



Sons accelerate maternal aging in a wild mammal

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Edited by Nils Chr. Stenseth, University of Oslo, Oslo, Norway, and approved January 21, 2020 (received for review August 22, 2019)

Aging, or senescence, is a progressive deterioration of physiological function with age. It leads to age-related declines in reproduction (reproductive senescence) and survival (actuarial senescence) in most organisms. However, senescence patterns can be highly variable across species, populations, and individuals, and the reasons for such variations remain poorly understood. Evolutionary theories predict that increases in reproductive effort in early life should be associated with accelerated senescence, but empirical tests have yielded mixed results. Although in sexually size-dimorphic species offspring of the larger sex (typically males) commonly require more parental resources, these sex differences are not currently incorporated into evolutionary theories of aging. Here, we show that female reproductive senescence varies with both the number and sex ratio of offspring weaned during early life, using data from a long-term study of bighorn sheep. For a given number of offspring, females that weaned more sons than daughters when aged between 2 and 7 y experienced faster senescence in offspring survival in old age. By contrast, analyses of actuarial senescence showed no cost of early-life reproduction. Our results unite two important topics in evolutionary biology: life history and sex allocation. Offspring sex ratio may help explain among-individual variation in senescence rates in other species, including humans.

cost of reproduction | offspring sex | senescence

The idea that reproduction entails costs upon future survival and/or reproduction is central to life-history evolution theory (1). Costs of reproduction play an important role in the evolution of reproductive tactics and can influence demography and population dynamics of many species (2, 3). These costs can vary according to environmental conditions and the characteristics of parents and offspring (4–6). In species where males are larger than females, including humans, the energy intake of sons before and after birth is typically higher than that of daughters (7, 8). The increased energetic costs of rearing sons depress maternal reproductive performance and survival probability in the subsequent breeding season in several mammal species (reviewed in ref. 9), with important implications for evolution of adaptive sex-ratio adjustment (10, 11). However, although some costs can occur only after a certain amount of physiological damage has accumulated (12), we know little about the long-term effects of offspring sex ratio on parental traits.

Both the disposable soma (13) and antagonistic pleiotropy (14) theories of aging predict that allocation to reproduction early in life should be favored by selection at the cost of faster demographic senescence (the age-related decline in survival probability and reproduction). Such early–late life trade-offs have been found in various mammals and birds (15), but results are mixed overall (16). Aging studies have used a variety of metrics to measure allocation to reproduction during early life, such as age at first reproduction and number of offspring produced or reared up to a certain age (15). Most studies, however, ignored the possibility that offspring can be divided into two fundamental categories: males and females. Helle et al. (17) showed that producing sons reduced the postmenopausal longevity of preindustrial Sami women, whereas the number of daughters tended to have the opposite effect. The generality of these findings, however, is controversial (18, 19). Notably, it has been suggested that the differential effects of sons and daughters on maternal longevity in human societies arise from sociocultural rather

than biological factors (18, 20). It is also important to note that longevity is an imperfect proxy for actuarial senescence, because life-span differences can result from variation in age-independent mortality as well as from differential increase in mortality risk with age (21). Thus, it remains uncertain whether sex allocation can mask links between early-life reproduction and senescence.

Here, we use the exceptionally detailed long-term monitoring of bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, Canada to assess the overall costs of reproduction and the costs of rearing more sons than daughters in terms of reproductive and actuarial senescence. Bighorn sheep are long-lived polygynous ungulates, with pronounced male-biased sexual size dimorphism already evident at birth (22) and a relatively simple social system compared to humans (23). Reproductive tactics differ greatly between the sexes. Males compete intensely for estrous females during the mating season (rut) but provide no parental care, whereas females provision offspring during 6 mo of gestation and 5 mo of lactation. There is evidence that short-term costs of reproduction are greater for mothers of sons than of daughters (22, 24, 25). Female survival starts to decrease after 7 y of age, marking the onset of actuarial senescence (26). Most females are primiparous at 2 or 3 y (27). Therefore, we defined reproduction early in life as occurring between 2 and 7 y inclusively (28). This period, associated with age-independent survival, is also known as the “prime age” (26). We have recently shown that in this population the number of sons weaned during early life is not associated with reduced maternal life span (9). However, links between sex allocation and senescence remain unexplored in any species. Similar to short-term costs of reproduction, long-term

Significance

Do sons and daughters have a differential cost over the long term? Sexual size dimorphism is widespread in animals and offspring of the larger sex commonly require more parental resources. The relationship between offspring sex ratio and maternal longevity has been tested in humans, producing mixed results and debates over the relative influence of biological and sociocultural factors. Meanwhile, links between offspring sex and reproductive aging have been neglected. We used data from a wild ungulate with high male-biased sexual dimorphism but without complicating sociocultural factors to show that females with many sons during early adulthood showed the strongest declines in reproductive success in old age. Our results underline the need to consider offspring sex in studies of aging.

Author contributions: M.D. designed research; M.D. performed research; M.D. analyzed data; and M.D., M.F.-B., and F.P. wrote the paper.

The authors declare no competing interest.

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Data deposition: The data reported in this paper have been deposited on Figshare, https://figshare.com/articles/Long-term_effects_of_sons_in_bighorn_sheep/11558973.

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1914654117/-DCSupplemental>.

First published February 18, 2020.

Table 1. List of reproductive traits of bighorn sheep females for which GLMMs were run, with units, timing of measurement, and sample sizes used

Trait	Units	Season of measurement*	No. of observations (no. of females) in full models	No. of observations (no. of females) per early-life sex ratio class [†]		
				More sons	More daughters	Equal
Annual reproductive success	Yes/no	Spring in y t+1	353 (90)	164 (40)	129 (35)	60 (15)
Fecundity	Yes/no	Spring in y t	364 (91) [‡]	168 (40)	133 (35)	63 (16)
Offspring survival to weaning	Yes/no	Autumn in y t	331 (87)	152 (39)	117 (33)	62 (15)
Offspring survival in winter	Yes/no	Spring in y t+1	199 (71)	94 (34)	67 (24)	38 (13)

*Y t refers to year of birth of focal offspring.

[†]Early-life sex ratio was fitted as a continuous variable in the models but divided into three groups for illustrative purposes.

