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2 Running Head Title: .Evolutionary Consequences of Trophy Hunting

3 **Predicting the Evolutionary Consequences of Trophy Hunting on a Quantitative Trait**

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12 **ABSTRACT**

13 Some ecologists suggest that trophy hunting (e.g. harvesting males with a desirable trait above a certain size)
14 can lead to rapid phenotypic change, which has led to an ongoing discussion about evolutionary consequences
15 of trophy hunting. Claims of rapid evolution come from the statistical analyses of data, with no examination
16 of whether these results are theoretically plausible. We constructed simple quantitative genetic models to
17 explore how a range of hunting scenarios affects the evolution of a trophy such as horn length. We show
18 that trophy hunting does lead to trophy evolution defined as change in the mean breeding value of the
19 trait. However, the fastest rates of phenotypic change attributable to trophy hunting via evolution that are
20 theoretically possible under standard assumptions of quantitative genetics are 1 to 2 orders of magnitude
21 slower than the fastest rates reported from statistical analyses. Our work suggests a re-evaluation of the
22 likely evolutionary consequences of trophy hunting would be appropriate when setting policy. Our work does
23 not consider the ethical or ecological consequences of trophy hunting.

24 **Keywords:** selection, hunting, quantitative genetics, integral projection models

25 Trophy hunting that is well managed, and based on robust monitoring protocols, can be a useful conservation
26 tool in areas where there is increasing demand for land from growing human populations (Di Minin et al.,
27 2016; Lindsey et al., 2006). The logic of the approach is that selectively hunting a small proportion of
28 males with large horns, antlers, or body size, will have few ecological and evolutionary consequences because
29 species with sexually selected characters usually exhibit a polygynous mating system in which males are not
30 limiting (Dickson et al., 2009; Milner-Gulland and Mace, 1998). However, a debate on the ethics, use, and
31 consequences, of trophy hunting is underway (Lindsey et al., 2016; Nelson et al., 2016; Ripple et al., 2016),
32 including an ongoing fast or slow evolution discussion on hunted bighorn sheep (*Ovis canadensis*; Coltman
33 et al., 2003; Pigeon et al., 2016; Traill et al., 2014). We contribute further to the trophy hunting debate by
34 constructing and analysing general quantitative genetic models of the effect of trophy hunting on phenotypic
35 evolution.

36 Proponents of trophy hunting argue that selling the rights to selectively hunt individuals with desirable
37 attributes is a useful way to raise money (Rodríguez-Muñoz et al., 2015). The argument is that if wildlife
38 populations can be monetized, they have value, and this worth makes the area in which the population
39 lives more easily protected from competing land use interests (Lindsey et al., 2007). Profit generated from
40 hunting can be invested in conservation, habitat improvement or in local communities, and any ecological
41 and evolutionary consequences of selective hunting on males is likely to be a small cost worth paying (e.g.,
42 Crosmary et al., 2015).

43 Those opposed to the approach argue either that trophy hunting is unethical, or that money raised
44 from trophy hunting rarely gets invested in local communities or in conservation. For example, in Africa,
45 monies raised from selling hunting rights can get subsumed into government coffers, and profits made by
46 outfitters do not always make it back to the local area or communities (Lindsey et al., 2014). In addition,
47 the ecological outcomes of hunting may be negative: in East Africa, unregulated trophy hunting influenced
48 a localized extirpation of lion (*Panthera leo*) populations (Packer et al., 2011), and unethical lion hunting
49 practices in Hwange National Park in Zimbabwe resulted in 72% of research animals being killed, including
50 30% of males < 4 years old that had yet to breed (Loveridge et al., 2007). Furthermore, hunting may lead
51 to evolution of selected traits as has frequently been speculated for some sheep populations (Douhard et al.,
52 2016; Festa-Bianchet et al., 2014; Pigeon et al., 2016).

53 One reason why the ecological and evolutionary consequences of trophy hunting have received recent
54 interest is that biologists have found that evolution can be observed on ecological timescales (Hairston et al.,

55 2005). This has spawned the field of eco-evolution (Schoener, 2011). There is compelling empirical evidence
56 of rapid, joint phenotypic and ecological change from a number of systems (e.g., Hairston et al., 2005; Ozgul
57 et al., 2010), but evidence of genetic change is much less widespread (Yoshida et al., 2003), partly because it is
58 harder to demonstrate. Quite frequently, phenotypic change is attributable to evolution without supporting
59 evidence of genetic change (Hendry, 2016), or without examining whether the rates of evolutionary change
60 reported are theoretically plausible (Coltman et al., 2003).

61 Coltman et al. (2003) report rapid phenotypic change in the face of hunting that was attributed to
62 evolution. Based on longitudinal data for the Ram Mountain bighorn population in Canada Coltman et al.
63 (2003) used statistical quantitative genetics to argue that selective hunting of, on average, 2 rams/year from
64 a population of, on average, approximately 70 bighorn sheep resulted in a 30% decline in horn size over 5
65 generations. In a second paper Pigeon et al. (2016) reported a new analysis that supports these claims. These
66 papers (Coltman et al., 2003; Pigeon et al., 2016) have become influential as opponents of trophy hunting
67 argue that the activity has rapid detrimental consequences on hunted populations. However, no papers
68 have yet examined whether the rates of change observed by Coltman et al. (2003) and Pigeon et al. (2016)
69 are plausible using the quantitative genetic theory that motivated their statistical analyses, even though
70 skepticism has been raised as to whether the phenotypic changes observed can be attributed to evolution
71 (e.g., Traill et al., 2014).

72 We developed novel, general theory to examine the likely evolutionary consequences of selective harvesting
73 on a single sex in a sexually reproducing species. We worked in the quantitative genetics framework because
74 the genetic architecture of trophy traits is rarely known (e.g., Kruuk et al., 2002). We start with a brief
75 summary of quantitative genetic theory that motivated our models, and which is widely used to examine
76 the evolution of phenotypic traits of unknown genetic architecture in free-living populations (Merilä et al.,
77 2001). We then describe the models we used, along with the parameter values we selected.

78 **METHODS**

79 We use the following notation. Expectations and variances of the distribution of $N(x, t)$ are denoted $\mathbb{E}(x, t)$
80 and $V(x, t)$ respectively. A subscript, either of f or m , is used to identify distributions or moments of
81 distributions taken over only females or males respectively. If this subscript is absent, the distribution is
82 taken over both sexes. We use a superscript R to identify distributions, or moments of distributions, that
83 have been operated on by selection.

