

Supporting Information

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SI Materials and Methods

Age- and Size-Structured Two-Sex Model. We extend the size-structured two-sex model introduced by ref. 1 such that the population is structured into age classes and size classes.

We denote with $n_f^{\text{stage}}(x, a, t)$ the number (or density) of females in stage “stage” that weigh x kg and are aged a y at time t . The term $n_m^{\text{stage}}(x, a, t)$ denotes the respective number (or density) of males. A sheep is in either of the following four stages: lamb (birth to first year, denoted with upper index “la”), yearling (aged 1–2 y, denoted with “ye”), adult (aged 3–7 y, denoted with “ad”), or senescent (aged 8–12 y, denoted with “se”). The number of all lambs (female and male) is denoted by n^{la} and is calculated with

$$\begin{aligned} n^{\text{la}}(x, 1, t+1) = & \left(\int f(x|y^{\text{ye}}, z^{\text{ad}})m(y^{\text{ye}}, z^{\text{ad}})n_f^{\text{ye}}(y^{\text{ye}}, t)n_m^{\text{ad}}(z^{\text{ad}}, t)R(y^{\text{ye}})dy^{\text{ye}}dz^{\text{ad}} \right. \\ & + \int f(x|y^{\text{ad}}, z^{\text{ad}})m(y^{\text{ad}}, z^{\text{ad}})n_f^{\text{ad}}(y^{\text{ad}}, t)n_m^{\text{ad}}(z^{\text{ad}}, t)R(y^{\text{ad}})dy^{\text{ad}}dz^{\text{ad}} \\ & + \int f(x|y^{\text{se}}, z^{\text{ad}})m(y^{\text{se}}, z^{\text{ad}})n_f^{\text{se}}(y^{\text{se}}, t)n_m^{\text{ad}}(z^{\text{ad}}, t)R(y^{\text{se}})dy^{\text{se}}dz^{\text{ad}} \\ & + \int f(x|y^{\text{ye}}, z^{\text{se}})m(y^{\text{ye}}, z^{\text{se}})n_f^{\text{ye}}(y^{\text{ye}}, t)n_m^{\text{se}}(z^{\text{se}}, t)R(y^{\text{ye}})dy^{\text{ye}}dz^{\text{se}} \\ & + \int f(x|y^{\text{ad}}, z^{\text{se}})m(y^{\text{ad}}, z^{\text{se}})n_f^{\text{ad}}(y^{\text{ad}}, t)n_m^{\text{se}}(z^{\text{se}}, t)R(y^{\text{ad}})dy^{\text{ad}}dz^{\text{se}} \\ & \left. + \int f(x|y^{\text{se}}, z^{\text{se}})m(y^{\text{se}}, z^{\text{se}})n_f^{\text{se}}(y^{\text{se}}, t)n_m^{\text{se}}(z^{\text{se}}, t)R(y^{\text{se}})dy^{\text{se}}dz^{\text{se}} \right) \end{aligned} \quad [\text{S1a}]$$

$$n_f^{\text{la}}(x, 1, t+1) = s C_{n_f, n_m} n^{\text{la}}(x, 1, t+1) \quad [\text{S1b}]$$

$$n_m^{\text{la}}(x, 1, t+1) = (1-s)C_{n_f, n_m} n^{\text{la}}(x, 1, t+1). \quad [\text{S1c}]$$

The number of yearlings is

$$n_f^{\text{ye}}(x, 2, t+1) = \int p^{\text{la}}(x, y^{\text{la}})n_f^{\text{la}}(y^{\text{la}}, 1, t)dy^{\text{la}} \quad [\text{S2a}]$$

$$n_m^{\text{ye}}(x, 2, t+1) = \int p^{\text{la}}(x, y^{\text{la}})n_m^{\text{la}}(y^{\text{la}}, 1, t)dy^{\text{la}}. \quad [\text{S2b}]$$