[‡]The difference in sample size between annual reproductive success and fecundity is due to 11 lambs that survived to weaning but whose winter survival was unknown.

costs of reproduction may be more commonly found on reproduction than on survival in long-lived species (12, 29). We thus expect that females rearing more sons than daughters in early life would show stronger senescence at old ages, particularly in terms of reproductive performance.

Results

We first analyzed how early-life reproduction influenced annual reproductive success in later life (≥ 8 y old) using generalized linear mixed models (GLMMs). We used the number (0, 1) of offspring surviving to 1 y as our measure of annual reproductive success. Details of sample sizes for annual reproductive success

and its components are in Table 1. There was considerable population-level age-related variation in reproductive success (Fig. 1A). To ensure that the age effect reflects an unbiased estimate of within-individual change, GLMMs included female identity as a random effect and female longevity as a fixed effect (Table 2). Females that reared more offspring during early life showed a faster decline in reproductive success with age (Fig. 2A), as revealed by the significant interaction between age and the number of offspring weaned between 2 and 7 y (Table 2). We found no such interaction when we considered the number of offspring produced rather than weaned between 2 and 7 y to measure early-life reproductive output (estimate \pm SE = -0.622 ± 0.574 ,

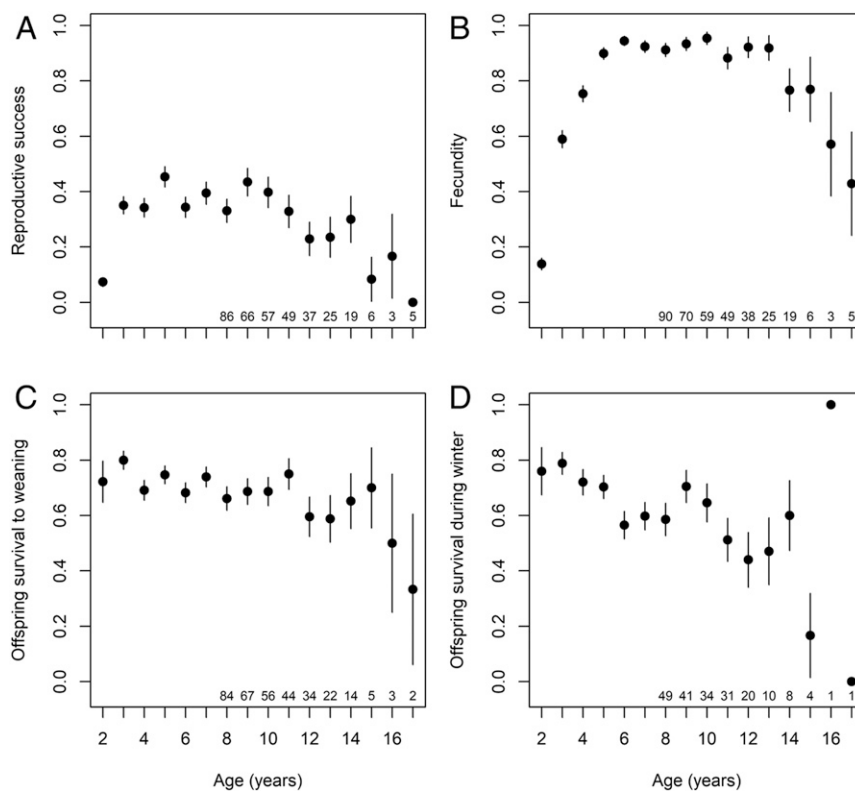


Fig. 1. Age-specific variation in (A) reproductive success and (B–D) its components in all adult female bighorn sheep at Ram Mountain (1972 to 2017). Points show population-level averages with SEs. All females older than 17 y ($n \leq 2$) are pooled within the 17-y age class. Numbers above the x axis are age-specific sample sizes used in the present analyses of senescence.

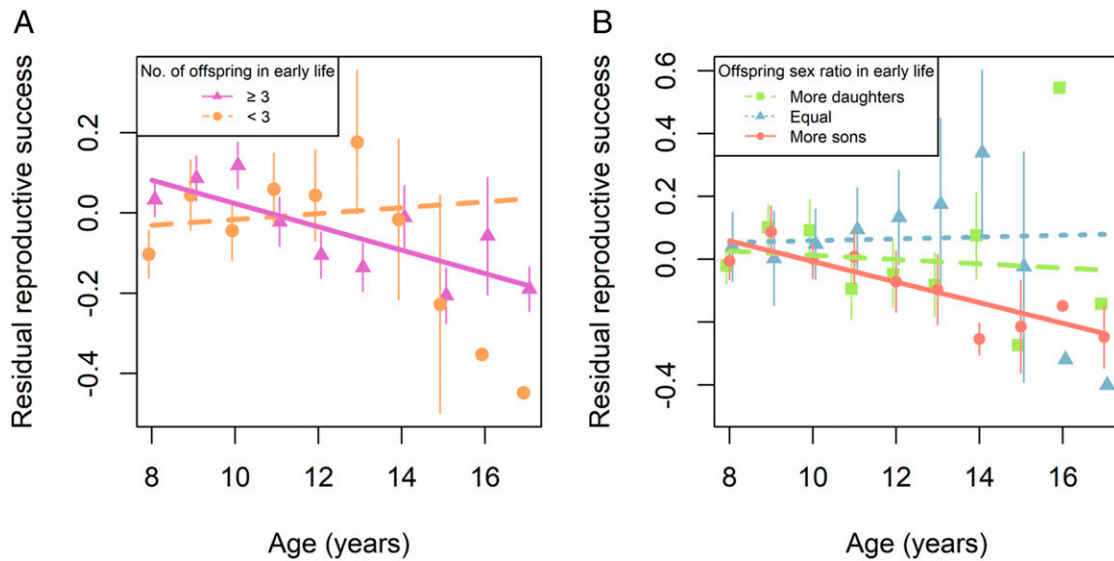


Fig. 2. Senescence in reproductive success of female bighorn sheep is modulated by reproduction in early life. (A) Reproductive success as a function of age among females aged 8 y and older that weaned less than three or at least three lambs when aged 2 to 7 y. (B) Reproductive success as a function of age among females that weaned more sons, more daughters, or an equal number of sons and daughters between 2 and 7 y. Shown are mean residuals (\pm SE) after accounting for other significant effects in the model (Table 2).

