# The Potential for Rapid Evolution in Response to Exploitation-Induced Selection

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**ABSTRACT:** The phenomenon of substantial and sustained evolutionary response to strong directional selection is well established in evolutionary theory and empirical studies. However, recent conceptual papers and modelling studies aimed at the question in bighorn sheep (*Ovis canadensis*) come to the opposite conclusion, suggesting that the scope for response to strong selection of highly heritable traits such as horn size is minimal. Here we address a series of errors in the most recent such paper (Coulson et al.'s 2018, in *The Journal of Wildlife Management* 82: 46–56), all of which predispose the model to predict a minimal response to selection. We explain the nature of the errors, re-run all analyses with and without errors, and provide additional results showing how established evolutionary principles govern evolutionary changes in mountain sheep horn size. Once the errors are corrected, the model in Coulson et al. (2018) predicts an evolutionary change in horn length of bighorn sheep very similar to published empirical estimates for the Ram Mountain population in Alberta: approximately 2.5 cm over 2–3 generations of intensive selective harvest.

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## INTRODUCTION

A surprising controversy attends the suggestion that persistent directional selection on a heritable trait, enforced by morphologically defined criteria for legal harvest, may cause evolutionary change in mountain sheep horns (Boyce and Krausman 2018). While it is widely accepted that harvest-induced selection based on body size or other physical traits can cause rapid evolutionary change in other species, for example in elephants (Campbell-Staton et al., 2021) and fish (Heino et al. 2015), strong reluctance exists to accept that morphologically defined criteria for legal harvest may have similar effects in bighorn sheep (*Ovis canadensis*; Heimer 2004, Heimer and Lee 2004, Traill et al., 2014, Boyce and Krausman 2018, Heffelfinger 2018, Coulson et al., 2018). Quantitative genetic methods applied to empirical data have reported an evolutionary component to changes in horn size in the individual-based, pedigreed, long-term study of bighorn sheep at Ram Mountain, Alberta (Festa-Bianchet et al. 2019) while the population was hunted (Coltman et al. 2003, Pigeon et al. 2016). Modelling studies, however, have claimed either that sustained evolutionary responses to sustained directional selection should not occur (Traill et al. 2014), or that the rate of evolutionary change reported for the Ram Mountain population is implausible (Coulson et al 2018).

The genetic basis of the evolutionary response of a population to directional artificial selection on a specific trait is well established in theory (Falconer 1992, Walsh and Lynch 2018), and corroborated experimentally (Clayton et al. 1957, Robertson 1966; Hill and Caballero 1992; Pélabon et al. 2021). The breeder's equation is highly instructive, providing the per-generation rate of evolutionary change in the of a trait, $\Delta\bar{z}$, as (1) $\Delta\bar{z} = h^2 S$ , where $h^2$ is the heritability (Wright 1921), proportion of phenotypic variation in a population that is due to heritable genetically based differences among individuals, and

$S$ is the selection differential, the difference in mean phenotype between breeding individuals and population mean phenotype, unweighted by fitness (Lush 1937, Robertson 1966, Price 1970). Heritability can be very high, often exceeding 50% of total phenotypic variance (i.e., $h^2 > 0.5$) for morphological traits (Hill 2010), even in free-ranging wild populations (Postma 2014), and is substantial for bighorn sheep horn morphology (Coltman et al. 2003, 2005, Wilson et al. 2005, Pigeon et al. 2016). Under artificial selection, the selection differential $S$ , may be very strong. Although responses to artificial selection are often somewhat less than predicted by the breeder's equation (Hill and Caballero 1992, Pélabon et al 2021), the equation generally makes robust predictions of the magnitude of the selection response for directional selection on specific traits. It is therefore surprising that many authors focusing on the potential for responses to artificial selection in wild sheep argue that substantial response to selection is unlikely. For example, Heffelfinger (2018) argues that many processes in nature, such as plasticity, maternal effects and environmental variability, will severely limit or oppose the response to selection. Although many ecological processes play out simultaneously, and interact, with evolutionary processes, all of ecology is not stacked in opposition to evolution. Kardos et al. (2018) provided a response to Heffelfinger's (2018) flawed perspective.

Similarly, a modelling paper by Traill et al. (2014) purported to show that very strong selection leads to only a minimal change in phenotype and no sustained response. To the contrary, a substantial body of theory indicates that sustained evolutionary responses are to be expected, and artificial selection has elicited sustained genetic responses in a diversity of species. Subsequent work by Janeiro et al. (2017; see also Hedrick et al 2014) demonstrated the error: Traill et al. (2014) use a notion of inheritance based on the regression of offspring trait values at one year of age or earlier on the value of traits in their fathers at the time of conception. Clearly, if genes act throughout development to influence values of traits in adults, genetic variation will have little or no manifest effects in offspring at recruitment, even if they inherit genes from their fathers that will affect their phenotype when they reach their fathers' ages (Janeiro et al. 2017). The biometric relations among kin will reflect inheritance only if traits are measured at equivalent ontogenetic stages has been recognised and been standard practice for some time (Galton 1886, 1888). More specifically, Janeiro et al. (2017) showed that the cross-age parent–offspring regression used in the Traill et al. (2014) model, despite vociferous claims (Coulson 2012) of its generality, did not subsume established theory of inheritance, and instead was guaranteed to always find no measurable evolution, no matter the true evolutionary dynamics of a trait.

Coulson et al. (2018) claimed that sustained responses to directional selection will occur, but that rates reported from the Ram Mountain population (Coltman et al. 2003, Pigeon et al. 2016) were orders of magnitude greater than is theoretically possible. Here, we re-run Coulson et al.'s (2018) simulation models and obtain results consistent with estimated rates based on quantitative-genetic analyses of Ram Mountain data (Coltman et al. 2003, Pigeon et al. 2016). We identify 5 features of the analysis and interpretations given in Coulson et al. (2018) that diverge markedly from the authors' stated intention of applying a model based on established quantitative genetic assumptions. We also clarify changes in the literature that have appeared since the publication of Coulson et al.'s (2018) paper.

## Distinguishing genetic and environmental contributions to trends in phenotype

After adjusting to age 4, the horns of mature bighorn sheep males on Ram Mountain, Alberta, Canada, declined in length by ~20 cm between 1972 and 2002 (approximately 5 generations; Coltman et al. 2003, Pigeon et al. 2016). After about 1985, environmental conditions deteriorated, partly through density-dependent effects (Jorgenson et al. 1998). Until 1996, the population was subjected to intense selection by trophy hunters: although only ~2.4 rams on average were harvested each year, this represented ~40% of males with legal-sized horns, most of which were taken before they reached peak reproductive age (Jorgenson et al. 1998, Coltman et al. 2003). Prior to the study by Coltman et al. (2003), the observed decline in horn size of adult males was thought to be primarily due to environmental effects; the possibility that unintentional artificial selection contributed to smaller horns was untested. Using linear mixed-effect models, Coltman et al. (2003), found: (1) a decline in horn length of 2–4-year-old males over time, which was significant even after accounting for age and resource availability ($\beta$ = 0.35 cm/year, $P$ < 0.001); (2) substantial heritability in horn length of 2–4-year-old males ($h^2$ =

0.69 after accounting for age and resource availability); and (3) a small but significant proportion of the change in horn length from 1972–2002 attributable to a change in breeding values, a measure of individuals' heritable genetic merit ($\beta$ = -0.075 cm/year, $P < 0.001$). The slope of the overall phenotypic trend, and that of the proportion attributable to genetic change (i.e., evolution) were clearly and separately reported in Coltman et al. (2003). The genetic contribution to the overall change was approximately 2.25 cm of the total 20 cm decline in horn length over the 30-year study period. Contrary to statements in Coulson et al. (2018), Coltman et al. (2003) did not argue, based on high heritability, that the phenotypic trend was primarily genetic.

