 3), and leads to declining sample sizes for the older age-classes. Figure 4 includes the simulated data projected after the death of each ram, showing the hypothetical size-at-age relationship in the absence of size-restricted harvest. After weighting sheep-years in the combined dataset by cumulative probability of escaping harvest under a 32% harvest of rams >4/5, the adjusted frequencies of occurrence are presented in Table II, and these have been translated into proportions in Table III to answer the question: *Of rams that reach a given age, how many would belong to each size-class?*

In Table IV, the frequencies from Table II have been transposed, and corrected to account for cumulative probability of escaping non-hunting mortality to answer the question: *How old are the sheep in a given size class?* A similar table is also included for female sheep, with appropriate survival rates applied to the adult females to distribute them across age-classes.

DISCUSSION

Incorporating size-restricted harvest in simulation modelling allows Alberta Environment and Parks to illustrate the likely outcomes of a variety of alternative management regimes in a data-driven manner. Using a scenario specific conversion table, sheep can be removed from the population based on their size while still retaining the high level of demographic detail provided by an age-structured model. The simulation model integrates many different types of data (e.g., inventories from aerial surveys, detailed demographic studies, radio collaring programs, habitat models, hunter harvest surveys, compulsory registration, annuli measurements). Using data from multiple sources encourages buy-in from a diverse group of experts and stakeholders because each can see how they are contributing to a big picture understanding of species management.

The objective of these simulations is to illustrate the relative trade offs between alternative management strategies in a format that is easily digestible for a wide range of stakeholders. The intent is not to predict the future with precision, but simply to compare relative differences. We have not attempted to propagate uncertainty through the simulation model, and so have not included confidence limits for the proportions reported in this paper. If the objective was to provide a reliable forecast (e.g., for populations in years between aerial survey inventories), confidence limits for these values could be generated using a subsampling or bootstrapping approach.

Model development to this point has relied on a provincially pooled size-at-age relationship to maximize sample size in each age class. Across Alberta, environmental conditions are likely to influence the way sheep grow to become legal, even in the absence of variable harvest effort. With the addition of the 2020 registrations, the dataset is expected to be large enough to develop regionally specific size-at-age relationships based on the sheep

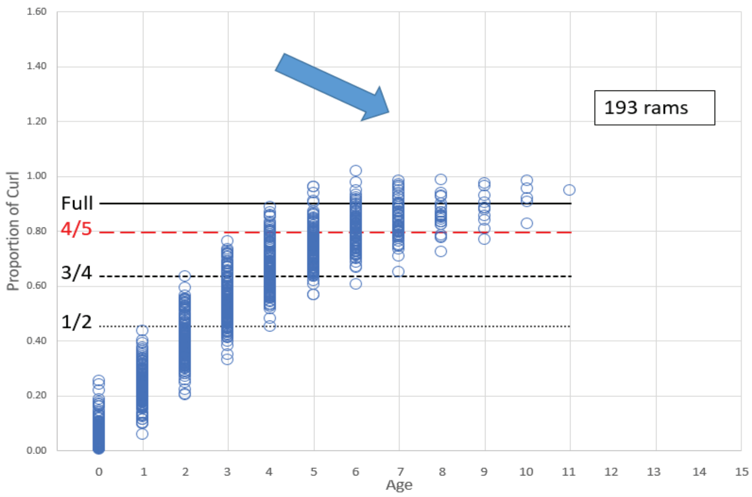

Figure 3. Horn curl data from 193 harvested rams showing size-at-age for 1331 sheep-years. Size class thresholds were averages derived from a subset of sheep where appropriate morphological measurements were taken. The arrow indicates the truncating effect of the current size restricted harvest regime on rams 5 years of age and older.

