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Ewe are what ewe wear: bigger horns, better ewes and the potential consequence of trophy hunting on female fitness in bighorn sheep

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In polygynous species, secondary sexual traits such as weapons or elaborate ornaments have evolved through intrasexual competition for mates. In some species, these traits are present in both sexes but are underdeveloped in the sex facing lower intrasexual competition for mates. It is often assumed that these underdeveloped sexually selected traits are a vestige of strong sexual selection on the other sex. Here, we challenge this assumption and investigate whether the expression of secondary sexual traits is associated with fitness in female bighorn sheep. Analyses of 45 years of data revealed that female horn length at 2 years, while accounting for mass and environmental variables, is associated with younger age at primiparity, younger age of first offspring weaned, greater reproductive lifespan and higher lifetime reproductive success. There was no association between horn length and fecundity. These findings highlight a potential conservation issue. In this population, trophy hunting selects against males with fast-growing horns. Intersexual genetic correlations imply that intense selective hunting of large-horned males before they can reproduce can decrease female horn size. Therefore, intense trophy hunting of males based on horn size could reduce female reproductive performance through the associations identified here, and ultimately reduce population growth and viability.

1. Introduction

In polygynous species where males use secondary sexual traits to compete for mates, the evolution of those traits in females is usually attributed to one or more of the following mechanisms: shared genetic architecture [1], intrasexual resource competition [1,2], predator defence [2] or male-mate choice [3]. The shared genetic architecture hypothesis, first recognized and described by Darwin [4] as 'correlated inheritance', states that although directional selection only affects male traits, the underlying genetic architecture (the same genes affect the trait in both sexes) results in females exhibiting underdeveloped forms of the same traits, despite no obvious fitness benefit for females [5]. Female traits maintained via shared genetic architecture, such as the long tail feathers of barn swallow (*Hirundo rustica*) [6], are thought to not affect female fitness. Alternatively, the intrasexual competition hypothesis holds that these traits may aid access to resources [7]. For example, female dung beetles (*Onthophagus sagittarius*) use horns to compete for dung, where they raise their offspring [8,9]. Additionally, secondary sexual characteristics in females can be an anti-predation adaptation, such as the horns of many female bovids [2]. Finally, female ornamentation may influence male-mate choice [3].

A common, often extremely sexually dimorphic, secondary sexual trait is the cranial weaponry of many ungulates. The use of cranial weaponry in male–male competition is well documented [9–11], but its function in females is debated. Stankowich & Caro [2] theorize that the horns of female bovids are an anti-predator adaptation, with larger more conspicuous species more likely to exhibit headgear [2,12]. Cranial weaponry may also function in female intrasexual competition; female reindeer (*Rangifer tarandus*) use antlers to compete for forage [13], and female Soay sheep (*Ovis aries*) with more developed horns win more intrasexual interactions [14]. Alternatively, shared genetic architecture may explain female cranial weaponry as a vestige of strong sexual selection in males for that trait [5]. Regardless of which mechanism is responsible for the development of horns in female ungulates, individual variation in cranial weaponry size may either influence or indicate variation in female fitness. If cranial weaponry functions as an anti-predator trait, individuals with larger horns may be better able to defend themselves. If weaponry size simply reflects overall body condition or resource acquisition, it may be correlated with body mass and therefore with reproductive success. Alternatively, given the high cross-sex heritability of headgear length in some ungulates [15], females who inherit alleles for more exaggerated headgear may also inherit alleles for other traits associated with greater fitness potential. For example, heavier mass as well as disease and parasite resistance are all correlated with the expression of male secondary sexual traits in diverse species [16–18]. Here we investigate if the expression of cranial weaponry in females is associated with reproductive fitness in a wild ungulate population.