The results of Coltman et al. (2003) attracted some controversy (Traill et al., 2014). Like other applications of the animal model of the time (e.g., Réale et al., 2003), Coltman et al. (2003) did not include year as an effect in the estimation of breeding values. Year should have been included to eliminate any bias in the estimate of changes in breeding value over time, as is now common practice following Postma (2006) and Hadfield et al. (2010). Including year in the estimation of breeding values indirectly accounts for unmodelled features of the environment that may lead to change in mean phenotype. Coltman et al.'s (2003) model, however, included a key variable, mean yearling ewe mass each year, which integrated the effects of population density (Festa-Bianchet et al. 2003). Inclusion of annual mean yearling ewe mass in the analysis of ram horn length had 2 important consequences. First, it likely captured much of the effect of density on horn size, minimising the risk that changing density could generate a spurious trend in breeding values. Second, since the index of density had a strong trend during the period analysed in Coltman et al. (2003), it indirectly captured the effects of other unmeasured environmental variables that may have been changing as well, and that normally would be accounted for by including an effect of year of measurement. A subsequent analysis by Pigeon et al. (2016) using the improved methods suggested by Postma (2006) and Hadfield et al. (2010) and including year as a covariate confirmed the general pattern identified by Coltman et al. (2003). Pigeon et al. (2016) found that breeding values declined by ~2.5 cm over approximately 2–3 generations during the period of intensive hunting, and that the decline stopped when the intense trophy hunt was stopped. Finally, Pigeon et al. (2016) estimated that the probability that the observed change in the genetic component of male horn length was attributable solely to genetic drift (as opposed to a response to selection) was <10%).

## What factors determine the rate of evolutionary change?

The breeder's equation, and other expressions for how different aspects of selection and genetic variation relate to one another in a range of circumstances (Robertson 1966, 1969; Lande 1979, 1980, Lande and Arnold 1983; Morrissey 2014; 2015) provide us with some understanding of what factors influence the rate of evolutionary change. Two general conclusions flow from the breeder's equation (Eq. 1): i) for a given strength of selection, higher heritability will generate faster responses to selection, and ii) for a given heritability, larger selection differentials will generate faster evolution. Therefore, the amount of phenotypic variation in a population constrains the possible strength of selection, because the mean of selected parents cannot differ much from the overall mean if the trait has little variation in the population. The more variation, the greater potential for selection to act.

Coulson et al. (2018) used 70 cm as an initial value for the mean horn length for four-year-old rams (from empirical data reported by Jorgenson et al. 1998). However, they used arbitrary values for initial additive genetic variance ($\sigma_A^2$) of 3 cm$^2$ and for total phenotypic variance ( $\sigma_z^2$ ) of 5 cm$^2$. For bighorn sheep, these parameters were estimated by Pigeon et al. (2016) as approximately $\sigma_A^2$ = 17.9 cm$^2$ and $\sigma_z^2$ = 45.0 cm$^2$. Earlier estimates in Coltman et al. (2005; $\sigma_A^2$ = 12.0 cm$^2$ and $\sigma_z^2$ = 30.6 cm$^2$) were also much larger than those used by Coulson et al. (2018). Thus, the best empirically supported estimate of heritability of horn length in 4-year-old bighorn rams is $h^2 = \frac{\sigma_A^2}{\sigma_z^2} = \frac{17.9}{45.0} \approx 0.4$ (Pigeon et al. 2016). In contrast, the initial heritability used in Coulson et al.'s models was $h^2 = \frac{\sigma_A^2}{\sigma_z^2} = \frac{3}{5} = 0.6$; thus, while the values for $\sigma_A^2$ and $\sigma_z^2$ are of a very different magnitude than published values for bighorn sheep horn length, the corresponding heritability value is at the higher end of the range of available estimates of $h^2$ , both for bighorn sheep horn size, and more generally for morphological traits in wild populations (Postma 2014). Does this make the genetic parameters in Coulson et al.'s (2018) model generous in assessing the potential for rapid evolution of horn size in bighorn sheep? That depends not only on heritability, but also on how the value of $\sigma_z^2$ influences the selection differential.

The selection scheme in Coulson et al.'s (2018) model allowed all below-average individuals to survive, whereas above-average individuals were culled with probability $\alpha$ ranging from 25 to 100%. This scheme can be viewed as an elaboration on truncation selection, which has well-known properties (reviewed in chapters 14 and 16 of Walsh and Lynch 2018). The Coulson et al. (2018) selection model can be described as follows: a fraction $\alpha$ of the population is subjected to negative truncation selection at the mean (some above-average individuals are culled, and the next generation is sired by the remaining individuals) and a fraction $1-\alpha$ is not subjected to selection. This formulation leads to a straightforward analytical expression for the relationship between $\alpha$ and the selection differential,

(2a) $$S = \sqrt{\frac{2}{\pi}}\sigma_z \frac{\alpha}{\alpha - 2},$$

where $\sigma_z$ is the square root of the phenotypic variance, or the phenotypic standard deviation. When $\alpha = 1$, all males with phenotype greater than the mean are culled (a scheme known as truncation selection at the mean), and the selection differential is

(2b) $$S = -\sqrt{\frac{2}{\pi}}\sigma_z .$$

The derivation of Eq. 2a,b follows from noting that the distribution after selection must follow a $\chi$ distribution with one degree of freedom (equal to a half-normal distribution; Eq. 2b) or a mixture of a $\chi$ and a Gaussian distribution (i.e., $\chi$ for a component $\alpha$ of the population, and Gaussian for a component $1-\alpha$; Eq. 2a). In the sex-limited model constructed here, this selection differential pertains to the selected sex, not to the entire adult population. Sex-limited selection is easily accommodated by existing evolutionary quantitative genetic theory (e.g., Lande 1982).

Focusing on the most intense selection scenario, Coulson et al.'s (2018) model gives a selection differential of $S = -\sqrt{\frac{2}{\pi}}\sigma_z = -\sqrt{\frac{2}{\pi}}\sqrt{5} = -1.78\text{cm}$. In contrast, exactly the same selection scheme applied using published estimates of the variance components yields $S = -\sqrt{\frac{2}{\pi}}\sigma_z = -\sqrt{\frac{2}{\pi}}\sqrt{45.0} = -5.35\text{cm}$. Thus, by using the arbitrary value of 5 for phenotypic variance, rather than the empirically estimated value of 45, Coulson et al. (2018) relegate the magnitude of selection, for any given culling scheme, to approximately one third of the value that would be relevant to bighorn sheep. It is unclear, given their intention to compare their model to bighorn sheep, for example by plotting their modelled evolutionary trajectories, and a purported evolutionary trajectory for horn length from Coltman et al. (2003) on the same graph, why Coulson et al. (2018) used the reported mean for the trait in question, but not the other critically important parameters of the trait's phenotypic distribution, especially a value of phenotypic variance with a reasonable order of magnitude. The differences in the selection differential and evolutionary prediction based on the breeder's equation between the estimated variance components and those used by Coulson et al. (2018) are substantial. This is demonstrated in Figure 1, by comparing part (a) (Coulson et al.'s 2018 variance components) with parts (c) and (e), which use available estimates of the additive genetic and total phenotypic variances for horn length of young adult males. Applying Coulson et al.'s (2018) model but changing it only by using published estimates of variance components makes it even more consistent with the estimated evolutionary change in horn length at Ram Mountain (Figure 1 c, e). This difference is driven more by the total phenotypic variance than the heritability; using the somewhat lower heritability empirically estimated for bighorn sheep horn length with reasonable values for the phenotypic variance also results in substantially greater selection (Figure 2a) and per generation evolutionary change of a trait under sex-limited selection (Figure 2b).