84 **A Quantitative Genetic Primer**

85 Quantitative genetics assumes that an individual's phenotype \mathcal{Z} consists of the sum of various components.
86 These components include a breeding value \mathcal{A} and the environmental component of the phenotype \mathcal{E} , with
87 contributions from epistasis and non-additive genetic effects also sometimes included in the sum (Lynch and
88 Walsh, 1998). Only \mathcal{A} and \mathcal{E} are considered here. An individual's breeding value describes the additive
89 genetic contribution to its phenotypic trait value. But what does this mean?

90 If alleles at a locus have an additive effect on a phenotypic trait, each allele can be assigned a value that
91 describes the contribution of that allele (in any genotype at that locus) to the phenotype. For example,
92 consider a bi-allelic locus with 3 genotypes, aa , aA and AA . Allele a has a value of 1g and allele A a value
93 of 2g. The breeding value of each genotype to body mass will be: $aa = 1 + 1 = 2$, $aA = 1 + 2 = 3$, and
94 $AA = 2 + 2 = 4$. Breeding values can be summed across genotypes at different loci to generate breeding values
95 for multi-locus genotypes. Under the additivity assumption, the dynamics of breeding values is identical to
96 the dynamics of alleles; this is not always the case when non-additive genetic processes like heterozygote
97 advantage and epistasis are operating (Falconer, 1975).

98 Many applications of quantitative genetics use the infinitesimal model (Fisher, 1930). This assumes that
99 an individual's breeding value for a phenotypic trait is made up from independent contributions from a large
100 (technically infinite) number of additive genotypes, each making a very small contribution to the phenotypic
101 trait. There is no interaction between alleles at a locus (dominance) or interactions between genotypes at
102 different loci (epistasis).

In additive genetic models used to predict evolutionary change, it is usually assumed that \mathcal{E} is determined
by developmental noise. An individual's environmental component can be considered as a random value
drawn from a Gaussian distribution with a mean and a constant variance: $\text{norm}(0, V(\mathcal{E}, t))$. \mathcal{A} and \mathcal{E} are
consequently independent. Thus,

$$\mathcal{Z} = \mathcal{A} + \mathcal{E}.$$

The distribution of breeding values is also assumed to be Gaussian, and

$$V(\mathcal{Z}, t) = V(\mathcal{A}, t) + V(\mathcal{E}, t).$$

103 These assumptions mean that, on average, the breeding value can be inferred from the phenotype – the
104 phenotypic gambit. The aim of statistical quantitative genetics is to correct the phenotype for nuisance
105 variables so the phenotypic gambit assumption is appropriate for the corrected phenotype (Lynch and Walsh,
106 1998).

Next, quantitative genetic theory makes the assumption that the mean of \mathcal{A} among parents is equal to that in offspring: e.g., $\mathbb{E}(\mathcal{A}, t + 1) = \mathbb{E}^R(\mathcal{A}, t)$. In 2-sex models this requires that the expected value of \mathcal{A} in an offspring is the mid-point of the breeding value of its parents. Given this assumption,

$$\Delta\mathbb{E}(\mathcal{Z}) = \mathbb{E}(\mathcal{Z}, t + 1) - \mathbb{E}(\mathcal{Z}, t) = \mathbb{E}(\mathcal{A}, t + 1) - \mathbb{E}(\mathcal{A}, t) = S(\mathcal{Z}) \frac{V(\mathcal{A}, t)}{V(\mathcal{Z}, t)}$$

107 where $\Delta\mathbb{E}(\mathcal{Z})$ is the difference in the mean of the phenotype between the offspring and parental generations,
108 $S(\mathcal{Z})$ is the selection differential on \mathcal{Z} and $\frac{V(\mathcal{A}, t)}{V(\mathcal{Z}, t)}$ the heritability (h^2) of a trait, and t represents generation
109 number. The selection differential describes the difference in the mean value of the character between those
110 individuals selected to reproduce and the entire population prior to selection (Price, 1970). Equation () is
111 the univariate breeders equation (Falconer, 1975).

112 If all assumptions of the univariate breeders equation are met, it will accurately predict evolution of a
113 trait assuming that the selection differential and the additive genetic and phenotypic variances have been
114 appropriately estimated. One exception where it can fail is if there are genetically correlated characters that
115 have not been measured, and which are under selection (Lande and Arnold, 1983).

Lande and Arnold (1983) developed a multivariate form of the breeders equation that states:

$$\Delta\mathbb{E}(\mathcal{Z}) = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$$

116 where $\Delta\mathbb{E}(\mathcal{Z})$ is a vector describing change in the mean of each of the phenotypic traits from the parental
117 to the offspring generation, \mathbf{S} is a vector of selection differentials on each character, \mathbf{G} is a genetic variance-
118 covariance matrix, and \mathbf{P} is a phenotypic variance-covariance matrix. If 2 traits are genetically correlated,
119 and both are under selection, to understand how 1 of the traits evolves it is necessary to understand how
120 the 2 traits are genetically and phenotypically correlated, and how strong selection is on each of the traits.

121 In both the univariate and multivariate breeders equations, the selection differentials capture total selec-
122 tion (Lande and Arnold, 1983). This means that both equations accurately capture selection on the trait(s)
123 even in the presence of unmeasured genetically correlated characters. Genetically correlated characters influ-
124 ence predictions of evolution in the breeders equations through their impact on estimates of the heritability
125 (in the univariate case) and the \mathbf{G} matrix (in the multivariate case).

126 A limitation of the breeders equation is it is not dynamically sufficient – it should not be used to make
127 predictions across multiple generations, particularly when evolution is sufficiently strong that it alters genetic
128 variances and covariances (Lande and Arnold, 1983). To construct a dynamic model, it is either necessary
129 to make assumptions about the genetic variance (it is sometimes assumed to be constant: (Lande, 1982))

130 or to track the dynamics of the entire distributions of \mathcal{A} and \mathcal{E} (Coulson et al., 2017) or \mathcal{A} and \mathcal{Z} (Barfield
131 et al., 2011; Childs et al., 2016). We model the dynamics of \mathcal{A} and \mathcal{E} .

132 **A Generic Model to Explore the Effects of Trophy Hunting on Evolution**

133 We developed a 2-sex, dynamic, quantitative genetic model to explore how hunting on one sex influences
134 phenotypic evolution. We iterate the population forwards on a per-generation time step.