The functions of horns in female bighorn sheep (*Ovis canadensis*) and their association with reproductive fitness are largely unknown. Horn length is highly genetically correlated across the sexes [15], thus females with long horns are expected to be both progeny and parents of longer-horned, typically higher-fitness males [10]. Jorgenson *et al.* [19] found that female yearlings with larger horns were more likely to have offspring earlier in life, however, that study did not control for a possible effect of body mass, which is also associated with age at primiparity [20,21]. Thus far, the relationships between horn size, body mass and age at primiparity have not been disentangled. Factors other than horn size known to be associated with reproductive traits include body mass [22] and population density [23], with density during early life being particularly important for reproductive potential [20,24]. Additionally, potential associations between female horns and reproductive fitness may lead to correlated, indirect effects on fitness via anthropogenic selective pressures on male horn length. Similar to other species, male bighorn sheep are subject to phenotype-based harvest [24–26]. Intense selective harvest can result in an evolutionary response in horn size, leading to a reduction in breeding values for horn length in both sexes [27]. Hence, if an association between female horn length and reproductive fitness exists in bighorn sheep, selective harvest of males may negatively affect population demography as seen in other species [28–30].

Despite the reproductive benefits conferred by horns to male bighorn sheep [10] in the absence of selective harvest [27,31], and the functionality of female weapons in some ungulates [13,14], little is known about the relationship between horn size and fitness in most ungulate species. Given the fitness benefits potentially conferred by cross-sex

shared genetic architecture [15,17], we hypothesize that females with longer horns may have higher reproductive fitness. We used approximately 45 years of longitudinal data to examine the effect of horn length, body mass, population density and other environmental variables on four components of reproductive fitness (age at primiparity, age at first offspring weaned, reproductive lifespan and fecundity) and lifetime reproductive success (LRS).

2. Methods

(a) Study site/population

Ram Mountain, Alberta (52º8′ N, 115º8′ W, 1082–2173 m elevation) is a rocky outcrop encompassing approximately 38 km^2 of alpine and sub-alpine terrain, approximately 30 km east of the main Rocky Mountain range. The sheep population is geographically and genetically distant [32] from the main species range. Monitoring started in 1971 [33] and is ongoing. The Ram Mountain population was historically subjected to trophy hunting of males based on horn size [27]. In 1996, a more restrictive regulation was introduced, and a moratorium has stopped sport hunting since 2011.

(b) Monitoring

Between late May and September, sheep were trapped in a corral baited with salt. At each capture, body mass was measured with a spring scale to the nearest 125 g. Horn length and base circumference (cm) were measured using a flexible tape. At first capture, a tissue sample was taken for DNA analyses and pedigree construction. Reproductive status was determined by observing lactation at capture, or by mother–offspring interactions. Mother–offspring pairs were determined by behavioural observations and confirmed by a genetic pedigree constructed using 26 microsatellite markers [10,34]. For this study, we analysed data from 1973 to 2018 for females of the 1973–2016 cohorts.

(c) Individual measurements

For females from the 1973 to 2016 cohorts, we recorded age at primiparity (years), age at first offspring weaned (years), yearly reproductive status (to examine reproductive lifespan), adjusted horn length (cm) and body mass (kg) to 15 September at two years to allow for comparison between individuals. Using repeated measurement of the same individual in the same season, horn length was adjusted using individual horn growth rates and mass was adjusted using mixed-effect models [35]. Age at primiparity was defined as the first occasion in which a female lactated (assessed by inspection of the udder during captures). We defined weaning as rearing offspring to mid-September. Our measure of reproductive lifespan was the number of years between first and last reproductive activity, defined as the last occasion in which a female lactated. Fecundity and LRS were examined for females from the 1973 to 2012 cohorts for which entire reproductive histories were available. Fecundity was the proportion of reproductive years in which an offspring was weaned and LRS was the total number of offspring weaned by each female. To control for environmental variation, we recorded population density, winter temperature and winter precipitation for the first year of life for each female and for each year from age two to primiparity or first weaning of offspring. As in previous publications, population density was the number of adult females in June. Mean winter temperature (°C) and mean winter precipitation (cm) were the average of monthly temperatures and precipitation recorded at the Environment Canada meteorological station in Nordegg (52º30′ N, 116º03′ W, elevation: 1320 m, about 20 km west of Ram

Table 1. Results of Cox mixed-effect models testing the association of female horn length and body mass at 2 years with age at primiparity, age at first offspring weaned and reproductive lifespan for female bighorn sheep at Ram Mountain, Alberta, 1973 to 2018. Each model included cohort, ID and year as random effects. Best model for each trait is in italics.