## What evolutionary responses should be expected from exploitation-induced selection in natural populations?

Coulson et al. (2018) simulated a range of selection strengths, the strongest being when all individuals with phenotypes above the mean are culled. That selection scheme generates a within-generation change in mean phenotype of approximately 0.8 phenotypic standard deviations (for a Gaussian trait; this can be obtained from Eq. 2; see also Bulmer 1976, Walsh and Lynch 2018). This change is stronger than typically observed strengths of natural selection (Kingsolver et al. 2001, Morrissey 2016) but is comparable to experimental

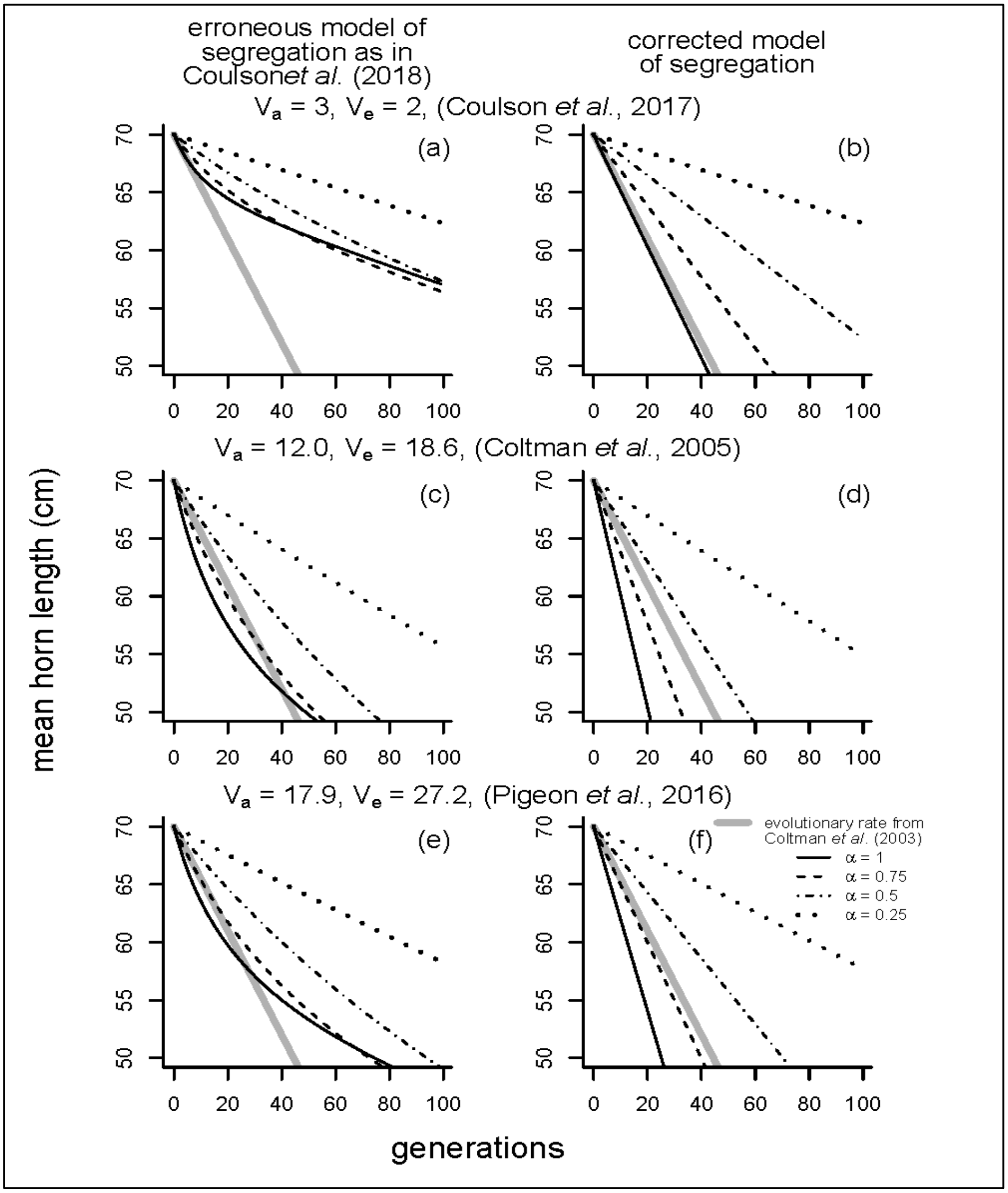

**Figure 1.** The genetic (evolutionary) trend in breeding values of bighorn sheep horn length reported in Coltman et al. (2003) in relation to the models in Coulson et al. (2018). In the left column, results from the Coulson et al. (2018) model are reproduced and plotted in relation to the inferred evolutionary trend in mean breeding value as estimated by Coltman et al. (2003). Coulson et al. (2018) erroneously related their results to the phenotypic trend. In the right column, Coulson et al.'s (2018) models are corrected for an error that conflated effects of selection on the linkage equilibrium component of the genetic variance with reductions in the genic variance and related to the same previous evolutionary inference. The culling parameter, α, is the probability of harvest of males with horns longer than the average (initially, 70 cm). At α = 1, all these above-average individuals are removed. The reference line (thick dashed grey) here represents the evolutionary inference reported in Coltman et al. (2003); Coulson et al. (2018) depict the much steeper phenotypic trend that was partly affected by environmentally-induced phenotypic changes, mostly acting via density changes in the Ram Mountain population, which is very much steeper but an incorrect representation of the evolutionary inference reported in Coltman et al. (2003).

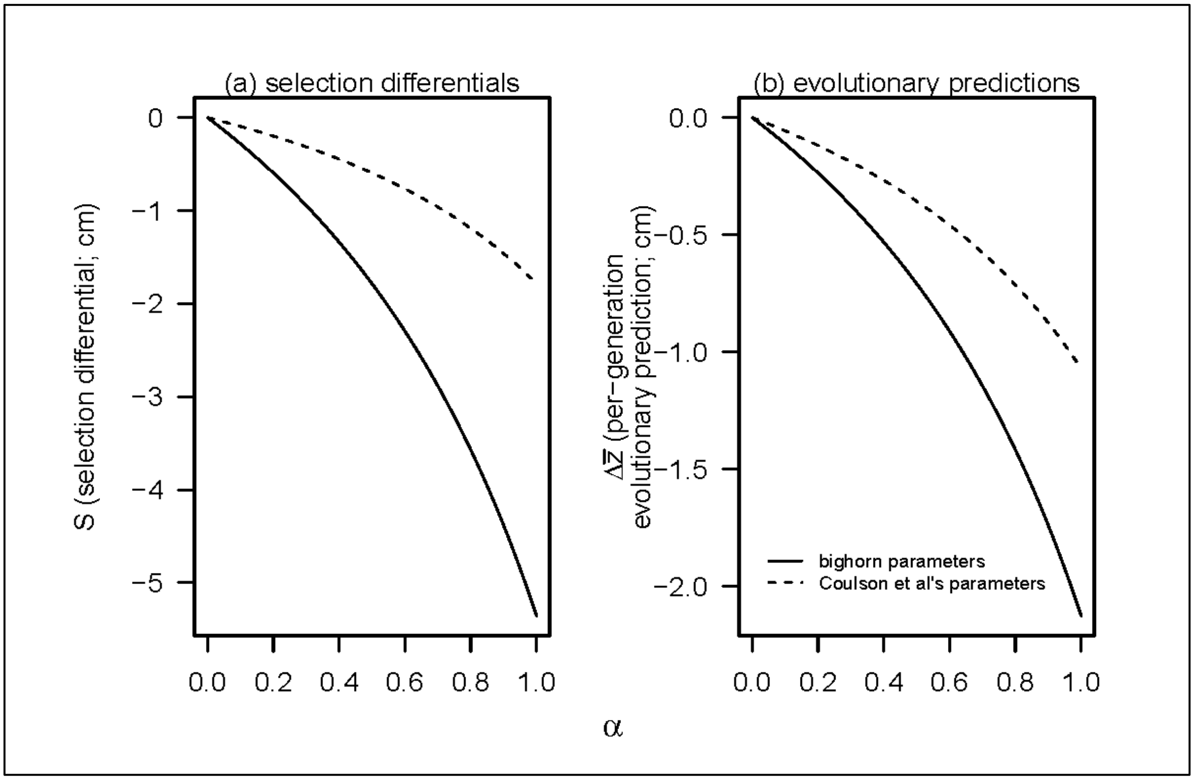

**Figure 2.** The strength of selection (a), and predictions of the initial per-generation evolutionary rate (b), using Coulson et al.'s (2018) selection scheme. The culling parameter $\alpha$ is the probability of harvest of males with above-average trait values.

artificial selection studies or agricultural breeding programs. For example, in a study specifically focused on the potential for responses to anthropogenic selection, Uusi-Heikkilä et al. (2015) applied truncation selection where the 75% of individuals with the largest trait values were culled. For a given phenotypic variance, this selection is 60% stronger than the most intense selection considered by Coulson et al. (2018).