135 We assume that in the absence of hunting, the trophy is not under selection in either sex and is con-
136 sequently not evolving. This provides us with a baseline scenario in the absence of hunting with which to
137 compare results from a range of hunting scenarios. We define a bivariate distribution $N(\mathcal{A}, \mathcal{E}, t)$ of breeding
138 values \mathcal{A} and the environmental component of the phenotype \mathcal{E} in generation t . At time $t = 0$ we assume
139 the distribution $N(\mathcal{A}, \mathcal{E}, t)$ is bivariate normal with means $\boldsymbol{\mu}$ and (co)variances $\boldsymbol{\Sigma}$. The 2 components of $\boldsymbol{\mu}$
140 are $\mathbb{E}(\mathcal{A}, t)$ and $\mathbb{E}(\mathcal{E}, t)$ at $t = 0$. $\boldsymbol{\Sigma}$ is a variance-covariance matrix,

$$\boldsymbol{\Sigma} = \begin{pmatrix} V(\mathcal{A}, t) & 0 \\ 0 & V(\mathcal{E}, t) \end{pmatrix}$$

141 Variances can be chosen to determine the heritability h^2 at time $t = 0$.

142 We assume that males and females have the same distribution of phenotypes and breeding values at birth,
143 and that the birth sex ratio is unity: $N_f(\mathcal{A}, \mathcal{E}, t) = N_m(\mathcal{A}, \mathcal{E}, t) = \frac{N(\mathcal{A}, \mathcal{E}, t)}{2}$.

144 Next we impose selection. There is no direct selection on females and the number of recruits they
145 produced is set to 2, the replacement rate, to ensure the female population remains the same size over time
146 and the population growth rate $\lambda = 1$. This assumes males are not limiting. The distribution of females
147 selected to reproduce is consequently $N_f^R(\mathcal{A}, \mathcal{E}, t) = 2N_f(\mathcal{A}, \mathcal{E}, t)$. The same function for males is used in the
148 absence of hunting.

149 When males are selectively hunted, we remove individuals from the distribution before assigning male
150 reproductive success. We then scale the resulting distribution of males to be the same size as the distribution
151 of females. For example, if all males of above mean trophy size are culled, the matings they would have had
152 are redistributed across those males that were below the mean trophy size and not hunted. In the case of a
153 Gaussian distribution of the trophy, their lifetime reproductive success would increase proportionally to the
154 number of males culled. The proportion p is calculated and the post-selection distribution $N_m^R(\mathcal{A}, \mathcal{E}, t) =$
155 $\frac{1}{p} S_m(\mathcal{A}, \mathcal{E}, t) N_m(\mathcal{A}, \mathcal{E}, t)$ is calculated where $S_m(\mathcal{A}, \mathcal{E}, t)$ is the function describing selection on the male
156 trophy. The distribution $N_m^R(\mathcal{A}, \mathcal{E}, t)$ is the distribution of the components of the phenotype of those males
157 selected to be fathers.

We impose selection on males by culling a proportion α of individuals that are above average size,

$$S_m(\mathcal{Z}, t) = \begin{cases} (1 - \alpha)\mathcal{Z}, & \text{if } \mathcal{Z} > \mathbb{E}(\mathcal{Z}, t) \\ \frac{1}{1-\alpha}\mathcal{Z}, & \text{otherwise, with } \alpha > 0 \end{cases}$$

158 This generates a distribution of fathers $N_m^R(\mathcal{A}, \mathcal{E}, t)$ that is equal in size to the distribution of mothers
159 $N_f^R(\mathcal{A}, \mathcal{E}, t)$.

160 We now have distributions of maternal and parental characters that are the same sizes and sufficient
161 for the female population to replace itself with some males reproducing with multiple mothers. We assume
162 random mating and calculate the distribution of parental midpoint breeding values $N^R(\mathcal{A}, t)$ by convolving
163 $\frac{N_m^R(\mathcal{A}, t)}{2}$ with $\frac{N_f^R(\mathcal{A}, t)}{2}$. To generate the distribution of offspring breeding values, we convolve this distribution
164 with a distribution of the segregation variance, defined as a Gaussian distribution with a mean of 0 and
165 a variance equal to half the additive genetic variance of the distribution $N^R(\mathcal{A}, \mathcal{E}, t)$: $\frac{V^R(\mathcal{A}, t)}{2}$ (Barfield
166 et al., 2011). Effects of increases in the additive genetic variance via mutation, or from other sources of
167 genetic variation being converted to additive genetic variance, can be captured by increasing the size of the
168 segregation variance. Finally, we generate a distribution of the environmental component of the phenotype
169 for each value of \mathcal{A} in the offspring distribution that is proportional to a Gaussian distribution with a mean
170 of 0 and an environmental variance that is the same as that in the previous generation. We now have the
171 bivariate distribution of the components of the phenotype in offspring $N(\mathcal{A}, \mathcal{E}, t + 1)$.

172 Taken together this gives the following recursion,

$$N_f(\mathcal{A}, \mathcal{E}, t) = \frac{N(\mathcal{A}, \mathcal{E}, t)}{2} \quad (1)$$

$$N_m(\mathcal{A}, \mathcal{E}, t) = \frac{N(\mathcal{A}, \mathcal{E}, t)}{2} \quad (2)$$

$$N_f^R(\mathcal{A}, \mathcal{E}, t) = 2N_f(\mathcal{A}, \mathcal{E}, t) \quad (3)$$

$$N_m^R(\mathcal{A}, \mathcal{E}, t) = \frac{1}{p}S_m(\mathcal{A}, \mathcal{E}, t)N_m(\mathcal{A}, \mathcal{E}, t) \quad (4)$$

$$N^R(\mathcal{A}, t) = N_f^R(\mathcal{A}, t) * N_m^R(\mathcal{A}, t) \quad (5)$$

$$N(\mathcal{A}, t + 1) = N^R(\mathcal{A}, t) * \text{norm}\left(0, \frac{V^R(\mathcal{A}, t)}{2}\right) \quad (6)$$

$$N(\mathcal{E}, t + 1) = \text{norm}(0, V(\mathcal{E}, t)) \quad (7)$$

$$N(\mathcal{A}, \mathcal{E}, t + 1) = [N(\mathcal{A}, t + 1), N(\mathcal{E}, t + 1)] \quad (8)$$

173 **Analysis of the Multivariate Breeders Equation** When evolutionary predictions fail to match obser-
174 vation, the existence of correlated unmeasured characters is often assumed (Merilä et al., 2001). However,

175 the potential impact of correlated characters on evolution assuming selection differentials have been appro-
176 priately measured is rarely investigated. We used the multivariate breeders equation to examine how such
177 characters can influence evolution, and in particular, whether they can generate rapid evolution in directions
178 opposite to those predicted by selection differentials which measure total selection on a trait (Lande and
179 Arnold, 1983).