model	age at primiparity			age at first offspring weaned			reproductive lifespan		
	d.f.	AICc	Δi	d.f.	AICc	Δi	d.f.	AICc	Δi
environment + horn length + body mass	*82.06*	*1707.26*	*0*	*117.14*	*1752.14*	*0*	137.76	1332.33	45.89
environment + body mass	83.58	1712.98	5.72	116.26	1754.47	2.33	141.28	1292.87	6.43
environment + horn length	83.76	1719.83	12.57	119.96	1759.49	7.35	141.88	1287.20	0.76
environment	85.99	1729.67	22.41	119.15	1767.65	15.51	*141.63*	*1286.44*	*0*

Table 2. Generalized mixed-effect models testing the association of horn length and body mass at 2 years with fecundity and LRS for female bighorn sheep at Ram Mountain, Alberta cohorts 1973–2012. Each model included cohort, ID and year as random effects. Best model for each trait is in italics.

model	fecundity			LRS		
	d.f.	AICc	Δi	d.f.	AICc	Δi
environment + horn length	7	1343.38	1.00	7	*701.23*	*0*
environment + horn length + body mass	8	1345.49	3.11	8	701.80	0.57
environment + body mass	7	1344.38	2.00	7	703.19	1.96
environment	6	*1342.38*	*0*	6	706.30	5.07

Mountain) from November to March (see also [21]). Prior to analysis all measurements were standardized by subtracting the mean and dividing by the standard deviation (s.d.), to compare the effect of variables with differing units of measurement.

(d) Statistical analysis

To analyse factors associated with age at primiparity, age at first offspring weaned and reproductive lifespan, we used R v. 4.0.3 [36], packages *survival* v. 3.2.13 [37] and *coxme* v. 2.2.16 [38] to calculate Cox mixed-effect survival models. We considered 12 models, four for each of the three sets of observations, to examine how environmental effects, adjusted horn length at age two and adjusted mass at age two were associated with age at primiparity, age at first weaning success and reproductive lifespan (tables 1 and 3). Female cohort, observation year and individual ID were included in all models as random effects. We obtained the hazard ratios for each fixed effect from *coxme*. We performed model selection on Cox mixed-effect survival models by ranking each set of four models by their Akaike information criterion corrected for small samples size (AICc) and selecting the model with the lowest AICc (table 1). We tested the validity of the best fitting models by their relationship between the Schoenfeld residuals [39] and time using the *survival* package [37]. Schoenfeld residuals are the difference between observed and predicted values for any covariate at any given event time and should have a non-significant relationship with time in valid models.

To analyse factors associated with fecundity and LRS, we used R package *lme4* v. 1.1–27.1 [40] to fit generalized linear mixed-effect models (GLMM). We considered eight models in total, four for each of the two sets of observations, to examine how environmental effects, adjusted horn length at age two and adjusted mass at age two were associated with fecundity and LRS (tables 2 and 4). Female cohort, grouped into 4-year periods to avoid overfitting, was included in all models as the sole random effect. Gaussian and Poisson error families were used for the fecundity and LRS models, respectively. We used *r2glmm* v. 0.1.2 [41] to calculate r^2 values for each fixed effect in Gaussian model. We calculated pseudo r^2 values for fixed effects in Poisson models by subtracting the marginal r^2 value of the model with the target variable from the marginal r^2 value of the whole model. Marginal r^2 values were calculated using the R package *Mumin* v. 1.43.17 [42]. We performed model selection on GLMMs by selecting the model with the lowest AICc (tables 1 and 2). We tested the fit of residuals from the best fitting models to a normal distribution by the Shapiro–Wilk normality test [43].

3. Results

Age at primiparity and age at first successful weaning datasets included 217 females, where horn length at 2 years ranged from 9.8 to 28.6 cm and body mass from 41.0 to 71.6 kg, with means of 19.0 cm (3.0 s.d.) and of 57.8 kg (5.7 s.d.), respectively. Age at primiparity ranged from 2 to 7 years, and age at first offspring weaned ranged from 2 to 9 years. The median age was 3 years for both variables (electronic supplementary material, figure S1). The reproductive lifespan dataset included 160 females, whose average horn length and body mass at 2 years were 19.6 cm (3.0 s.d.) and 58.8 kg (4.9 s.d.), respectively. Reproductive lifespan ranged from 1 to 15 years, with a median of six (electronic supplementary material, figure S1). LRS and fecundity were known for 152 females and ranged from 1 to 12 lambs weaned and 20% to 100% annual fecundity, with a median of four and mean of 74.6%, respectively (electronic supplementary material, figure S1). The average horn length and body mass at 2 years in these datasets were 19.2 cm (3.1 s.d.) and 58.3 kg (5.5 s.d.), respectively. Temporal trends