The number of adults of ages $a = 3, \dots, 7$ is

$$n_f^{\text{ad}}(x, 3, t+1) = \int p^{\text{ye}}(x, y^{\text{ye}})n_f^{\text{ye}}(y^{\text{ye}}, 2, t)dy^{\text{ye}} \quad [\text{S3a}]$$

$$n_m^{\text{ad}}(x, 3, t+1) = \int p^{\text{ye}}(x, y^{\text{ye}})n_m^{\text{ye}}(y^{\text{ye}}, 2, t)dy^{\text{ye}} \quad [\text{S3b}]$$

$$n_f^{\text{ad}}(x, a+1, t+1) = \int p^{\text{ad}}(x, y^{\text{ad}})n_f^{\text{ad}}(y^{\text{ad}}, a, t)dy^{\text{ad}} \quad [\text{S3c}]$$

$$n_m^{\text{ad}}(x, a+1, t+1) = \int p^{\text{ad}}(x, y^{\text{ad}})n_m^{\text{ad}}(y^{\text{ad}}, a, t)dy^{\text{ad}}. \quad [\text{S3d}]$$

The number of senescents of ages $a = 8, \dots, 12$ is

$$n_f^{\text{se}}(x, 8, t+1) = \int p^{\text{ad}}(x, y^{\text{ad}})n_f^{\text{ad}}(y^{\text{ad}}, 7, t)dy^{\text{ad}} \quad [\text{S4a}]$$

$$n_m^{\text{se}}(x, 8, t+1) = \int p^{\text{ad}}(x, y^{\text{ad}})n_m^{\text{ad}}(y^{\text{ad}}, 7, t)dy^{\text{ad}} \quad [\text{S4b}]$$

$$n_f^{\text{se}}(x, a+1, t+1) = \int p^{\text{se}}(x, y^{\text{se}})n_f^{\text{se}}(y^{\text{se}}, a, t)dy^{\text{se}} \quad [\text{S4c}]$$

$$n_m^{\text{se}}(x, a+1, t+1) = \int p^{\text{se}}(x, y^{\text{se}})n_m^{\text{se}}(y^{\text{se}}, a, t)dy^{\text{se}}. \quad [\text{S4d}]$$

See Table S6 for a complete list of model parameters and functions. The functions $p^{\text{stage}}(x, y)$ denote the probability of lambs, yearlings, adults, and senescents to survive one time step and change weight from y to x . The factor s in Eqs. S1b and S1c denotes the sex ratio, that is, the proportion of females at birth. The mating probability between an x female and a y male is proportional to $m(x, y)$ and we require that $\int m(x, y)dy = 1$ for all x (that means all females are mated, but it would suffice to require “ ≤ 1 ”). The number of offspring per breeding event is denoted by $R(x)$. The offspring distribution is denoted by $f(x|y, z)$, which gives the probability that an offspring has trait x if its parents have traits y and z .

The normalization constant C_{n_f, n_m} in Eqs. S1b and S1c is set to

$$C_{n_f, n_m} = \frac{\int_{y_{\min}}^{\infty} (n_f^{\text{ye}}(y, t) + n_f^{\text{ad}}(y, t) + n_f^{\text{se}}(y, t)) dy}{\int_0^{\infty} m(y, z) \left(\sum_{\text{stage}} n_f^{\text{stage}}(y, t) n_m^{\text{stage}}(z, t) \right) dy dz} \quad [\text{S5}]$$

with y_{\min} denoting the minimal trait value for reproduction. Eq. S5 imposes a constraint such that the overall number of birth events or parturitions is set to the overall number of females that are large enough to reproduce.

Mating. We construct the mating function $m(x, y)$ such that

$$m(x, y) = \begin{cases} 0, & \text{if female is lamb or male is either lamb or yearling} \\ (\text{male age}) * (1 + y), & \text{otherwise,} \end{cases} \quad [\text{S6}]$$

that is, the mating advantage of bigger males increases linearly with their body weight and intercept and slope increase with male age. The mating function is then normalized such that $\int m(x, y)dy = 1$ for all x and all stages but female lambs.

