Coulson Dynamic Price and Breeder's equations for variable environments

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ABSTRACT

The Breeder's and Price equations are static models of evolution. Recent work has demonstrated how components of these equations, such as selection differentials and heritabilities, can be calculated for each time-step from dynamic, evolutionarily-explicit, structured population models. These dynamic models consist of functions that describe how environmental factors impact associations of genotypes and phenotypic traits with survival, reproduction, development, and non-genetic inheritance. Because evolutionarily explicit versions of these structured models can include feedbacks and can capture all the routes via which environmental variation can impact evolution, they i) provide a more powerful predictive tool for modelling eco-evolution in natural settings than existing approaches, and ii) reveal how key evolutionary parameters incorporated into static models change with time as evolution, or environmental change, proceeds.

17 INTRODUCTION

18 Eco-evolutionary dynamics occur when selection on heritable phenotypic traits and the population
 19 growth rate within a focal species change together (Hairston Jr et al. 2005). Eco-evolutionary
 20 feedbacks then arise when a change in the population growth rate alters the strength of selection
 21 within a species, and vice versa (Patel et al. 2018). By using dynamic, evolutionarily-explicit,
 22 structured models (Coulson et al. 2017) to examine the dynamics of both population growth and
 23 terms in the Breeder's and Price equations (Coulson et al. 2010, Childs et al. 2016), we show how
 24 eco-evolutionary dynamics and feedbacks influence evolution, phenotypic trait dynamics, and
 25 population growth. Our approach is based on understanding the interplay of fitness functions with
 26 functions that describe development, and genetic and non-genetic inheritance (see also (Wallace
 27 et al. 2013)). Fitness functions define how the association between phenotypic trait values and
 28 individual absolute fitness (or survival and reproductive components of fitness) varies with
 29 environmental drivers; development functions characterise the phenotypic development of
 30 surviving individuals over a time-step as a function of their environment; inheritance functions
 31 capture both genetic inheritance and environmentally-induced, non-genetic inheritance (Childs et
 32 al. 2016, Coulson et al. 2017).

33 Adaptive evolution requires directional selection on a heritable phenotypic trait (Fisher 1930). The
 34 strength of selection is determined by the phenotypic variance and the association between the
 35 phenotypic trait and absolute fitness, and is measured with a selection differential (Price 1970,
 36 Lande and Arnold 1983). Selection alters the distribution of the trait within a population within a
 37 generation. For evolution to occur, this change must, at least partially, be reflected in the
 38 distributions of alleles that determine trait values within the population (Falconer 1960). Rules of
 39 genetic inheritance mean that allele frequencies among selected parents are expected to be
 40 observed in offspring, although processes such as mutation and genetic drift can lead to

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41 departures from this expectation (Crow and Kimura 1970). For eco-evolutionary dynamics and
 42 feedbacks to occur, it is necessary, but not sufficient, that the strength of selection is influenced by
 43 the population growth rate. The selection differential can be written as the covariance between
 44 phenotypic trait values and individual absolute fitness, divided by the mean individual absolute
 45 fitness (Heywood 2005). When the mean individual absolute fitness over a time-step is shorter
 46 than a generation, it is the population growth rate (Fisher 1930). The strength of selection is
 47 consequently influenced by the population growth rate, as long as the covariance between
 48 phenotypic trait values and individual absolute fitness does not vary systematically with the
 49 population growth rate.

50 A dynamical consequence of selection being partially determined by the covariance between
 51 phenotypic trait values and individual absolute fitness, is that if the mean of one quantity changes,
 52 the mean of the other will also change. This is true as long as i) the function linking the two
 53 quantities does not change with time, and ii) there is variation in each quantity within the
 54 population. For example, evolution of a phenotypic trait will cause an increase in mean absolute
 55 fitness (i.e. the population growth rate) (Fisher 1930). Under these scenarios, both eco-
 56 evolutionary dynamics and feedbacks will occur (Coulson et al. 2017). This is because i) the mean
 57 of the phenotypic trait and the population growth rate will evolve together, ii) an increase in the
 58 population growth rate will increase the size of the denominator in the selection differential, iii)
 59 this will reduce the strength of selection which will, in turn, iv) reduce the rate of evolution of the
 60 population growth rate. The speed of the eco-evolutionary dynamics, and the magnitude of the
 61 eco-evolutionary feedback, both depend upon the association between phenotypic trait values
 62 and individual absolute fitness, the phenotypic variance, and the form of the map between
 63 genotype and phenotype.

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64 In artificial settings it is possible to control i) the association between phenotypic trait values and
 65 individual absolute fitness, ii) the phenotypic variance, and iii), to some extent, the way that
 66 environmental variation might influence the genotype-phenotype map (Falconer 1960). Such
 67 control does not exist in the natural world, where density-dependent feedbacks and
 68 environmental variation can generate temporal change in each of these three quantities. For
 69 example, if evolution occurs while the association between phenotypic trait values and individual
 70 absolute fitness remains constant in time, populations grow hyper-exponentially (Witting 2002).
 71 This is not observed in nature because density-dependent processes such as food limitation and
 72 predation prevent long-term hyper-exponential (or even exponential) population growth.
 73 Negative density-dependence operates to lower the elevation of the association between
 74 phenotypic trait values and individual absolute fitness, which in turns reduces mean individual
 75 absolute fitness (the population growth rate) (Coulson et al. 2017).
 76 We use evolutionarily-explicit, density-dependent, structured population models to examine how
 77 environmental variation can alter the form of the association between phenotypic trait values and
 78 individual absolute fitness, the genotype-phenotype map, and the phenotypic variance, thereby
 79 impacting eco-evolution and potentially leading to eco-evolutionary feedbacks.

80 THEORETICAL UNDERPINNINGS

81 Understanding eco-evolutionary dynamics and feedbacks requires dynamic models. However,
 82 standard evolutionary theory widely used by empiricists is static, in that it only provides
 83 predictions over a single time-step (Falconer 1960, Morrissey et al. 2010). Nonetheless, this static
 84 theory is useful as selection differentials on which it is based provide exact descriptions of the
 85 strength of observed selection on phenotypic traits (Lande and Arnold 1983), and the Price
 86 equations builds on this to provide a complete description of evolution (Price 1970). If models of

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eco-evolution are to link with the understanding these static models have provided, they must predict time series of components of these static models (Coulson et al. 2010, Coulson et al. 2017, Coulson et al. 2018). We consequently start by considering these models.