$P = 0.279$). There was a trend for an interaction between offspring sex ratio in early life and age (Table 2). For a given number of offspring, females that weaned more sons than daughters before the age of 8 y showed the fastest decline in reproductive success in old age (Fig. 2B).

We then fitted separate GLMMs for three components of female reproductive success: fecundity, offspring survival to weaning, and offspring winter survival (Fig. 1 B–D). Fecundity decreased with increasing population density and was higher for females that weaned a lamb the previous year than for those that did not (Table 3). After accounting for the effects of density and previous reproductive status, the decline in fecundity with age tended to be faster when many offspring were weaned early in life (Table 3 and *SI Appendix*, Fig. S1). However, we did not find that this decline was affected by sex ratio of offspring weaned during early life (*SI Appendix*, Table S2). There was no evidence for interactions between age and early-life sex ratio or early-life number of offspring on offspring survival to weaning (*SI Appendix*, Table S2). The final model for offspring survival to weaning only included previous reproductive status and a positive effect of the number of offspring weaned during early life (Table 3). We found evidence for early–late life trade-offs when considering lamb winter survival (Table 3). Females that weaned more offspring between 2 and 7 y showed the strongest decline in offspring winter survival in old age (Fig. 3A). In addition, offspring winter survival declined more rapidly in old age among females that weaned more sons than daughters before age 8 y (Fig. 3B). These results show that the influence of early-life reproduction on senescence in reproductive success arises mainly through its influence on offspring survival during winter.

One possible explanation of these results is that females with many sons during early life produced relatively light lambs later in life. To explore this possibility, we tested how reproduction during early life influenced senescence in weaning mass of offspring. Weaning mass decreased with maternal age from 8 y onward (slope \pm SE = -2.472 ± 0.735 , $P = 0.001$), but this relationship did not depend on early-life reproduction (interaction between early-life sex ratio and age, estimate \pm SE = -1.280 ± 1.676 , $P = 0.447$; interaction between early-life number of offspring and age, estimate \pm SE = -2.022 ± 1.825 , $P = 0.270$).

There was no main effect of early-life sex ratio (slope \pm SE = 0.308 ± 0.924 , $P = 0.740$) or early-life number of offspring (slope \pm SE = 1.621 ± 0.989 , $P = 0.104$). Thus, long-term costs of early reproduction on late-age offspring winter survival persisted after accounting for the positive effect of weaning mass (*SI Appendix*, Table S3).

Our analyses indicate that variation in early-life reproduction affected reproductive senescence but provide no evidence that early-life reproduction affected survival senescence (Table 4). The number of offspring weaned between 2 and 7 y was only a significant predictor of late-life baseline mortality (Table 4). Females that had greater weaning success before the age of 8 y showed higher survival probabilities in late life, independent of their age (Fig. 4A). There was a trend for survival to increase when females weaned more sons than daughters before the age of 8 y (Table 4 and Fig. 4B).

Table 2. Final GLMM of annual reproductive success, calculated as the number (0, 1) of offspring surviving to 1 y, in female bighorn sheep that survived to at least age 8 y

Effects	Estimate	SE	P value
Fixed effects			
Intercept	-0.783	0.253	
Longevity	1.045	0.380	0.006
Age	-1.365	0.415	0.001
Population density	-0.992	0.444	0.026
Early-life no. of offspring	0.840	0.368	0.022
Early-life sex ratio	-0.266	0.287	0.355
Early-life no. of offspring \times age	-1.654	0.786	0.035
Early-life sex ratio \times age	-1.092	0.646	0.091
Random effects			
	Variance	SD	
Female Identity	0.001	0.039	
Year	0.894	0.945	

The final model includes 359 observations from 91 females. Annual reproductive success was measured in June of year $t+1$. Early-life reproduction was estimated between 2 and 7 y of age and the other fixed effects were measured in June of year t (year of birth of focal offspring). For a summary of nonsignificant variables see *SI Appendix*, Table S1.

Table 3. Final GLMMs to explain senescence in components of reproductive success in female bighorn sheep

Response and explanatory variables	Estimate	SE	$\chi^2_{(df)}$	P value
Fecundity				
Fixed effects				
Intercept	2.725	0.473		
Age	-3.004	0.680		<0.001
Longevity	1.835	0.758		0.015
Population density	-1.292	0.520		0.013
Reproductive status in year t-1*			14.22 ₍₂₎	<0.001
Weaned a daughter	2.210	0.695		0.001
Weaned a son	1.136	0.505		0.025
Early-life no. of offspring	1.589	0.546		0.004
Early-life no. of offspring \times age	-1.411	0.779		0.070
Random effects				
Female Identity	Variance	SD		
Year	1.245	1.116		
	<0.001	<0.001		
Offspring survival to weaning				
Fixed effects				
Intercept	1.324	0.308		
Reproductive status in year t-1			5.71 ₍₂₎	0.057
Weaned a daughter	-0.613	0.342		0.073
Weaned a son	-0.751	0.345		0.029
Early-life no. of offspring	0.711	0.307		0.021
Random effects				
Female Identity	Variance	SD		
Year	0.178	0.422		
	0.565	0.752		
Offspring survival during winter				
Fixed effects				
Intercept	0.573	0.304		
Longevity	0.932	0.456		0.041
Offspring sex [†]	-0.929	0.355		0.009
Age	-1.240	0.518		0.017
Population density	-1.148	0.471		0.015
Early-life no. of offspring	0.204	0.474		0.666
Early-life sex ratio	-0.728	0.396		0.066
Early-life no. of offspring \times age	-1.902	1.063		0.073
Early-life sex ratio \times age	-2.000	1.012		0.048
Random effects				
Female Identity	Variance	SD		
Year	<0.001	<0.001		
	0.630	0.794		

The final model for fecundity (evidence of lactation in late May/early June of year t) includes 470 observations from 119 females. The final model for offspring survival to weaning (late September in year t) consists of 420 observations from 113 females. The final model for offspring survival during winter (whether the lamb seen in late September did or did not survive to June of year t+1) includes 203 observations from 72 females. Early-life reproduction was estimated between 2 and 7 y of age. The others fixed effects were measured in June of year t, with the exception of reproductive status in year t-1. For a summary of nonsignificant variables see *SI Appendix, Table S2*.