Table 3. Coefficients, hazard ratio (HR) and p-values from best Cox mixed-effect survival models of associations of environmental variation, body mass and horn length on age at primiparity and at first offspring weaned for female bighorn sheep at Ram Mountain, Alberta between 1973 and 2018.

variable	age at primiparity			age at first lamb weaned			reproductive lifespan		
	coefficient (s.e.)	HR	p	coefficient (s.e.)	HR	p	coefficient (s.e.)	HR	p
fixed effects									
adjusted mass at two years	0.335 (0.133)	1.398	0.012	0.413 (0.166)	1.511	0.013			
adjusted horn length at 2 years	0.293 (0.133)	1.340	0.028	0.454 (0.169)	1.574	0.007			
density experienced as a lamb	−0.508 (0.425)	0.601	0.230	−0.943 (0.344)	0.389	0.006	−0.696 (0.389)	0.499	0.073
winter precipitation experienced as a lamb	−0.024 (0.324)	0.976	0.940	−0.075 (0.284)	0.927	0.790	0.587 (0.409)	1.799	0.150
winter temperature experienced as a lamb	0.386 (0.303)	1.471	0.200	0.070 (0.250)	1.073	0.780	0.779 (0.364)	2.180	0.032
yearly density	−0.163 (0.470)	0.849	0.730	0.391 (0.337)	1.478	0.250	−0.680 (0.269)	0.507	0.011
yearly winter precipitation	0.437 (0.256)	1.548	0.088	−0.021 (0.152)	0.979	0.890	−0.037 (0.169)	0.964	0.830
yearly winter temperature	0.068 (0.275)	1.070	0.810	−0.203 (0.165)	0.812	0.220	0.079 (0.164)	1.082	0.630
	variance			variance			variance		
random effects									
cohort	1.564			1.057			0.016		
ID	0.282			1.283			0.147		
year	1.327			0.165			<0.001		

Table 4. Estimates from best generalized mixed-effect models examining associations of environmental variation and horn length with reproductive lifespan, environmental variation with fecundity, and horn length, body mass and environment with LRS for female bighorn sheep at Ram Mountain, Alberta, cohorts 1973–2012.

	fecundity			LRS		
variable	coefficient (s.e.)	p	r^2	coefficient (s.e.)	p	r^2
fixed effects						
adjusted horn length at 2 years				0.131 (0.049)	0.007	0.050
density experienced as a lamb	−0.271 (0.127)	0.032	0.057	−0.027 (0.077)	0.721	0.006
winter precipitation experienced as a lamb	−0.002 (0.317)	0.994	0	−0.014 (0.055)	0.797	0.007
winter temperature experienced as a lamb	−1.422 (0.930)	0.126	0.020	−0.071 (0.055)	0.198	0.035
	variance			**variance**		
random effects						
grouped cohort	62.45			0.041		

for horn length, fecundity, reproductive lifespan and LRS were characterized by a decline until the early to mid-1990s followed by an increase (figure 1). Conversely, age at primiparity and at first offspring weaned increased until the 1990s then declined. Electronic supplementary material, figure S2 reports temporal trends in environmental variables.

For factors associated with age at primiparity and age at first offspring weaned, the best model contained adjusted horn length at age two, adjusted mass at age two and all environmental effects (tables 1 and 3). In these models, adjusted horn length and adjusted mass at age two had hazard ratio of 1.34 and 1.40, respectively, for the likelihood of transitioning from a nonparous to a primiparous state at any age, and 1.57 and 1.51, respectively, for the likelihood of transitioning from a non-weaning to a weaning state at any age. Thus, for every additional 3.0 cm (1 s.d.) of horn length and 5.5 kg (1 s.d.) of mass, the likelihood of being primiparous increased by 39.8% and 34.0%, respectively, and for every additional 3.0 cm (1 s.d.) of horn length and 5.5 kg (1 s.d.) of mass, the likelihood of first weaning an offspring increased by 57.4% and 51.1%, respectively (figure 2). These likelihoods increased exponentially with every year spent nonparous or non-weaning.

