COMMENTARY

Late-life costs of raising sons in bighorn sheep

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Senescence, the physiological decline associated with aging, is pervasive in nature. The age at onset and rate of senescent decline vary widely among species, among populations of the same species, and even among individuals within the same population (1). Understanding the reasons for this variability is of great importance for the field of biogerontology, as well as from an evolutionary and ecological perspective (2). In evolutionary terms, senescence can be explained by a decline in the strength of natural selection with age (3). Because not all individuals survive to the oldest ages, genes with late-acting negative effects are able to accumulate in the genome [mutation accumulation (3)], and genes that confer an advantage in early life may spread even if they are costly in later life [antagonistic pleiotropy (4)]. The disposable soma theory can be considered as a physiological manifestation of antagonistic pleiotropy and posits that optimal resource allocation between growth, maintenance, and reproduction comes with fitness consequences late in life (5). Both antagonistic pleiotropy and disposable soma theories therefore predict trade-offs in performance between early and late life (6), and high resource allocation to reproduction early in life is expected to be associated with accelerated senescence (4, 5). Douhard et al. (7) examine whether the rate of senescence in a wild population of bighorn sheep (*Ovis canadensis*) is dependent on allocation of resources to reproduction in early life, testing key predictions of evolutionary and life-history theory (Fig. 1).

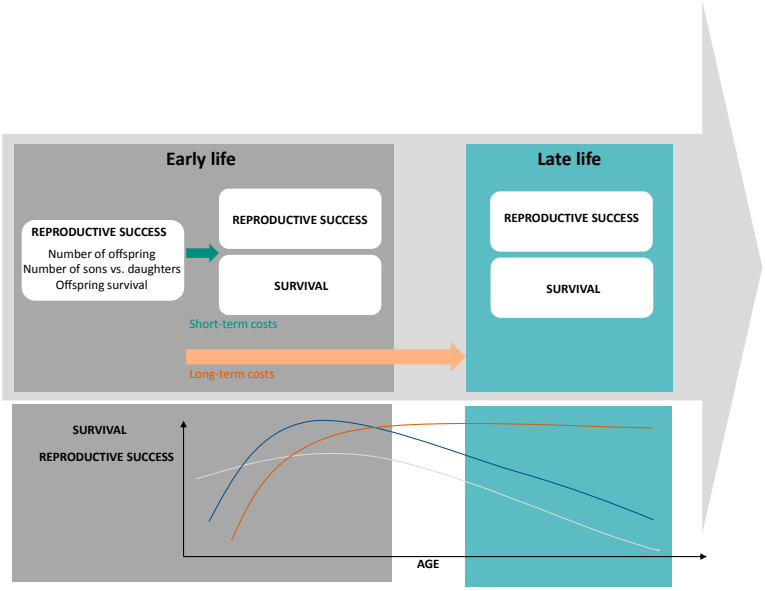

Fig. 1. Reproduction early in life can be measured through various traits, such as the number of offspring produced, number of sons vs. daughters produced (sex ratio), and offspring survival. Early-life reproduction may induce short-term (blue arrow) and/or long-term (orange arrow) costs on subsequent reproduction and/or survival. Early-life reproduction may thus influence patterns of age-related declines in survival and/or reproductive success.

In classically sexually selected species, males compete intensively for access to mating opportunities and exhibit sexual size dimorphism. In mammals, such phenotypic differences between males and females may be apparent from birth, with sons being heavier than daughters, and often increase throughout lactation, since male offspring suckle milk more frequently and for longer than their female counterparts (8). Sons may therefore generate higher costs of reproduction for mothers, and short-term costs have been documented in ungulates including bighorn sheep: The offspring of bighorn mothers who weaned sons in the previous year show slower growth over the summer and are less likely to survive to independence (9) than those of mothers that raised daughters.

Bighorn females show declines in survival probability and reproductive performance after 7 y of age, but the rate of senescence varies among individuals (10). According to the principles of energy allocation (11), antagonistic pleiotropy, and disposable soma, mothers that wean more offspring and/or more sons should experience accelerated senescence (Fig. 1). In their study, Douhard et al. (7) test these predictions and find that bighorn females who successfully weaned more offspring between 2 y and 7 y of age suffered more-rapid declines in reproductive success in later life. Importantly, for a given number of offspring

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weaned in early life, females that weaned more sons showed faster reproductive senescence. This highlights a previously unexplored long-term cost of rearing sons. The effects were only apparent when considering the number of offspring successfully weaned, rather than the number born, supporting previous findings of higher short-term costs of lactation than gestation in sheep and other ungulates (9). Interestingly, the effects were evident in reproductive performance only: The number and sex ratio of offspring weaned in early life did not influence the decline in survival probability in senescent mothers (known as actuarial senescence). The detection of costs in reproduction rather than survival aligns with findings in other long-lived vertebrates, where the variance in reproduction tends to be greater than that in survival, at least in prime-age individuals, making it easier to detect such costs (12).