Helpfully, when an appropriate phenotypic variance is used, the range of culling parameter values used in Coulson et al. (2018) is relevant to selection caused by quota-free trophy hunting of bighorn sheep, as currently practiced in most of Alberta, Canada. For the years in which trophy hunting occurred at Ram Mountain, we calculated the mean horn length at age 4 of all individuals and of rams that were not shot. Horn measurements were collected throughout the summer from rams caught in a corral trap (Jorgenson et al.1998). Because most trophy hunting mortality occurs between ages 4 and 7, and the peak reproduction for males is mostly after this age period (Coltman et al. 2002; Martin et al. 2016), the difference in these mean phenotypes approximates the hunting-induced selection differential for horn size at age 4. Males that were not shot had horns on average 2 cm shorter than all males together, or one-third of a phenotypic standard deviation. Coulson et al.'s (2018) culling scheme, with $\sigma_z = \sqrt{45}$ and $\alpha = {}^{1}/_{2}$ returns a selection differential of about 1.8 cm, using Eq. 2a.

Combined with a heritability ($h^2$, see eq. 1) of approximately 0.4 (Pigeon et al. 2016), this sex-limited selection should generate evolutionary change of about 0.4 cm per generation ($\Delta\bar{z} = \frac{1}{2}h^2 S = \frac{1}{2} \cdot 0.4 \cdot 2\,cm = 0.4\,cm$). Thus, using a value for phenotypic variance empirically estimated for bighorn sheep, the general evolutionary quantitative genetic framework used by workers in the bighorn sheep and similar systems makes evolutionary predictions of similar magnitude to those predicted by the model published by Coulson et al. (2018), at least in the first few generations. Over the longer term an additional issue about how the segregational variance is handled becomes important. This matter will be considered later. We first examine another erroneous aspect of Coulson et al. (2018) about the detectability of change.

**How large a change in mean phenotype is detectable?**

Coulson et al. (2018) draw lines on their figures representing a change from the initial mean phenotype of 1.96 standard deviations of phenotype, and they suggest that this represents the limit of detectability of changes in mean phenotype. However, uncertainty of any statistic (in this instance, the sample mean) is related to natural variability as well as to sample size. It is thus not related to the standard deviation, but rather to the standard error. Differences in mean phenotype of at least 1.96 standard errors, not standard deviations, are detectable (in the sense of a one-sample, two-tailed test of significance at the 0.05 threshold for the *p*-value, which seems to be Coulson et al.'s 2018 intention, though it is unstated). With sample sizes relevant to bighorn sheep, or many studies of natural populations with 100 or more observations, 1.96 standard errors and 1.96 standard deviations differ by approximately a factor of 10. Moreover, the 1.96 standard error limit of detectability applies to a test for the difference of a mean of a single sample to a hypothesized null value. The question at hand relates to detecting a change in a quantity over time, which depends on additional factors, such as a regression model's residual variance and the variance of the predictor variable. It is not clear why Coulson et al. (2018) expect that the detectability limit relevant to a one-sample two-tailed test would apply to the methods actually used to decompose phenotypic changes in natural populations into their genetic and environmental components. Nonetheless, armed with an understanding of the distinction between biological and statistical variation (standard deviation vs. standard error), it will often be possible to characterise ecologically relevant changes in phenotype; by calling on mixed-model methods, inferences of its genetic components are possible as well.

Coulson et al.'s (2018) figures 1–3 included lines depicting their understanding of the limit of detectability of an evolutionary change, but it does not occur at the stated value of $70 - 1.96\sqrt{5}$ cm of horn length, as would be expected given their stated parameter values. Inspection of their code (available at *https://github.com/tncoulson/JWM-Coulson-et-2017*) reveals that the line plotted uses a phenotypic variance of 13 $cm^2$ rather than 5 $cm^2$ as otherwise used in their models. Why the authors used larger, yet still arbitrary, values of the phenotypic variance to generate their figure is unclear.

**How large a change in a trait is important?**

In bighorn sheep at Ram Mountain, a part of the change in mean phenotype for horn morphology was attributable to evolution (Coltman et al. 2003, Pigeon et al*.*, 2016). The effects of other factors, such as density, were much larger (Douhard et al., 2017). That does not render evolutionary change unimportant.

Over all, but the shortest time scales, no one factor will be the overwhelming driver of most characteristics of populations that may be of ecological, social, cultural, recreational or economic significance. It is disconcerting to see suggestions to managers to dismiss one source of change if it is not the sole driver of an important property of a population. The estimated evolutionary change in horn length breeding value at Ram Mountain between 1975 and 1996 was about 2.5 cm (Pigeon et al. 2016). That is at the low end of the range of changes in age-adjusted average horn length observed in heavily harvested populations of bighorn sheep (Festa-Bianchet et al. 2014) and Stone sheep (*Ovis dalli stonei*; Douhard et al. 2016) over longer periods. A few centimetres of horn growth make the difference between a ram that is legal to harvest and one that is not (see Figure 1 in Pelletier et al. (2012) and Festa-Bianchet et al. 2014) and could therefore be very relevant to both ram survival and management. Additionally, evolutionary change differs from other effects on traits in an important way: it is not immediately reversible. The timescales required to reverse any undesirable evolutionary effects of exploitation under future management scenarios are likely much longer than the timescales on which the effects of management actions on density or forage availability, for example, could be expected to occur.

What do Coulson et al.'s (2018) models say about whether intense trophy hunting may have important evolutionary consequences? Coulson et al.'s (2018) interpretation is that the potential is very small. However, this conclusion is obtained by comparing their model results to the *phenotypic*, not evolutionary, trajectory for bighorn sheep horn size at Ram Mountain, which experienced a rapid decline for a variety of reasons as discussed. It is unclear how a primarily ecologically based decline in horn size in a given population should be the measure by which the magnitude of evolution should be judged.

A useful way of making rates of evolutionary change comparable across species or traits is to express evolutionary change in units of standard deviations of phenotype (Haldane 1949, Huxley 1942). If we reproduce results of Coulson et al.'s (2018) model outputs, but express them in units of standard deviations, we get a very different impression (Figures 3a, 3b). Coulson et al.'s (2018) strongest selection scenarios can change mean phenotype by as much as one phenotypic standard deviation in 5 years, given the reasonable value of heritability that they employ. Even their weakest selection scenario can induce a change so large that the mean phenotype is outside the original phenotypic range (i.e., cumulative evolution of ~2 standard deviations) over 100 generations. To illustrate the magnitude of these changes expressed in standard deviations, Figure 3c shows the shift in the distribution of phenotype over 20 generations.