180 We assume 2 traits Z_1 and Z_2 . We predict 1 generation ahead, so we do not use t for time to
181 simplify notation. We define bivariate Gaussian distributions of the traits' breeding values \mathcal{A}_1 and \mathcal{A}_2
182 ($\text{norm}(\boldsymbol{\mu}(\mathcal{A}), \boldsymbol{\Sigma}(\mathcal{A}))$) and environmental components of the phenotype ($\text{norm}(\boldsymbol{\mu}(\mathcal{E}), \boldsymbol{\Sigma}(\mathcal{E}))$). From this we
183 construct a bivariate Gaussian distribution of the phenotype $\text{norm}(\boldsymbol{\mu}(\mathcal{Z}), \boldsymbol{\Sigma}(\mathcal{Z})) = \text{norm}(\boldsymbol{\mu}(\mathcal{A}), \boldsymbol{\Sigma}(\mathcal{A})) +$
184 $\text{norm}(\boldsymbol{\mu}(\mathcal{E}), \boldsymbol{\Sigma}(\mathcal{E}))$.

185 We now impose selection on the phenotype with the following fitness function $W(\mathcal{Z}, t) = \beta_0 + \beta_1 Z_1 + \beta_2 Z_2$.
186 We estimate selection differentials on the 2 phenotypic traits as $\mathbf{S} = \boldsymbol{\Sigma}^{-1}(\mathcal{Z})\boldsymbol{\beta}$ where $\boldsymbol{\beta} = (\beta_1, \beta_2)^T$ where
187 T is the vector transpose and \mathbf{S} is a vector containing the selection differentials s_1 and s_2 . We also calculate
188 the univariate fitness functions $W(\mathcal{Z}) = \beta_0^* + \beta_1^* Z_1$ and $W(\mathcal{Z}) = \beta_0' + \beta_2' Z_2$ using methods from instrumental
189 variable analyses (Coulson et al., 2017; Kendall, 2015). From these functions, we calculated the univariate
190 selection differentials s_1^* and s_2' . We calculate univariate heritabilities using the relevant additive genetic
191 variances and phenotypic variances for each trait. We then compare predictions of evolutionary change
192 between the multivariate breeder's equation and the two univariate breeder's equations.

193 Model Parameters

194 We set $\boldsymbol{\mu} = [70 \text{ cm}, 0]$. The value of 70 cm is approximately the mean horn length of 4-year old rams
195 reported by (Coltman et al., 2003, Figure 2) at the start of their study. The value of zero is the mean of the
196 environmental component of the phenotype as is usually assumed in quantitative genetics (Falconer, 1975).

197 To explore the effects of hunting on the evolution of a trophy, we ran simulations with a range of initial
198 genetic, environmental and phenotypic variances. We conducted simulations to demonstrate the effects
199 of altering the additive genetic variance and the total phenotypic variance. For example, the simulations
200 reported in fig. 1 and fig 2. both have identical initial additive genetic variances of $V(\mathcal{A}, 1) = 3$ but they
201 have different environmental variances of $V\mathcal{E}, 1 = 2$ and $V\mathcal{E}, 1 = 0.1$ respectively. The simulations reported
202 in Fig. 3 demonstrate the effect of increasing the phenotype variance by increasing the additive genetic
203 variance compared to those simulations reported in Fig. 1 and Fig. 2: $V(\mathcal{A}, 1) = 5$ and $V(\mathcal{E}, 1) = 2$.

204 We also examined the consequences of injecting additional genetic variance into the population at each

205 time step by setting the segregation variance to the constant initial value chosen at the beginning of the
206 simulation. For all parameter sets, we explored the effect of removing 25%, 50%, 75%, and 100% of males
207 of above average horn size (e.g., $\alpha = [0.25, 0.5, 0.75, 1]$).

208 To demonstrate how correlated characters affect phenotypic evolution over a single generation, we ran a
209 number of simulations of the multivariate breeder's equation. In each simulation we set $w = 0.3 + 0.1\mathcal{A}_1 +$
210 $0.1\mathcal{A}_2$ and $\boldsymbol{\mu}(\boldsymbol{Z}) = (6, 6)$. These values are arbitrary in that any values could be used to reveal the effects we
211 demonstrate. We then ran 12 simulations. In each simulation $V(\mathcal{A}_1, t = 0) = 2$ and $V(\mathcal{A}_2, t = 0) = 2$. We
212 then examine 3 genetic covariance structures within 4 different distributions of the environmental components
213 of the phenotype. The first assumes no genetic covariance, the second a negative genetic covariance of -1.41
214 and the third a positive genetic covariance of 1.41. We chose the second and third values because they
215 are the 2 limits that the covariance can take to ensure the variance-covariance matrix is positive-definite.
216 The 4 distributions of the environmental components of the phenotype are selected such that phenotypic
217 variances and covariances are dominated by the additive genetic variances and covariances, and for cases
218 where approximately half of the phenotypic variances and covariances are attributable to the additive genetic
219 variances and covariances. We then explored the effects of positive and negative covariances between the
220 environmental components of the phenotypes on evolutionary dynamics.

221 RESULTS

222 Selective trophy hunting led to an evolutionary response in all of our simulations (Fig. 1-3). In our initial
223 simulation with a starting heritability of 0.6, the phenotypic mean declined from a initial value of 70 to
224 between 57 and 62.5 depending upon the proportion of the population culled. There was relatively little
225 difference in the mean phenotype after 100 generations when 50%, 75%, or 100% of males of above average
226 trophy value were harvested; all simulations achieved a decline from 70 to 57 over 100 generations. In contrast,
227 evolution was notably slower when only 25% of above average trophy sizes were culled per generation (Fig.
228 1(A)). The phenotypic variation and heritability showed similar rates of change. This is expected because
229 variation in the environmental component of the phenotype at birth is constant across generations. The
230 rate of loss of phenotypic variation and decline in the heritability scaled with harvesting rate (Fig. 1(B,C)).
231 When all males above the mean trophy value were harvested, additive genetic variance was initially rapidly
232 eroded, before starting to decline more slowly. This change was reflected in the dynamics of the phenotypic
233 variance (Fig. 1(B)). These rates of change in the variance affected the dynamics of the mean phenotype.
234 Although the initial rate of evolution correlated with harvesting pressure, over the course of 100 generations

235 evolution was fastest when 75% of above average males were harvested. None of our scenarios predicted
236 phenotypic change at the rate reported by Coltman et al. (2003). In our initial simulations it took between
237 40 and 100 generations before the mean phenotype evolved to a value that would be significantly different
238 from its initial value (regardless of sample size). Finally, altering the initial heritability by reducing the initial
239 additive genetic variance slowed the rate of evolutionary change as expected. In contrast, as the additive
240 genetic variance and consequently heritability increased, so too did the rate of evolution (Fig. 1(D)).