Although mating success in bighorn rams increases with age, and older males use horn and body size as weaponry to achieve dominance over younger rams (2), our assumption of a linear relationship between body weight and mating success is somewhat simplistic. In fact, there is little effect of mass on mating success among small and medium to large males, whereas large rams do have a substantial mating advantage. Nevertheless, for the sake of simplicity we assume a linear relationship. With this setting, adults and senescents have similar shares of all of the matings (51% adults, 49% senescents). Also, 15% of the matings are allotted to the oldest age class (senescents that are 12 y old) and 50% to the heaviest quarter of reproducing male rams.

Growth and survival. The probability p_s to survive to the next time step for a bighorn of weight x and each stage is calculated by

$$p_s^{\text{stage}}(y) = \frac{e^{\text{intercept} + y \cdot (\text{body mass slope})}}{1 + e^{\text{intercept} + y \cdot (\text{body mass slope})}} \quad [\text{S7}]$$

with the parameters (intercept, slope) taken from Table S1. The probability of a bighorn growing from weight x to y is proportional to $\tilde{p}_g(x, y)$:

$$\tilde{p}_g(x, y) = \frac{1}{\sqrt{2\pi}\sigma^2(x)} e^{-\frac{(y-\mu(x))^2}{2\sigma^2(x)}}, \quad [\text{S8}]$$

where

$$\sigma^2(x) = (\text{residuals intercept}) + x \cdot (\text{residuals slope}) + x^2 \cdot (\text{residuals slope}^2) \quad [\text{S9}]$$

for all sexes and stages but male adults and senescents. For the latter we have set

$$\sigma^2(x) = (\text{residuals intercept}) + x \cdot (\text{residuals slope}), \quad [\text{S10}]$$

because the year effects would otherwise reduce the value of σ^2 below zero too often. Although with the linear fit in Eq. S10 this occurs more seldom, we have to apply a minimal value for sigma that is found in Table S3. The mean value of the growth distribution in Eq. S8 is calculated by $\mu(x) = (\text{body mass intercept}) + x \cdot (\text{body mass slope})$. All intercepts and slopes are listed in Table S3. To obtain the probability to gain weight from x to y we calculate $p_g(y|x) = \tilde{p}_g(x, y)/C$ such that $\int p_g(y|x)dy = 1$, that is, with $C = \int \tilde{p}_g(x, y)dy$. With $p_s(x)$ and $p_g(y|x)$ we calculate the probability that an x -weighed individual survives and grows to weight y by $p(x, y) = p_s(x)p_g(y|x)$.

Recruitment. The probability $R(x)$ to give birth to one lamb for a ewe of weight x and each stage is calculated by

$$R(x) = \frac{e^{\text{intercept}+x \cdot (\text{body mass slope})}}{1 + e^{\text{intercept}+x \cdot (\text{body mass slope})}} \quad [\text{S11}]$$

with the parameters (intercept, slope) taken from Table S2.

Inheritance. The probability $f(x|y, z)$ that a lamb weighs x when it was born to a mother weighing y and a father weighing z is calculated by

$$f(x|y, z) = \frac{1}{\sqrt{2\pi}\sigma^2(y, z)} e^{-\frac{(x-\mu(y, z))^2}{2\sigma^2(y, z)}} \quad [\text{S12}]$$

with

$$\mu(y, z) = (\text{mass intercept}) + y \cdot (\text{female body mass slope}) + z \cdot (\text{male body mass slope}), \quad [\text{S13}]$$

and

$$\sigma^2(y, z) = (\text{residuals intercept}) + y \cdot (\text{residuals female slope}) + z \cdot (\text{residuals male slope}). \quad [\text{S14}]$$

Intercepts and slopes are listed in Table S4. We normalize $f(x|y, z)$ such that $\int f(x|y, z)dx = 1$.