*Reference category: no lamb weaned.

[†]Reference category: female.

Discussion

Patterns of demographic senescence are highly variable both between and within species (e.g., refs. 30–32) and part of those variations can be accounted for by differences in allocation to reproduction during early life. We found that reproductive senescence in female bighorn sheep varies with both the number and sex ratio of offspring weaned during early life. Our results represent evidence that offspring sex ratio can explain individual variation in rates of senescence.

Sex allocation theory predicts that parents should adjust offspring sex ratio when the fitness returns of producing sons and daughters vary (33). While studies of invertebrates have provided clear support for sex allocation theory, there is no consistent pattern in vertebrates (11, 34). Sex allocation in vertebrates can be influenced by many selective forces, potentially operating in opposite directions. For instance, if both mothers and fathers have adaptive control over offspring sex ratio, their interests may

diverge (35). Recently, we have shown in this population that offspring sex ratio varies according to complex interactions between maternal previous weaning success, maternal condition, or environmental conditions (36, 37), and that males with higher reproductive success have a higher proportion of sons (38). For most mammals, it may be easier to determine the consequences rather than the causes of offspring sex-ratio bias. Across mammalian orders, male-biased sexual size dimorphism is prevalent (39). Because they are larger, sons commonly require more resources than daughters. In some species, daughters share their mother's home range after weaning, with potential additional costs to mothers through increased competition (40, 41). However, the social organization of bighorn sheep is characterized by weak postweaning mother–daughter associations (23).

Costs of reproduction documented here depend on how long offspring lived. While female sheep that weaned many lambs during early life showed accelerated declines in reproductive

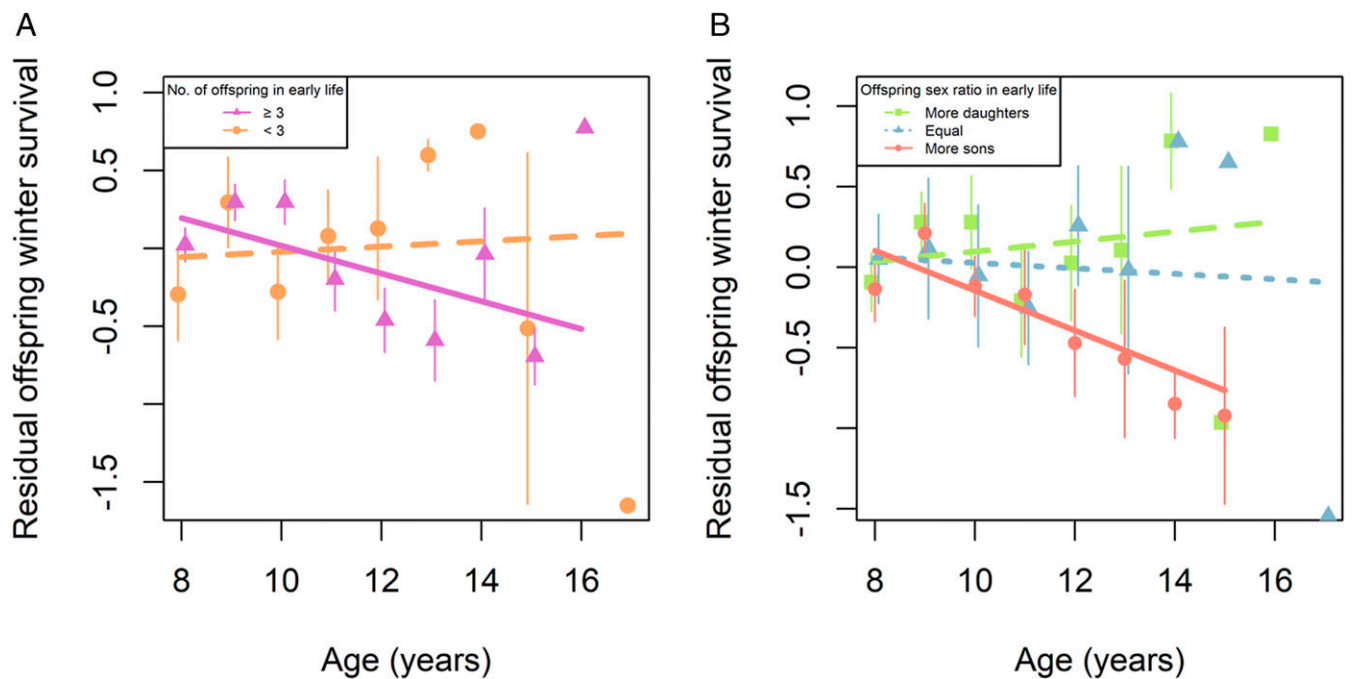


Fig. 3. Effects of reproduction in early life on senescence in offspring winter survival (whether the weaned lamb did or did not survive to 1 y of age) in bighorn sheep females aged 8 y and older. (A) Age-related changes in lamb winter survival among females that weaned less than three or at least three lambs when aged 2 to 7 y. (B) Age-related changes in lamb winter survival among females that weaned more sons, more daughters, or an equal number of sons and daughters between 2 and 7 y. Shown are mean residuals (\pm SE) after accounting for other significant effects in the model (Table 3).

success in old age, reproductive senescence was not related to the number of offspring born during early life. These results support the contention that costs of gestation are lower than those of lactation (6). In several dimorphic mammals, including bighorn sheep, sons suckle more frequently and for longer duration than daughters (7, 22). Bighorn ewes that weaned a son are about 10 to 12% less likely to wean an offspring the following year than ewes that weaned a daughter (25). As this cost of weaning sons does not hold when restricting the analysis to females aged 8 y and older, it appears that short-fitness costs of sons do not affect all females equally and fall primarily on young adults (i.e., <8 y old). As short-term and long-term costs of reproduction have been studied in isolation, their relative influence on fitness-related traits remains largely unexplored (12). In older bighorn ewes, the consequences of rearing sons were expressed as cumulative effects over the long term, rather than from one year to the next.