241 In our second simulation, we increased the initial heritability by reducing the environmental variation.
242 This had a relatively small impact on the rates of evolution (Fig. 2(A)), although the reduction in the
243 phenotypic variance (Fig. 2(B)) did reduce rates of evolution at the highest levels of off-take (Fig. 2(A)).
244 Increasing the additive genetic variance, and consequently the phenotypic variance, also increased rates of
245 evolutionary change slightly (Fig. 3(A,B)), although rates of evolution were still between 1 and 2 orders
246 of magnitude slower than reported by Coltman et al. (2003) and Pigeon et al. (2016). The time series of
247 selection differentials estimated across males and females for these simulations are given in Fig. S1.

248 In all simulations, setting the segregation variance to a constant value generated linear selection because
249 selection does not rapidly erode the additive genetic variance (Fig. S2). However, even when all males of
250 above average horn size are culled, the rate of evolution is still > 5 times slower than that reported by
251 Coltman et al. (2003).

252 We next compared evolutionary dynamics predicted by the univariate and bivariate breeders equation to
253 examine whether correlated characters could lead to rapid evolution in the opposite direction to selection,
254 or to evolutionary stasis. The degree of correlation between 2 characters increased the rate of evolution
255 when the sign of the phenotypic covariance (-/+) was the same as the sign of the product of the selection
256 differentials on each trait (Fig. 4(A)-(D)). As the proportion of phenotypic variation attributable to additive
257 genetic variation tended to unity, predictions from the univariate and bivariate breeders equation converged
258 (Fig. 4(A)). Similarly, although not reported, at the other limit, as the proportion of phenotypic variance
259 attributable to additive genetic variance tended to zero, no evolution was predicted by either the univariate
260 or bivariate breeders equation and predictions converged. Departures between the 2 equations were greatest
261 when intermediate proportions of the phenotypic variances and covariances were attributable to the additive
262 genetic variances and covariances (Fig. 4(B)-(D)). Both additive genetic covariances, and covariances in the
263 environmental component of the phenotype, could lead to divergence between the univariate and bivariate
264 breeders equation (Fig. 4(B)-(D)).

265 Although covariances in $\Sigma(\mathcal{E})$ and $\Sigma(\mathcal{A})$ could affect rates of evolution, when selection differentials were
266 large, covariances could not generate stasis or lead to evolution in the opposite direction to that predicted by
267 selection (Fig. 4, blue lines). However, as selection got weaker, correlated characters could prevent selection,
268 and even lead to very small evolutionary change in the opposite direction to that predicted by evolution (Fig.
269 4, red lines). However, effect sizes were small and would be challenging to detect without large quantities of
270 data.

271 DISCUSSION

272 Our simulations show that selective harvesting can alter the evolutionary fate of populations, and can result
273 in declines in trophy size. However, even under intensive trophy hunting, it is expected to take many tens
274 of generations before the mean trophy size has evolved to be significantly smaller than it was prior to the
275 onset of selective harvesting (see also Mysterud and Bischof, 2010; Thelen, 1991). Our results also show that
276 although correlated characters can have impacts on phenotypic evolution, they cannot be invoked to explain
277 rapid phenotypic change in the opposite direction to that predicted from univariate selection differentials.

278 Our models are kept deliberately simple and make a number of assumptions. First, we iterate the
279 population forwards on a per-generation step. This means there is no age structure, and that a single
280 breeding value determines trophy size throughout life. For some traits there is evidence of age-specific
281 breeding values (Wilson et al., 2005), and these could influence evolutionary rates (Lande, 1982). Males are
282 typically shot once they have reached adulthood, which means direct selection via hunting does not occur in
283 younger ages. The indirect effect of trophy hunting at older ages on phenotypes and fitness at younger ages
284 is determined by genetic correlations across ages. As we show in our analysis of the multivariate breeders
285 equation, evolution is most rapid when the genetic correlations are close to the limit and align with the
286 direction of selection. Given trophy sizes typically experience positive selection at all ages (Coltman et al.,
287 2002; Preston et al., 2003), this means that the rate of evolution will be greatest when genetic correlations
288 are close to unity. At the limit, this would mean that the same breeding value would determine trophy
289 size throughout life – an assumption of our model. Our model consequently likely predicts faster rates of
290 evolution than would be predicted from a model with age-structured breeding values and the same selection
291 regime that we assume.

292 A second assumption we make is that the trait is not subject to selection before selective harvesting
293 is imposed. Trophy size positively correlates with fitness in species that are not harvested (Preston et al.,
294 2003). Trophies may consequently be expected to be slowly evolving to be larger in the absence of selective

295 hunting. If that were the case, then the effect of trophy hunting would have to be greater than in our models
296 to lead to evolution of smaller trophies at the rates we report. This is because selective harvesting would have
297 to counteract evolution for larger trophies in the absence of harvesting, before then leading to a reduction
298 in trophy size. Our model would over-estimate the evolutionary impact of trophy hunting in such a case.

299 Males in sexually dimorphic species with trophies form dominance hierarchies (Pelletier and Festa-
300 Bianchet, 2006). If a dominant male with large trophies is shot, it may be reasonable to assume that
301 surviving males with large trophies that are towards the top of the dominance hierarchy would secure the re-
302 productive success the shot male would have enjoyed. We do not model this process. Instead, we redistribute
303 the reproductive success across all remaining males. This egalitarian redistribution of reproductive success
304 likely exaggerates the evolutionary consequences of trophy hunting because individuals with small trophies
305 are benefiting from those with large trophies being shot. Our model, although simple, has consequently been
306 formulated to likely exaggerate the consequences of trophy hunting on trophy evolution.