We start with the Breeder's equation. Following standard quantitative genetic theory, we assume that an individual's phenotypic trait value z_t can be decomposed into a breeding value A_t and an environmental component E_t , so that $z_t = A_t + E_t$. Next, we write the Breeder's equation in terms of individual absolute fitness w_t (Heywood 2005) and assume an annual life history and an annual population census such that viability selection can be ignored and mean absolute fitness is equal to the mean recruitment rate $\bar{w}_t = \bar{r}_t$, where $\bar{r}_t$ is defined as the per capita production of offspring between times t and $t + 1$ that survive to enter the population at time $t + 1$.

$$\Delta \bar{z}_t = \frac{\text{cov}(w_t, A_t + E_t)}{\bar{w}_t} \frac{\text{var}(A_t)}{\text{var}(A_t + E_t)}. \quad (1)$$

$\Delta \bar{z}_t$ is the change in the mean phenotypic trait value over a generation (=time-step for our annual life history) (Lush 1943), the first term on the right-hand side is a phenotypic selection differential, and the second is the narrow-sense heritability h^2 . The variance in the breeding values at time t is denoted $\text{var}(A_t)$ – the additive genetic variance. Equation (1) assumes that change in $\bar{A}_t$ caused by selection within the parental generation is transmitted to the offspring generation, and that change in $\bar{E}_t$ is not.

We can rewrite equation (1) as $\Delta \bar{z}_t = \frac{\beta_1 \text{var}(A_t)}{\bar{w}_t}$ where β_1 is the slope of a linear regression between individual absolute fitness and individual phenotypic trait values (the derivative $\frac{d\bar{w}_t}{d\bar{z}_t}$). Note that this makes β_1 different from a selection gradient (Lande and Arnold 1983), which is computed using relative fitness values (e.g. $\beta_1 / \bar{w}_t$ in our notation).

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108 In this formulation, $\bar{w}_t = \bar{r}_t$ is mean fitness and the population growth rate. Assuming that β_1 and
 109 $var(A_t)$ do not systematically vary with $\bar{w}_t$, it is apparent that the rate of evolution $\Delta\bar{z}_t$ and the
 110 population growth rate $\bar{w}_t$ are intimately linked. For example, if we assume a linear fitness
 111 function $w_t = \beta_0 + \beta_1 z_t$ we can write:

$$112 \quad \Delta\bar{z}_t = \frac{\beta_1 var(A_t)}{\beta_0 + \beta_1 [\bar{A}_t + \bar{E}_t]}. \quad (2)$$

113 The equations above assume that selection is the only process that alters $\bar{A}_t$ or $\bar{E}_t$ from one
 114 generation to the next. This is one reason why the Breeder's equation does not provide a
 115 complete description of evolution of the mean of a phenotypic trait. Non-genetic inheritance and
 116 phenotypic plasticity, that can influence the value of $\bar{E}_t$ and contribute to evolutionary dynamics,
 117 are processes that are not included in the Breeder's equation. Put another way, the Breeder's
 118 equation assumes that the genotype-phenotype map does not vary with time due to processes
 119 that can alter $\bar{E}_t$. These processes can be captured, along with selection, with the Price equation
 120 (Price 1970).

121 The Price equation provides a complete description of the change in the mean of a phenotypic
 122 trait over a generation. Continuing to assume $z_t = A_t + E_t$,

$$123 \quad \Delta\bar{z}_t = \frac{cov(w_t, A_t + E_t)}{\bar{w}_t} + [\bar{A}_{t+1} - \bar{A}_{\omega,t}] + [\bar{E}_{t+1} - \bar{E}_{\omega,t}]. \quad (3)$$

124 $\bar{A}_{\omega,t}$ and $\bar{E}_{\omega,t}$ respectively describe the mean of the breeding value and environmental component
 125 of the phenotype among selected parents.

126 The first term on the right-hand side is a selection differential. The second term describes how
 127 imperfect genetic inheritance (e.g., mutation, recombination) could alter the mean breeding value
 128 between offspring and their parents, and the third how non-genetic inheritance (e.g., epigenetics)

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129 alters the mean environmental component of the phenotypic trait between offspring and their
130 parents.

131 The Breeder's equation is a special form of the Price equation that assumes that $[\bar{A}_{t+1} - \bar{A}_{\omega,t}] =$
132 0 and $\frac{cov(w_t, E_t)}{\bar{w}_t} = -[\bar{E}_{t+1} - \bar{E}_{\omega,t}]$. Biologically this means that genetic inheritance does not change
133 $\bar{A}_t$ (i.e. there is no transmission bias), and that $\bar{E}_t$ at birth remains identical in each generation.
134 The first of these assumptions is reasonable for large populations; the second is justified if the
135 environmental component of the phenotypic trait is determined by completely random
136 developmental noise (Falconer 1960) and not by any variation in the environment. If the
137 environmental component of the phenotypic trait is dependent upon non-random aspects of the
138 external environment (including non-genetic inheritance), then the assumption will be violated
139 (Kruuk et al. 2002). If this is the case, the Price equation is required to describe evolution.

140 In an annual life history $\bar{w}_t = \bar{r}_t$; in a non-annual life history, the population growth rate and mean
141 fitness over a time-step are the sum of mean survival and mean recruitment, $\bar{w}_t = \bar{s}_t +$
142 $\bar{r}_t$. Replacing $\bar{w}_t$ with $\bar{r}_t + \bar{s}_t$ and expanding (3) we can write the Price equation in terms of fitness
143 and transition functions acting through survival, recruitment, development and genetic and non-
144 genetic inheritance on the distribution of z . In this form, the Price equation applies to iteroparous
145 species:

$$\Delta \bar{z}_t = \frac{cov(s_t, A_t + E_t)}{\bar{w}_t} + \quad (4a) \quad \text{Effect of viability selection on components of the phenotype.}$$

$$+ \frac{cov(r_t, A_t + E_t)}{\bar{w}_t} + \quad (4b) \quad \text{Effect of fertility selection on components of the phenotype.}$$

$$+ \frac{\bar{r}_t}{\bar{w}_t} [\bar{A}'_{t+1} - \bar{A}_{\omega_r,t}] + \quad (4c) \quad \text{Effect of genetic inheritance on the mean breeding value. } \bar{A}'_{t+1} \text{ is the mean breeding value amongst recruits; } \bar{A}_{\omega_r,t} \text{ is the mean breeding value among}$$

selected parents. Equals zero: inheritance does not change the mean breeding value between selected parents and their offspring.

$$+ \frac{\bar{s}_t}{\bar{w}_t} [\bar{A}''_{t+1} - \bar{A}_{\omega_s,t}] + \quad (4d)$$

Development of the breeding value within surviving individuals. $\bar{A}''_{t+1}$ is the mean breeding value amongst surviving individuals at time $t+1$; $\bar{A}_{\omega_s,t}$ is the mean breeding value at time t amongst individuals that will survive from time t to time $t+1$. Equals zero: breeding values do not change within individuals as they age.

$$+ \frac{\bar{r}_t}{\bar{w}_t} [\bar{E}'_{t+1} - \bar{E}_{\omega_r,t}] + \quad (4e)$$

Effect of non-genetic inheritance on the mean environmental component of the phenotypic trait: non-genetic inheritance can change the mean of the environmental component of the phenotype between selected parents and their offspring.

$$+ \frac{\bar{s}_t}{\bar{w}_t} [\bar{E}''_{t+1} - \bar{E}_{\omega_s,t}]. \quad (4f)$$

Effect of phenotypic plasticity on the development of the mean environmental component of the phenotypic trait: the environmental component of the phenotype can change within individuals as they age.

