Fitness functions, genetic and non-genetic inheritance, and why ecological dynamics and evolution are inevitably linked

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ABSTRACT

Fitness functions are at the heart of ecology and evolution as they simultaneously determine both population dynamics and the strength of selection. We link the Breeders and Price equations with structured population models constructed from fitness functions to show how ecological and evolutionary dynamics are intimately linked, and to characterise all of the ways that environmental variation can influence selection and evolution. We show i) how multi-generational predictions of evolution are sensitive to assumptions about phenotypic plasticity and non-genetic inheritance, ii) that factors that reduce the per time-step population growth rate such as negative density-dependence and antagonistic species interactions are generally expected to accelerate rates of evolution compared to cases when they are absent, iii) that evolution is expected to occur fastest when it is cryptic (all other things being equal) and iv) that eco-evolutionary dynamics are likely widespread and can be studied using evolutionarily explicit structured population models.

INTRODUCTION

Biologists now appreciate that ecological and evolutionary dynamics can occur on the same time scale, and this has spawned the field of eco-evolution (Hairston Jr et al. 2005). Research in this field has flourished with a profusion of reviews (Post and Palkovacs 2009) (Hendry 2016), empirical analyses of observational (Coulson et al. 2011, Travis et al. 2014) and experimental (Yoshida et al. 2003, Cameron et al. 2013) data, and theory papers (Cotto et al. 2017, Coulson et al. 2017). Yet it is not always clear how work in eco-evolution links to existing ecological and evolutionary understanding. In this paper, we show how key theory in ecology and evolutionary biology can be linked by using a series of simple models constructed around fitness functions that can be empirically estimated.

There is a large literature on eco-evolution, and a number of modelling approaches have been championed. These approaches range from coupled equations describing the dynamics of population size and the mean of a phenotypic trait, through individual-based models, to those that track the dynamics of distributions of genotypes and heritable phenotypes (Yoshida et al. 2003, Hairston Jr et al. 2005, Coulson et al. 2011, DeLong and Gibert 2016, Coulson et al. 2017, Doebeli et al. 2017). Parallel developments among modellers working in discrete (Coulson et al. 2011) and continuous (Doebeli et al. 2017) time has concluded that a powerful approach to modelling eco-evolution is to use models of the dynamics of entire distributions of genotypes and phenotypes where fitness is an emergent property rather than defined *a priori*. At the heart of these models are fitness functions that describe the association between heritable individual characteristics with survival and reproduction that can include aspects of the biotic and abiotic environment. These models can be formulated to be dynamic forms of the Breeders' and Price equations that are at the heart of evolutionary theory (Coulson et al. 2010, Childs et al. 2016). However, the

consequences of these linkages ecological and evolutionary understanding have not widely explored (Lowe et al. 2017).

Fitness functions describe how phenotypic traits influence fitness or its survival and recruitment components (Parker and Smith 1990). These functions are central to understanding both ecological (Easterling et al. 2000) and evolutionary dynamics (Lande 1982) as they determine population growth, and the strength of selection. Because of the key role that fitness functions play in both ecology and evolution, they offer a logical starting point from which to develop eco-evolutionary theory that is consistent with current understanding. Yet not all eco-evolutionary theory is derived from such a starting point. Equations can be coupled to describe the dynamics of population size and the mean of a phenotypic trait (Patel et al. 2018), but the coupling can be phenomenological such that it does not capture known biological constraints.

Evolutionary theory has demonstrated that the mean of a phenotypic trait and the population growth rate can change simultaneously as a consequence of the shape of fitness functions (Fisher 1930). In particular, for annual species, individual fitness is lifetime reproductive success (LRS) and mean LRS is the population growth rate: selection on a phenotypic trait can lead to phenotypic evolution as well as an increase in mean LRS and consequently the population growth rate (Fisher 1930). In spite of this realisation, little evolutionary theory has investigated the simultaneous evolution of phenotypic traits and population growth for non-annual life histories (but see (Lande 1982, van Tienderen 2000)) for two reasons. First, weak selection is often assumed such that the dynamics of populations occur on a shorter time scale to the dynamics of phenotypic trait means (Lande 1982). Such an assumption simplifies model analysis by separating ecological and evolutionary dynamics, but in cases where ecological and evolutionary change occurs on the same time scales, models of weak selection can provide only limited insight. Second, evolutionary models frequently define selection as a fixed per-generation parameter rather than an emergent

consequence of the form of the survival and reproductive fitness functions (e.g. (Charlesworth 1994)). Under this assumption it is straightforward to model evolution but it is problematic to define the population dynamics as a function of parameters describing selection.

Evolutionary models incorporate rules of genetic inheritance, be they clonal or sexual; ecological models do not. Instead, ecological models assume either no covariance between parental and offspring phenotypic trait values (Easterling et al. 2000), or incorporate a phenomenological association that is identified from statistical analyses (Coulson 2012). However, many ecological models are constructed from fitness functions (Ellner et al. 2016). A number of authors have used ecological models built from fitness functions to simultaneously consider the selective, phenotypic and population dynamical consequences of altering fitness functions (Coulson et al. 2010, Childs et al. 2016). These models have demonstrated, for both annual and iteroparous species, that the population growth rate and the strength of selection on a phenotypic trait vary simultaneously when fitness functions are altered. However, unlike evolutionary models, these models cannot be used to study rates of evolution (Chevin 2015). In spite of this, some evolutionary inference can be gained via sensitivity analyses of ecological models (Caswell 2001) where a parameter in the model is altered in a way that mimics evolution and the simultaneous impact of the change on population growth and phenotypic trait means is investigated (Traill et al. 2014).

Ecological and evolutionary models constructed from fitness functions have consequently revealed that selection, phenotypic traits and population dynamics can change simultaneously when the form of fitness functions is altered. However, many empiricists verbally articulate a view of eco-evolution whereby ecological change results in evolution, which in turn results in further ecological change, and so on *ad infinitum* (Pelletier et al. 2009, Hendry 2016). Such a narrative is not consistent with ecological and evolutionary understanding, but it is clear why it has arisen. The majority of theoretical models linking the dynamics of populations and the mean phenotype

assume continuous time (Hairston Jr et al. 2005, Terhorst et al. 2018). One equation describes how population size within a species changes as a function of the mean phenotypic trait value, while another captures change in the mean phenotypic trait value as a function of population size. Because time is continuous and population and phenotypic change is instantaneous, population size and the mean phenotypic trait change together. However, some authors have interpreted time as if it were discrete in these models, leading to a verbal narrative that phenotypic change and population change happen in a stepwise linear sequence rather than together (Hendry 2016). A better way to visualise simultaneous eco-evolutionary change is to ask how biotic or abiotic change impacts fitness functions, and how change to these functions impacts ecological and evolutionary dynamics (Coulson 2012).

Empiricists often work in discrete time because they collect and analyse data from population censuses collected at regular time intervals (Clutton-Brock 1988). For example, capture-mark-recapture analyses take a mix of individual-, population- and environment-level attributes and use them to explain variation in survival rates from one time step to the next, while simultaneously correcting for imperfect detection probabilities (White and Burnham 1999). Approaches such as these can be used to estimate discrete time fitness functions, and these functions can be incorporated into discrete time population dynamic models (Lefkovitch 1965, Easterling et al. 2000, Caswell 2001, Ellner and Rees 2006) to produce point estimates of the simulated processes at fixed intervals of time.

Discrete time ecological models project over fixed time intervals such as a week, month, or year. Discrete time evolutionary models typically provide projections on a per generation time scale (Falconer 1960, Lynch and Walsh 1998). Models such as the Breeders' and Price equations are consequently usually parameterised using LRS. Fisher (1930) demonstrated that LRS is individual absolute fitness for species with an annual life history, and some empiricists have extended this

logic to iteroparous species (Morrissey et al. 2010). However, in iteroparous species, where different individuals can live for different lengths of time and breed on a different number of occasions and at different ages (Clutton-Brock 1988), mean LRS is not mean fitness or the population growth rate (Grafen 1988). For iteroparous species it is consequently not straightforward (and may be impossible) to link population dynamics and evolution using LRS as a measure of fitness as can be done for annual life histories (Sæther and Engen 2015). It seems improbable that a general theory of eco-evolution that is applicable to iteroparous species can be derived from models of LRS. An alternative approach is needed. Discrete-time ecological models provide a logical starting point (Childs et al. 2016).

Discrete time structured ecological models of iteroparous species based on fitness functions have recently been extended to incorporate rules of genetic inheritance (Barfield et al. 2011, Coulson et al. 2011, Childs et al. 2016, Coulson et al. 2017, Rees and Ellner 2019). These models can be shown to be generalised, dynamic forms of the Breeders' and Price equations for iteroparous species that can be easily parameterised with data collected from regular population censuses (Coulson et al. 2010, Childs et al. 2016). When viewed from this perspective the models reveal novel insights into eco-evolution. We demonstrate this by first constructing and analysing simple models before proceeding to more realistic models that are developed by extending existing models of Soay sheep (*Ovis aries*) (Coulson 2012).