307 When predictions from simple models like ours fail to match with observation, the existence of genetically
308 correlated unmeasured characters is often invoked as an explanation (Merilä et al., 2001). Changing the
309 degree of generic covariation between two characters can significantly alter selection differentials on both
310 characters (e.g., Fig. 4). However, this does not mean that the failure to measure a correlated character will
311 lead to incorrect estimates of a selection differential on a trait. In fact, the failure to measure a correlated
312 character will have no impact on the estimate of a selection differential of a focal character (Coulson et al.,
313 2017; Kingsolver et al., 2001; Lynch and Walsh, 1998). Estimates of selection differentials on a univariate
314 character will consequently always give an upper limit on the rate of evolution of a character that conforms
315 to the assumptions of the phenotypic gambit.

316 Genetic and environmental covariation with unmeasured characters can affect the response to selection.
317 The effect is most likely to be strongest when characters have heritabilities in the vicinity of 0.5 and co-
318 variances are close to their limits. The further from this proportion that variance and covariances get, the
319 less biased predictions of evolution in the presence of unmeasured correlated characters becomes. Large
320 covariances that act to reduce the strength of selection can lead to low rates of evolutionary change in the
321 opposite direction to selection, but the effect is small and could only be detectable in very large data sets.
322 We consequently conclude that if the phenotypic gambit is assumed and significant selection on a trait is
323 observed, then unmeasured correlated characters can act to slow, or increase, rates of evolution compared to
324 those predicted by the univariate breeders equation, but they cannot result in evolutionary change that is

325 greater than the univariate selection differentials, or lead to evolutionary stasis. We conclude that although
326 our models on the effect of hunting on a trophy are simple, they will not be too wide of the mark, particularly
327 for large initial heritability for a trophy.

328 Although our models are simple, they provide some novel insights. In particular, our strongest selection
329 regimes result in initial increased rates of evolution. However, they erode the additive genetic covariance
330 more quickly than less stringent hunting regimes, rapidly slowing the rate of evolution. Over longer periods,
331 evolutionary rates are highest at intermediate rates of hunting compared to higher hunting rates. These
332 results show how important it is to track the dynamics of the additive genetic variance when predicting
333 evolution in the face of strong selection over multiple generations (see also Barfield et al., 2011; Childs et al.,
334 2016; Coulson et al., 2017; Lande, 1982). Assuming a constant additive genetic variance in the face of strong
335 selection would lead to predictions of elevated rates of evolution over multiple generations.

336 In most of our simulations we assume that the directional selection we impose erodes the additive genetic
337 variance as is often assumed in quantitative genetics (Falconer, 1975). We do this by constraining the
338 segregation variation to be equal to half the additive genetic variance among parents (Barfield et al., 2011;
339 Childs et al., 2016). However, we also relax this assumption by maintaining a constant segregation variance
340 that is not eroded in the face of selection. This mimics processes, including mutation, that generate additive
341 genetic variance. By doing this we linearize the longer-term response to selection, such that evolution
342 continues to alter the trait value at a greater evolutionary rate over a longer period of time than is possible
343 when selection erodes the additive genetic variance. However, even under these circumstances, statistically
344 significant evolution is predicted to take between 10 and 20 generations even under strong selection when all
345 males of above average horn size are culled.

346 What do our results contribute to bighorn sheep management? Their primary contribution is to suggest
347 that very fast phenotypic change of quantitative characters that is sometimes observed in these populations
348 cannot be due to rapid evolution, at least not under the assumptions of quantitative genetics, for 2 reasons.
349 First, the upper rates of change reported (Coltman et al., 2003) are approximately 2 orders of magnitude
350 faster than models of intensive selective harvesting can achieve. Second, the traits that are hypothesised
351 to evolve, horn length and body size, are subject to positive selection at some ages, even in the presence
352 of harvesting (Traill et al., 2014), yet body and horn size have become smaller (Coltman et al., 2003).
353 Unmeasured correlated characters cannot explain this. So what causes the rapid phenotypic change that is
354 sometimes observed? There are a number of possibilities.

355 First, the environment may have deteriorated rapidly, leading to a change in the mean of the environ-
356 mental component of the phenotype (Kruuk et al., 2002; Merilä et al., 2001), perhaps in a similar manner
357 as reported in a desert bighorn sheep population (*Ovis canadensis nelsoni*; Hedrick, 2011). Second, the
358 phenotypic gambit on which statistical quantitative genetic analyses are based, may be violated (Hadfield
359 et al., 2007). This could occur if genotype-by-environment interactions, dominance variation or epistasis
360 have contributed to the observed phenotypic trends (Falconer, 1975). Quantitative genetics theory and em-
361 pirical methods exists to deal with each of these processes (Lynch and Walsh, 1998), but statistical methods
362 to estimate these processes either require large population sizes or additional data that may not be avail-
363 able for this population. Third, the association between body size and horn length and fitness may not
364 be causal (Merilä et al., 2001), but both may reflect an individuals ability to extract resources from the
365 environment. Individuals that are good at doing this grow to large sizes, produce large trophies, and have
366 high fitness. If the ability to extract resources from the environment is not determined by a simple additive
367 genotype-phenotype map, then neither will be the association between body size and horn length and fitness.

368 Although our models reveal that very rapid evolution attributable to selective hunting is not a plausible
369 explanation for the observed phenotypic declines, our models are not parameterized for bighorn sheep.
370 Ideally the theoretical quantitative genetic approach we use here and in Coulson et al. (2017) should be
371 parameterized for bighorn sheep before any management recommendations are made. The only data set
372 we are aware of that may be sufficient to parameterize models within our framework are from the bighorn
373 sheep population at Ram Mountain (Coltman et al., 2003; Pigeon et al., 2016). These data have not been
374 made publicly available, and the data in Pigeon et al. (2016) are embargoed until 2026. In addition, Festa-
375 Bianchet and Pelletier (coauthors on Coltman et al. (2003) and Pigeon et al. (2016)) are signatories on Mills
376 et al. (2015), which argues against making long-term individual-based data open access. Given it seems
377 unlikely that these valuable data will not be made publicly available any time soon, we implore Coltman
378 and colleagues to use their data to construct and analyze the class of model we use here. Until this is done,
379 we recommend that the conclusions of Coltman et al. (2003) and Pigeon et al. (2016) are not used to inform
380 wildlife management policies given their conclusions are not theoretically plausible.

