Selection and evolution of causally-covarying traits

Michael B. Morrissey

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School of Biology, University of St Andrews

contact
email: michael.morrissey@st-andrews.ac.uk
phone: +44 (0) 1334 463738
fax: +44 (0) 1334 463366
post: Dyers Brae House
      School of Biology, University of St Andrews
      St Andrews, Fife, UK, KY16 9TH

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Abstract

When traits cause variation in fitness, the distribution of phenotype, weighted by fitness, necessarily changes. The degree to which traits cause fitness variation is therefore of central importance to evolutionary biology. Multivariate selection gradients are the main quantity used to describe components of trait-fitness covariation, but they quantify the direct effects of traits on (relative) fitness, which are not necessarily the total effects of traits on fitness. Despite considerable use in evolutionary ecology, path analytic characterizations of the total effects of traits on fitness have not been formally incorporated into quantitative genetic theory. By formally defining “extended” selection gradients, which are the total effects of traits on fitness, as opposed to the existing definition of selection gradients, a more intuitive scheme for characterizing selection is obtained. Extended selection gradients are distinct quantities, differing from the standard definition of selection gradients not only in the statistical means by which they may be assessed and the assumptions required for their estimation from observational data, but also in their fundamental biological meaning. Like direct selection gradients, extended selection gradients can be combined with genetic inference of multivariate phenotypic variation to provide quantitative prediction of microevolutionary trajectories.
Introduction

Natural selection is the phenomenon where effects of traits on fitness necessarily result in within-generation changes in the distribution of phenotype, weighted by fitness (Godfrey-Smith, 2007). When heritable traits are selected, and in the absence of antagonistic selection of genetically correlated traits, the effect of a trait on fitness also results in changes in the distribution of breeding values. This change of the distribution of breeding values transmits within-generation phenotypic change to the next generation. This fundamental evolutionary mechanism has led to a range of approaches and perspectives on how to explain phenotype-fitness relationships in terms of causal and correlative effects, and how to quantify the ultimate evolutionary consequences of selection (Endler, 1986; Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Price, 1970; Robertson, 1966; Schluter, 1988; Shaw and Geyer, 2010). The main partitioning of selection is the decomposition of a selection differential $S$, the covariance of a trait with relative fitness, into that resulting from direct effects, as represented by selection gradients $\beta$, and correlative effects (Walsh and Lynch, 2012), resulting from selection of phenotypically-correlated traits. Generally, selection gradients are characterized as describing the causal effects of a trait on fitness, i.e., representing “selection for” (Endler, 1986; Sober, 1984), rather than the total association of traits and fitness (“selection of”), and so are often the most central parameters in empirical and theoretical studies of natural selection.

Arnold (1983) provided the basis for a thought experiment that can be used to elucidate the importance of the distinction between direct and total causal effects of traits on fitness. Consider two characters: an aspect of morphology, and an aspect of organismal performance, and also their relationships with fitness. Assume that morphology influences fitness via an effect on performance, which itself influences fitness, but that morphology does not affect fitness independently of performance. Figure 1 illustrates these relationships graphically. Arnold (1983) considered the problem of inference of selection and prediction of evolution of morphology, especially in light of the fact that it may be hard to simultane-
ous and meaningfully measure morphology and fitness on a sufficiently large number of individuals to make robust inferences in any given single study. Arnold (1983) emphasised how to use Wright’s (1921; 1934) path rules to make inferences of the selection of morphology, given separate inferences about the effects of morphology on performance, and of performance on fitness. van Tienderen (2000) extended the approach, showing how demographic principles can be used to evaluate performance (i.e., demographic rates, life history traits) - fitness relationships, and how to relate these to other traits, such as morphology.

In the morphology-performance-fitness model, a selection gradient of morphology can be obtained as the product of the coefficients describing the morphology-performance and performance-fitness relationships. The product of this selection gradient and the genetic variance of the morphological trait yields a prediction of evolutionary change in performance. Multivariate evolutionary prediction follows in a standard manner in order to predict evolutionary trajectories of multiple aspects of morphology (Arnold, 1983; Lande, 1979). However, simultaneous evaluation of selection and evolution of morphology and performance is not so straightforward.