More specifically we develop eco-evolutionary models of strong selection. We start by considering the Breeders' (Falconer 1960) and Price (Price 1970) equations of evolution of the mean phenotype before extending these static models to form evolutionarily explicit dynamic demographic models based on fitness functions that incorporate phenotypic development and genetic and non-genetic inheritance. We do this by dividing the modelled phenotypic traits into their additive genetic and environmental components (Falconer 1960). An additive function

determines how the two components combine to form the phenotypic trait, before fitness functions operate on the entire trait, altering the bivariate distribution of both components (and the conditional distributions of each) (Coulson et al. 2017). Additional functions then describe how both the additive genetic and environmental components of the phenotypic trait are inherited (the latter through non-genetic inheritance), and how the environmental component develops throughout an individual's life, potentially as a function of the external biotic or abiotic environment. Once constructed, models can be iterated and the dynamics of selection, population size or growth rate, the phenotypic trait, and its additive genetic (i.e. evolution) and environmental components (i.e. phenotypic plasticity) investigated.

DEVELOPMENT OF THEORY

Selection

In seasonal breeders, absolute fitness of individual i over a time-step $w_{i,t}$ is always the sum of a reproductive component $r_{i,t}$ and a survival component $s_{i,t}$: $w_{i,t} = r_{i,t} + s_{i,t}$. The reproductive component $r_{i,t}$ is the number of offspring produced between time *t* and *t+1* that survive to enter the population at time *t+1*, scaled by the genetic relatedness between parent and offspring, while the survival component $s_{i,t}$ equals one if the focal individual itself survives to time *t+1*, and zero otherwise (Watson and Galton 1875). The definition holds for non-seasonal breeders as long as all individuals born over the time-step can be considered as being within the same cohort.

In populations where immigration and emigration can be ignored, the mean of individual absolute fitness is the per-time-step population growth rate $\bar{w}_t$. In addition, the mean of the reproductive components of individual fitness is the mean reproductive rate $\bar{r}_t$, and the mean of the survival component is the mean survival rate $\bar{s}_t$. Consequently $\bar{w}_t = \bar{r}_t + \bar{s}_t$ (Coulson et al. 2005).

Selection on a phenotypic trait z at time t is measured with a selection differential $\omega_{z,t}$. $\omega_{z,t}$ describes the difference between the mean phenotypic trait value of selected individuals at time t $\bar{z}_{\omega,t}$ and the mean phenotypic trait value of the entire population prior to selection at time t $\bar{z}_t$: $\omega_{z,t} = \bar{z}_{\omega,t} - \bar{z}_t$ (Price 1970). $\omega_{z,t}$ can be written as a quantity that includes $w_{i,t}$, $\bar{w}_t$ and $z_{i,t}$ – the phenotypic trait value of individual i at time t:

$$\omega_{z,t} = \frac{\frac{1}{N_t}\sum_{i=1}^{N_t}\left[w_{i,t} - \bar{w}_t\right]\left[z_{i,t} - \bar{z}_t\right]}{\bar{w}_t} \tag{1}$$

where N_t is the population size at time t. Equation (1) can be expanded into its reproductive and survival components such that

$$\omega_{z,t} = \frac{\bar{r}_t}{\bar{w}_t}\frac{\frac{1}{N_t}\sum_{i=1}^{N_t}\left[r_{i,t} - \bar{r}_t\right]\left[z_{i,t} - \bar{z}_t\right]}{\bar{r}_t} + \frac{\bar{s}_t}{\bar{w}_t}\frac{\frac{1}{N_t}\sum_{i=1}^{N_t}\left[s_{i,t} - \bar{s}_t\right]\left[z_{i,t} - \bar{z}_t\right]}{\bar{s}_t}. \tag{2}$$

The first term on the right-hand side of equation (2) is a fertility selection differential and the second is a viability selection differential (Falconer 1960). $\frac{1}{N_t}\sum_{i=1}^{N_t}\left[w_{i,t} - \bar{w}_t\right]\left[z_{i,t} - \bar{z}_t\right]$ are covariances, and express them as a function $cov(w_t, z_t)$. Note that functions that take arguments are denoted with round parentheses. We now drop the subscripts i to simplify notation.

It is clear from equations (*1*) and (*2*) that over a time-step the population growth rate $\bar{w}_t$ and the strength of selection $\omega_{z,t}$ are related, and that the strength of selection is expected to change with the population growth rate. The reason for this is that the denominator of relative fitness over a time step is the population growth rate. However, will the population growth rate $\bar{w}_t$ change in response to selection and evolutionary change? The answer is (usually) yes, but understanding why requires formulating the Breeders' equation.

The Breeders' equation

We start by writing the Breeders' equation in terms of individual absolute fitness (Heywood 2005). We assume an annual life history and an annual population census such that viability selection can be ignored and $\bar{w}_t = \bar{r}_t$,

$$\Delta\bar{z}_t = \frac{cov(w_t, A_t + E_t)}{\bar{w}_t}\frac{var(A_t)}{var(A_t + E_t)}. \quad (3)$$

Where $\Delta\bar{z}_t$ is the change in the mean phenotypic trait value over a generation (=time-step for our annual life history) (Lush 1943). We have now split the phenotypic trait z into its additive genetic component A_t (the breeding value) and an environmental component E_t such that $z_t = A_t + E_t$. We assume that z_t does not have any non-additive genetic components, such as dominance or epistatic components or maternal effects (Falconer 1960). The variance in the breeding values at time t is denoted $var(A_t)$ – the additive genetic variance.

Equation (*3*) states that a proportion $\frac{var(A_t)}{var(A_t+E_t)} = h^2$ (the narrow-sense heritability) of selection is realised as evolution. This 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. The equation consequently assumes that $\Delta\bar{z}_t$ is entirely attributable to change in $\bar{A}_t$. We can rewrite equation (3) as

$$\Delta\bar{z}_t = \frac{\beta_1 var(A_t)}{\bar{w}_t}, \quad (4)$$

where β_1 is the slope of a linear regression between individual absolute fitness and the individual phenotypic trait values (also the derivative $\frac{d\bar{w}_t}{dz_t}$). 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). Mean individual fitness at time t, $\bar{w}_t$, is dependent upon the distribution of the

phenotypic trait and the form of the fitness function. For a linear fitness function $w_t = \beta_0 + \beta_1 z_t$ we can write

$$\bar{w}_t = \beta_0 + \beta_1 \bar{z}_t. \tag{5}$$

For non-linear fitness functions mean fitness will not necessarily be expected fitness at the mean value of the phenotypic trait due to non-linear averaging (Ellner et al. 2016). However, as long as $\bar{w}_t$ systematically changes with $\bar{z}_t$ as evolution alters $\bar{z}_t$, we can see that $\bar{w}_t$ (which is also the population growth rate) will also change. For linear functions we can write:

$$\Delta\bar{z}_t = \frac{\beta_1 var(A_t)}{\beta_0 + \beta_1[\bar{A}_t + \bar{E}_t]}. \tag{6}$$

The equations above assume that selection is the only process that alters $\bar{A}_t$ or $\bar{E}_t$ over a time-step, and this is one reason why the Breeders' equation does not provide a complete description of the dynamics of the mean of a phenotypic trait. What processes other than selection might influence evolution? Non-genetic inheritance, ontogenetic development, and phenotypic plasticity provide three possibilities. These can be captured, along with selection, with the Price equation.

The Price equation

The Price equation (Price 1970) provides a complete description of the change in the mean of a phenotypic trait over a time-step. As before, we start by assuming an annual population census of a species with an annual life history such that $\bar{w}_t = \bar{r}_t$,. The Price equation states that

$$\Delta\bar{z}_t = \frac{cov(w_t, z_t)}{\bar{w}_t} + [\bar{z}_{t+1} - \bar{z}_{\omega,t}] \tag{7}$$

where $\bar{z}_{\omega,t}$ is the mean phenotypic trait of individuals selected to produce offspring (i.e. the parents), and $\bar{z}_{t+1}$ is the mean phenotypic trait of offspring. The first term on the right-hand side is

a selection differential, while the second term describes how imperfect inheritance (through mutation, recombination and non-genetic processes) alters the mean phenotypic trait between times t and $t+1$.