Mixed models used here control for repeated measures of individuals and for selective disappearance (an age-related change

in the population mean of a phenotypic trait due to mortality), which can mask within-individual senescence patterns (42–44). The significant positive effect of longevity on reproductive traits (Tables 2 and 3) indicates that selective disappearance affects population structure: Older females with poorer reproductive performance had shorter life spans. After accounting for selective disappearance, we found that females that weaned many sons during early life showed accelerated senescence in lamb winter survival. This long-term cost of reproduction is evident alongside significant effects of individual reproductive potential (often referred to as individual quality; ref. 45) on late-life reproductive performance. For example, the number of lambs weaned between 2 and 7 y of age was positively correlated with the number of lambs weaned after 7 y of age. We have previously failed to detect any cost of early-life reproduction on future longevity for females in this population (9, 28). On the contrary, longevity was positively correlated with both the number of lambs and the number of sons weaned between the ages of 2 and 7 y (28). Here we show that

Table 4. A comparison of Gompertz models testing for effects of early-life reproduction on baseline mortality and rate of change in mortality with age (actuarial senescence) of female bighorn sheep aged ≥ 7 y

Model	Structure	Models to be compared	$\chi^2_{(df)}$	P value
1	Baseline (early-life no. of offspring \times early-life sex ratio) + rate (early-life no. of offspring + early-life sex ratio)			
2	Baseline (early-life no. of offspring + early-life sex ratio) + rate (early-life no. of offspring + early-life sex ratio)	1 vs. 2	1.13 ₍₁₎	0.288
3	Baseline (early-life no. of offspring + early-life sex ratio) + rate (early-life no. of offspring)	2 vs. 3	0.16 ₍₁₎	0.688
4	Baseline (early-life no. of offspring + early-life sex ratio) + rate	3 vs. 4	2.02 ₍₁₎	0.155
5	Baseline (early-life no. of offspring) + rate	4 vs. 5	2.98 ₍₁₎	0.084
6	Baseline + rate	5 vs. 6	7.35 ₍₁₎	0.007

The full model used a survival dataset of 106 females.

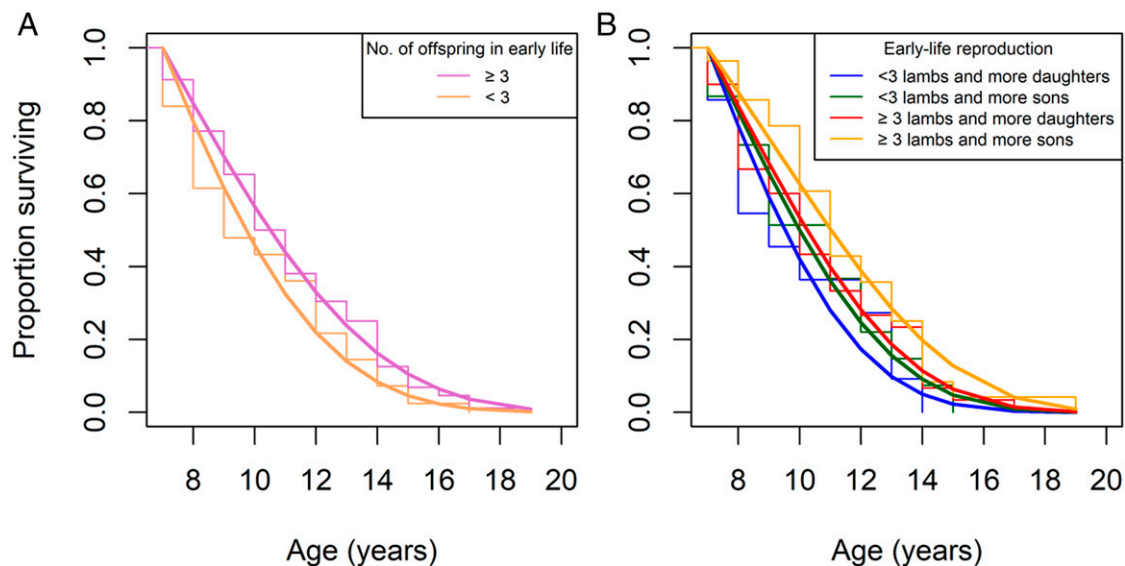


Fig. 4. Effects of early-life reproduction on survival later in life in bighorn females. (A) Proportion of females surviving to the following year among those that weaned less than or at least three lambs between 2 and 7 y. (B) Proportion of females surviving to the following year according to combinations of early-life number of offspring and early-life sex ratio. Curves with equal sex ratio were omitted for clarity but can be found in *SI Appendix, Fig. S2*.

these effects arise through an age-independent change in baseline mortality rather than a change in the rate of actuarial senescence. Similar to short-term reproductive costs (29), long-term costs of reproduction in long-lived species may be more likely to manifest in terms of future reproduction than on survival, because longevity strongly influences fitness in these species (46). Our results are in line with the view that a high allocation to reproduction in early life affects some but not all traits at old ages (15) and underline the importance of studying multiple traits.

A remaining question is the nature of the mechanisms linking early-life reproductive effort to senescence in offspring winter survival. It is well known that reductions in milk production and quality affect juvenile growth (e.g., refs. 47 and 48), which, in turn, influences their survival (49). However, we found that the costs of early-life reproduction were independent of weaning mass of lambs born later in life. That result does not necessarily imply that lactation performance is not involved. The composition and amount of milk may influence offspring survival through mechanisms other than growth, as shown in the Columbian ground squirrel (*Urocitellus columbianus*) (50), for example, through long-term effects on immune function (51). Estimating the effects of age and reproductive history on quantity and quality of milk produced by females is an important next step toward our understanding of processes governing maternal effect senescence in the wild.

To date, most research into the evolution of senescence has focused on age-dependant declines in survival and fecundity. However, it is also important to consider the detrimental effects of increasing maternal age manifested in offspring traits (52). If we had simply analyzed fecundity and survival patterns, we would have concluded, wrongly, that there is no long-term effect of sons on maternal senescence in bighorn sheep. Data from a pre-industrial Finnish human population suggest that women with higher early-life fecundity (defined as the number of children born to a woman before age 25 y) experienced accelerated senescence in child survival, but not in annual probability of giving birth (53). While sons have a greater negative influence than daughters on maternal longevity and health in some human populations (17, 20, 54–56), the differential effects of sons and daughters on parental senescence remain to be investigated in our own species.