If morphology influences performance, three important consequences follow. First, the phenotypic covariance (partial covariance, formally, but these are equivalent in this simple case) of morphology and performance will be non-zero. Second, the genetic covariance will be non-zero; essentially, if morphology affects performance, breeding values for the morphological trait are consequentially a component of the breeding values for performance. Third, the effect of morphology on fitness will be non-zero, providing that performance indeed influences fitness. This illustrates two related and potentially non-intuitive features of selection gradients that necessitate care in their interpretation. First, selection gradients are not necessarily interpretable simply as ‘effects’ of a traits fitness. Rather, selection gradients describe the direct components of effects of traits on fitness. In the morphology-performance-fitness model, the selection gradient for morphology is zero, if morphology and

1van Tienderen (2000), page 676, suggests that causal relationships among the set of focal phenotypic traits can be accommodated, but does not provide guidance as to how.
performance are considered simultaneously, but the true value is non-zero if performance is not simultaneously considered. So, second, the selection gradient is partially a function of the (arbitrary) inclusion of traits that may mediate a focal character’s ultimate effect on fitness.

The dependence of selection gradients on the choice (or constraints) of what traits are included in a study is not necessarily a case of selection being erroneously estimated, i.e., it is distinct from the “missing variable” problem (Hadfield, 2008; Morrissey et al., 2010; Rausher, 1992). A univariate analysis of selection, genetics, and predicted evolution of morphology, where the genetic variance of morphology is multiplied by a selection gradient representing the total regression of relative fitness on morphology, would provide a correct evolutionary prediction. Similarly, a bivariate analysis, where the genetic variance-covariance matrix of morphology and performance was post-multiplied by a vector containing the partial regressions, where the partial regression of relative fitness on morphology is zero, would yield a correct evolutionary prediction as well. The “missing variable problem” would occur if an unmeasured variable existed that caused covariance of morphology and/or performance with fitness, beyond the causal effects of the traits themselves (Morrissey et al., 2010).

Clearly, partitioning total selection, i.e. the selection differential, $S$, into direct and indirect selection neither results in full characterization of the different possible aspects of relationships among traits and fitness, nor does it match intuition. A selection coefficient describing the total effect, not simply the direct effect, of a trait on fitness will have substantial interpretive advantages. Definition of this third selection coefficient, effectively an “extended-sense” selection gradient $\eta$, allows the primary division of types of selection coefficients to be based on causation, rather than on direct versus indirect effects. As such, total selection is thought of as the result of causal effects of a focal trait on fitness, summarized by $\eta$, and indirect selection due to incidental correlations. $\eta$, the total causal

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*Or more generally, the partial derivatives of relative fitness with respect to the two phenotypic traits, averaged over the distribution of the traits. This is an issue of what selection gradients mean, not an issue of the methodological means by which estimated selection gradients are obtained.*
effect of a trait on fitness, can then be further considered in terms of its component direct
and indirect but causal components. In addition to matching intuition about causation,
selection and evolution, empirical evaluation of $\eta$ for a given focal trait or set of focal traits
(say, morphology) is invariant to whether or not other traits (i.e., performance, life history)
that mediate the focal trait’s or traits’ ultimate effect(s) on fitness are simultaneously
considered.

Path analysis (Wright, 1934) of natural selection provides a means of simultaneously
modelling how traits affect fitness and how phenotypic traits affect one another (Walsh
and Lynch, 2013). As such, path analysis can provide insights, both quantitative and
qualitative, into the mechanisms by which phenotypic traits cause fitness variation (Latta
and McCain, 2009; Scheiner et al., 2000). The morphology-performance-fitness model is a
simple path model. The procedure of obtaining the total effect of morphology on fitness as
the product of the regressions of fitness on performance and performance on morphology
is a simple application of Wright’s path rules. The qualitative benefits of a path analytic
perspective for making inferences about natural selection have been discussed from several
perspectives (Arnold, 1983; Conner, 1996; Crespi and Brookstein, 1989; Kingsolver and
Schemske, 1991; Latta and McCain, 2009; Scheiner et al., 2000; Shipley, 1997). While
these authors have appreciated and clearly demonstrated the value of characterizing the
causal effects of traits on one another and on fitness, the distinction between compound
path-based selection coefficients and (traditional, direct) selection gradients has not been
made clear. Consequently, some conclusions have been drawn based on the notion that
path-based inferences of selection and traditional selection gradients represent different in-
ferences (statistical, philosophical, or both) of the same biological quantity (Scheiner et al.,
2002, 2000), but this is not the case. In addition to the previous lack of formal consider-
ation of the mathematical and philosophical distinctions and commonalities between path
coefficients and selection gradients in the traditional sense, the role of path coefficients in
quantitative genetic theory has not yet been formally considered.