For factors associated with reproductive lifespan, the best model contained only environmental variables (tables 1 and 3). This model, however, was only weakly supported over one containing horn length at age two and environmental variables, with a delta AICc of 0.76. The Schoenfeld residuals of Cox survival models (electronic supplementary material, table S2) revealed a significant relationship between birth density and age (time) in the primiparity model, as expected due to temporal trends in density. We subsequently repeated this model series twice, once with birth density removed and again with an interaction between birth density and age included (electronic supplementary material, table S3). These models showed the same pattern as the original models when ranked by AICc; therefore, age at primiparity was associated with both horn length and mass at 2 years in addition to environmental effects.

For factors associated with fecundity, the best model contained only environmental effects (tables 2 and 4). For LRS, the best model contained adjusted horn length at 2 years and all environmental effects (tables 2 and 4; figure 3). In this model, r^2 value for adjusted horn length was 0.050.

The residuals of these models were normally distributed according to Shapiro–Wilk normality tests [43].

4. Discussion

Variation in age at primiparity and age at first offspring weaned in female bighorn sheep was associated with both horn length and body mass when controlling for environmental factors. Additionally, we found an association between LRS and horn length when controlling for environmental factors. Both female mass and environmental factors were associated with age at primiparity and age at first offspring weaned [19–21]. However, horn size appeared to explain more variation than body mass in age at first offspring weaned, and to be the most explanatory variable of variation in LRS. Thus, larger horns correlate with higher reproductive fitness in both male [10] and female bighorn sheep.

The relationship between horn length and female reproductive fitness may result from shared genetic architecture, if alleles for greater fitness are associated with alleles for larger headgear. Female horn length could indicate variation in condition or other aspects of individual reproductive potential through its association with other traits linked to the shared genetic architecture for horns [17]. Therefore, due to the high degree of cross-sex heritability of horn length [15], females who inherit alleles for larger horns are also likely to inherit alleles for greater fitness phenotypes, a positive relationship already observed in other fitness-related traits in this population [17], and similar to correlations observed in other species [16,18]. This hypothesis suggests that selective harvesting of males based on horn size could deplete alleles for traits associated with greater female reproductive fitness in bighorn sheep.