381 Quantitative genetics theory is powerful, elegant, and based on irrefutable logic (Falconer, 1975; Lande
382 and Arnold, 1983). The statistical methods used to estimate evolutionary change are also extremely powerful
383 when assumptions that underpin the analyses are met (Lynch and Walsh, 1998). We recommend that when
384 evolution is inferred from these statistical analyses, quantitative genetic theory based on the assumptions

385 that underpin the analyses is used to check that reported patterns are plausible. For example, could a
386 correlated character that results in the same selection differential that is observed on the trait generate the
387 observed patterns? This is particularly important when statistically identified rates of evolution are very
388 rapid, or occur in the opposite direction to that predicted. If patterns from these statistical analyses are
389 not theoretically possible, some key assumption underpinning the statistical analysis has been violated, and
390 conclusions from the statistical analyses are unreliable. Simple quantitative genetic models rarely provide
391 predictions that match with observation in the wild (Merilä et al., 2001). When this happens, and predictions
392 and observation cannot be reconciled, the use of phenotype-only models (Ellner et al., 2016), or models with
393 more complex genotype-phenotype maps (Yang, 2004), can provide useful insight into causes of phenotypic
394 change, particularly when these models capture observed dynamics accurately, as they frequently do (Coulson
395 et al., 2010; Merow et al., 2014).

396 **Management Implications**

397 Our work suggests that highly selective trophy hunting will result in evolutionary change, but that it will
398 not be particularly rapid. Evolutionary change would be more rapid if both sexes were selectively targeted
399 as is unfortunately the case for African elephant (*Loxodonta africana*) populations in some countries (Selier
400 et al., 2014). When harvesting is less selective, or coupled with habitat change, the evolutionary consequences
401 of selective harvesting may be harder to detect (Crosmaroy et al., 2013; Garel et al., 2007; Monteith et al.,
402 2013; Rivrud et al., 2013). Our work does not tackle the ethics or ecological consequences of trophy hunting,
403 nor do we account for potential economic benefits of hunting for local communities, whether these be in
404 Canada (Hurley et al., 2015) or in the developing world (Lindsey et al., 2007). These issues should be given
405 considerably more weight when designing population management and conservation strategies compared to
406 the likelihood of rapid evolution.

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532 **FIGURE LEGENDS**

533 Figure 1. The effect of different trophy hunting regimes on the dynamics of the phenotype and the heritability.
534 The dynamics of the mean (A), the variance (B) and the heritability (C) all depend upon the proportion
535 of males of above average trophy (e.g., horn) size that are culled (numbers next to lines). In (A) the red
536 horizontal line represents 1.96 standard deviations from the initial mean trophy size. We selected the starting
537 mean phenotypic value in (A) to be the same as that reported by Coltman et al. (2003). The blue horizontal
538 line is the mean phenotype Coltman et al. (2003) reported 5 generations later. The near vertical blue line
539 represents the rate of the change in the phenotypic mean they report. The line can be compared with the
540 lines from our simulations. In these simulations, the initial additive genetic variance was set at 3.0, and the
541 environmental variance at 2.0. We also report the dynamics of the mean phenotype when 25% of above-
542 average trophy sizes are harvested as a function of increasing additive genetic variance and the heritability
543 (D). In each of the four simulations reported in (D) we set the initial phenotypic variance at 5 by using
544 values for the initial additive genetic variances as (4.99,3.75,2.5,1.25) and for the environmental variances as
545 (0.01,1.25,2.5,1.75). These give initial heritabilities of 0.99,.075,0.5 and 0.25 (values next to the lines).

546 Figure 2. The effect of different trophy hunting regimes on the dynamics of the phenotype. The dynamics
547 of the mean (A), and the variance (B) for cases when the phenotype is determined almost entirely by
548 the additive genetic variance. In each simulation the initial additive genetic variance was set to 3.0 and
549 the environmental variance to 0.1. The blue horizontal line is the mean phenotype Coltman et al. (2003)
550 reported 5 generations later. The near vertical blue line represents the rate of the change in the phenotypic
551 mean they report. The line can be compared with the lines from our simulations.

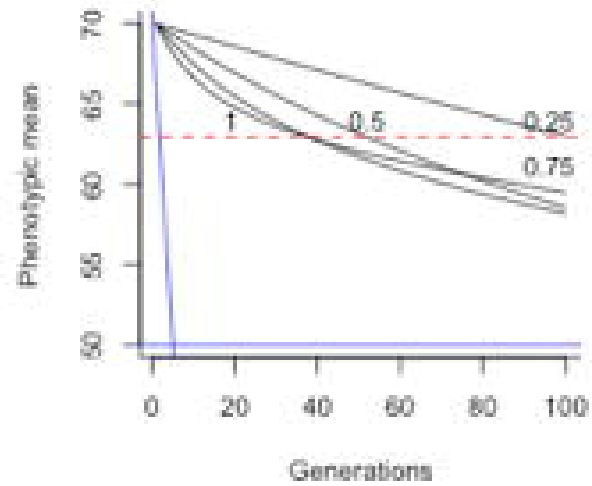
552 Figure 3. The effect of different trophy hunting regimes on the dynamics of the phenotype. The dynamics
553 of the mean (A) and the variance (B) to demonstrate the effect of a high heritability and large phenotypic
554 variance. In each simulation the initial additive genetic variance was set to 5.0 and the environmental
555 variance to 2.0. The blue horizontal line is the mean phenotype Coltman et al. (2003) reported 5 generations
556 later. The near vertical blue line represents the rate of the change in the phenotypic mean they report. The
557 line can be compared with the lines from our simulations.

558 Figure 4. A comparison of the dynamics of the multivariate and univariate breeders equation for different
559 degrees of additive genetic and environmental variances and covariances. Each figure reports 3 simulations:
560 no genetic covariance (black lines), strong positive genetic covariances that reinforce selection (blue lines),

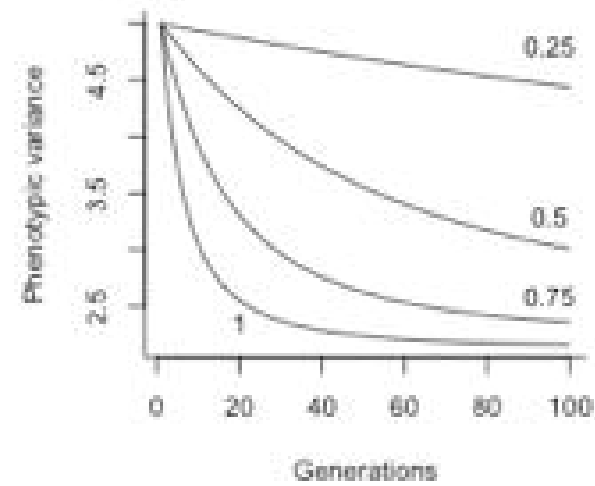
561 and strong negative genetic covariances that oppose selection (red lines). Solid lines represent selection
562 differentials on each trait and dotted lines represent responses to selection. Horizontal and vertical dot-
563 dashed lines show predictions of evolution from the univariate breeders equation for each trait. The farther
564 the right hand end of the dashed lines are from the intersection of the horizontal and vertical dot-dashed
565 lines, the greater the disparity between predictions from the univariate and multivariate breeders equation.
566 We simulated that all phenotypic variation is attributable to genetic (co)variances (A), approximately half
567 of phenotypic variance is attributable to additive genetic variance (B), and the effect of a positive (C) and
568 negative (D) covariance in the environmental components of the phenotypes on rates of evolution. The
569 genetic and environmental (co)variance used in each simulation can be found in Table S1.