As we go on to develop dynamic models, it becomes useful to separate out the Price equation into terms that operate on the breeding value A_t, and on the environmental component E_t of the phenotype. We start by rewriting equation (*6*) as,

$$\Delta\bar{z}_t = \frac{cov(w_t, A_t + E_t)}{\bar{w}_t} + \left[\bar{A}_{t+1} - \bar{A}_{\omega,t}\right] + \left[\bar{E}_{t+1} - \bar{E}_{\omega,t}\right]. \quad (8)$$

The first term on the right-hand side describes how selection alters components of the mean phenotype. The second term describes how imperfect genetic inheritance could alter the mean breeding value between offspring and their parents. The third term describes how non-genetic inheritance including ecological processes such as variation in resource acquisition alters the mean environmental component of the phenotypic trait between offspring and their parents. Note that we can separate $\frac{cov(w_t,A_t+E_t)}{\bar{w}_t} = \frac{cov(w_t,A_t)}{\bar{w}_t} + \frac{cov(w_t,E_t)}{\bar{w}_t}$. This is useful to demonstrate linkages between the Price and Breeders' equation (below), but can erroneously suggest that selection at a point in time can operate independently on different components of the phenotype. It cannot if we assume $z_t = A_t + E_t$. Selection operates on the entire phenotype, altering the distribution of the components that combine to produce it. For selection to operate in contrasting ways on each component of the phenotype as sometimes argued (Morrissey et al. 2010, Bonnet et al. 2017) it is necessary to specify a genotype-phenotype maps where $z_t \neq A_t + E_t$ (Appendix 1).

How do the Price and Breeders' equation relate to one another? The Breeders' equation is a special form of the Price equation (Eqn. 8) that assumes that $[\bar{A}_{t+1} - \bar{A}_{\omega,t}] = 0$ 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 $\bar{A}_t$ (i.e. there is

no transmission bias), and that $\bar{E}_t$ at birth remains identical in each generation. The first of these assumptions is reasonable for large populations; the second is justified if the environmental component of the phenotypic trait is determined by completely random developmental noise (Falconer 1960). If the environmental component of the phenotypic trait is dependent upon non-random aspects of the external environment, then the assumption will be violated (Kruuk et al. 2002). If this is the case, the Price equation is required. We can write down a form of the Price equation based on the Breeders' equation by combining equations (*4*) and (*8*): $\Delta\bar{z}_t = \frac{\beta_1 var(A_t)}{\bar{w}_t} + \left[\bar{E}_{t+1} - \bar{E}_{\omega,t}\right]$. This formulation assumes that $[\bar{A}_{t+1} - \bar{A}_{\omega,t}] = 0$ as in the Breeder's equation.

We now relax the annual life cycle assumption and expand the Price equation into its survival and reproductive components:

$$\Delta\bar{z}_t = \frac{cov(s_t, A_t + E_t)}{\bar{w}_t} + \qquad (9a)$$

Effects of viability selection on components of the phenotype.

$$+\frac{cov(r_t, A_t + E_t)}{\bar{w}_t} + \qquad (9b)$$

Effect of fertility selection on components of the phenotype.

$$+\frac{\bar{r}_t}{\bar{w}_t}[\bar{A}'_{t+1} - \bar{A}_{\omega_r,t}] + \qquad (9c)$$

Effect of genetic inheritance on the mean breeding value. $\bar{A}'_{t+1}$ is the mean breeding value amongst recruits; $\bar{A}_{\omega_r,t}$ is the mean breeding value among selected parents. Equals zero: inheritance does not change the mean breeding value between selected parents and their offspring.

$$+\frac{\bar{s}_t}{\bar{w}_t}[\bar{A}''_{t+1} - \bar{A}_{\omega_s,t}] + \qquad (9d)$$

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 amongst individuals that will survive from time *t* to time *t+1*. Equals zero: breeding values do not change within individuals as they age.

$$+\frac{\bar{r}_t}{\bar{w}_t}[\bar{E}'_{t+1} - \bar{E}_{\omega_r,t}] + \qquad (9e)$$

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 the selected parents and their offspring.

$$+\frac{\bar{s}_t}{\bar{w}_t}[\bar{E}''_{t+1} - \bar{E}_{\omega_s,t}]. \qquad (9f)$$

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

In this formulation we assume that all processes remain constant with age. This assumption could be relaxed using the approach in Coulson and Tuljapurkar (2008).

From equation (*9*) it is clear that change in the mean of a phenotypic trait over a time-step is dependent on the strength of viability and fertility selection on the phenotypic trait, and on how phenotypic plasticity and imperfect inheritance might alter its mean breeding value and environmental component. Components 9(c) and 9(d) are usually assumed to be zero, as inheritance is not assumed to change the mean breeding value between selected parents and their offspring (9(c)), and as breeding values are not assumed to change within individuals as they age (9(d)).

Making the Breeders' and Price equations dynamic

Each of the terms in the static Breeders' and Price equations are emergent properties of the distribution of the phenotypic trait (and its components) at time t, fitness functions, and functions that determine the terms in equations 9(c) to 9(f) (Coulson et al. 2010, Childs et al. 2016). In order to make the Price and Breeders' equations dynamic, it is consequently necessary to specify fitness functions that determine selection, as well as functions that determine development and inheritance of the environmental component of the phenotypic trait, and inheritance of the additive genetic component (Coulson et al. 2017). These functions then iterate forward the

dynamics of the distribution of $z_t = A_t + E_t$. We start by considering the dynamics of the univariate distribution of z_t for an annual species before extending the model to track the bivariate distribution of A_t and E_t for iteroparous life histories.

A reproductive fitness function, $R(z_t)$, can be used to map the distribution of the individual phenotypic traits z_t at time t, $n(z_t)$, to a new distribution of the phenotypic trait at time $t+1$, $n(z'_{t+1})$ (Ellner et al. 2016),

$$n(z'_{t+1}) = \int H(z'_{t+1}|z_t)R(z_t)n(z_t)dz\,. \tag{10}$$

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

To produce a model that projects terms in the Breeders and Price equation over a time step, z_t can be replaced with $A_t + E_t$ (Coulson et al. 2017). First, write,

$$n(A'_{t+1}, E'_{t+1}) = \int H(A'_{t+1}, E'_{t+1}|A_t, E_t)R(A_t + E_t)n(A_t, E_t)dAdE. \tag{11}$$

The transition function $H(A'_{t+1}, E'_{t+1}|A_t, E_t)$ can be formulated to capture the second term on the right-hand side of the Breeders' equation (3) or the last two terms on the right-hand side of the Price equation (8), and so can describe genetic or non-genetic inheritance rules. A dynamic form of the Breeders' equation (3) requires $H(A'_{t+1}, E'_{t+1}|A_t, E_t)$ to be specified such that it produces a distribution of $n(A'_{t+1}, E'_{t+1})$ that has means of $\bar{A}'_{t+1} = \bar{A}_{\omega,t}$ and $\bar{E}_t = \bar{E}_{t+1}$ and a

variance-covariance matrix $\begin{pmatrix} var(A_t) & 0 \\ 0 & var(E_t) \end{pmatrix}$ where $var(A_t)$ can be selected to be a constant or to erode with time as a function of selection, and $var(E_t)$ is constant (Childs et al. 2016, Coulson et al. 2017, Rees and Ellner 2019). There are a number of ways this can be achieved (Appendix 2). Any formulation of $H(A'_{t+1}, E'_{t+1}|A_t, E_t)$ that results in $\bar{A}'_{t+1} \neq \bar{A}_t$ and/or $\bar{E}_t \neq \bar{E}_{t+1}$ provides a dynamic form of the Price equation (8). Once the transition and fitness functions are parameterised, derivations from Coulson *et al.* (2010) can then be used to create time series of $\Delta\bar{z}_t$, β_0, β_1, $var(A_t)$, $\bar{A}_t$ and $\bar{E}_t$ for different parameterisations of $H(A'_{t+1}, E'_{t+1}|A_t, E_t)$ and $R(A_t + E_t)$ and different starting values of $n(A_t, E_t)$.