We observed temporal changes in reproductive traits that appeared to be associated with trophy hunting activity in this population. Female horn length at age 2 years decreased and age at primiparity and first weaning success increased until the near cessation of trophy hunting in 1996, after which horn length at age 2 years increased and age at primiparity and at first weaning success decreased. These patterns mirror the trends of expected breeding value for horn length in both sexes and male horn circumference observed by Pigeon et al. [27] and further exemplify how reducing hunting
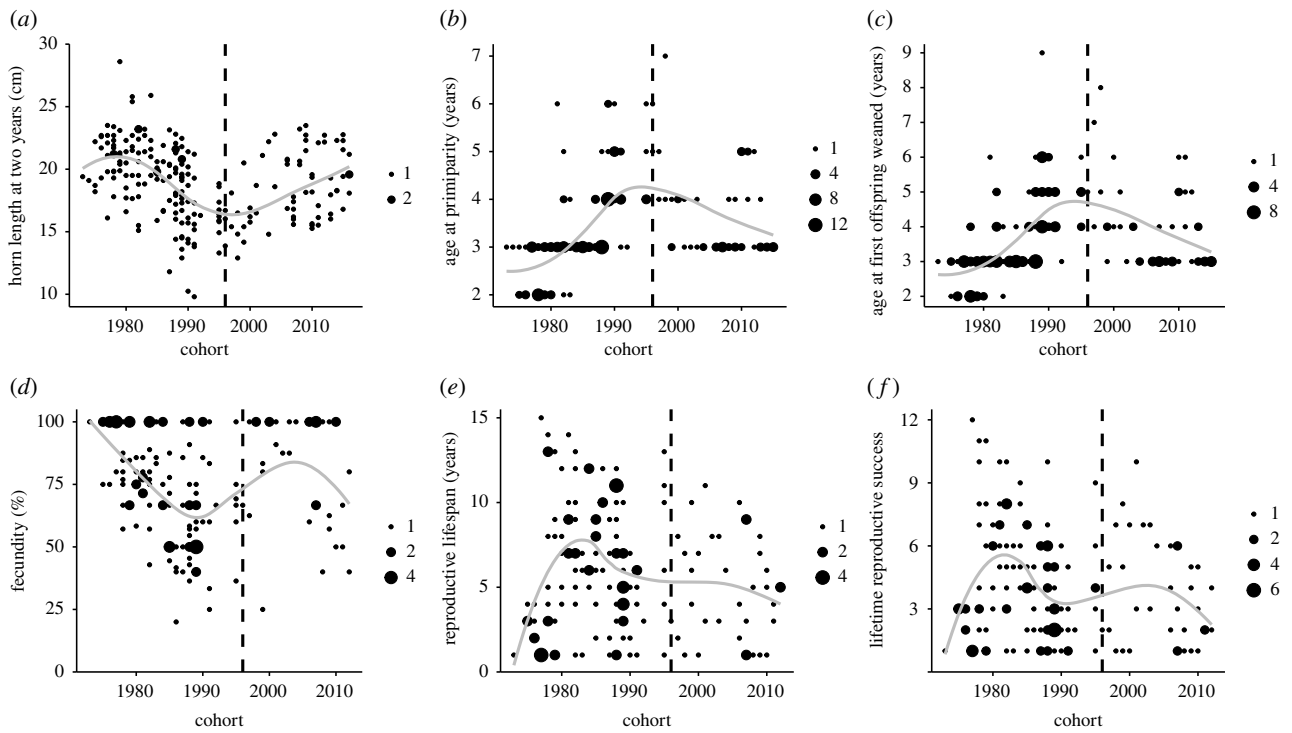
Figure 1. (a) Horn length at 2 years and (b) age at primiparity for female bighorn sheep from cohorts 1973 to 2015, and (c) age at first offspring weaned, (d) fecundity, (e) reproductive lifespan and (f) LRS for female bighorn sheep from cohorts 1973 to 2012 at Ram Mountain, Alberta, Canada. Dashed vertical line represents the near cessation of trophy hunting in 1996. Smooth line was fitted using loess. Point size represents overlapping data points.
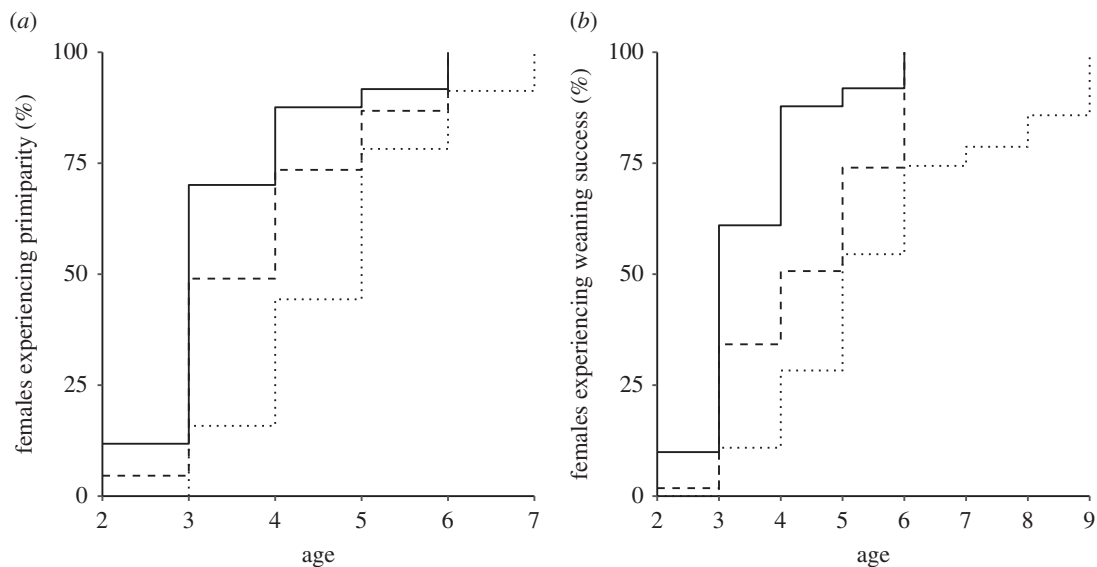