146 This provides a complete description of all of the processes that can influence change in the mean
 147 phenotype in an iteroparous species over a time-step. The formulation does assume $z_t = A_t + E_t$
 148 and that all processes remain constant with age. The latter assumption could be relaxed using the
 149 approach in (Coulson and Tuljapurkar 2008). Note that some authors have further decomposed
 150 $cov(r_t, A_t + E_t)$ into $cov(r_t, A_t) + cov(r_t, E_t)$ and assumed that these two quantities can change
 151 independently of one another (Bonnet et al. 2017). We do not do this here as this violates the
 152 additivity assumption of $z_t = A_t + E_t$ of quantitative genetics (Appendix 1) that we are currently
 153 employing.

154 Each of the terms in the static Breeder's and Price equations are emergent properties of the
 155 distribution of the phenotypic trait (and its components) at time t , fitness functions determining
 156 terms in equation (4a) and (4b), and transition functions determining terms in equations (4c) to
 157 (4f) (Coulson et al. 2010, Childs et al. 2016). Integral projection models (IPMs), which calculate

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158 changes in the distribution of a continuous trait by integrating over a series of fitness and
159 transition functions (Coulson et al. 2010, Childs et al. 2016) provide a framework with which to
160 make the Price and Breeder's equations dynamic. To do this, it is consequently necessary to
161 specify these functions (Coulson et al. 2017) that can then be combined into a model to iterate
162 forward the dynamics of the distribution of $z_t = A_t + E_t$.

163 In the case of an annual life history, a reproductive fitness function, $R(A_t + E_t)$, is used to map
164 the bivariate distribution of breeding values and environmental components of the phenotype at
165 time t , $n(A_t, E_t)$, to a new distribution at time $t + 1$, $n(A'_{t+1}, E'_{t+1})$ (Ellner et al. 2016),

$$166 \quad n(A'_{t+1}, E'_{t+1}) = \int [H(A'_{t+1}, E'_{t+1} | A_t, E_t) R(A_t + E_t) n(A_t, E_t)] dA_t dE_t. \quad (5)$$

167 $H(A'_{t+1}, E'_{t+1} | A_t, E_t)$ is a transition function that describes the probability of transitioning from
168 trait value $A_t + E_t$ at time t to all possible trait values $A'_{t+1} + E'_{t+1}$ at time $t + 1$ (Easterling et al.
169 2000). Trait value $z_t = A_t + E_t$ is expressed in the focal individual, while trait values $z'_{t+1} =$
170 $A'_{t+1} + E'_{t+1}$ are expressed in offspring. The transition function is needed when predicting
171 evolutionary change over multiple time-steps if offspring that recruit to the population at time $t +$
172 1 and their parents at time t do not perfectly resemble one another.

173 $H(A'_{t+1}, E'_{t+1} | A_t, E_t)$ can be formulated to capture the second term on the right-hand side of the
174 Breeder's equation (1) or the last two terms on the right-hand side of the Price equation (3), and
175 so can describe genetic and non-genetic inheritance. A dynamic form of the Breeder's equation (1)
176 requires $H(A'_{t+1}, E'_{t+1} | A_t, E_t)$ to be specified such that it produces a distribution $n(A'_{t+1}, E'_{t+1})$
177 that has means of $\bar{A}'_{t+1} = \bar{A}_{\omega,t}$ and $\bar{E}'_{t+1} = \bar{E}_{\omega,t}$ and a variance-covariance matrix

178 $\begin{pmatrix} \text{var}(A_t) & 0 \\ 0 & \text{var}(E_t) \end{pmatrix}$ where $\text{var}(A_t)$ can be selected to be a constant, or to change with time as a

179 function of selection, and $\text{var}(E_t)$ is constant (Childs et al. 2016, Coulson et al. 2017, Rees and

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180 Ellner 2019). There are a number of ways this can be achieved (Appendix 2). Any formulation of
 181 $H(A'_{t+1}, E'_{t+1} | A_t, E_t)$ that results in $\bar{A}'_{t+1} \neq \bar{A}_{\omega,t}$ and/or $\bar{E}'_{t+1} \neq \bar{E}_{\omega,t}$ provides a dynamic form of
 182 the Price equation (3, 4). Once the transition and fitness functions are parameterised, derivations
 183 from Coulson *et al.* (2010) can then be used to create time series of each of the components in the
 184 various forms of the Price and Breeder's equations described above.

185 Equation (5) can be extended to incorporate per-time-step survival and recruitment functions to
 186 allow models of iteroparous species. Models now include two transition functions: a development
 187 function $G(E'_{t+1} | A_t, E_t)$ operating on surviving individuals, and an inheritance function
 188 $D(E'_{t+1} | A_t, E_t)$ that captures the similarity between parental and offspring traits (Easterling et al.
 189 2000, Ellner and Rees 2006, Coulson 2012). The development function operates with a survival
 190 fitness function $S(A_t + E_t)$ that determines the strength of viability selection, while the
 191 inheritance function operates with the recruitment fitness function $R(A_t + E_t)$ that determines
 192 the strength of fertility selection:

$$193 \quad n(A'_{t+1}, E'_{t+1}) = \int \left[D(E'_{t+1} | A_t, E_t) R(A_t + E_t) + \dots \right] n(A_t, E_t) dA_t dE_t. \quad (6)$$

194 Each process that can contribute to the change in the mean phenotype in an iteroparous species
 195 (i.e. Equation(4)) is captured in this IPM: term (4a) is determined by $S(A_t + E_t)n(A_t, E_t)$, term
 196 (4b) by $R(A_t + E_t)n(A_t, E_t)$, terms (4c) and (4e) by $\int D(E'_t | A_t, E_t) R(A_t + E_t) n(A_t, E_t) dA_t dE_t$
 197 and terms (4d) and (4f) by $\int G(E'_t | A_t, E_t) S(A_t + E_t) n(A_t, E_t) dA_t dE_t$ (Childs et al. 2016).