Materials and Methods

Study Area and Population. The Ram Mountain population of bighorn sheep has been studied since the early 1970s. Ram Mountain is about 30 km east of the Rocky Mountains in Alberta, Canada (52° N, 115° W, elevation 1,700 to 2,200 m), with about 38 km² of alpine and subalpine habitat. Population density, measured as the number of females 2 y and older in June, varied markedly over the study (57). Female bighorn sheep are highly philopatric. They conceive in mid-November or early December and give birth in late May or early June (58) to a maximum of one offspring per year from age 2 y onward. Weaning occurs at ~4 to 5 mo of age (59).

Sheep were captured several times each year from late May to late September in a corral trap baited with salt. Individuals were marked with visual collars and plastic ear tags at their first capture, usually as lambs, so their exact age was known. Biopsies for genetic analysis were collected since 1987. Genetic data were used to determine paternity, confirm behavioral maternity assignments (discussed below), and identify mothers of the few individuals first captured at 1 y of age (yearling). The winter survival of 11 lambs born before 1987 that were unmarked or lost both ear tags during the winter was unknown because yearlings generally did not associate with their mothers (23). At each capture, we recorded body mass and examined the udder to classify females as lactating or not. Females can retain visibly swollen udders up to 3 wk after lamb death (24).

Intensive and continuous observations during summer provided precise data on individual survival and reproduction. The resighting probability of adult females is 0.99 (26). Date of last sighting is therefore a reliable indicator of age at death. Lamb–mother associations were established through repeated observations of suckling behavior.

Our work was approved by the Animal Care Committee of the Université de Sherbrooke (protocols MFB2018-01 and FP2016-01) affiliated with the Canadian Council on Animal Care.

Quantification and Statistical Analysis. Similarly to previous studies of this population (9, 28), we chose the age of 7 y as the cutoff between early and late life because survival decreases with age beyond 7 y (26). Reproduction early in life therefore occurred between 2 and 7 y inclusively. This period overlaps the latest age at first reproduction (9). We measured the number and sex ratio of lambs weaned rather than produced during early life for two reasons. First, energetic costs of gestation are generally lower than those of lactation (6). Second, the sex of lambs that died at or shortly after birth was unknown because no lamb was seen, yet milk or colostrum was expressed by the mother at capture. There was no relationship between the number of offspring weaned during early life and the sex ratio of those offspring ($\beta = -0.009 \pm 0.10$, $P = 0.932$). Although the number of offspring weaned during early life is a continuous measure in all analyses, it is grouped (<3 and ≥3) for illustrative purposes. Similarly, sex ratio of lambs weaned

during early life was fitted as a continuous variable in all models but divided into three groups (“more sons,” “equal,” and “more daughters”) in figures and Table 1. The distributions of early-life reproductive variables are presented in *SI Appendix, Fig. S3*.

We first analyzed the effects of early-life reproduction on annual reproductive success for each calendar year a female was alive and aged 8 y and more. Reproductive success is often defined as the number of offspring weaned. In bighorn sheep, lambs are usually weaned in late September but some females continue to nurse their lambs into autumn (60). Furthermore, the effects of maternal reproductive effort during lactation on lamb survival are delayed by several months, as they mostly manifest themselves during the winter (61). Annual reproductive success was therefore scored as whether or not a female produced a lamb surviving to 1 y of age. Analysis of reproductive success included all adult females regardless of whether or not they had given birth. Reproductive success was analyzed in GLMMs with the R package lme4, using a binomial distribution. The full GLMM included the fixed terms of interest: age, the number of offspring weaned during early life, the sex ratio of those offspring, and all two-way interactions. Unfortunately, sample size was insufficient to assess the three-way interaction between age, early-life number of offspring, and early-life sex ratio. We controlled for selective disappearance from the breeding population by including female longevity as a linear covariate. We also considered as potential covariates several variables known to influence annual reproduction: reproductive status the previous year (coded as “failed,” “weaned a male,” or “weaned a female”) (25) and population density in the year of the lamb’s birth (62). We fitted female identity and breeding year as random factors to control for unmeasured sources of between-female and between-year variation.

Reproductive success can be decomposed into 1) fecundity (evidence of lactation), 2) offspring survival to weaning, and 3) offspring winter survival (from weaning to 1 y of age). We analyzed the effects of early-life reproduction on each of these three components using GLMMs. We fitted the same fixed and random effects as the full model of reproductive success described above. Lamb sex was added as a factor in models of offspring winter survival. The reduced model of offspring winter survival was rerun with lamb mass in mid-September as an additional explanatory variable. Lamb mass was adjusted to September 15 using LMMs for lambs that were weighted at least twice between June and September (67%) and linear

models for lambs weighted once (33%) (63). Sample sizes (Tables 1–3) varied between full and reduced models because of some missing values for explanatory variables.

We assessed the effects of early-life reproduction on survival senescence using parametric survival analyses with a Gompertz equation (hereafter called Gompertz models). The Gompertz model has the structure $H_t = Ae^{Bt}$, where the hazard function (H_t , the force of mortality) depends on baseline mortality A and increases exponentially with age according to parameter B , which quantifies the rate of survival senescence. The higher B is, the more intense the senescence. The Gompertz distribution provides accurate estimates of survival senescence in large herbivores, including bighorn sheep (64). Gompertz models were fitted using the package flexsurv (65).

Full models were simplified by testing successively the first-order interactions and, if interactions were not statistically significant, the main effects of covariates. We used likelihood ratio tests and Wald statistics to assess statistical significance. Variables were included in final models if they had a P value < 0.10 . However, main effects were always retained if they were involved in interactions. Random factors were kept in the models independently of their proportion of explained variance. Parameter estimates are presented \pm SE. We reported standardized regression coefficients obtained by standardizing all continuous explanatory variables. Because the models included factors, we standardized continuous variables by centering and dividing them by two SDs (66).