Equations (*10*) and (*11*) can be extended to incorporate per-time step survival and recruitment functions to allow models to be constructed for iteroparous species. Models now include two transition functions: an development function $G(z'_{t+1}|z_t)$ operating on surviving individuals, and an inheritance function $D(z'_{t+1}|z_t)$ that captures the similarity between parental and offspring traits (Easterling et al. 2000, Ellner and Rees 2006, Coulson 2012). The development function operates with a survival fitness function $S(z_t)$, while the inheritance function operates with the recruitment fitness function $R(z_t)$:

$$n(z'_{t+1}) = \int [D(z'_{t+1}|z_t)R(z_t) + G(z'_{t+1}|z_t)S(z_t)]n(z_t)dz. \qquad (12)$$

Equation (*12*) can be extended to project forwards the dynamics of the phenotypic trait partitioned into A_t and E_t. Selection operates on the phenotypic trait $z_t = A_t + E_t$, potentially altering the size, location and shape of the conditional distributions of both A_t and E_t, before inheritance and development functions then operate on the post-selection distribution of A_t and E_t:

$$n(A'_{t+1}, E'_{t+1}) = \int [D(A'_{t+1}, E'_{t+1}|A_t, E_t)R(A_t + E_t) + G(E'_{t+1}|A_t, E_t)S(A_t + E_t)]n(A_t, E_t)dA_t dE_t. \qquad (13)$$

How does this equation relate to equation (9)? Term 9(a) is determined by $S(A_t + E_t)n(A_t, E_t)$, term 9(b) by $R(A_t + E_t)n(A_t, E_t)$, terms 9(c) and 9(e) by $\int D(E'_{t+1}|A_t, E_t)R(A_t + E_t)n(A_t, E_t)dA_t dE_t$ and terms 9(d) and 9(f) by $\int G(E'_{t+1}|A_t, E_t)S(A_t + E_t)n(A_t, E_t)dA_t dE_t$ (Childs et al. 2016).

RESULTS

From equation (*6*) it is clear that the rate of evolution of a trait over a time step will i) scale linearly with the additive genetic variance for the trait (Falconer 1960, Lynch and Walsh 1998), ii) will reduce as the elevation (intercept) of the fitness function (β_0) is increased, iii) will slow as the mean phenotype is increased (assuming $\bar{A}_t$ and $\bar{E}_t$ are both positive), and iv) has a complex association with the linear slope of the phenotype with fitness (β_1) as this term appears in both the numerator and denominator. All these results follow from the fact that as absolute fitness of the population increases, the among individual variance in absolute fitness remains approximately unchanged, which means the relative fitness differences are declining. If we used an exponential fitness function we would achieve constant relative fitness and a constant rate of evolution.

The transition terms in the Price equation provide a way to capture processes other than selection that influence either $\bar{E}_t$ or $\bar{A}_t$ (Price 1970, Coulson and Tuljapurkar 2008). For example, if $\Delta\bar{A}_t - \Delta\bar{E}_t = 0$ then $\Delta\bar{Z}_t = 0$ and phenotypic change due to evolution is countered by change in the environmental component of the phenotype, a phenomenon termed cryptic evolution (Merilä et al. 2001a).

A simple evolutionarily explicit IPM

A simulation model of an annual semelparous species with a linear fitness function (equation (11)) provides graphical representation of the theoretical insights. We ran four model scenarios. In

scenarios 1) and 3) selection erodes additive genetic variation, while in scenarios 2) and 4) additive genetic variation is not eroded by selection. In scenarios 1) and 2) the mean and variance of the environmental component of the phenotype remains constant across generations, while in scenarios 3) and 4) the mean of the environmental component declines with time such that $\bar{E}_t = 10 - 0.05t$. Scenarios 1) and 2) are dynamic forms of the Breeders' equation, while scenarios 3) and 4) are dynamic forms of the Price equation. The last two scenarios capture a process where some aspect of the environment can determine the dynamics of the environmental component of the phenotype (Kruuk et al. 2002).

Evolution, defined as a change in the mean breeding value, was fastest when additive genetic variance was not eroded by selection, and when there was a negative temporal trend in $\bar{E}_t$ (Figure 1(A)). The negative temporal trend in $\bar{E}_t$ accelerated the rate of evolution via its effect on reducing mean fitness. In spite of accelerating the rate of evolution, the trending values of $\bar{E}_t$ with time slowed the rate of phenotypic change as positive change in $\bar{A}_t$ was countered by negative change in $\bar{E}_t$ (Figure 1(B)). Mean fitness evolved fastest when additive genetic variance was not eroded, and $\bar{E}_t$ did not decline with time (Figure 1(C)). Increased levels of the additive genetic variance in the phenotypic trait increased the rate of change in $\bar{w}_t$. Linear selection reduced the additive genetic variance if it was not replaced in each generation (Figure 1(D)). When there was no temporal trend in $\bar{E}_t$, the association between the mean breeding value and mean fitness was linear (Figure 1(E)), while it was slightly curvilinear when $\bar{E}_t$ trends with time. As the fitness function was linear, there was by definition a linear association between the mean phenotypic trait and mean fitness, with a slope of β_1 (Figure 1(F)).

We can graphically illustrate the evolutionary, phenotypic trait, and fitness dynamics of this simple model with a plot of A_t against E_t that includes fitness clines (Figure 2(a)). Each diagonal dashed line represents equivalent values of the phenotypic trait made from different combinations of A_t

and E_t. Because the fitness function is linear and includes no additional terms beyond β_0 and β_1, these dashed lines also represent fitness. The darker the colour of the line, the larger the value of z_t and fitness. The central solid line contours represent the bivariate distribution of A_t and E_t at time $t = 0$ when simulations are begun. The coloured arrows represent phenotypic change. When evolution is cryptic and $\Delta\bar{A}_t - \Delta\bar{E}_t = 0$, then A_t increases at the same rate as E_t decreases and neither z_t, nor $\bar{w}_t$ change. Because $\bar{w}_t$does not change (blue arrow), evolution proceeds rapidly as the denominator in the selection differential remains constant with time. Dynamics forms of the Price equation are required to capture such cryptic evolution. The green line represents dynamics predicted by dynamic forms of the Breeders' equation with $\bar{A}_t$ and $\bar{w}_t$, evolving, but the $\bar{E}_t$ remaining constant with time. Evolution occurs more slowly than when it is cryptic because $\bar{w}_t$ increases with time, increasing the denominator of the selection differential. The red line captures evolutionary dynamics where change in the mean breeding value and the mean environmental component of the phenotype act in the same direction, increasing both $\bar{Z}_t$ and $\bar{w}_t$. A dynamic form of the Price equation is required to capture such dynamics, and evolution proceeds even more slowly than in the previous two examples, because $\bar{w}_t$ increases even faster. Finally, the purple arrow represents no evolution, but phenotypic change due solely to change in $\bar{E}_t$ – i.e. via non-genetic inheritance (or phenotypic plasticity in iteroparous species). A dynamic form of the Price equation is required to capture such dynamics.

A more realistic model using data from Soay sheep

The assumption of linear fitness (equation (*5*)) in the previous simulation is unrealistic because litter size and survival rates are bounded. In addition, in variable environments, survival or transition functions for the environmental component of the phenotype depend on environmental factors such as the population size or phenotypic or age structure of the focal species or of an interacting one (Kruuk et al. 2002, Bassar et al. 2017). Moreover, although breeding values remain

constant with age, the environmental component of the phenotypic trait can change within individuals – phenotypic plasticity (Falconer 1960). We consequently developed a density-dependent model, where fitness is separated into its survival and recruitment components, and where the environmental component of the phenotype can develop within surviving individuals, and can vary between parents and their offspring.

T*o* examine these complexities, we constructed a non-linear, iteroparous Soay sheep model that extends insights from the simple model in three ways. First, we consider an iteroparous life history (equation (*13*)), second, the incorporation of density-dependence in the survival and recruitment functions has the effect of reducing the intercepts of the fitness functions with time as $\overline{w}_t$ evolves and population size increases, and third, the non-linear fitness functions mean that the derivative of mean fitness to the phenotype (i.e. the slope β_1 in equation (4)) can vary as evolution proceeds. Density dependence was included in all functions in the baseline model. We then removed the effect of density in each function in the model in turn.

Figure (2(b)) shows the joint dynamics of $\bar{A}_t$ and $\bar{E}_t$ for each of the simulations. We do not include fitness clines such as those in Figure (2(a)) because the incorporation of density-dependence complicates the association between $\bar{Z}_t$ and $\overline{w}_t$, with the different models exhibiting different associations (Figure 2(c)). The blue points demonstrate that as evolution proceeds $\bar{Z}_t$ can change, but the mean of a fitness component can remain constant if the fitness function changes with time. However, if $\overline{w}_t$ does evolve at some rate with z_t, the derivative β_1 (red lines) can change with time if fitness functions are non-linear. Both of the processes operate in the modified Soay sheep model.

Removing density-dependence from the recruitment and inheritance functions in the modified sheep model increased the rate of evolution of body size, while removing it from the survival and

development function decreased it (Figure 2(b)). By far the largest effect was caused by perturbing the survival function.

Temporal changes in $\bar{E}_t$ were negative in all models due to density-dependence, with the greatest rate of change observed when density-dependence was removed from the recruitment function (Figure 2(b)). In all models, $\bar{E}_t$ trended to smaller values. This negative trend partially countered the positive trends in $\bar{A}_t$, such that $\bar{z}_t$ increased with time in all models (Figure 3(b)), but to a lesser extent than change in $\bar{A}_t$.