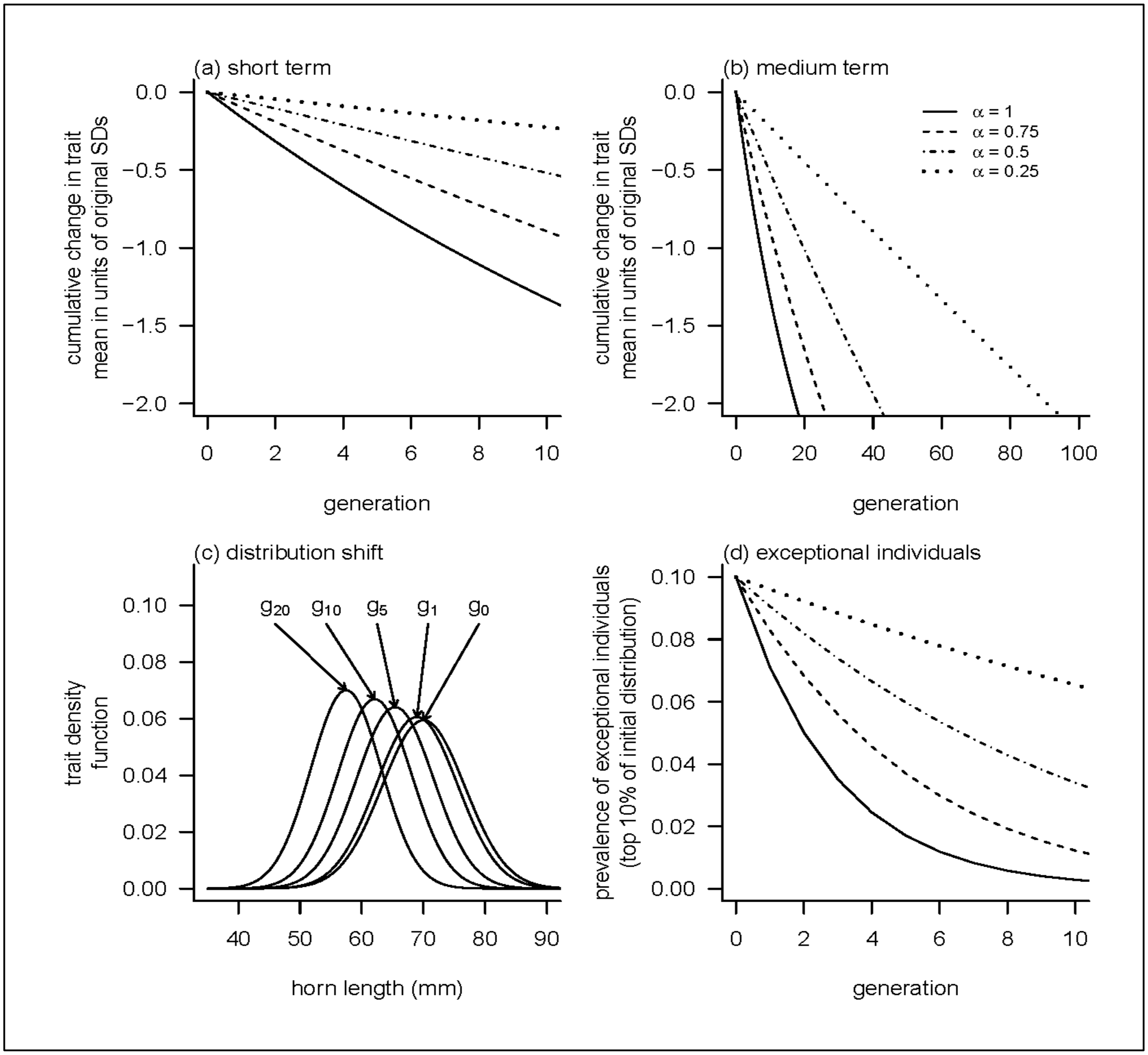

**Figure 3.** Depictions of Coulson et al.'s (2018) model results in phenotypic standard deviations, to allow comparison across species and traits. These results use published estimates of variance components for young adult male bighorn sheep horn length instead of Coulson et al.'s (2018) arbitrary values, and a correct model of segregation. Equivalent plots using Coulson et al.'s (2018) variance components and erroneous model of segregation are in Figures S1 and S2. Panels (a) and (b) re-plot results from Figure 1b, over short (<10 generation) and medium (<100 generation) time scales; the latter (b) is the x-axis time scale used in Coulson et al. (2018). Panel (c) is an additional depiction of the change in standard deviations, showing the changes in the full distribution of a normal trait. 'g' refers to the number of generations of selective harvest. Panel (d) represents evolutionary change as the decrease in the prevalence of individuals with exceptional trait values, defined as those in the top 10% of the initial distribution of the trait.

In the context of the potential evolutionary consequences of intense trophy hunting, we can construct an even more directly informative representation of the magnitude of the evolutionary changes predicted by the Coulson et al. (2018) models. Imagine that to enter the record book, a trophy must have horns in the top 10% of the range currently expressed in its population. With Coulson et al.'s (2018) selection scenarios, at what rate would evolutionary change reduce the prevalence of record-book animals from the initial frequency of 10%? The answer, derived from Coulson et al.'s (2018) models, is presented in Figure 3d. The strongest selection scenario essentially eliminates trophy animals in about five generations. Even the weakest selection (25% harvest of trophy males) considered by Coulson et al. (2018) generates a reduction in the prevalence of record book animals by over a third in 6–7 generations. These are timescales very relevant to wildlife management: 6 generations of bighorn sheep is about the time elapsed since the 4/5-curl minimum legal size was established in Alberta in 1968.

Results in Figure 3 are plotted based on Coulson et al.'s (2018) model but using published variance component estimates and the corrected model of segregation (see below; the model iterated to generate Figure 1e, f). Using Coulson et al.'s (2018) arbitrary variance components (Figure S1) actually generates even more rapid evolution in terms of phenotypic standard deviations, because evolutionary change in standard deviations is more dependent on heritability than on genetic variance. Model results using both the arbitrary variance components and Coulson et al.'s (2018) erroneous model of segregation also generate substantial evolutionary change (see below and Figure S2). This model, praised by Boyce and Krausman (2018) for suggesting that rapid evolution is unlikely, actually predicts *faster* evolution of small horns (in units of phenotypic standard deviations) than what has been reported empirically over much of the range of selection intensity that it considered.

## Segregation, genic vs. genetic variance, and the potential for sustained evolutionary responses to harvest-induced selection

In Coulson et al.'s (2018) models, the response to selection is attenuated over time. Indeed, in the absence of mutation or gene flow, selection will ultimately erode genetic variation. When genetic variation is gone, the response to selection must stop. Unfortunately, the behaviour of Coulson et al.'s (2018) models arises from a simple mistake. This section will correct that mistake and explore what is known about potential evolutionary responses to sustained strong directional selection, such as that induced by intense phenotype-based exploitation. After considering the issue from first principles, we examine the nature of this additional error in Coulson et al.'s (2018) model.

### *The effect of selection influence genetic variance: principles*

If many loci contribute variation to a continuous trait, then the response to selection in a single generation will result from very small changes in allele frequencies at many loci. Because non-trivial evolutionary change can result from very small allele frequency changes at each of many individual loci, selection of quantitative traits has modest effects on the genetic variance in the short term, allowing sustained and rapid evolutionary change. These are basic properties of the 'infinitesimal model' of variation in quantitative traits (Bulmer 1980).

In the long term, selection changes allele frequencies. In the very long term, in the absence of migration or mutation, selection will erode genetic variation, attenuating the response to selection. In the short term, however, selection causes linkage disequilibrium. Directional and stabilizing selection both cause alleles with positive and negative effects on selected traits to become associated in gametes (and thus individuals), reducing the genetic variance (Felsenstein 1965; Bulmer 1971, 1974).

How genetic variance is influenced by both selection and recombination is most transparently handled by the Bulmer equation (Bulmer 1971):

$$\Delta d = -\frac{d}{2} + \frac{h^4}{2}\delta(\sigma_z^2) \qquad (3)$$

where $d$ is the contribution of linkage disequilibrium to the additive genetic variance; as such, $\sigma_A^2 = \sigma_a^2 + d$, where $\sigma_a^2$ is the linkage equilibrium value of the additive genetic variance, or the genic variance. $\Delta d$ is thus the change in the disequilibrium contribution to $\sigma_A^2$ from one generation to the next. $h^4$ is the square of the heritability, and $\delta(\sigma_z^2)$ is the within-generation change in phenotypic variance caused by selection. The first term on the right-hand side of (Eq. 3) reflects the partial deterioration of previously accumulated linkage disequilibrium contributions to the additive genetic variance, assuming a large genome such that most loci are unlinked. The second term represents the new linkage disequilibrium contribution to $d$ generated by selection in the current generation. Recombination is powerful: in a scenario involving many loci spread throughout the genome, recombination by itself restores half of the accumulated effect of linkage disequilibrium on $\sigma_A^2$ to the linkage equilibrium value (i.e., the genic variance) each generation. In contrast, the contribution of selection to changing $\sigma_A^2$ is modest, as it depends on half the squared heritability. Since heritability varies between zero and one, half its square is typically a small value.