Data Availability. The data reported in this paper have been deposited on Figshare (67).

ACKNOWLEDGMENTS. We thank the many assistants and students who contributed to data collection over decades; D. Coltman, J. Jorgenson, A. Hubb, and C. Feder for invaluable support; and J.-F. Lemaître and three anonymous reviewers for constructive comments on earlier drafts of the manuscript. This work was supported by a Fonds de recherche du Québec – Nature et technologies Merit Scholarship Program for Foreign Students (PBEEE) to M.D. Research on bighorn sheep at Ram Mountain is mostly supported by Natural Sciences and Engineering Research Council of Canada Discovery grants and Alberta Conservation Association grants to M.F.-B. and F.P. and a Canada Research Chair to F.P.

1. S. C. Stearns, *The Evolution of Life Histories* (Oxford University Press, New York, 1992).
2. G. Proaktor, T. Coulson, E. J. Milner-Gulland, The demographic consequences of the cost of reproduction in ungulates. *Ecology* **89**, 2604–2611 (2008).
3. A. Kuparinen, D. C. Hardie, J. A. Hutchings, Evolutionary and ecological feedbacks of the survival cost of reproduction. *Evol. Appl.* **5**, 245–255 (2012).
4. S. Hamel, S. D. Côté, M. Festa-Bianchet, Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology* **91**, 2034–2043 (2010).
5. S. Descamps, S. Boutin, A. G. McAdam, D. Berteaux, J.-M. Gaillard, Survival costs of reproduction vary with age in North American red squirrels. *Proc. Biol. Sci.* **276**, 1129–1135 (2009).
6. T. H. Clutton-Brock, S. D. Albon, F. E. Guinness, Fitness costs of gestation and lactation in wild mammals. *Nature* **337**, 260–262 (1989).
7. T. H. Clutton-Brock, *The Evolution of Parental Care* (Princeton University Press, Princeton, NJ, 1991).
8. R. M. Tamimi *et al.*, Average energy intake among pregnant women carrying a boy compared with a girl. *BMJ* **326**, 1245–1246 (2003).
9. M. Douhard *et al.*, Maternal longevity and offspring sex in wild ungulates. *Proc. R. Soc. B Biol. Sci.* **286**, 20181968 (2019).
10. M. Gomendio, T. H. Clutton-Brock, S. D. Albon, F. E. Guinness, M. J. Simpson, Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature* **343**, 261–263 (1990).
11. A. Cockburn, S. Legge, M. C. Double, “Sex ratios in birds and mammals: Can the hypotheses be disentangled?” in *Sex Ratios: Concepts and Research Methods*, C. W. Hardy, Ed. (Cambridge University Press, Cambridge, UK, 2002), pp. 266–286.
12. S. B. Kroeger, D. T. Blumstein, K. B. Armitage, J. M. Reid, J. G. A. Martin, Cumulative reproductive costs on current reproduction in a wild polytocous mammal. *Ecol. Evol.* **8**, 11543–11553 (2018).
13. T. B. L. Kirkwood, M. R. Rose, Evolution of senescence: Late survival sacrificed for reproduction. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **332**, 15–24 (1991).
14. G. C. Williams, Pleiotropy, natural selection and the evolution of senescence. *Evolution* **11**, 398–411 (1957).
15. J.-F. Lemaître *et al.*, Early-late life trade-offs and the evolution of ageing in the wild. *Proc. Biol. Sci.* **282**, 20150209 (2015).
16. J.-F. Lemaître, L. Cheynel, M. Douhard, V. Ronget, J.-M. Gaillard, “Trade-offs” in *Encyclopedia of Biomedical Gerontology*, S. I. S. Rattan, Ed. (Elsevier, 2020), pp. 367–375.
17. S. Helle, V. Lummaa, J. Jokela, Sons reduced maternal longevity in preindustrial humans. *Science* **296**, 1085 (2002).
18. J. Beise, E. Volland, Effect of producing sons on maternal longevity in premodern populations. *Science* **298**, 317, author reply 317 (2002).
19. D. Cesarini, E. Lindqvist, B. Wallace, Is there an adverse effect of sons on maternal longevity? *Proc. Biol. Sci.* **276**, 2081–2084 (2009).
20. B. Van de Putte, K. Matthijs, R. Vlietinck, A social component in the negative effect of sons on maternal longevity in pre-industrial humans. *J. Biosoc. Sci.* **36**, 289–297 (2004).
21. G. Péron, J.-F. Lemaître, V. Ronget, M. Tidière, J.-M. Gaillard, Variation in actuarial senescence does not reflect life span variation across mammals. *PLoS Biol.* **17**, e3000432 (2019).
22. J. T. Hogg, C. C. Hass, D. A. Jenni, Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behav. Ecol. Sociobiol.* **31**, 243–251 (1992).
23. M. Festa-Bianchet, The social system of bighorn sheep: Grouping patterns, kinship and female dominance rank. *Anim. Behav.* **42**, 71–82 (1991).
24. M. Festa-Bianchet, Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). *J. Anim. Ecol.* **58**, 785–795 (1989).
25. C. H. Bérubé, M. Festa-Bianchet, J. T. Jorgenson, Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav. Ecol.* **7**, 60–68 (1996).
26. J. T. Jorgenson, M. Festa-Bianchet, J.-M. Gaillard, W. D. Wishart, Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* **78**, 1019–1032 (1997).
27. M. Festa-Bianchet, J. T. Jorgenson, M. Lucherini, W. D. Wishart, Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology* **76**, 871–881 (1995).
28. C. H. Bérubé, M. Festa-bianchet, J. T. Jorgenson, Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565 (1999).
29. S. Hamel *et al.*, Fitness costs of reproduction depend on life speed: Empirical evidence from mammalian populations. *Ecol. Lett.* **13**, 915–935 (2010).
30. O. R. Jones *et al.*, Diversity of ageing across the tree of life. *Nature* **505**, 169–173 (2014).
31. N. Kawasaki, C. E. Brassil, R. C. Brooks, R. Bonduriansky, Environmental effects on the expression of life span and aging: An extreme contrast between wild and captive cohorts of *Telostylinus angusticollis* (Diptera: Neridae). *Am. Nat.* **172**, 346–357 (2008).
32. J.-F. Lemaître, J.-M. Gaillard, L. B. Lackey, M. Clauss, D. W. H. Müller, Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Exp. Gerontol.* **48**, 162–167 (2013).
33. S. A. West, *Sex Allocation* (Princeton University Press, Princeton, NJ, 2009).
34. B. Geffroy, M. Douhard, The adaptive sex in stressful environments. *Trends Ecol. Evol.* **34**, 628–640 (2019).
35. M. Douhard, The role of fathers in mammalian sex allocation. *Mammal Rev.* **48**, 67–74 (2018).
36. M. Douhard, M. Festa-Bianchet, F. Pelletier, Maternal condition and previous reproduction interact to affect offspring sex in a wild mammal. *Biol. Lett.* **12**, 20160510 (2016).