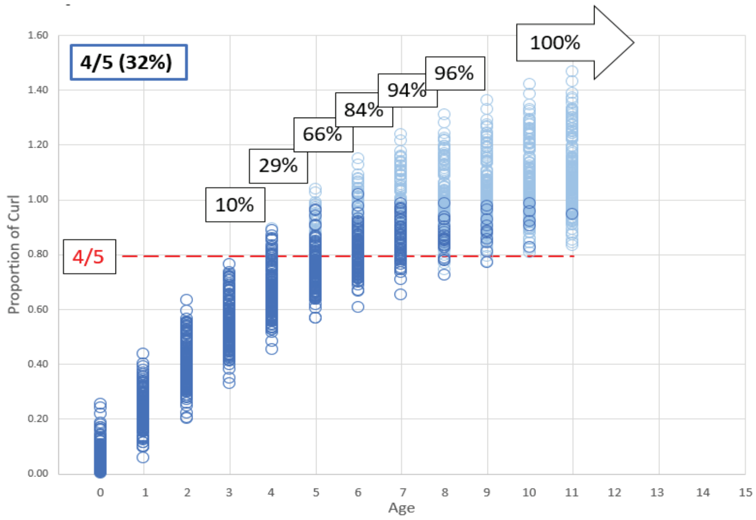

Figure 4. Raw data plus 985 sheep-years that were projected after death to erase survivor bias. The proportion of each age class exposed to harvest mortality reflects weighting of sheep-years by the cumulative probability of that individual escaping harvest to that point, and is based on a minimum size restriction of 4/5 curl, and a Trophy harvest rate of 32% (to approximate the realized harvest regime in north of the Athabasca River to the provincial boundary).

that were harvested in Northern, Central, and Southern Alberta to explore this hypothesis further.

In analyses conducted to date, sheep that have lost their first annulus from both horns have not been included in the dataset. Such sheep account for about 8% of registrations provincially, mostly from southern Alberta. Therefore, the size-at-age relationship presented here describes sheep that wear down the lamb tips, but don't suffer brooming beyond the first annulus. Excluding broomed rams from our dataset further limits the sample sizes available for the older age-classes. We can also expect a slight positive bias in the horn size of older age-classes, although this might not greatly affect the size class assignment if brooming occurs primarily after a ram has reached Full curl.

Table II. Frequency of sheep-years by age and size-class, with bolded values adjusted to reflect the survivor bias expected under a 4/5 curl size restriction when 32% of legal rams are harvested annually. No rams aged 12-15 years were observed in the dataset, so rams in these age classes were presumed to all be Full curl for the purposes of this exercise.

COUNT	Lamb	1/4	1/2	3/4	4/5	Full	Legal	Total
0	193							193.0
1		193						193.0
2		155	38					193.0
3		23	144	26				193.0
4		1	68	104	20		20	193.0
5			5	127	**38.0**	**16.6**	41	186.6
6			1	57	**84.2**	**26.9**	74	169.1
7				21	**64.2**	**48.4**	37	133.6
8				6	**37.9**	**53.6**	15	97.5
9				3	**21.5**	**43.7**	3	68.3
10					**9.1**	**38.3**	3	47.4
11					**3.7**	**28.5**	0	32.2
12						**21.9**	0	**21.9**
13						**14.9**	0	**14.9**
14						**10.1**	0	**10.1**
15						**6.6**	0	**6.6**

Table III. ***Of rams that reach a given age, how many would belong to each size-class?*** Conversion from age to size: Frequencies from Table II, rescaled to proportion of sheep of each size, for each age-class. There is no correction for non-hunting mortality, because this is presumed to be dependent on age, not size.