The equations for the dynamics of the mean (the breeder's equation; Eq. 1) and variance (the Bulmer equation; Eq. 3) can be coupled to make evolutionary predictions, as we do below. First, however, we use Eq. 3 for a closer look at the short-term effects of selection on genetic variance.

Under truncation selection at the mean, the strongest selection scenario in Coulson et al.'s (2018) paper, the change in the variance takes a particularly simple form (derivable from more general expressions given in Bulmer 1976): the proportional reduction in the phenotypic variance is related to the square of the selection intensity $\bar{\iota}$, as

$$\text{(4)} \qquad \frac{\sigma_z^{*2}}{\sigma_z^2} = (1 - \bar{\iota}^2) \text{ ,}$$

where $\bar{\iota} = {}^{S}\!/_{\sigma_z}$ and $\sigma_z^{*2}$ is the phenotypic variance after selection. Consequently,

$$\text{(5)} \qquad \delta(\sigma_z^2) = \sigma_z^{*2} - \sigma_z^2 = -\sigma_z^2 \bar{\iota}^2 \text{ .}$$

These are fairly general equations. In the specific scenario of truncation selection on a sex-limited trait, or any male-specific selection, there are no within-generation changes in the mean and variance in females. We will therefore proceed with the sex-limited version of equations (1) and (5), which if $S$ represents selection in one sex are

$$\text{(6a)} \qquad \Delta\bar{z} = \frac{1}{2} h^2 S.$$

$$\text{(6b)} \qquad \delta(\sigma_z^2) = -\frac{1}{2}\sigma_z^2 \bar{\iota}^2 = -\frac{1}{2} S^2.$$

We can now iterate the evolutionary trajectory, but we will first take a more analytical look at the behaviour of the genetic variance under the consistent directional selection of truncation selection at the mean.

Bulmer (1976) showed that the equilibrium value of the disequilibrium contribution to the genetic variance, $\tilde{d}$, is given by $\tilde{d} = \tilde{\delta}(\sigma_z^2)\tilde{h}^4$ where $\tilde{\delta}(\sigma_z^2)$ is the reduction phenotypic variance, and $\tilde{h}^4$ is the square of the heritability, both at their equilibrium values. The implications of this formula are not intuitive, because both terms on the right-hand side are themselves functions of $\tilde{d}$. Its basic message, however, is quite straightforward. Because the equilibrium heritability is a number between 0 and 1, its square is typically a modest value. Consequently, even under sustained selection, the disequilibrium contribution will reach a modest maximum equilibrium value. To achieve a result more specific to the modified truncation selection model considered here, and one given entirely in terms of equilibrium parameter values, we need only substitute (eq. 2b) and (eq. 6b) into the Bulmer equation (eq. 3) and solve for the equilibrium values, where $\Delta d = 0$ (Bulmer 1974). The equilibrium value of $d$, i.e., $\tilde{d}$, and writing the environmental variance as $\sigma_e^2$, is

$$\text{(7)} \quad \tilde{d} = \frac{-(2+\pi)\sigma_a^2 - \pi\sigma_e^2 + \sqrt{-4(1+\pi)\sigma_a^4 + \left(2\sigma_a^2 + \pi(\sigma_a^2 + \sigma_e^2)^2\right)}}{2+2\pi}.$$

Being a solution to a quadratic equation, (7) is complex. General solutions in terms of equilibrium values are necessarily of this form, see equations 16.13a and 16.13d in Walsh and Lynch (2018).

*The effect of selection on the genetic variance: models of artificial selection in bighorn sheep*

The general theory of short-term effects of selection on the genetic variance can be evaluated for the instructive case where we assume that estimated variance components in bighorn sheep are the linkage equilibrium values. They are not—they have, of course, been influenced by past processes including selection—but this will give us an idea of the likely magnitude of $\tilde{d}$ under Coulson et al.'s (2018) most intensive selection scheme (100% harvest of above-average males). For the variance components given by Pigeon et al. (2016), $\sigma_a^2 = 17.9$ and $\sigma_e^2 = 27.1$, $\tilde{d} = -1.89$. This represents approximately a 10% reduction in the genetic variance; in terms of the phenotypic standard deviation, it is a reduction in variability of approximately 2%. It is well known that the Bulmer effect is typically modest, even for strong selection (e.g., Turelli and Barton 1994). An illustration of equation (7) is a graphical depiction of the effects of linkage disequilibrium at equilibrium, for a range of heritabilities. Figure 4 shows this for heritabilities between 0 and 1, using the observed phenotypic variance of horn length in young adult male bighorn sheep: the effects of even strong truncation selection

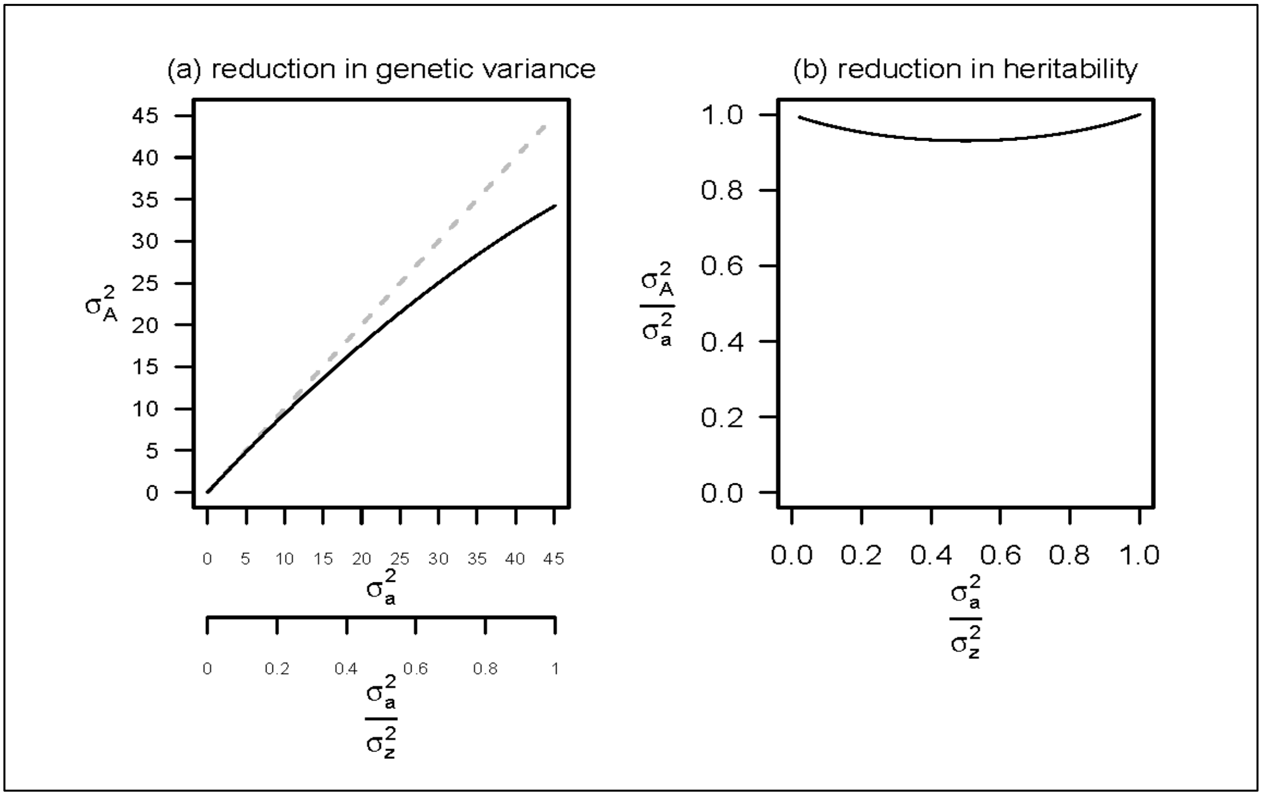

**Figure 4.** The effect of selection on additive genetic variance ($\sigma_A^2$; panel a) and heritability ($h^2$ or $\frac{\sigma_A^2}{\sigma_z^2}$; panel b). The dashed line in (a) represents equality of the genic and additive genetic variance, which would occur in the absence of selection-induced linkage disequilibrium. Both $\sigma_A^2$ and $h^2$ are depicted for ranges of the linkage equilibrium value of heritability between zero and one. The phenotypic variance is set at $\sigma_z^2$ = 45.0 cm$^2$, the observed value for young adult horn length in bighorn sheep males.

such as culling all above-average individuals, on the genetic variance are quite modest. The feature of Coulson et al.'s (2018) results that intense selection through trophy hunting will rapidly erode genetic variance in horn size is thus contrary to theory.