I show how path analysis-based extended selection gradients relate quantitatively to
genetic variation and evolutionary change by deriving an equation that relates extended selection gradients to genetic variation in order to quantitatively predict evolutionary change. I then provide two examples of the estimation and interpretation of extended selection gradients in an evolutionary quantitative genetic context. In the first, I present a comparison of extended and direct selection gradients of Soay sheep *Ovis aries* (Clutton-Brock and Pemberton, 2004) neonatal traits. This provides a simple situation where the biological meanings of the traits, and of their relationships with fitness, are fairly intuitive, allowing illustration of the interpretive differences between $\beta$ and $\eta$. I then show the incorporation of the path analytic approach into both the decomposition of phenotypic and genetic (co)variances, and the simultaneous quantification of selection gradients, using data from a laboratory rearing experiment based on a population of recombinant inbred lines derived from contrasting ecotypes of the wild oat *Avena barbata* (Gardner and Latta, 2008; Latta and McCain, 2009). The examples demonstrate (i) how $\beta$ and $\eta$ can differ qualitatively, including how they can take different signs, and (ii) consequently how biological interpretations that are typically sought regarding the selective meaning of trait variation must be assessed via the extended view of selection gradients.

**Multivariate evolutionary prediction using extended selection gradients**

Expected evolutionary change based on (path coefficient-based) estimates of extended selection gradients can be obtained starting with the Lande equation (Lande, 1979),

$$\Delta \bar{z} = G \beta,$$

(1)

where $\Delta \bar{z}$ is the expected per-generation change in the vector of mean phenotype, $G$ is the matrix of additive genetic variances and covariances, and $\beta$ is a vector of direct selection gradients, i.e., the average partial derivatives of relative fitness integrated over
the distribution of the phenotype. In path analytic terms, $\beta$ are the coefficients associated with arrows directly between traits and relative fitness. To express the rest of the formula in terms of path coefficients, $G$ needs to be related to causal effects of traits on one another (path arrows among traits). Given a matrix of path coefficients $b$, the total causal effects of each trait on every other trait are

$$\Phi = (I - b)^{-1}. \quad (2)$$

Following McArdle and McDonald (1984) and Gianola and Sorensen (2004), $G$ is determined in part by $\Phi$ according to

$$G = \Phi G_c \Phi^T, \quad (3)$$

where $G_c$ represents the additive genetic component of sources of variance and covariance among traits, beyond those attributable to causal relationships among traits. Diagonal elements of $G_c$ represent the additive genetic components of exogenous inputs of variation to a system of structural equations, often denoted $U$ on path diagrams. Off-diagonal elements of $G_c$, if any, represent the additive genetic component of covariances that are extrinsic to causal relations, often denoted with curved double-headed arrows on path diagrams.

Substitution of equation 3 into equation 1 gives $\Delta \bar{z} = \Phi G_c \Phi^T \beta$. Within this expression, the extended selection gradients, $\eta$, or total effects of each trait on relative fitness, are $\eta = \Phi^T \beta$. In scalar form, this is $\eta_x = \sum_{y=1}^{n} \Phi_{xy} \beta_y$, defining the total effects on fitness as the sum of the products of the effects of the traits on one another and on relative fitness. So the evolution of the mean vector in terms of extended selection gradients is