37. J. G. A. Martin, M. Festa-Bianchet, Sex ratio bias and reproductive strategies: What sex to produce when? *Ecology* **92**, 441–449 (2011).
38. M. Douhard, M. Festa-Bianchet, D. W. Coltman, F. Pelletier, Paternal reproductive success drives sex allocation in a wild mammal. *Evolution* **70**, 358–368 (2016).
39. P. Lindenfors, J. L. Gittleman, K. E. Jones, "Sexual size dimorphism in mammals" in *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*, D. J. Fairbairn, W. D. Blanckenhorn, T. Székely, Eds. (Oxford University Press, 2007), pp. 16–21.
40. A. B. Clark, Sex ratio and local resource competition in a prosimian primate. *Science* **201**, 163–165 (1978).
41. T. H. Clutton Brock, S. D. Albon, F. E. Guinness, Competition between female relatives in a matrilineal mammal. *Nature* **300**, 178–180 (1982).
42. M. van de Pol, S. Verhulst, Age-dependent traits: A new statistical model to separate within- and between-individual effects. *Am. Nat.* **167**, 766–773 (2006).
43. D. H. Nussey, T. N. Coulson, M. Festa-Bianchet, J.-M. Gaillard, Measuring senescence in wild animal populations: Towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406 (2008).
44. S. Bouwhuis, B. C. Sheldon, S. Verhulst, A. Charmantier, Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proc. R. Soc. B Biol. Sci.* **276**, 2769–2777 (2009).
45. A. J. Wilson, D. H. Nussey, What is individual quality? An evolutionary perspective. *Trends Ecol. Evol.* **25**, 207–214 (2010).
46. T. H. Clutton-Brock, *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (University of Chicago Press, Chicago, IL, 1988).
47. T. Landete-Castillejos, A. Garcia, L. Gallego, Calf growth in captive Iberian red deer (*Cervus elaphus hispanicus*): Effects of birth date and hind milk production and composition. *J. Anim. Sci.* **79**, 1085–1092 (2001).
48. J. A. E. Mellish, S. J. Iverson, W. Don Bowen, Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **72**, 677–690 (1999).
49. V. Ronget *et al.*, Causes and consequences of variation in offspring body mass: Meta-analyses in birds and mammals. *Biol. Rev. Camb. Philos. Soc.* **93**, 1–27 (2018).
50. A. L. Skibiel, W. R. Hood, Milk matters: Offspring survival in columbian ground squirrels is affected by nutrient composition of mother's milk. *Front. Ecol. Evol.* **3**, 111 (2015).
51. D. Hasselquist, J. Å. Nilsson, Maternal transfer of antibodies in vertebrates: Trans-generational effects on offspring immunity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 51–60 (2009).
52. J. A. Moorad, D. H. Nussey, Evolution of maternal effect senescence. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 362–367 (2016).
53. A. D. Hayward, I. Nenko, V. Lummaa, Early-life reproduction is associated with increased mortality risk but enhanced lifetime fitness in pre-industrial humans. *Proc. Biol. Sci.* **282**, 20143053 (2015).
54. L. S. Hurt, C. Ronsmans, M. Quigley, Does the number of sons born affect long-term mortality of parents? A cohort study in rural Bangladesh. *Proc. Biol. Sci.* **273**, 149–155 (2006).
55. A. Galbarczyk, M. Klimek, I. Nenko, G. Jasienska, Sons may be bad for maternal health at older age: New evidence for costs of reproduction in humans. *J. Gerontol. A Biol. Sci. Med. Sci.* **74**, 648–651 (2019).
56. Ø. Næss, L. H. Mortensen, Å. Vikanes, G. D. Smith, Offspring sex and parental health and mortality. *Sci. Rep.* **7**, 5285 (2017).
57. M. Douhard *et al.*, Environmental and evolutionary effects on horn growth of male bighorn sheep. *Oikos* **126**, 1031–1041 (2017).
58. C. Feder, J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, J. Jorgenson, Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia* **156**, 773–781 (2008).
59. M. Festa-Bianchet, Nursing behaviour of bighorn sheep: Correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim. Behav.* **36**, 1445–1454 (1988).
60. M. Festa-Bianchet, Condition-dependent reproductive success in bighorn ewes. *Ecol. Lett.* **1**, 91–94 (1998).
61. J. G. A. Martin, M. Festa-Bianchet, Bighorn ewes transfer the costs of reproduction to their lambs. *Am. Nat.* **176**, 414–423 (2010).
62. M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**, 367–379 (1998).
63. J. G. A. Martin, F. Pelletier, Measuring growth patterns in the field: Effects of sampling regime and methods on standardized estimates. *Can. J. Zool.* **89**, 529–537 (2011).
64. J.-M. Gaillard, A. Viallefont, A. Loison, M. Festa-Bianchet, Assessing senescence patterns in populations of large mammals. *Anim. Biodivers. Conserv.* **27**, 47–58 (2004).
65. C. H. Jackson, flexsurv: A platform for parametric survival modeling in R. *J. Stat. Softw.* **70**, 1–33 (2016).
66. A. Gelman, Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873 (2008).
67. M. Douhard, M. Festa-Bianchet, F. Pelletier, Long-term effects of sons in bighorn sheep. Figshare. https://figshare.com/articles/Long-term_effects_of_sons_in_bighorn_sheep/11558973. Deposited 9 January 2020.