198 METHODS

199 Our aim here is to incorporate environmental trends and feedbacks caused by density-
 200 dependence into the functions in equations (5) and (6). We will examine how this impacts the
 201 association between phenotypic trait values and individual absolute fitness, the phenotypic

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202 variance, and the map between genotype and phenotype, and how, ultimately, this generates
203 temporal dynamics in the components of the Breeder's and Price equations, rates of evolution,
204 phenotypic trait dynamics, and population growth.

205 We start with a model of the form of equation (5) with the phenotypic trait separated into its
206 additive genetic and environmental components, $z_t = A_t + E_t$, but where fitness is not separated
207 into its survival and recruitment components. We assume a linear association between phenotypic
208 trait values and individual absolute fitness and iterate $n(A_t, E_t)$ given the following
209 parameterisation,

$$210 \quad w(A_t + E_t) = -0.2 + 0.05(A_t + E_t), \quad (7)$$

211 and a starting bivariate normal distribution $n(A_{t=1}, E_{t=1})$ with means $\bar{A}_t = \bar{E}_t = 10$ and a
212 variance-covariance matrix $\sigma^2 = \begin{pmatrix} 2 & 0 \\ 0 & 2 \end{pmatrix}$. The choice of parameter values is for illustration rather
213 than representing any particular system. The mean of the breeding value distribution does not
214 change between parents and their offspring.

215 We ran four model scenarios. In scenarios 1) and 2) the mean and variance of the environmental
216 component of the phenotype remained constant across generations, while in scenarios 3) and 4)
217 the mean of the environmental component declined with time such that $\bar{E}_t = 10 - 0.05t$. In
218 scenarios 1) and 3) selection eroded additive genetic variation, while in scenarios 2) and 4) it did
219 not. Scenarios 1) and 2) are dynamic forms of the Breeder's equation, while scenarios 3) and 4)
220 are dynamic forms of the Price equation. The last two scenarios capture a process where some
221 aspect of the environment can determine the dynamics of the environmental component of the
222 phenotype (Kruuk et al. 2002).

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223 The linear assumption of the simple model is unrealistic because litter size and survival rates are
 224 bounded. In addition, in variable environments, survival, recruitment, development and
 225 inheritance functions for the environmental component of the phenotype depend on
 226 environmental factors such as the population size (Kruuk et al. 2002, Bassar et al. 2017).
 227 Moreover, although breeding values remain constant with age, the environmental component of
 228 the phenotypic trait can change within individuals – phenotypic plasticity (Falconer 1960). We
 229 consequently developed a more complex, density-dependent model, where fitness is separated
 230 into its survival and recruitment components, and where the environmental component of the
 231 phenotype can develop within surviving individuals, and can vary between parents and their
 232 offspring. We took a published density-dependent Integral Projection Model (IPM) of the
 233 dynamics of body size from females in an individually marked population of Soay sheep (*Ovis*
 234 *aries*) living on the island of Hirta in the St. Kilda archipelago in Scotland (Coulson 2012). The
 235 published IPM was modified to be of the form of equation (6). Functions and parameter values are
 236 provided in Appendix 3.

237 We selected the starting population structure of each evolutionarily explicit simulation by using
 238 the equilibrium population structure from an ecological simulation where the additive genetic
 239 variance was set to 0 so evolution cannot occur. Each simulation was run for 100 time-steps.

240 As well as the baseline model, in which the survival, recruitment, development and inheritance
 241 functions were all density-dependent, we ran four simulations where we set the density-
 242 dependence parameter to 0 in either the survival fitness function, the recruitment fitness
 243 function, the development function, or the inheritance function for E_t . Although this is a large
 244 perturbation, it reveals interesting dynamics whereby perturbing one function influences the role
 245 of other functions on eco-evolution.

246 RESULTS

247 In our evolutionarily explicit IPM with a linear fitness function, evolution, defined as a change in
 248 the mean breeding value $\Delta \bar{A}_t$, was fastest when additive genetic variance was not eroded by
 249 selection, and when, simultaneously, there was a negative temporal trend in the mean
 250 environmental component of the phenotype $\bar{E}_t$ (Figure 1(A)). The negative temporal trend in $\bar{E}_t$
 251 accelerated the rate of evolution by reducing the population growth rate $\bar{w}_t$ (Figure 1(B)). In spite
 252 of accelerating the rate of evolution, the trending values of $\bar{E}_t$ with time slowed the rate of
 253 phenotypic change, as positive change in $\bar{A}_t$ was countered by negative change in $\bar{E}_t$ (Figure 1(C)).
 254 The population growth rate $\bar{w}_t$, which is also mean fitness, increased fastest when additive genetic
 255 variance was not eroded, and $\bar{E}_t$ did not decline with time (Figure 1(C)). As expected, linear
 256 selection reduced the additive genetic variance if it was not replaced in each generation (Figure
 257 1(D)). When there was no temporal trend in $\bar{E}_t$, the association between the mean breeding value
 258 and the population growth rate was linear (Figure 1(E)), while it was slightly curvilinear when $\bar{E}_t$
 259 declined with time. As the association between phenotypic trait values and individual absolute
 260 fitness was linear, there was, by definition, a linear association between the mean phenotypic trait
 261 and the population growth rate, with a slope of β_1 (Figure 1(F)).

262 We can combine these insights to graphically illustrate the evolutionary, phenotypic, and
 263 population-growth dynamics our results reveal with a plot of A_t against E_t that includes fitness
 264 clines (Figure 2(A)). Each diagonal dashed line represents equivalent values of the phenotypic trait
 265 z_t made from different combinations of A_t and E_t . Because the association between phenotypic
 266 trait values and individual absolute fitness was linear and included no additional terms beyond β_0
 267 and β_1 , these dashed lines also represent the population growth rate. The darker the colour of the
 268 line, the larger the value of z_t and the population growth rate. The central solid line contours
 269 represent the bivariate distribution of A_t and E_t at time $t = 0$ when simulations are begun. The

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270 green, red and purple arrows represent phenotypic change. When evolution was cryptic (blue
271 arrow), meaning that neither $\bar{z}_t$, nor $\bar{w}_t$, changed, $\bar{A}_t$ increased at the same rate as $\bar{E}_t$ decreased
272 such that $\Delta\bar{A}_t - \Delta\bar{E}_t = 0$. Because $\bar{w}_t$ did not change in this situation, evolution proceeded rapidly
273 as the denominator in the selection differential remained constant with time. Dynamic forms of
274 the Price equation are required to capture such cryptic evolution. The green line represents
275 dynamics predicted by dynamic forms of the Breeder's equation, with $\bar{A}_t$ and $\bar{w}_t$ evolving, thus
276 resulting in phenotypic change, but $\bar{E}_t$ remaining constant with time. Evolution occurred more
277 slowly than when it was cryptic because $\bar{w}_t$ increased with time, increasing the denominator of
278 the selection differential. The red line captures evolutionary dynamics where the mean breeding
279 value and the mean environmental component of the phenotype change in the same direction,
280 increasing both $\bar{z}_t$ and $\bar{w}_t$. A dynamic form of the Price equation is required to capture such
281 dynamics, and evolution proceeded even more slowly than in the previous two examples, because
282 $\bar{w}_t$ increased even faster. Finally, the purple arrow represents no evolution, but phenotypic
283 change due solely to change in $\bar{E}_t$ – i.e. via non-genetic inheritance (or phenotypic plasticity in
284 iteroparous species). A dynamic form of the Price equation is required to capture such dynamics.