Proportion	Lamb	1/4	1/2	3/4	4/5	Full	Total
0	1.000						1.000
1		1.000					1.000
2		0.803	0.197				1.000
3		0.119	0.746	0.135			1.000
4		0.005	0.352	0.539	0.104		1.000
5			0.027	0.681	0.204	0.089	1.000
6			0.006	0.337	0.498	0.159	1.000
7				0.157	0.481	0.362	1.000
8				0.062	0.389	0.550	1.000
9				0.044	0.315	0.641	1.000
10					0.191	0.809	1.000
11					0.116	0.884	1.000
12						**1.000**	**1.000**
13						**1.000**	**1.000**
14						**1.000**	**1.000**
15						**1.000**	**1.000**

In this exercise, the measured annuli lengths have been used to model growth of a horn around a two dimensional circle, without accounting for a horn that actually traces a helix in three dimensions. The resulting positive bias in proportion of curl is likely of minimal concern because it also affects the class distinguishing thresholds that were determined relative to the morphological landmarks specified in the *Wildlife Regulation*: Sheep-years would still be assigned appropriately to size-classes, even if the proportion of curl value appears to be exaggerated. To confirm this assumption, size-class assignments using 2D and 3D approximations of the horn growth will be

Table IV. ***How old are the sheep in a given size class?*** Conversion from size to age showing the relative proportion of ages within each size class. The frequencies from Table II have been weighted by cumulative survival from non-hunting mortality sources, and rescaled to reflect the proportion of sheep of each age, for each size class. A similar table is also provided for female sheep, to distribute them across ages in a realistic manner.

Proportion	0	1	2	3	4	5	6	7	8	9	10	11	**12**	**13**	**14**	**15**	Total
Ann. Survival	0.54	0.82	0.89	0.85	0.86	0.84	0.83	0.8	0.79	0.77	0.74	0.71	0.69	0.3	0	0	
Cum. Survival	1	0.540	0.443	0.394	0.335	0.288	0.242	0.201	0.161	0.127	0.098	0.072	0.051	0.035	0.011	0.000	
Lamb (M)	1.000																1.000
1/4		0.572	0.377	0.050	0.002												1.000
1/2			0.172	0.579	0.232	0.015	0.002										1.000
3/4				0.101	0.345	0.362	0.137	0.042	0.010	0.004							1.000
4/5					0.110	0.180	0.335	0.212	0.100	0.045	0.015	0.004					1.000
Full						0.112	0.152	0.227	0.202	0.130	0.088	0.048	**0.026**	**0.012**	**0.003**	**0.000**	1.000
From/To	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
Harv. Survival	1	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	
Ann. Survival	0.54	0.85	0.95	0.94	0.93	0.92	0.91	0.89	0.88	0.88	0.86	0.82	0.81	0.8	0.77	0.7	
Cum. Survival	1	0.540	0.459	0.436	0.410	0.381	0.351	0.319	0.284	0.250	0.220	0.189	0.155	0.126	0.101	0.077	
Lamb (F)	1.000																1.000
Ewe		0.126	0.107	0.101	0.095	0.089	0.082	0.074	0.066	0.058	0.051	0.044	0.036	0.029	0.023	0.018	1.000

compared in the coming years using a subset of the sheep registered in 2020, from which additional measurements were taken to capture the depth of spiral (i.e., from anterior edge of the horn base to the horn tip).

More sophisticated statistical methods could possibly be used to account for survivor bias in the size-at-age relationship, though these would likely rely on a similar approach to erasing the existing bias and reintroducing an appropriate one. The horn growth model used to project data beyond the death of an individual sheep is crude, but the projected data appear consistent with what might be expected. However, such a conclusion is conjectural and would benefit from a more objective assessment of the reliability of the horn growth projection model.

To date, we have not accounted for potential changes in horn growth rate that might be observed in future as a result of climate change (e.g., Loehr *et al.* 2010), changes in population density (e.g., Monteith *et al.* 2018), genetic effects of artificial selection (e.g., Pigeon *et al.,* 2016; Douhard *et al.* 2016), or behavioural/energetic consequences of departing from a ‘natural’ male age structure (Schindler *et al.* 2020). While this is a limitation of how the size-at-age relationship is currently being applied, the approach captures the current range of variability in how rams grow to become available for harvest. Using the best available knowledge to explicitly describe size-restricted harvest in population modelling is essential to ensure stakeholders have a clear understanding of the expected trade-offs when exploring the likely outcomes of alternative management, and so they are able to provide informed opinions on how bighorn sheep should be managed in the public interest.

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