Stochasticity. We have included stochasticity (mimicking environmental effects) into the functions of survival, growth, recruitment, and inheritance. Each parameter that enters one of the four functions is perturbed by an error term drawn from a Gaussian distribution with zero mean and a variance equalling the fitted year effect. The values for the year effect for each parameter are found in Tables S1–S4.

In the case that a parameter is perturbed outside its natural range, for instance, if the perturbed variance of the growth function would be negative, then the parameter is set to the minimal or maximal value of its range. In the example of the variance, we require that the perturbed value is not smaller than 0.001 (adult males) or 0.045 (senescent males).

The model is run for 1,100 time steps (years) and we assume that the dynamics settle within the first 100 time steps. That means we assume that any bias introduced by initial settings will have vanished by that time. We obtain our results, for example, the stationary distribution, by averaging over the last 1,000 time steps of the model run. The stochastic population growth rate is the geometric mean over the same period.

1. Schindler S, Neuhaus P, Gaillard JM, Coulson T (2013) The influence of nonrandom mating on population growth. *Am Nat* 182(1):28–41.

2. Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C (2002) Age-dependent sexual selection in bighorn rams. *P Roy Soc B-Biol Sci* 269(1487):165–172.

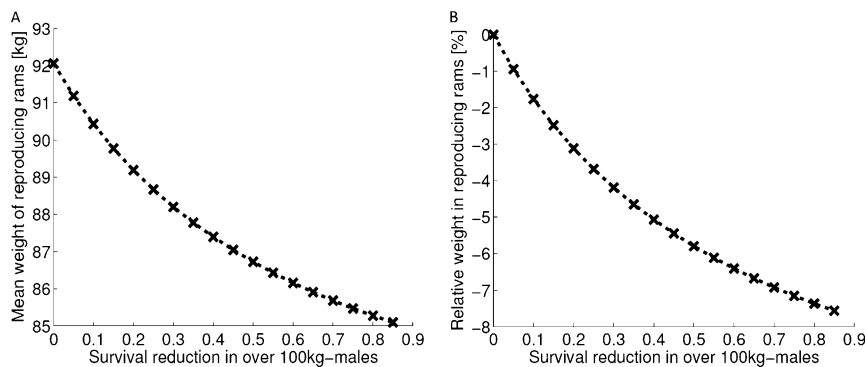


Fig. S1. (A) The difference in mean weight (kilograms) of reproducing male bighorn following an increase in hunting intensity. Hunting intensity was estimated by reducing the survival in rams over 100 kg by 5, 10, 15, 20, and 25 up to 85%. The black crosses represent the differences in mass for breeding males following harvest and where the inheritance function slope is based on field data. (B) The relative percentage difference in mean weight (kilograms) of reproducing male bighorn following an increase in hunting intensity. Hunting intensity was estimated by reducing the survival in rams over 100 kg by 5, 10, 15, 20, and 25 up to 85%. The black crosses represent the relative differences in mass for breeding males following harvest and where the inheritance function slope is based on field data.