$$\Delta \bar{z} = \Phi G_c \eta. \quad (4)$$

It remains to consider how exogenous genetic variances and covariances are to be obtained. $G_c$ and its components are not generally considered among the parameters of
interest in evolutionary quantitative genetics, but have specific evolutionary meaning and
are obtainable through modifications of familiar mixed-model techniques (Henderson, 1973;
Kruuk, 2004; Wilson et al., 2010). Standard structural equation modelling packages (e.g.,
SEM; Fox 2006, Listrel; Joreskog and Van Thillo 1972) for implementing path analyses
intrinsically estimate total exogenous variances and covariances, even if these are not typ-
ically considered parameters of particular interest. The key to the decomposition of the
total exogenous (co)variances into genetic and residual components is to view a path model
as a system of mixed model equations. The twist, however, is that any trait that has a
effect on any other trait is part of the response (i.e., its value is modelled), and also serves
as a predictor of the observed values of other traits. If there are neither simultaneous (e.g.,
$A \rightarrow B, B \rightarrow A$) relationships nor recursive loops (e.g., $A \rightarrow B, B \rightarrow C, C \rightarrow A$), the com-
ponents of $b$ and $G_\epsilon$ can be estimated from separate mixed models describing parts of the
path model. Path coefficients are simply continuous fixed effects, and exogenous variances
are obtained as random effects, conditional on any fixed effects representing path coeffi-
cients. If a path model involves exogenous covariances, then components of $G_\epsilon$ pertaining
to these variables would be estimated using a multi-response mixed model. Decomposition
of exogenous (co)variances into genetic, residual, and potentially other components can be
implemented using standard mixed model techniques. For example, using general pedi-
gree information, additive genetic exogenous variance components can be estimated using
animal models (Henderson, 1973; Kruuk, 2004; Wilson et al., 2010) in which fixed effects
are included to estimate path coefficients. All component mixed models must be simul-
taneously evaluated in path models that contain recursive or simultaneous relationships
(Gianola and Sorensen, 2004), but such features of path models do not generally appear
in studies of natural selection.
Example 1: Selection of neonatal traits in Soay sheep

The purpose of this example is (i) to consider the differences between estimates of $\beta$ and $\eta$ in the context of covariances among traits in a real dataset, and (ii) to consider the ways in which interpretations about natural selection can be made given estimates of $\beta$ and $\eta$. Here, I consider the relations among birth date, twin status, birth weight, weight in August, and their selection via relationships with relative fitness in the first year of life of female Soay sheep lambs on St Kilda, Outer Hebrides, Scotland, during the period of 1985 to 2009. The fitness component is overwinter survival. In total, the analysis was conducted on complete records of all traits and overwinter survival for 1284 individuals. More detail about the study system is available in Clutton-Brock and Pemberton (2004).

Covariances among birth date, twin status, birth weight, August weight, and relative fitness (overwinter survival scored as 0 and 1, divided by year-specific mean survival) are given in table 1. A plausible model relating the traits to one another and to relative fitness is

$$ w_i = \mu_w + b_w,awt \cdot awt_i + b_w,bwt \cdot bwt_i + b_w,twn \cdot twn_i + b_w,bdy \cdot bdy_i + e_i(w) \quad (5a) $$

$$ awt_i = \mu_{awt} + b_{awt,bwt} \cdot bwt_i + b_{awt,twn} \cdot twn_i + b_{awt,bdy} \cdot bdy_i + e_i(awt) \quad (5b) $$

$$ bwt_i = \mu_{bwt} + b_{bwt,twn} \cdot twn_i + b_{bwt,bdy} \cdot bdy_i + e_i(bwt) \quad (5c) $$

where $w$ represents relative fitness, $awt$ represents weight in August (kg), $bwt$ represents birth weight (kg), $twn$ represents twin status (scored as zero or one), and $bdy$ represents birth date (day of the year). $i$ indexes individuals, $e_i$ terms are residual errors of the bracketed quantities, and $\mu$ are intercepts. I evaluated the three multiple regressions in equation 5 using MCMCglmm (Hadfield, 2010). This allowed statistical uncertainty in both direct and extended selection gradient estimates to be evaluated by integration over the joint posterior distributions of the solutions to equation 5.