*How does sustained selection change both the mean and variance of a trait?*

Established theory (eight decades for the breeder's equation, four for the Bulmer equation) suggests that the genetic variance for a polygenic trait under sustained directional selection should be only fractionally reduced at equilibrium, while Coulson et al.'s (2018) model rapidly eliminates genetic variation. In addition to theory, much empirical evidence supports the notion that genetic variation can persist for directionally selected traits over many generations, allowing very large and sustained responses to selection. Classic artificial selection studies of quantitative traits with sustained responses include, for example, abdominal bristle number in *Drosophila spp.* (Yoo 1980) and oil content in maize (Dudley 2007), and striking examples of rapid and sustained response to artificial selection in livestock are well known, for example, the well-documented and dramatic increases in growth and feed efficiency in broiler chickens (Zuidhof et al., 2014).

Coulson et al. (2018) intended their model to be based on standard statistical mechanics for inheritance of a continuous trait under the infinitesimal model (Bulmer 1980). However, the implementation contains yet another error. The segregational variance (the variance of differences between individuals' breeding values and the means of their parents' breeding values) is half the value of the additive genetic variance at linkage equilibrium (i.e., the genic variance), not the value including linkage equilibrium at a given time. The consequence of this new error is a mistaken erosion of genetic variation over time, which does not correspond to any known process in population genetics. The error does, however, make it appear more likely that selection through trophy hunting will be inconsequential. Coulson et al. (2018) did in fact apply the correct infinitesimal model of quantitative genetic variation (i.e., where the segregational variance is half of the genic variance), but relegated the associated results to a supplement, presenting the erroneous results that generate less cumulative evolutionary changes in the main document. The difference between iterating the coupled breeder's and Bulmer equations as opposed to Coulson et al.'s (2018) erroneous models is given in the contrast between the columns of Figure 1.

Of course, selection will change allele frequencies in a way that must ultimately erode genetic variation. The joint breeder's and Bulmer equations do not account for this allele frequency change. They only account for the effects of selection on the genetic variance via the generation of non-random association of alleles across loci. To explore the possibility that Coulson et al.'s (2018) model represents a reasonable rate of erosion of genetic variance, we ran individual-based simulations using their selection scenario. We used a demo-genetic scenario close to the infinitesimal model and with little drift (1,000 loci all with equal effects and initially balanced allele frequencies) and a population size of 1,000 males and 1,000 females. We also used a scenario involving fewer loci of larger effects (100 loci, also with equal effects and initially balanced allele frequencies) and a more realistic population size for many managed populations (100 males and 100 females). Both scenarios are much better modelled by the standard mechanics provided by the breeder's and Bulmer equations, in the short and medium terms (Figure 5a–c).

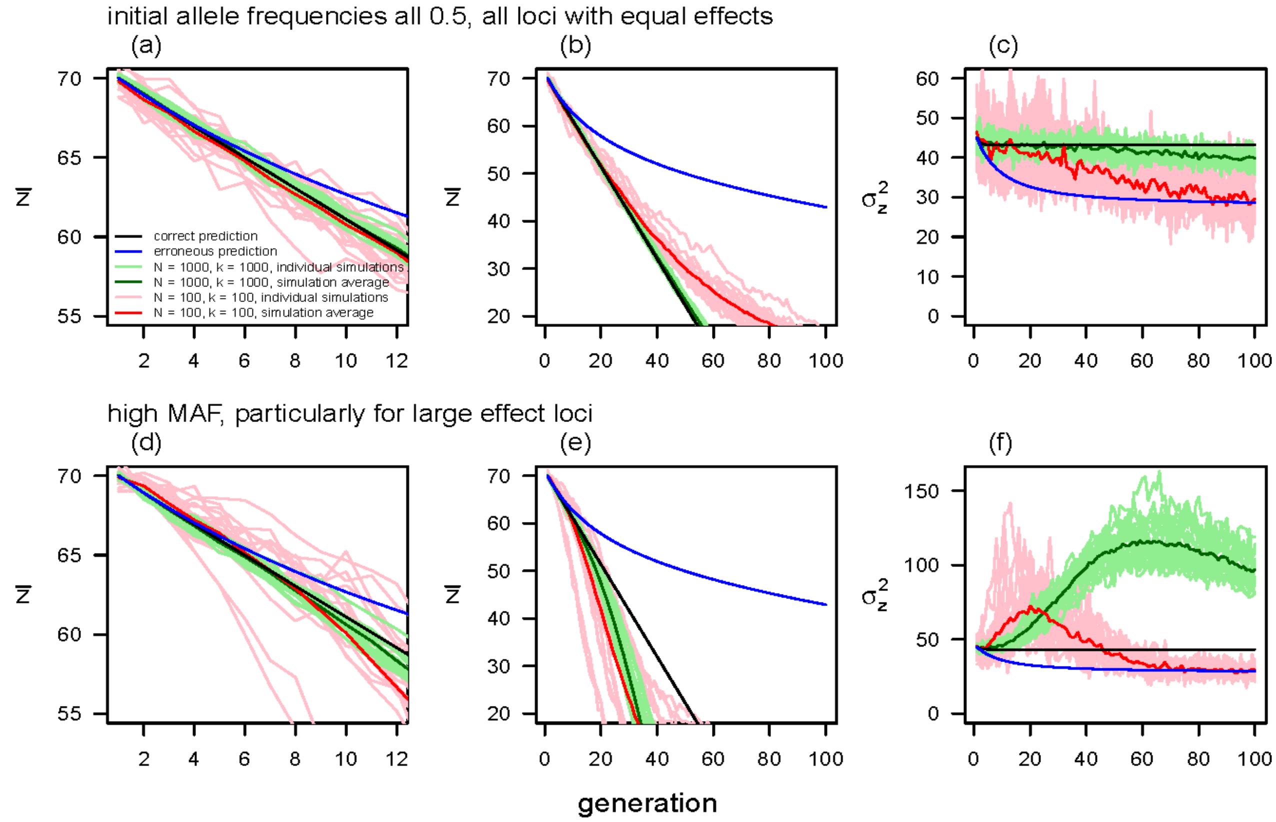

**Figure 5.** Comparison of established quantitative genetic models with numerical simulations of evolutionary responses to selection of polygenic characters. Initial conditions reflect estimates of the population mean value for horn size in 4-year-old bighorn rams (approx. 70 cm), the additive genetic variance ($\sigma_A^2 = 17.9$ cm$^2$) and the phenotypic variance ($\sigma_z^2$ = 45.0 cm$^2$). In simulations in panels (a–c), $k$ = 100 or 1000 loci are simulated with equal initial allele frequencies. In panels (d–f), the same numbers of loci are considered, but their frequencies and allelic effects are simulated from more natural distributions: loci with lower minor allele frequency are more common, and most loci with large effects have low minor allele frequencies. Panels (a) vs (b) and (d) vs (e) depict the same results, but with axes adjusted to focus on short-term (a, d) and longer-term (b, e) change. These figures, except for the blue lines, use the phenotypic and additive genetic variances estimated for bighorn sheep; equivalent plots with the arbitrary (smaller) variance components used by Coulson et al. (2018) are in Figure S.