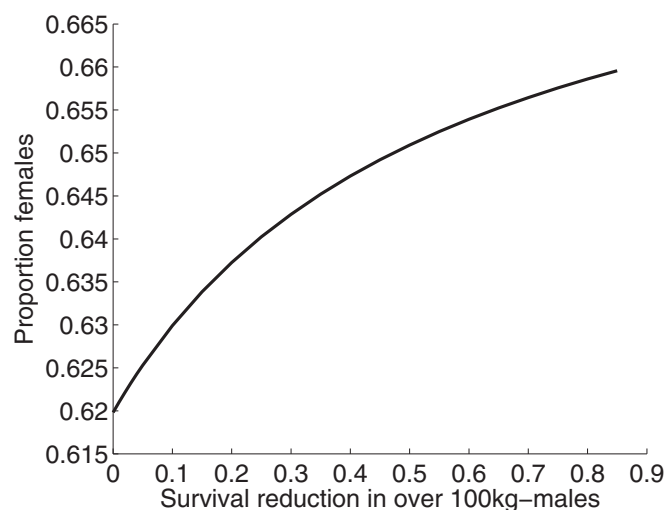


Fig. S2. The change in sex ratio in the Ram Mountain bighorn sheep population following an increase in the intensity of selective harvest. The figure indicates the proportion of females (all ages) to males following a reduction in survival of males over 100 kg at 1% up to 85%.

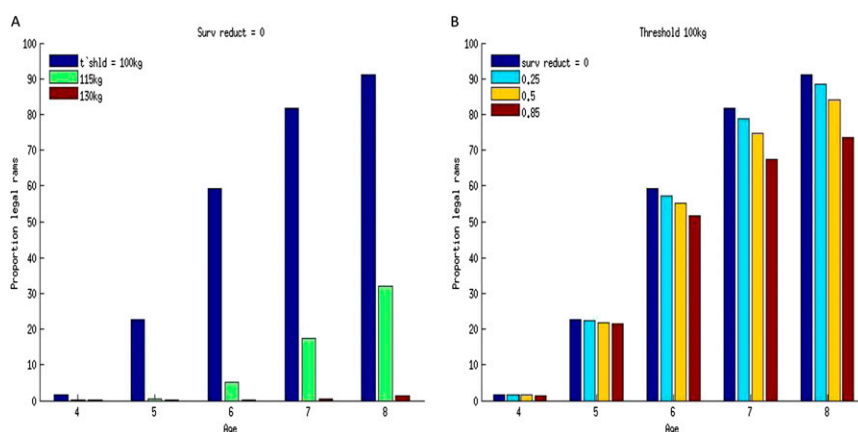


Fig. S3. The 100-kg harvest threshold shown by make age group. We show the (A) proportion of males in each age group above the critical 100-kg threshold for harvest and (B) mortality rates of each age group above the critical 100-kg threshold.

Table S1. Parameter values for the generalized linear mixed models (with the error family specified as binomial) used to determine the survival function for all age-size groups and both sexes

Parameters	Survival models							
	Female				Male			
	Lamb	Yearling	Adult	Senescent	Lamb	Yearling	Adult	Senescent
Sample size, n	337	224	948	473	357	225	718	76
Fixed effects								
Intercept	-0.863	-3.948	2.779	-6.293	-3.470	-0.823	4.324	-4.852
Body mass slope	0.046	0.127	-0.003	0.108	0.124	0.048	-0.031	0.049
Cause of mortality							0.161	0.129
Random effects								
Year SD	1.054	0.243	0.505	0.655	1.08	0.000	0.000	1.17
ID SD			0.000	0.000			0.000	0.000

Table S2. Parameter values for the generalized linear mixed models used to determine the recruitment function for female bighorn yearlings, adults, and senescents

Parameters	Recruitment models for females		
	Yearling	Adult	Senescent
Sample size, n	238	1,033	375
Fixed effects			
Intercept	-14.622	-5.367	-6.266
Body mass slope	0.252	0.092	0.094
Random effects			
Year SD	1.124	0.958	0.723
ID SD		0.408	0.457

Note that the recruitment function within the integral projection model (IPM) accounted for lamb survival (*Materials and Methods*). Also note that the male mating function was developed separately, as described in *SI Materials and Methods*. Sample size, n is given for each pooled age group.