$\bar{w}_t$ (the per-time step population growth rate) evolved at similar rates in the baseline model and models where density-dependence was removed from the recruitment, inheritance and development functions. In contrast, $\bar{w}_t$ evolved much more slowly when density-dependence was removed from the survival function (Figure 3(c)), although initial population size was much larger in the density-independent survival model than in any of the other models (Figure 2(b)). The additive genetic variance increased slightly with time when density-dependence was removed from the survival and recruitment functions, but remained constant when development and inheritance were density-independent (Figure 3(d)).

Removing density-dependence from each fitness functions impacted evolutionary, phenotypic and population size change via a number of different routes. First, removing density-dependence resulted in different starting population sizes and structures (Figure 4(a)-(e)). In the baseline model and the model with density-dependence removed from the inheritance function, there was clear bimodality in the distributions $z_t$throughout the simulation (Figures 3(a,e)). The bimodality reflects a population with similar proportions of smaller juveniles and larger adults. There is weaker evidence of a bimodal distribution at time $t = 1$ for the other three models, with bimodality weakening as the simulations proceeded (Figures (3(b-d)). In the models with density-

independent survival and inheritance, small juveniles are comparatively rare, and their frequency decreases as the simulations proceed. In contrast, in the density-independent recruitment model, the population is dominated by small juveniles and becomes increasingly so as the simulation proceeds.

The rates of evolution of the phenotypic trait and mean fitness are determined by i) β_1, ii) $\overline{w}_t$ (which depends upon $n(z_t)$ and the fitness functions), and iii) $var(A_t)$. Because the models are density-dependent, the mean population growth rate tends towards unity, and differs little between the simulations (Figure 3(c)). Relatively little of the dynamical difference between the models is consequently due to differences in $\overline{w}_t$ across simulations. Similarly, because the additive genetic variance remains approximately constant in all simulations (Figure 3(d)) this too is not a major driver of the dynamics we report from the sheep model.

Most of the dynamical differences between the simulations are consequently caused by processes generating variation in β_1: the covariance between individual phenotypic traits and individual absolute fitness (equation 1) and the phenotypic variance. These two terms tend to show similar temporal dynamics (Figure 4(f, g, h)) resulting in the derivative between the mean survival and the phenotype (the strength and direction of viability selection) remaining approximately constant in the baseline model and the density-independent growth and inheritance function models (Figure 3(i)). In contrast, the derivative trended downwards as the simulation proceeded in the density-independent survival and recruitment models (Figure 3(i)). Similar patterns were observed for the derivative of mean recruitment to the mean phenotype (not shown).

These temporal changes in the derivatives of the mean fitness components to the phenotypic trait value resulted in approximately constant survival and recruitment rates in the density-independent survival model, weakly trending decreases in survival rates and weakly trending

increases in recruitment rates in the baseline, density-independent development and density-independent inheritance models, and stronger temporal trends for decreased survival and increased recruitment rates in the density-independent recruitment model (Figure 4(j)). In other words, the patterns we report in mean fitness are caused by opposing trends in fitness components in these simulations.

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

The Soay sheep population is primarily regulated via density-dependent survival. When density is removed from the survival function, the population consequently increases to a large size, in turn reducing recruitment rates, development rates, and the mean value of the environmental component of the phenotype. Large individuals, however, have very high survival, at a point when the derivative of mean survival to body weight is very shallow – i.e. β_1 is close to zero and evolution of both the mean phenotypic trait and mean fitness is slow.

4. DISCUSSION

In a paper that is proving highly influential, Doebeli et al. (2017) constructed continuous time models of the dynamics of a heritable character distribution. He noted that fitness was an emergent property of birth and death processes that themselves are determined by individual attributes and the environment. By defining fitness functions that link individual attributes to birth and death and including aspects of the biotic and abiotic environment into these functions, Doebeli et al. (2017) demonstrates that these models provide a powerful tool to investigate cultural evolution, multi-level selection, social evolution and inclusive fitness, and eco-evolution. Discrete-time versions of Doebeli's (2017) approach have been used to link life history, population dynamics, quantitative genetics, and population genetics (Childs et al. 2004, Barfield et al. 2011, Coulson et al. 2011, Steiner et al. 2014, Coulson et al. 2017). Doebeli et al. (2017) are correct that structured demographic models, in both continuous and discrete time, provide remarkably powerful tools to unify many disparate areas of biology (see also (Lowe et al. 2017)). In this paper, we build upon these observations by demonstrating that terms in the Price and Breeders' equation are emergent properties of the functions that link individual attributes to birth and death, and demonstrate how different assumptions about the form of these functions influence values of parameters in these two equations that have been central to evolution for over half a century.

The dynamic forms of the Breeders' and Price equations we develop from demographic models build on existing approaches by Lande (Lande 1982), Barfield et al. (Barfield et al. 2011), Childs et al.(Childs et al. 2016), Coulson et al. (Coulson et al. 2011, Coulson et al. 2017) and Rees and Ellner (Rees and Ellner 2019). The approach is powerful as it allows the simultaneous study of population dynamics with the evolution of phenotypic traits, life histories, and mean fitness (Coulson et al.

2011). In this paper we use simple dynamic models to demonstrate how our approach generate dynamics of terms in the Breeders' and Price equations.

The first insight our work provides concerns eco-evolution. A widely championed view of eco-evolution is that ecological change generates evolutionary change and so on *ad infinitum* (Hendry 2016). The logic behind this interpretation is that ecology and evolution are two separate processes that can influence one another (Pelletier et al. 2009). Our approach reveals that ecological change and evolution occur simultaneously when an environmental process alters either the fitness, development or inheritance functions in demographic models (see also (Coulson et al. 2011, Childs et al. 2016, Coulson et al. 2017)). For example, the reduction in size of a predator population may increase the elevation of fitness functions, simultaneously increasing the population growth rate and reducing the strength of selection and the rate of evolution.

Our view of eco-evolution is based on the logic that a population can be represented by a multivariate distribution of genotypes and phenotypes (Easterling et al. 2000, Ellner and Rees 2006). The dynamics of this distribution are then determined by fitness, development and inheritance functions. The dynamics of the distribution's volume (size) are the population dynamics, while the dynamics of the mean genotype (and sometimes phenotypic trait) capture evolution (Smallegange and Coulson 2013). These models can also be used to study the dynamics of life history descriptors such as generation length and LRS (Ellner and Rees 2006, Steiner et al. 2012, Steiner et al. 2014), and examine life history evolution (Childs et al. 2003, 2004). The fitness, development, and inheritance functions that underpin these models can vary as a function of age, sex, location, and genotype, and they can include aspects of the biotic and abiotic environment such as the size and structure of the focal species or of other species in the community, or climatic variation (Ellner and Rees 2006, Coulson 2012, Schindler et al. 2015, Ellner et al. 2016, Bassar et al. 2017).

There are two criticisms that have been levelled at the demographic modelling approach that we use. First, that models tend to be data driven rather than mechanistic (Chevin 2015, Janeiro et al. 2017), and second, that the data required to parameterise models for natural systems can be prohibitive. It is correct that most models of real systems have been phenomenological rather than mechanistic. However, following observations that particular mechanisms were not included in early models, the structured modelling approach has been extended to incorporate a number of mechanisms. Genetic inheritance (Coulson et al. 2011, Childs et al. 2016), dynamic energy budgets (Smallegange et al. 2017), and resource dependence (Bassar et al. 2017) have now been explicitly included into models, with ongoing work including additional mechanisms.

The more complex a model is, the harder it will be to parameterise, and analyse. However, it is possible to collect the required data from many systems, and complex models have been parameterised, and analysed, for a number of them (Merow et al. 2014, Rees et al. 2014, Ellner et al. 2016). We are not advocating that simpler models (or even individual-based models that are often even more parameter-rich than the ones we develop) be abandoned. Instead, we are demonstrating how structured models can be remarkably powerful at linking ecology and evolution. The choice of model to construct always depends upon the question, the data available, and the desired degree of analytical, or numerical, tractability. All models are wrong, and criticising any modelling approach for what it does not include is easy; the challenge is selecting the approach that is least wrong for the question at hand.

The question we are interested in is how might perturbations impact the fitness, development, and inheritance functions that constitute demographic models, and how do such impacts simultaneously influence population dynamics, phenotypic trait dynamics, and evolution? To study evolution, we examine how environmental variation can impact terms in the Breeders' and Price equations.