With few loci and a small population size, and without any immigration or mutation, genetic variation is typically eroded within the time frame represented in Coulson et al.'s (2018) figures (see our Figure 5c); however, the cumulative evolution that occurs before genetic variation is eroded is much greater: despite this latest error, the model predicts evolution similar to that reported for bighorn sheep at Ram Mountain (Pigeon et al. 2016).

*How does the effect of selection on genetic variance depend on genetic architecture?*

Although selection will erode genetic variation in the long term, that erosion will not necessarily be immediate. In the simulations considered up to this point (Figure 5a-c), the initial conditions have allele frequencies of 0.5 for each of the alternate alleles. For any allelic substitution effects, this allele frequency generates the maximum possible genetic variance. Consequently, genetic variance can only be eroded. In reality, most polymorphisms will have much lower minor allele frequencies (MAF), and furthermore, it is likely that for any ecologically important trait that has experienced past selection, the polymorphic loci with the largest allelic substitution effects will be those with low MAF (Wright 1937, Park 2011). We therefore conducted a second set of simulations, where high and low initial allele frequencies were most common, and loci with these high and low initial frequencies had some of the largest effects, in terms of substitution of one allele for the other, on the trait. Figure S4 shows an example of the resulting joint distribution of allele frequencies and allelic substitution effects.

When an allele is rare, it contributes very little genetic variance to a trait, even if it has a large effect on phenotype relative to the other alleles at the same locus. If that allele is selected against, its elimination results in very little change in the genetic variance. However, when a rare allele is positively selected and its frequency increases, its contribution to genetic variance can increase substantially. Consequently, while directional selection will eventually erode genetic variation, in the medium term, selection can substantially increase the genic and genetic variances (Bürger and Lynch 1995; Bürger 2000). This is illustrated in the simulations using a range of allele frequencies and distributions of effects on phenotype (Figure 2d–f). Selection can cause substantial increases in genetic variance, accelerating the response to selection over ecologically relevant periods of time. Thus, the erroneous model of segregation in Coulson et al. (2018) does not necessarily coincide with any probable departures from any model of selection such as the breeder's equation, with or without Bulmer's mechanics for fine details of transient changes in the genetic variance of quantitative traits.

We reproduced all analyses depicted in Figure 5 using Coulson et al.'s (2018) values of $\sigma_A^2 = 3$ and $\sigma_z^2 = 5$. Although these values correspond to a somewhat higher heritability, Coulson et al.'s (2018) selection scheme leads to less evolutionary change due to the lower phenotypic variance (Figure S3). Coulson et al.'s (2018) parameters, using the observed mean of 70 cm, and arbitrary values of $\sigma_A^2$ and $\sigma_z^2$ result in evolutionary rates of about half those generated using the published estimates.

## The present findings considering recently published works

In 2017, after a clearly marked 'version of record' of Coulson et al.'s (2018) had appeared online, and while an earlier version of the present article was under review at *The Journal of Wildlife Management*, the version of record of Coulson et al.'s (2018) article was changed extensively, without alerting readers of these changes. Additionally, in 2019, *The Journal of Wildlife Management* published materials that would appear to pre-empt and contradict conclusions of the present article, re-drawing, but deleting key components, of figures from the present article in a correspondence (Boyce et al. 2019) that was ostensibly published to respond to other matters (Festa-Bianchet 2019).

One of the substantive changes relative to the original version of record of Coulson et al., (2018) was the addition of statements to key figure captions in Coulson et al. (2018; modified version of record) to the effect that the evolutionary rates from model results were not intended to be instructive about evolution of horn size in bighorn sheep. These assertions are surprising. The clearly stated conclusions of Coulson et al. (2018; both the original version of record and the modified version) are that their models disprove the plausibility of rates of evolution inferred for horn size of Ram Mountain bighorn sheep (Coltman et al. 2003, Pigeon et al. 2016). Additionally, the statements added to figure captions asserting that comparisons were not intended to be made in relation to bighorn sheep are contradicted by the very fact that the figures plotted the phenotypic change in horn size in Ram Mountain bighorn sheep as the sole comparison to the Coulson et al. (2018) model results.

A second substantive change was the inclusion of a paragraph in the discussion of Coulson et al. (2018; modified version of record). The new paragraph states that Coltman et al. (2003) concluded that most of the observed phenotypic change in horn length at Ram Mountain was due to evolution, because heritability of horn length is relatively high. In fact, Coltman et al. (2003) categorically did not conclude that most of the phenotypic change was genetically based. We have already explained this point, but we repeat it here considering the changes to Coulson et al. (2018): Coltman et al. (2003) reported an estimated phenotypic decline of 3.5 mm per year, and the inference of the genetic contribution to that decline was 0.75 mm per year. Furthermore, the inference of the rate of genetically based (i.e., evolutionary) change was in no way based on a notion that high heritability means that phenotypic change can be assumed to equate to genetic change; rather, the estimate was based on a model-based estimate of the genetic trend.

Boyce et al. (2019) responded to various points raised by Festa-Bianchet (2019) in relation to the special section on wild sheep management (The Journal of Wildlife Management, volume 82, issue1). The point that Coulson et al.'s (2018) arbitrarily small phenotypic variance results in a distorted picture of the potential for evolution was *not* included in Festa-Bianchet's (2019) communication. It was addressed in an earlier version of the present article, which was in review at The Journal of Wildlife Management at the time, but was ultimately not published there. Nonetheless, Boyce et al. (2019) included an apparent response about the phenotypic variance.

Boyce et al. (2019) contend that a larger value of the phenotypic variance would not lead to appreciably more rapid evolution than Coulson et al. (2018) reported. In support of this contention, Boyce et al. (2019) present the results depicted in figure 1e of the present article. However, Boyce et al. (2019) only plot the lowest culling rate (25%; recall that Coulson et al. (2018) considered culling rates up to 100% for males with above average horn size). Furthermore, while Coulson et al. (2018) plotted their results with a y-axis range from 50-70 cm of horn length (a scale we retain for ease of comparison), the plot in Boyce et al. (2019) uses a range from 0-70 cm. While their figure consequently gives the impression of a shallow slope, the full results (Fig 1e of the present paper) show that a faithful reproduction of Coulson et al.'s (2018) results with an appropriate phenotypic variance indeed greatly changes the scope for evolutionary change. Why Boyce et al. (2019) presented material that has the appearance of negating results of ours that were in review at the time at the same journal is not clear.

## CONCLUSION

Coulson et al.'s (2018) conclusion that estimated rates of evolution in response to trophy hunting in the Ram Mountain population are orders of magnitude greater than is theoretically possible rests on a series of errors. Foremost, they portray research on Ram Mountain as assigning the entire phenotypic change as genetically based. Multiple papers quantified both genetic and non-genetic sources of variation and trends in ecologically important traits in bighorn sheep, including horn size (e.g., Coltman et al. 2003, 2005, Wilson et al. 2005, Pigeon et al. 2016). Taken together with other mistakes, including an erroneous model of segregation, confusion of standard deviation with standard error, and the peculiar mixture of some parameter values from bighorn sheep, such as the population mean and phenotypic trend, but not others (esp., variance components), are puzzling.

We submit that Coulson et al.'s (2018) claim, that the magnitude of evolutionary change in response to exploitation is theoretically implausible, is deeply flawed. By correcting key errors made by Coulson et al. (2018), we have shown a clear congruence of theory and data. We note that all these errors support the claim that hunting-induced evolutionary change in mountain sheep horns is irrelevant to management. We welcome further work motivated to better understand these trends, and to help guide future management decisions. It is important that work continues to refine our theoretical and empirical understanding of evolution as a consequence of exploitation.

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