Table S3. Parameter values and residuals for the generalized linear mixed models used to determine the development or growth function for all age groups and both sexes

Parameters	Development models						
	Female				Male		
	Lamb	Yearling	Adult	Senescent	Lamb	Yearling	Adult + senescent
Sample size, n	202	213	966	309	205	188	589
Fixed effects							
Body mass intercept	25.87	25.865	34.563	16.542	24.498	21.196	38.876
Body mass slope	0.716	0.692	0.515	0.772	0.909	0.929	0.673
Residuals intercept	26.921	14.359	79.056	52.926	30.597	76.71	13.153
Residuals slope	-1.296	-0.356	-1.727	-1.469	-1.351	-1.987	-0.12
Residuals slope ²	0.025	0.006	0.011	0.011	0.028	0.015	0.001
Minimal residual							0.001 [males] 0.045 [sen]
Random effects							
Intercept SD for year	2.818	2.447	1.989	2.219	2.716	2.98	3.936
Intercept SD for ID			1.635	0.0			2.671
Year SD for residuals	31.76	21.27	18.65	0.0	0.0	0.0	6.175

Table S4. Parameter values and residuals for the generalized linear mixed model used to determine the inheritance function for both males and females

Parameters	Inheritance model, male and female, pooled adult and senescent age groups
Sample size, n	233
Fixed effects	
Mass intercept	8.113
Female body mass slope	0.227
Male body mass slope	0.02 (0.0195)
Residuals intercept	9.25
Residuals female slope	-0.124
Residuals male slope	0.06
Random effects	
Year SD	2.834
ID SD	1.869 [Ewe ID] + 0.897 [Ram ID]
Residuals year SD	1.213

We use the random effect intercept SD value for year in the IPM.

Table S5. Possible outcomes (following literature review) affecting population growth rate and body mass distribution following the selective harvest of large males

Parameter	Female	Male
Fecundity	Reduced female fertility rates (1) and recruitment will likely lead to reduced population growth rate and a shift in age structure toward older animals and subsequent shift in mean body mass.	Reduced mating opportunity for large males may lead to reduced population growth rate, and shift in age structure, dependent on the frequency and severity of mortality.
Survival	If increased male mortality reduces female survival, then population growth rate will decrease, but it is unclear how body size distribution will be influenced.	Direct offtake reduces mean survival, with reduced population growth rate and possible shift in mean body mass distribution.
Growth	An increase in male mortality may bring about a shift in female growth rates, potentially upward. This will bring about a subsequent shift in female survival and fecundity.	An increase in male mortality may lead to reduced growth rates.
Offspring size	If a reduction in male adult survival leads to reduced female lamb body size, then a subsequent decrease in lamb survival will lead to reduced population growth rate and a shift in mean female body size.	If mean male lamb size decreases, then this will lead to a decline in survival and a subsequent decline in population growth rate. There will also be a shift toward smaller male lambs overall.

Scenarios are based on the functions used to construct an IPM, and for both sexes.

1. Milner-Gulland EJ, et al. (2003) Conservation: Reproductive collapse in saiga antelope harems. *Nature* 422(6928):135.

Table S6. List of notations

Notation	Description
a	Age
t	Time
x, y, z	Body weight
$y^{1a}, y^{ye}, y^{ad}, y^{se}$	Body weight of a lamb, yearling, adult or senescent
n^{la}	Numbers or densities
n_f^{la} and n_m^{la}	Number of lambs, equivalent to the number of surviving offspring
n_f^{ye} and n_m^{ye}	Number of female or male lambs
n_f^{ad} and n_m^{ad}	Number of female or male yearlings
n_f^{se} and n_m^{se}	Number of female or male adults
	Reproduction
s	Proportion of female offspring
C_{n_f, n_m}	Normalization constant, equivalent to the number of parturitions
$m(x, y)$	Mating probability between x female and y male is proportional to $m(x, y)$
$R(x)$	Probability to produce one offspring of a female weighing x
$f(x y, z)$	Probability that an offspring has trait x if its parents have traits y and z
	Growth and survival
$p^{1a}(x, y), p^{ye}(x, y), \dots, p^{ad}(x, y)$ and $p^{se}(x, y)$	Probability of a lamb, yearling, adult or senescent to survive to the next time step and change the body weight from y to x