Further investigation revealed that the higher cost of raising males in early life arose through reductions in the survival of offspring produced in later life (7). The authors find no evidence that the frequency of breeding or offspring survival over the summer months was impacted by the sex ratio of lambs in early life. However, the offspring of these senescent mothers were less likely to survive the winter, resulting in an overall reduction in reproductive success. This indicates that accelerated senescence may compromise maternal provisioning, resulting in the offspring being less able to endure the thermoregulatory demands and food limitation experienced during the harsh winter period. Perhaps surprisingly, the authors find that this effect was independent of the mass of the offspring at weaning, a trait that is likely to reflect much of the variation in maternal provisioning. They suggest that unmeasured factors such as maternal antibodies may be responsible, which are known to have an important influence on the development of the offspring immune profile. Overall, it appears that the mothers transfer the increased costs of producing males onto their future offspring, leading to a transgenerational consequence of senescence (13). The same is true for the short-term costs (9), which aligns with the conservative reproductive strategy expected in a long-lived species that should prioritize their own survival over that of their offspring (9, 12).

Although predicted by theory, allocation trade-offs are notoriously challenging to detect in wild systems because resource acquisition, as well as allocation, may vary among individuals. Such individual heterogeneity may mask trade-offs at the population level (14), making age-related declines difficult to detect (15). Douhard et al. (7) find that females with higher average reproductive success in later life also tend to live longer. Using statistical tools to control for this "selective disappearance" of poorer breeders enabled them to better capture senescence among the survivors. The authors also find that the baseline rate of mortality (although not the rate of senescence) is positively associated with the number of offspring weaned in early life, suggesting that mothers who successfully raise more offspring are also more robust.

Douhard et al.'s (7) study relies on the long-term monitoring of a free-ranging bighorn sheep population that began in the early 1970s. Individuals have been marked as lambs and resighted via physical captures and observations throughout life. From these individual trajectories, components of reproductive success and survival have been estimated annually. Moreover, biopsies for genetic analyses collected since 1987 allowed genetic maternity assignment in addition to behavioral maternity assignment. Assessing how allocation to sons in early life influences demographic performance later in life would have been impossible without such longitudinal data collected for many years. This study thus provides additional support for the pivotal role played by long-term studies in our understanding of ecological and evolutionary processes *in natura* (16). The recent technological advances for tracking wild animals, such as GPS, environmental DNA, or biologging sensors, as well as the development of genetic analyses, will undoubtedly offer new insights into the underlying mechanisms shaping life-history trade-offs in a large range of biological systems. It should be noted that, even using a dataset as remarkable as that of the bighorn sheep, sample size may still be limited. Studies of senescence are, by definition, restricted to individuals that reach old age. In Douhard et al.'s study, analyses were restricted to female sheep that reached "late life" (Fig. 1), that is, survived to at least age 8 y. Their analyses were therefore based on 72 to 119 females, which translated into increased uncertainty around some estimated parameters. The restricted number of individuals that reach old age highlights an important question about the relative importance of short- versus long-term costs of reproduction in terms of individual contributions to the next generation, which are yet to be evaluated.

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It is also interesting to consider how much of the observed among-individual variation in senescence rates is actually explained by offspring sex ratio. Theoretical and empirical evidence is accumulating in that among-individual variation in senescence rates is likely explained by several interacting factors, including genetics and environmental conditions experienced throughout life (2). The relative contribution of offspring sex ratio to the observed among-individual variation in senescence rates remains to be carefully explored. Future research should also address whether this trade-off has a genetic basis, which is required to be fully consistent with antagonistic pleiotropy (17). Finally, it would be interesting to consider to what extent the results from bighorn sheep may resonate in other species, including humans. Humans and bighorn sheep are both mammals exhibiting sexual size dimorphism. Previous studies in historical human populations have found associations between the number of sons produced and maternal longevity (18), although none have examined effects on the rate of senescence. However, other studies have found contrasting results (19, 20), calling into question their generality and the potential for confounding effects. While it is tempting to establish a comparison between sex allocation in a wild mammalian population and in humans, these two species differ in many respects. For instance, low parasite burdens, advanced medical care, contraception, absence of lactation, and extended postreproductive lifespan may prevent the occurrence/detection of trade-offs between allocation to sons early in life and late-life consequences on demographic performance in humans, at least in modern societies. Moreover, the prediction positing that females from highly dimorphic mammalian species that wean more sons than daughters early in life should exhibit accelerated senescence is deeply rooted in the principle of allocation, and so plentiful

resources and sociocultural factors are likely to mask potential reproductive trade-offs. We thus reiterate the caution expressed by several authors that many confounding factors, often unknown, may complexify the study of reproductive trade-offs in humans (19, 20).

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