285 We now turn to the more complex Soay sheep model that extends insights from the linear model
286 in three ways: i) it is for an iteroparous life history, ii) it incorporates density-dependence in the
287 survival and recruitment functions (thus reducing the intercepts of the fitness functions with time
288 as evolution proceeds), and iii) it has non-linear fitness functions (meaning that the slope of the
289 association between phenotypic trait values and individual absolute fitness will vary as evolution
290 proceeds).

291 Figure (2(B)) shows the joint dynamics of $\bar{A}_t$ and $\bar{E}_t$ for each of the simulations of body size in
292 female Soay sheep. We do not include fitness clines such as those in Figure (2(A)) because the
293 incorporation of density-dependence complicates the association between $\bar{z}_t$ and $\bar{w}_t$. Before we

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294 explore these results in further detail, it is helpful to appreciate that change in $\bar{z}_t$ can alter both
 295 the elevation (blue dots) and slope (red lines) of the expected association between phenotypic
 296 trait values and individual absolute fitness (red lines; Figure 2(C)). The way a system evolves
 297 depends on both the rate that phenotypic change alters the location of the distribution of
 298 phenotypic trait values on a fitness function, and the rate at which evolution of the population
 299 growth rate alters the form of the fitness function itself.

300 Compared to the baseline model where all four functions were density-dependent, removing
 301 density-dependence from the recruitment and inheritance functions in the modified sheep model
 302 increased the rate of evolution of body size, while removing it from the survival and development
 303 function decreased it (Figure 2(B)). By far the largest effect was caused by perturbing the survival
 304 function.

305 Temporal changes in $\bar{E}_t$ were negative in all models, with the greatest change observed when
 306 density-dependence was removed from the recruitment function (Figure 2(B)). This negative trend
 307 only partially countered the positive trends in $\bar{A}_t$ (Figure 3(A, B)), such that $\bar{z}_t$ increased with time
 308 in all models (Figure 3(B)), but to a lesser extent than $\bar{A}_t$ (Figure 3(A)).

309 $\bar{w}_t$ evolved at similar rates in the baseline model and models where density-dependence was
 310 removed from the recruitment, inheritance and development functions (Figure 3(C)). In contrast,
 311 $\bar{w}_t$ evolved much more slowly when density-dependence was removed from the survival function
 312 (Figure 3(C)), although initial population size was much larger in the density-independent survival
 313 model than in any of the other models (Figure 2(B)). The additive genetic variance increased
 314 slightly with time when density-dependence was removed from the survival, recruitment and
 315 development functions, but remained constant when inheritance was density-independent, as
 316 well as in the baseline model (Figure 3(D)).

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317 Removing density-dependence from each fitness function impacted evolutionary, phenotypic and
 318 population-size change via a number of different routes. First, removing density-dependence
 319 resulted in different starting population sizes and structures (Figures 4(A)-(E)). In the baseline
 320 model and the model with density-dependence removed from the development function, there
 321 was clear bimodality in the distribution of z_t throughout the simulation (Figures 4(A, E)). The
 322 bimodality reflects a population with similar proportions of smaller juveniles and larger adults.
 323 There was weaker evidence of a bimodal distribution at time $t = 1$ for the other three models,
 324 with bimodality weakening as the simulations proceeded (Figures 4(B-D)). In models with density-
 325 independent survival and inheritance, small juveniles were comparatively rare from the start, and
 326 became rarer still over time. In contrast, in the density-independent recruitment model, the
 327 population was initially dominated by small juveniles, but then also became increasingly
 328 dominated by larger adults as the simulation proceeded.

329 The rates of evolution of the phenotypic trait and mean fitness are determined by i) β_1 , ii) $\bar{w}_t$
 330 (which depends upon $n(z_t)$ and the fitness functions), and iii) $var(A_t)$. Because the models were
 331 density-dependent, the mean population growth rate tended towards unity, and differed little
 332 between simulations (Figure 3(C)). Relatively little of the dynamical difference between the
 333 models was consequently due to differences in $\bar{w}_t$ across simulations. Similarly, because the
 334 additive genetic variance remained approximately constant in all simulations (Figure 3(D)), this too
 335 was not a major driver of the dynamics we report from the sheep model.

336 Most of the dynamical differences between the simulations were consequently caused by
 337 processes generating variation in β_1 : the covariance between individual phenotypic trait values
 338 and individual absolute fitness and the phenotypic variance. These two terms tended to show
 339 similar temporal dynamics (Figure 4(F-H)). Consequently, the derivative between mean survival
 340 and the phenotype (the strength and direction of viability selection) remained approximately

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341 constant in the baseline model and the density-independent development and inheritance
342 models, while it trended downwards as the simulation proceeded in the density-independent
343 survival and recruitment models (Figure 4(I)). Similar patterns were observed for the derivative of
344 mean recruitment to the mean phenotype (not shown).

345 These temporal changes in the derivatives of the mean fitness components to the phenotypic trait
346 value resulted in approximately constant survival and recruitment rates in the density-
347 independent survival model, weak decreases in survival rates and weak increases in recruitment
348 rates in the baseline, density-independent development and density-independent inheritance
349 models, and stronger temporal trends for decreased survival and increased recruitment rates in
350 the density-independent recruitment model (Figure 4(J)). In other words, the patterns we report
351 in mean fitness were caused by opposing trends in fitness components in these simulations.

352 The dynamics of β_1 that generated these contrasting patterns across the different simulations
353 were determined by the shape of the fitness function (Figure 2(C)). As density increased, the
354 intercept of the logistic fitness functions became smaller due to the density-dependence terms in
355 the models. In contrast, as mean body size increased, the body size distribution moved to the right
356 on the x-axis of figure 2(C). To some extent, these two processes tended to cancel one another
357 out, such that mean survival and mean recruitment tended to change relatively slowly. The one
358 exception to this pattern is in the density-independent recruitment model, where increasing body
359 size increased recruitment rates but did not lower the intercept of the function. Instead, mean
360 survival rates decreased as density increased because mean fitness evolved.