Figure 2. Associations of three different classes of female horn length at 2 years with (a) proportion of primiparous females and (b) proportion of females that weaned their first offspring across ages. Dotted line, dashed line and solid line represent short, medium and long horn classes, respectively. Females with standardized horn lengths less than −0.5 s.d., between −0.5 and 0.5 s.d. or greater than 0.5 s.d., respectively, were assigned to the short, medium and long horn length classes, respectively. Only females that experienced primiparity or weaned at least one offspring were included: (a) $n = 189$ and (b) $n = 182$.

pressure can mitigate human-mediated evolutionary changes [25]. Additionally, reproductive lifespan decreased from a peak in about 1980 until the cessation of trophy hunting. Many populations of mountain sheep in Canada are subjected to similar trophy hunting regimes as that experienced by the Ram Mountain population prior to 1996. Across Alberta, declining male horn length has been observed over the past approximately 40 years [44,45]. Assuming other populations also exhibit cross-sex heritability of horn length [15], harvested populations may also experience delayed age at primiparity and the subsequent reduction in population growth as a cross-sex correlated response to harvest selection.

While plausible, we cannot conclusively determine that the correlation between horn length and reproductive fitness results from shared genetic architecture. Individual variation in nutritional intake, parasite load, non-additive genetic effects or other unmeasured environmental effects could also mediate the correlation between horn growth and reproductive fitness. However, if environmental variability was the main driver of the relationships we reported, we would have expected body mass to play a greater role than horn length, as body mass directly affects female reproductive potential [22].

Our findings suggest that secondary sexual traits, particularly cranial weaponry, in females of sexually dimorphic
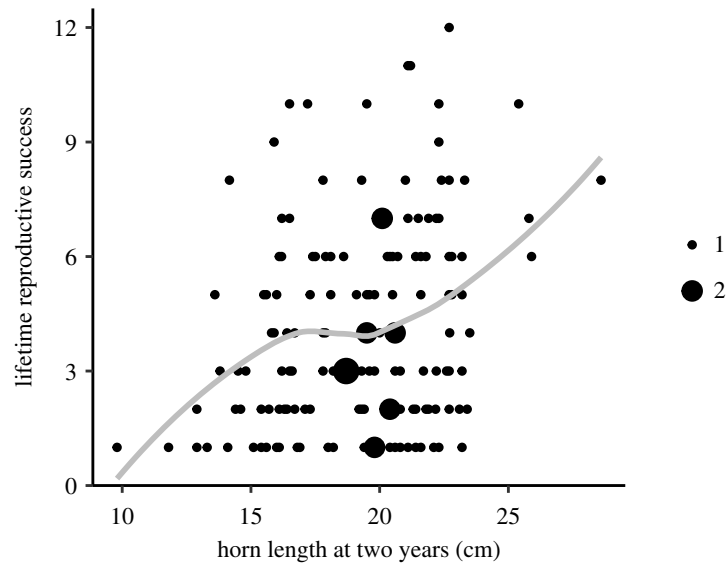
Figure 3. Associations of horn length at 2 years with LRS for female bighorn sheep at Ram Mountain, Alberta, cohorts 1973–2012. Grey lines fitted with loess, for ease of interpretation.

species may be more than ornamental vestiges of intense selection in males, as they are associated with fitness variation in females. These traits might confer direct benefits in intrasexual competition or indirect benefits via shared genetic architecture. Female horn length could increase intrasexual competitiveness, given that the use of horns in intrasexual resource competition has been observed in numerous other species [8,9,13,14]. However, there is no evidence that horn size determines the outcome of dominance interactions in female bighorn sheep [46]. Regardless of the underlying mechanism, the association of female horn length at 2 years with early reproductive success and LRS highlights a potential important conservation issue for trophy-hunted populations of bighorn sheep. Intense selective harvest has been linked to an evolutionary decline in horn length in both sexes [27]. Although female horn length was not a target of selective hunting, it declined because of cross-sex heritability [15]. Here, we show that females with smaller horns have delayed primiparity and age at first successful weaning, leading to a reduction in LRS. Therefore, selective harvest may indirectly select for females with lower overall reproductive fitness, which may negatively affect population dynamics. Our study exemplifies how species subjected to selective harvesting regimes may exhibit decreases in overall population fitness [25,26] with demographic and evolutionary effects [28–30] extending beyond changes in the trait targeted by trophy hunters [24,27].

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