Our results reveal that there are multiple ways that the environment can impact evolution. The first route is via its impact on mean fitness that can influence the strength of selection. We explicitly separate the covariance between a phenotypic trait and relative individual fitness – a quantity central to evolution – into the covariance between the phenotypic trait and absolute individual fitness, divided by mean absolute individual fitness (Heywood 2005). This is a mathematically trivial alteration to standard derivations, but is biologically illuminating, as over a time step, mean individual absolute fitness is the population growth rate (Watson and Galton 1875, Engen et al. 2009). Population ecologists have long studied the population growth rate (Caswell 2001), and by separating it out of the selection differential, the understanding they have garnered can be used to gain insight into the dynamics of selection. In particular, population ecologists have revealed how intraspecific competition for resources, interspecific interactions, and the abiotic environment can impact the distribution of per-time step population growth rates (Turchin 2003): these drivers have the potential to impact the temporal dynamics of selection via the temporal dynamics of mean fitness.

Writing relative fitness in terms of absolute fitness also allows us to reformulate the Breeders' and Price equations so that the numerator of the equation now contains the derivative of mean fitness to the phenotypic trait value. Much ecological research has revealed how phenotypic traits such as body size are associated with demographic rates (components of absolute fitness), and how these associations can vary with aspects of the biotic and abiotic environment (Merow et al. 2014, Ellner et al. 2016). In general, recruitment and survival rates tend to be higher in good environments. However, because these fitness components are bounded, as their means increase, the derivative of fitness to phenotypic trait values is (often) expected to decrease as favourable environments act to increase the intercept of fitness functions. Because favourable environments also result in higher per-time step population growth rates, we may expect selection to be weaker

in favourable rather than in harsh environments. Such a pattern has been observed in some cases (Wilson et al. 2006) but is not universal (Siepielski et al. 2017). Examining how the derivative of components of fitness to phenotypic traits changes with aspects of the environment across a range of species will help to understand why.

The third route via which the environment can impact selection is via change in the mean of the environmental component of the phenotype (Nussey et al. 2007). Non-genetic change in the mean phenotype via phenotypic plasticity or non-genetic inheritance can impact the rate of phenotypic change (Reed et al. 2011, Coulson et al. 2017), which in turn can influence both mean fitness (Figure 2(a)), or the derivative of mean fitness to the phenotype (Figure 2(c)).

We only consider additive genotype-phenotype maps such that $z_t = A_t + E_t$ where A_t and E_t are on the same scale of measurement (Fisher 1930). When genotype-by-environment interactions occur, the environment can influence evolution (and consequently ecological dynamics) via an alternative route (Via and Lande 1985). Some authors have argued that selection acts on the environmental and additive genetic components of the phenotype in contrasting ways (Morrissey et al. 2010, Bonnet et al. 2017), thus invoking a genotype-by-environment interaction. Indeed, it seems plausible that genotype-by-environment interactions are widespread in natural settings. Our approach can be extended to include non-additive genotype-phenotype maps (Coulson et al. 2017).

Given the multiple routes via which environmental variation can impact ecology and evolution it is perhaps unsurprising how difficult it has proven to predict evolution in variable environments (Merilä et al. 2001b), yet understandable why models such as the Breeders' equation do tend to make more accurate predictions in the more constant environments under which most artificial selection regimes are imposed (Lynch and Walsh 1998). Our approach does provide a way to

explore how different forms of environmental variation operating via different components of the life history might simultaneously impact ecological dynamics and evolution.

The modelling framework we work within allows the effects of phenotypic plasticity and non-genetic inheritance on evolution, phenotypic change, and ecology to be explored. Results are consistent with current quantitative genetic understanding, but our approach significantly advances our ability to understand how environmental variation, and processes other than selection such as phenotypic plasticity and non-genetic inheritance, can impact evolutionary outcomes over multiple time-steps. Because life-history descriptors like generation length and life expectancy can be calculated from integral projection models (Steiner et al. 2012, Steiner et al. 2014), it is also possible to explore how phenotypic evolution impacts life history. The next steps involve constructing models for interacting species, incorporating multiple traits, and parameterising models for a range of systems.

Materials and Methods

All models were coded in R.

A simple evolutionary IPM

We start with a model of the form of equation (*11*) with the phenotypic trait separated into its additive genetic and environmental components $z_t = A_t + E_t$, but where fitness is not separated into its recruitment and survival components. We assume a linear fitness function and iterate $n(A_t, E_t)$ given the following parameterisation,

$$w(A_t + E_t) = -0.2 + 0.05(A_t + E_t) \tag{14}$$

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

Each simulation is run for 50 generations. For each simulation we report the rate of evolution (defined as $\Delta\bar{A}_t$), the rate of change in the mean phenotype $\Delta\bar{z}_t$, the population growth rate (mean fitness $\bar{w}_t$), trends in the additive genetic variance, covariances between $\Delta\bar{A}_t$ and $\Delta\bar{z}_t$ with $\bar{w}_t$ and all terms in equations (*1*)-(*9*).

A more complex Soay sheep model

We took a published density-dependent IPM of the dynamics of body size from the female component of an individually marked population of Soay sheep (*Ovis aries*) living on the island of Hirta in the St. Kilda archipelago in Scotland (Coulson 2012). The published IPM was of the form of

equation (*12*), and was modified to be of the form of equation (*13*). Functions and parameter values are provided in Appendix 3.

The Soay sheep model consisted of the following parameterisations:

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

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

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

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

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

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

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

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

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

We started each simulation with mean values of $\bar{A}_t = 5.5$ and $\bar{E}_t = 19.5$, an additive genetic variance of 4 and a variance in the environmental component of 6.

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

The parameterisation above describes the baseline model. We ran four simulations where we set the density-dependence parameter to 0 in either the survival fitness function, the recruitment fitness function, the development or inheritance functions for E_t. Although this is a large perturbation, it reveals some interesting dynamics. We then compared the dynamics of the breeding value, the mean phenotypic trait, and mean fitness across the simulations.

None of the simulations reached an equilibrium because of the positive slopes for the phenotypic trait in the fitness functions and some additive genetic variance is always maintained.

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 red lines represent sim 2), where additive genetic variance is not eroded by selection, and the mean and variance in the environmental component of the phenotypic trait remain constant with time. The black line represents sim 1), where the additive genetic variance is eroded and the mean and variance in the environmental component of the phenotypic trait remain constant with time. The green (sim 4)) and blue line (sim 3)) are the same as sim 2) and sim 1), except we impose a weak temporal trend in the mean of the 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, when non-genetic inheritance or phenotypic plasticity, impacts the environmental component of the phenotype in a manner that exactly counters gains to the additive genetic component of the phenotype attributable to selection. (B) The bivariate dynamics of the mean breeding value and the mean environmental component of the phenotypic trait over time in each simulation for the modified sheep model. The starting point of each simulation is towards the bottom of the figure. The increasing size of the thick lines represent how population size (as a consequence of the dynamics of mean fitness) changes as the simulation progresses. Bivariate distributions of the components of the phenotypic trait are drawn as contour plots at time t=1, t=50 and t=100 for the simulation where density was removed from the recruitment (fitness) function. Evolution is captured by the length of the line in the y-axis, while change in the environmental component of the phenotypic trait is captured by change in the x-axis. (C) The derivative of mean fitness to the mean phenotype (red line) can vary as either the mean phenotypic trait increases when linear functions are non-linear, or when environment drivers such as an increase in density act to lower the intercept of the fitness function (black lines).