361 To sum up, our results show that the Soay sheep population is primarily regulated via density-
362 dependent survival. When density was removed from the survival function, the population
363 consequently increased to a large size, in turn reducing recruitment rates, development rates, and

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364 the mean value of the environmental component of the phenotype. Large individuals, however,
365 had very high survival, at a point when the derivative of mean survival to body weight was very
366 shallow – i.e. β_1 was close to zero and evolution of both the mean phenotypic trait and mean
367 fitness was slow.

368 DISCUSSION

369 The structured, evolutionarily-explicit models we developed to examine the dynamics of terms in
370 the Breeder's and Price equations build on existing approaches by Lande (Lande 1982), Barfield et
371 al. (Barfield et al. 2011), Childs et al. (Childs et al. 2016), Coulson et al. (Coulson et al. 2011,
372 Coulson et al. 2017) and Rees and Ellner (Rees and Ellner 2019). The approach is powerful as it
373 allows the simultaneous study of population dynamics and the evolution of phenotypic traits, life
374 histories, and mean fitness (Coulson et al. 2011). In this paper we use dynamic models to generate
375 dynamics of components of the Breeder's and Price equations.

376 Population dynamics and phenotypic evolution are both determined by three drivers: i) the
377 distribution of phenotypic trait values, ii) the fitness functions that determine how expected
378 survival and reproductive rates vary with phenotypic trait values and the environment, and iii)
379 details of the genotype-phenotype map (Lande 1982, Lynch and Walsh 1998). The latter can
380 include phenotypic plasticity, and genetic and non-genetic inheritance (in all its forms). Our
381 models reveal how rates of evolution (defined as $\Delta \bar{A}_t$), of phenotypic change, and of change in the
382 population growth rate, are determined by factors that influence each of these three drivers.

383 In the absence of any processes that alter these drivers with time, genetic change, phenotypic
384 change, and population growth rate change will occur simultaneously (Witting 2002). In the case
385 of a linear association, the rate of change of each will slow with time. This is an example of eco-
386 evolutionary feedbacks. If the association between the phenotypic trait and fitness is exponential,

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387 then the rate of change is constant. This is because the slope of the association between the
388 phenotypic trait and fitness changes with time as the mean phenotype evolves.

389 In natural systems, because populations cannot increase in size indefinitely, the association
390 between the phenotypic trait and fitness must be influenced by processes such as density-
391 dependence or environmental change, to prevent the population growing hyper-exponentially.
392 These processes are typically modelled as being additive (Ellner et al. 2016), and act to reduce the
393 intercept of the association between the phenotypic trait and fitness, as evolution increases the
394 mean value of the phenotypic trait (Smallegange and Coulson 2013). However, these processes
395 can also interact with the phenotypic trait to alter the slope of the association. In our models, the
396 survival and fertility (fitness) functions can capture all these processes (Coulson et al. 2017).

397 Environmental drivers such as density-dependence and climatic variation can influence the rate of
398 evolution, phenotypic change, and the population growth rate, by directly impacting the
399 phenotypic trait via processes other than selection – e.g. phenotypic plasticity and non-genetic
400 inheritance (Nussey et al. 2007, Reed et al. 2011). These processes can affect the rate of evolution,
401 phenotypic trait dynamics, and the ecology of a system. In particular, these drivers can alter the
402 mean or variance of the trait, by changing the environmental component of the trait (Coulson et
403 al. 2017). In our models, these effects are captured by the development and inheritance functions
404 – where the latter also captures genetic inheritance.

405 In natural systems, environmental drivers typically impact fitness, development and inheritance
406 functions simultaneously, and potentially in different ways in different ages and sexes (Simmonds
407 et al. 2019). A consequence of this is that the environment can simultaneously influence evolution,
408 phenotypic trait dynamics, and the population growth rate (e.g. ecology) in multiple, interacting
409 ways (Coulson et al. 2011). For example, density-dependence can alter the association between a

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410 phenotypic trait and fitness, and alter the mean and variance of the environmental component of
411 the phenotype.

412 The Breeder's equation was developed as a model to predict evolution over a single time-step in
413 artificial environments when humans specify the association between the phenotypic trait and
414 fitness to produce a desired number of offspring from those individuals they allow to reproduce
415 (Lush 1943, Falconer 1960, Lynch and Walsh 1998). In addition, they minimise the effect of
416 environmental drivers on the phenotypic trait by typically providing *ad libitum* food and removing
417 predation- and disease-related causes of death. Under these circumstances, the Breeder's
418 equation performs well. Yet, when it has been used as a retrospective tool to explain evolution in
419 natural systems it has typically failed (Merilä et al. 2001). This is because processes that can alter
420 the rate of evolution in natural settings are not included in the model, and are treated as nuisance
421 variables to be corrected for in statistical analyses (Kruuk 2004). However, these processes can
422 influence evolution (and ecology) and should consequently be included in predictive models if
423 they are found to explain significant variation in statistical analyses used to estimate additive
424 genetic variances and the strength of selection. Our approach allows for these processes to be
425 explicitly incorporated into predictive models (Childs et al. 2016, Coulson et al. 2017, Simmonds et
426 al. 2019).

427 The Breeder's equation does not incorporate all the processes that can generate phenotypic
428 change (Morrissey et al. 2010). This observation limits the utility of estimates of additive genetic
429 variances and heritabilities from free-living populations (Kruuk 2004), because, if these processes
430 are important, they should be incorporated into predictive models. The Price equation, on the
431 other hand, does provide an exact description of phenotypic evolution (Price 1970). However, it is
432 a tautology (Heywood 2005), and simply describes the difference between two means. It is
433 consequently a very useful tool to retrospectively decompose phenotypic change into all factors

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434 that contributed to it (Coulson and Tuljapurkar 2008), but it is not dynamically sufficient, and
 435 consequently cannot be used to make predictions of future dynamics. The structured population
 436 models we develop are dynamically sufficient, and provide a dynamic form of the Price equation
 437 (Childs et al. 2004, Coulson et al. 2010). In previous work, we have demonstrated how these
 438 models can be parameterised for real systems (Simmonds et al. 2019).