570 **Summary to the electronic Table of Contents** We show that the widely cited results claiming rapid
571 evolution of trophy size in bighorn sheep in response to selective trophy hunting are theoretically impossible
572 given standard assumptions of quantitative genetics.

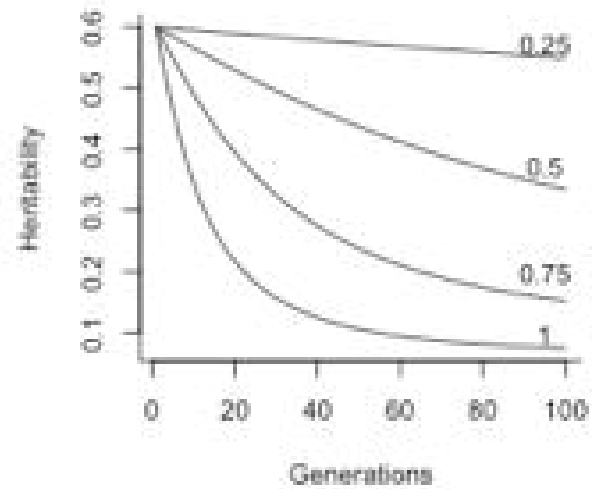
(A) Dynamics of the mean phenotype



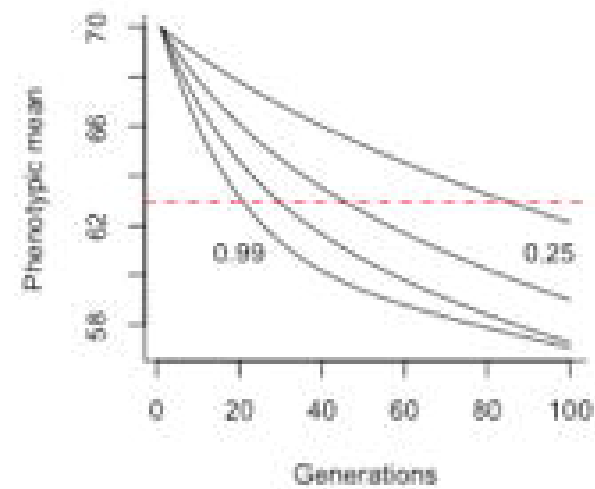
(B) Dynamics of the phenotypic variance



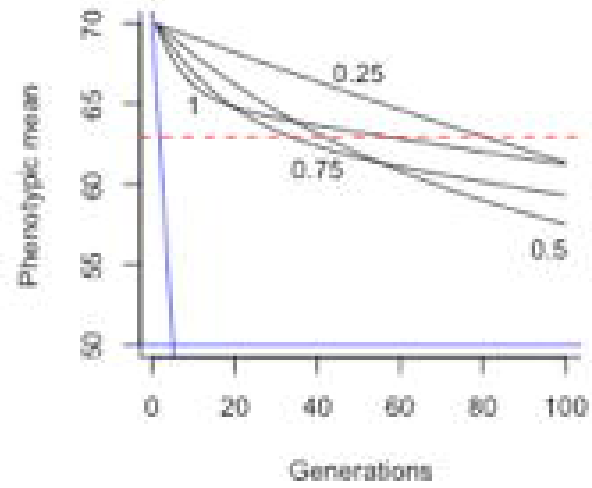
(C) Dynamics of the heritability



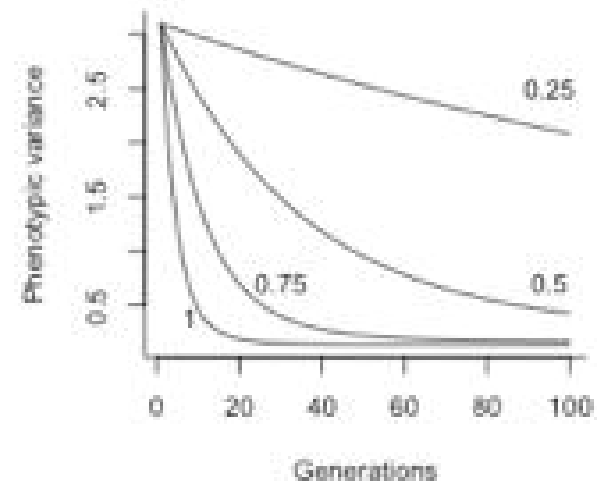
(D) Dynamics of the mean phenotype



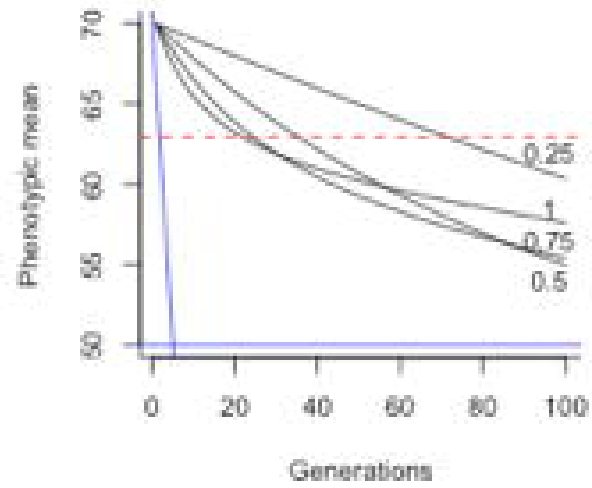
(A) Dynamics of the mean phenotype



(B) Dynamics of the phenotypic variance



(A) Dynamics of the mean phenotype



(B) Dynamics of the phenotypic variance