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

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

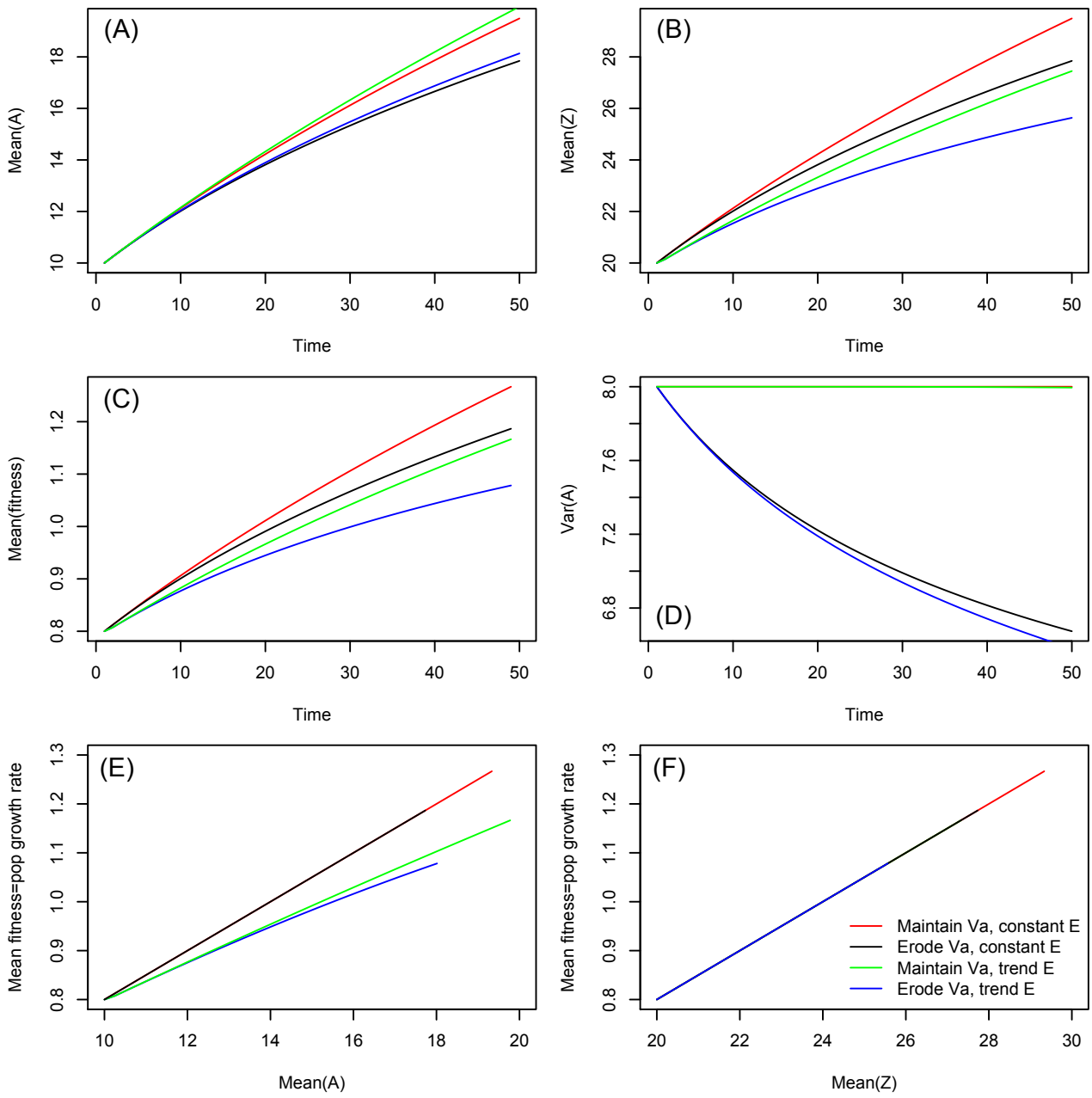
(A)
Mean(A)
Time
(B)
Mean(Z)
Time
(C)
Mean(fitness)
Time
(D)
Var(A)
Time
(E)
Mean fitness=pop growth rate
Mean(A)
(F)
Mean fitness=pop growth rate
Mean(Z)
Maintain Va, constant E
Erode Va, constant E
Maintain Va, trend E
Erode Va, trend E

Figure 1

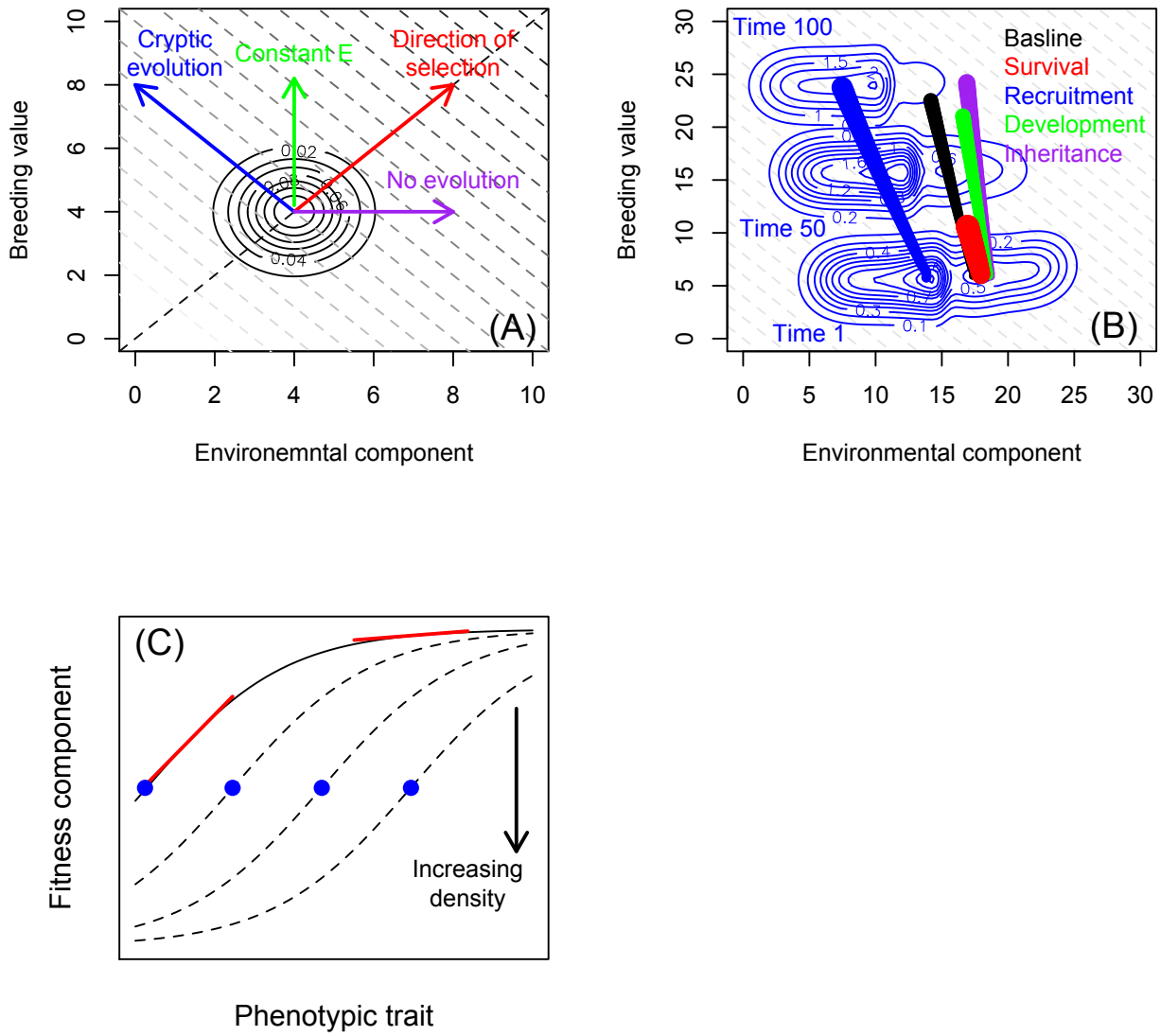
Cryptic evolution
Constant E
Direction of selection
No evolution
(A)
Breeding value
Environemntal component
Time 100
Time 50
Time 1
Basline
Survival
Recruitment
Development
Inheritance
(B)
Breeding value
Environmental component
(C)
Fitness component
Increasing density
Phenotypic trait

Figure 2.