439 The class of structured models we have developed to predict evolutionary change in natural
 440 systems is widely used in ecology (Caswell 2001). A consequence of this is that our models can be
 441 used to predict simultaneous ecological and evolutionary change (Coulson et al. 2011). Eco-
 442 evolution is frequently described as ecological change generating evolutionary change, which in
 443 turn generates ecological change, and so on *ad infinitum* (Hendry 2016). The logic behind this
 444 interpretation is that ecology and evolution are two separate processes that can influence one
 445 another (Pelletier et al. 2009). Our work challenges this interpretation, as we show that ecological
 446 change and evolution occur simultaneously, as a consequence of ecological change or evolution
 447 altering fitness, development and inheritance functions (see also (Coulson et al. 2011, Childs et al.
 448 2016, Coulson et al. 2017)).

449 Our approach is based on the logic that a population can be represented by a multivariate
 450 distribution of genotypes and phenotypes (Easterling et al. 2000, Ellner and Rees 2006). The
 451 dynamics of this distribution are then determined by survival and reproduction, development and
 452 inheritance functions. We consider these four processes as fundamental. The dynamics of the
 453 distribution's volume (size) are the population dynamics, while the dynamics of the mean
 454 genotype (and sometimes phenotypic trait) capture evolution (Smallegange and Coulson 2013).
 455 These models can also be used to study the dynamics of life history descriptors such as generation
 456 length and lifetime reproductive success (Ellner and Rees 2006, Steiner et al. 2012, Steiner et al.
 457 2014), and to examine life history evolution (Childs et al. 2003, 2004). The fundamental processes

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458 that these models capture can vary as a function of age, sex, location, and genotype, and they can
459 include aspects of the biotic and abiotic environment such as the size and structure of the focal
460 species or of other species in the community, climatic variation, or variation in resource
461 availability (Ellner and Rees 2006, Coulson 2012, Schindler et al. 2015, Ellner et al. 2016, Bassar et
462 al. 2017). These models consequently offer a flexible framework to explore how populations will
463 ecologically and evolutionarily respond to environmental change.

464 In this paper we provide two simple models to demonstrate the utility of our approach. However,
465 more complex models can be developed by extending such models. For example, we can relax the
466 assumption of an additive genotype-phenotype map, and extend models for multiple traits, age-
467 and sex-structure (Schindler et al. 2015, Coulson et al. 2017). It is also possible to construct models
468 of interacting species (Bassar et al. 2017). Although there will doubtless be challenges in
469 parameterising some versions of these models, the approach we describe here offers enormous
470 potential to improve predictions of eco-evolution in natural settings.

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Figure 1. Evolution of (A) the mean breeding value, (B) the mean phenotypic trait, (C) mean fitness, and (D) the additive genetic variance in simple models over 50 generations. The black line represents sim 1), where the additive genetic variance is eroded and the mean and variance of the environmental component of the phenotypic trait remain constant with time. The red lines represent sim 2), where additive genetic variance is not eroded by selection, and the mean and variance of the environmental component of the phenotypic trait remain constant with time. The blue (sim 3)) and green line (sim 4)) are the same as sim 1) and sim 2), except we impose a weak temporal downward trend on the mean environmental component of the phenotypic trait. (E) In models with no temporal trend in the environmental component of the phenotypic trait, the relationship between the mean breeding value and mean fitness is linear, while it is slightly curvilinear in models with temporal trends in E . In contrast, there is (F) a linear association between the mean phenotypic trait and mean fitness in all four models.

Figure 2. The dynamics of phenotypic traits and mean fitness. (A) Because the breeding value and the value of the environmental component of a phenotypic trait sum to produce the phenotypic trait, there are multiple ways the same phenotypic trait value can be produced (dashed grey lines). If the phenotypic trait linearly influences fitness, these phenotypic trait clines also represent fitness clines, generating linear fitness contours. Larger values of the trait, and of mean fitness, are depicted with darker dashed lines. Depending upon the dynamics of the environmental component of the phenotype, selection can fail to climb across contours, or can climb at a range of rates even for the same, constant, derivative of mean fitness to the mean phenotype (i.e. phenotypic slope in the linear fitness function). Because mean fitness remains lowest when evolution is cryptic, all other things being equal, selection will also be strongest, and evolution fastest. Cryptic evolution occurs when non-genetic inheritance or phenotypic plasticity impact the environmental component of the phenotype in a manner that exactly counters gains to the

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591 additive genetic component of the phenotype attributable to selection. (B) The bivariate dynamics
592 of the mean breeding value and the mean environmental component of the phenotypic trait over
593 time in each simulation for the modified sheep model. The starting point of each simulation is
594 towards the bottom of the figure. The increasing width of the thick lines represent how population
595 size (as a consequence of the dynamics of mean fitness) changes as the simulation progresses.
596 Bivariate distributions of the components of the phenotypic trait are drawn as contour plots at
597 time $t=1$, $t=50$ and $t=100$ for the simulation where density-dependence was removed from the
598 recruitment (fitness) function. Evolution is captured by the length of the thick line in the y-axis,
599 while change in the environmental component of the phenotypic trait is captured by change in the
600 x-axis. (C) The derivative of mean fitness to the mean phenotype (red line) can vary as either the
601 mean phenotypic trait increases when fitness functions are non-linear (blue dots), or when
602 environmental drivers such as increasing population density lower the intercept of the fitness
603 function (dashed black lines).

604 Figure 3. Evolution of (A) the mean breeding value, (B) the mean phenotypic trait value, (C) mean
605 fitness, and (D) the additive genetic variance in the modified sheep model. The baseline model
606 (black lines) has negative density-dependence in each function, while the coloured lines represent
607 simulations where density-dependence has been removed from one particular function.

608 Figure 4. Dynamics of the phenotypic trait distribution in the baseline model (A) and in models
609 with negative density-dependence removed from each function (B-E). Distributions are drawn at
610 times $t=1$, $t=50$ and $t=100$. These dynamics are determined in part by selection (the derivative of
611 mean fitness to the mean phenotypic trait value) that consists of (F, G) covariances between the
612 trait and components of fitness, and (H) the phenotypic variance in the trait. (I) derivative of mean
613 survival to the mean phenotype (similar patterns for recruitment not shown) and (J) the temporal
614 dynamics of mean survival and recruitment rates.

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Figure 1

621

622

623 Figure 2.

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624

625 Figure 3.

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626

627 Figure 4.

628

629 **Appendix 1**

630 A key premise of the standard quantitative genetic approach is that the genotype-phenotype map
631 can be described as $z = A + E$ (Falconer 1960). If a phenotypic trait is measured in a particular
632 unit, say length in millimetres, then A and E also take these units. The second premise is that
633 selection operates on the entire phenotype via a selection differential. If we consider a linear
634 fitness function $E(w) = \beta_0 + \beta_1 z$ we can also write $E(w) = \beta_0 + \beta_1(A + E) = \beta_0 + \beta_1 A + \beta_1 E$.
635 This equation says the effect of a one-unit change on fitness in the additive genetic and
636 environmental components of the phenotype is identical.