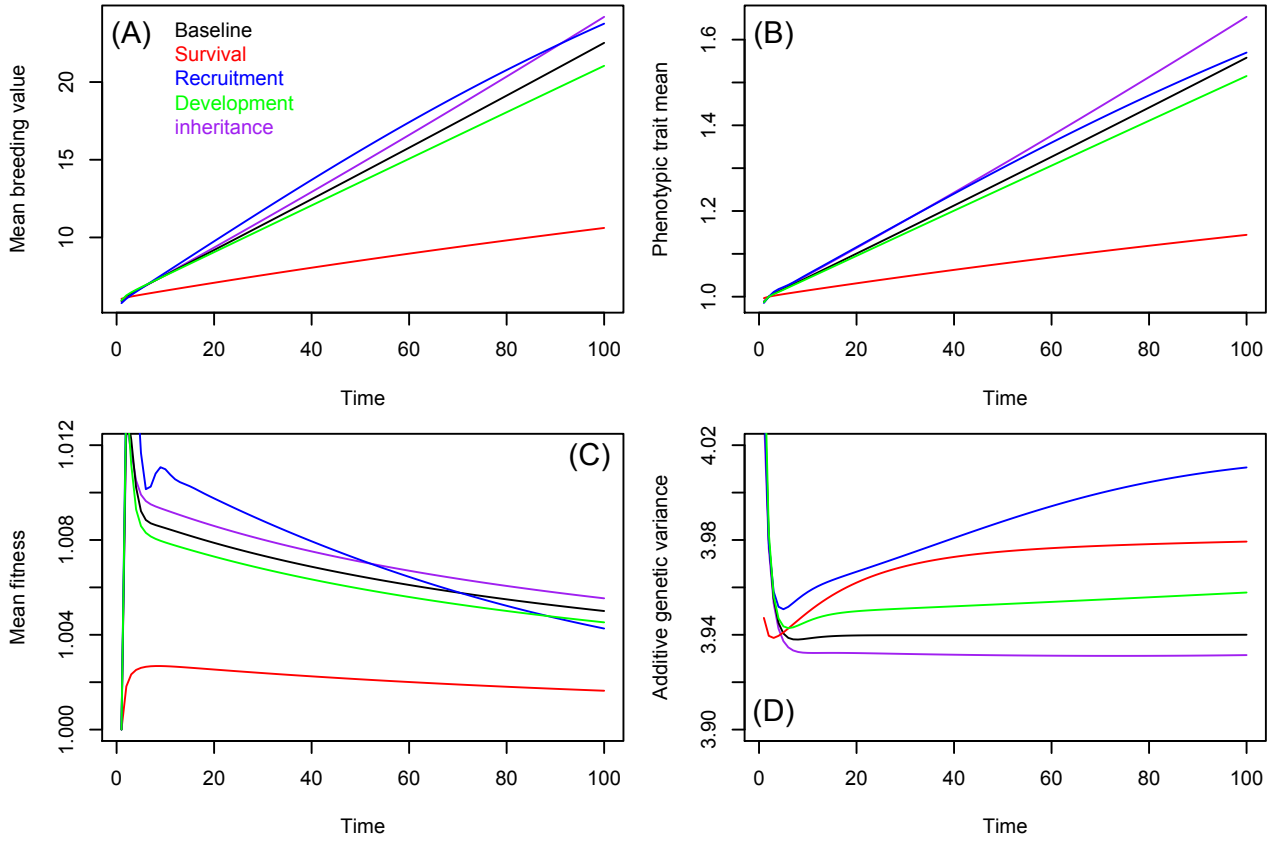
(A)
Baseline
Survival
Recruitment
Development
inheritance
Mean breeding value
10
15
20
0
20
40
60
80
100
Time
(B)
Phenotypic trait mean
1.0
1.2
1.4
1.6
0
20
40
60
80
100
Time
(C)
Mean fitness
1.000
1.004
1.008
1.012
0
20
40
60
80
100
Time
(D)
Additive genetic variance
3.90
3.94
3.98
4.02
0
20
40
60
80
100
Time

Figure 3.

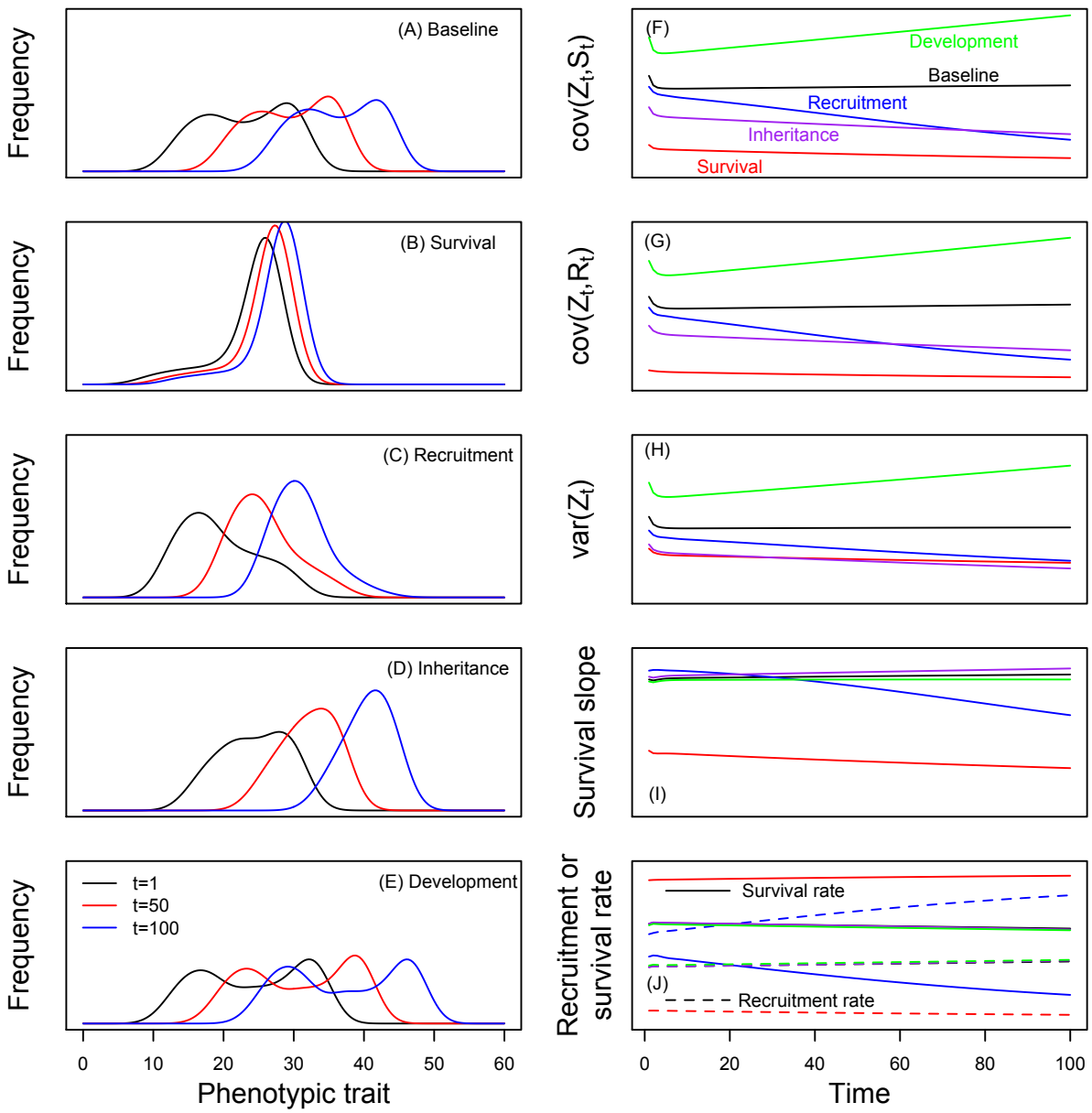
Frequency
(A) Baseline
(B) Survival
(C) Recruitment
(D) Inheritance
(E) Development
t=1
t=50
t=100
0
10
20
30
40
50
60
Phenotypic trait
cov(Zt,St)
(F)
Development
Baseline
Recruitment
Inheritance
Survival
cov(Zt,Rt)
(G)
var(Zt)
(H)
Survival slope
(I)
Recruitment or survival rate
Survival rate
(J)
Recruitment rate
0
20
40
60
80
100
Time

Figure 4.

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Appendix 1

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

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

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

where $\frac{cov(w,A)}{var(A)} = \frac{cov(w,E)}{var(E)}$. If $\frac{cov(w,A)}{var(A)} \neq \frac{cov(w,E)}{var(E)}$ then $Z \neq A + E$ but will be of the form $Z = A + \gamma E$ where $\gamma \neq 1$.

Some authors have argued that selection can operate in contrasting ways on the environmental and additive genetic components of the phenotype while assuming $z_t = A_t + E_t$ (Morrissey et al. 2010). In the most extreme cases they argue that selection on the breeding value is in one direction, while selection on the environmental component of the phenotype is in a contrasting direction such that $\gamma < 0$ while A_t and E_t do not covary (Bonnet et al. 2017). Although mathematically possible, such a genotype-phenotype map seems biologically implausible. We have been unable to identify a biologically plausible genotype-phenotype map where 1 unit increase in A_t will result in an increase in fitness while a 1 unit increase in E_t will result in a decrease without invoking some dependence of A_t and E_t on one another.

A more plausible genotype-phenotype map would involve phenotypic plasticity where a breeding value A_t produces a different phenotypic value z_t in different environments. If $z_t = A_t + E_t$ this requires E_t to vary with the environment θ, such that E can be made a function of the environment $E(\theta_t)$. Phenotypic plasticity can then be captured with a number of formulations 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 formulation, the mean and variance of E_t can vary with the environment, but the genotype-phenotype map remains $z_t = A_t + E_t$ such that the slope between the environmental component of the phenotype and fitness equals the slope between the additive genetic component of the phenotype and fitness. In contrast, in the second formulation, the breeding value-by-environment interaction means that the slope between fitness and each component of the phenotype differs. Empirical evidence of so-called "selection on the environmental component of the phenotype" (Bonnet et al. 2017) is consequently likely evidence of a genotype-by-environment interaction: something that cannot be detected with widely used statistical analyses of observational data (Kruuk 2004).

Appendix 2

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

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

Does the distribution of breeding values in mid-parents and offspring have the same mean?	yes	yes	yes	yes
Does the distribution of breeding values in parents and offspring have the same shape?	No	No	No	yes

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