637 A linear regression slope is defined as the covariance between the response and predictor
638 variable, divided by the variance in the predictor variable. Consequently,

$$639 \quad \bar{w}_t = \beta_0 + \frac{\text{cov}(w, A)}{\text{var}(A)} A + \frac{\text{cov}(w, E)}{\text{var}(E)} E,$$

640 where $\frac{\text{cov}(w, A)}{\text{var}(A)} = \frac{\text{cov}(w, E)}{\text{var}(E)}$. If $\frac{\text{cov}(w, A)}{\text{var}(A)} \neq \frac{\text{cov}(w, E)}{\text{var}(E)}$ then $z \neq A + E$. Instead, the genotype-phenotype
641 map will be of the form $z = A + \gamma E$, where $\gamma \neq 1$. In general, this means that any difference in
642 slopes of the breeding values and the environment components of the phenotype with fitness can
643 only occur if the genotype-phenotype map has changed with time during the period over which
644 data were collected to parameterise models.

645 Some authors have argued that selection can operate in contrasting ways on the environmental
646 and additive genetic components of the phenotype while assuming $z_t = A_t + E_t$ (Morrissey et al.
647 2010). In the most extreme cases they argue that selection on the breeding value is in one
648 direction, while selection on the environmental component of the phenotype is in a contrasting
649 direction such that $\gamma < 0$ while A_t and E_t do not covary (Bonnet et al. 2017). Although
650 mathematically possible, such a genotype-phenotype map seems biologically implausible. We

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651 have been unable to identify a biologically plausible genotype-phenotype map where a one-unit
652 increase in A_t will result in an increase in fitness, while a one-unit increase in E_t will result in a
653 decrease, without invoking some dependence of A_t and E_t on one another.

654 A more plausible genotype-phenotype map would involve phenotypic plasticity, where a breeding
655 value A_t produces a different phenotypic value z_t in different environments. If $z_t = A_t + E_t$ this
656 requires E_t to vary with the environment θ , such that E can be made a function of the
657 environment $E(\theta_t)$. Phenotypic plasticity can then be captured with a number of formulations
658 such as $z_t = A_t + E(\theta_t)$ or $z_t = A_t + E(\theta_t) + \alpha A_t E(\theta_t)$ (Coulson et al. 2017). In the first
659 formulation, the mean and variance of E_t can vary with the environment, but the genotype-
660 phenotype map remains $z_t = A_t + E_t$ such that the slope between the environmental component
661 of the phenotype and fitness equals the slope between the additive genetic component of the
662 phenotype and fitness, but $\bar{E}_t$ change with time, altering the numerical form of the genotype-
663 phenotype map. In contrast, in the second formulation, the breeding value-by-environment
664 interaction means that the slope between fitness and each component of the phenotype differs.
665 Empirical evidence of so-called "selection on the environmental component of the phenotype"
666 (Bonnet et al. 2017) is consequently likely evidence of a genotype-by-environment interaction:
667 something that cannot be detected with widely used statistical analyses of observational data
668 (Kruuk 2004).

669 **Appendix 2**

670 Four approaches can be used to specify how inheritance alters the distribution of breeding values
 671 between selected parents and their offspring. Approach 1: A convolution of the distribution of
 672 breeding values in mothers and fathers is taken to construct a distribution of mid-parental values
 673 assuming random mating. The distribution of mid-parental values is then convolved with a normal
 674 distribution with a mean of 0 and a constant variance to construct the distribution of breeding
 675 values in offspring. Approach 2: Breeding values in the offspring generation are assumed to be
 676 normally distributed, with a mean equal to that of the mid-point parental breeding value
 677 distribution, and a constant variance that does not change across generations. Approach 3: The
 678 distribution of breeding values of parents is operated on by an inheritance function which
 679 maintains the mid-parental mean value and injects Gaussian distributed segregation variance
 680 around each mid-point breeding value. Approach 4: The distribution of breeding values in parents
 681 and offspring is identical. As long as selection does not generate distributions with substantial
 682 skew or kurtosis, the first three of these approaches give very similar predictions. Various
 683 properties of these four approaches are summarised in Table A2.1

684 Table A2.1. Properties of transition functions for breeding values.

	Approach 1	Approach 2	Approach 3	Approach 4
Are the breeding values in offspring normally distributed?	not necessarily	yes	not necessarily	not necessarily

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687 **Appendix 3**

688 The Soay sheep model consisted of the following parameterisations:

689
$$S(A_t + E_t) = \frac{1}{1 + e^{-(0.2392 + 1.1175(A_t + E_t) - 0.0043N_t)}}$$

690
$$R(A_t + E_t) = \frac{1}{1 + e^{-(1.7839 + 0.1090(A_t + E_t) - 0.0032N_t)}}$$

691
$$G(A'_{t+1}|A_t) = A_t$$

692
$$G(E'_{t+1}|E_t) = \text{norm}(\mu_G(E_t), \sigma_G^2(E_t)),$$

693 where $\mu_G(E_t) = 10.603 + 0.6049E_t - 0.0026N_t$ and $\sigma_G^2(E_t) = 2.874 - 0.0124E_t$

694
$$D(A'_{t+1}|A_t) = \text{norm}(\mu_D^\omega(A_t), \sigma_D^2(A_t)),$$

695 where $\mu_D^\omega(A_t)$ is the mean breeding value post-fertility selection, and $\sigma_D^2(A_t)$ is the additive
696 genetic variance in offspring at birth, which we assumed to be constant and Gaussian distributed.

697 Finally,

698
$$D(E'_{t+1}|E_t) = \text{norm}(\mu_D(E_t), \sigma_D^2(E_t)),$$

699 where $\mu_D(E_t) = 9.8065 + 0.2544E_t - 0.0069N_t$ and $\sigma_D^2(E_t) = 4.581 - 0.1196E_t$.

700 We started each simulation with mean values of $\bar{A}_t = 5.5$ and $\bar{E}_t = 19.5$, an additive genetic
701 variance of 4 and a variance in the environmental component of 6. Because the genetic variances
702 influence the rate of evolution, and selection operate on the entire phenotype, the model results
703 are insensitive to the starting values of $\bar{A}_t$ and $\bar{E}_t$. Rather it is their sum that determines dynamics.

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704 In an initial (unreported) model we tracked a multivariate distribution of age-related breeding
 705 values with genetic correlations close to unity. We simplified the model to so each age-related
 706 trait has the same breeding value – i.e. genetic correlations are equal to unity. The simplification
 707 made no material difference to the results we report.