The estimates of $\beta$ from equation 5a, the fixed components of which are essentially
Lande and Arnold’s (1983) multiple regression analysis for directional (direct) selection gradients, and estimates of $\eta$ obtained by applying path rules to coefficients obtained from equations 5a-c, are given in table 2. Figure 2 shows the relationships described in equation 5 as a path diagram, with representation of path strengths (variance-standardized, i.e. partial correlations, except for regressions of relative fitness on the traits, which are the partial regressions of $w$ on the variance-standardized traits) as thickness of arrows.

August weight has a substantial direct effect on fitness, while the other traits have smaller direct effects (table 2, figure 2). However, in this model, twin status and birth weight have effects as well on fitness as well, but they are largely indirect. Birth weight has a positive effect on fitness via its effect on August weight, jointly with the fact that August weight affects fitness. Similarly, while twin status has little or no direct effect on fitness, it does have negative effects on both birth weight and August weight, and consequently a negative total, if mostly indirect, effect on fitness.

The interpretation of extended selection gradients is well-illustrated by this example. Twin status and birth weight have very small direct influence on fitness, and therefore small $\beta$. Insofar as it is reasonable to assume that these traits may have causal effects on August weight and fitness, it is very worth quantifying the total effect of this trait on fitness if we are trying to understand the adaptive significance of variation in birth weight. $\eta$ most closely reflects the concept of “selection for” (Endler, 1986; Sober, 1984) birth weight, as it reflects the selective significance of birth weight in a way that existing selection coefficients do not.

These results do not necessarily represent a comprehensive study of selection of lamb traits via variation in first year overwinter survival in female Soay sheep. For example, the study population experiences substantial environmental variation with respect to population density, food availability and weather (Clutton-Brock and Pemberton, 2004; Coulson et al., 2001), and the relationships among traits and between traits and fitness may vary in important ways with environmental conditions (Catchpole et al., 2000). I present this example as a simple calculation of $\eta$ given a path diagram, and of the interpretive differences
between $\eta$ and $\beta$.

Example 2: Path model-based simultaneous inference of selection and genetics in wild oats

The purpose of this section is to illustrate the simultaneous estimation of extended selection gradients and genetic and residual exogenous variances for the purpose of quantitative path model-based microevolutionary prediction. The focal dataset in this section is from Gardner and Latta’s (2008) experiment in which recombinant inbred lines of wild oat *Avena barbata*, derived from contrasting ecotypes, were grown in the lab to evaluate relationships among a number of phenological, vegetative, and reproductive traits. The experimental design using inbred lines greatly simplifies the statistical inference of genetic parameters. However, the (co)variances among individuals attributable to line must be interpreted as broad-sense genetic parameters, i.e., representing total genetic effects, not only additive genetic effects. Extension to analysis of classical breeding designs (Lynch and Walsh, 1998) and general pedigrees (Gianola and Sorensen, 2004; Henderson, 1973; Kruuk, 2004; Wilson et al., 2010) is relatively straight forward (see section 2), once the basic principle is clear. Closely following Latta and McCain (2009), I adopted the path model structure in figure 3 as an *a priori* set of causal assumptions about covariances among the phenological, vegetative, and reproductive traits, and relative fitness, based on the number of reproductive
spikes. The set of mixed models characterizing this causal scheme is

\[ w_i = \mu_7 + b_{7,1} \cdot \text{mass}_i + b_{7,5} \cdot \text{rpt}_i + b_{7,6} \cdot \text{mrt}_i + g_{\text{line}_i}(w) + e_{\epsilon,i}(w), \]  

\[ \text{mrt}_i = \mu_6 + b_{6,4} \cdot \text{mass}_i + b_{6,3} \cdot \text{dtf}_i + g_{\text{line}_i}(\text{mrt}) + e_{\epsilon,i}(\text{mrt}), \]  

\[ \text{rpt}_i = \mu_5 + b_{5,4} \cdot \text{mass}_i + b_{5,3} \cdot \text{dtf}_i + g_{\text{line}_i}(\text{rpt}) + e_{\epsilon,i}(\text{rpt}), \]  

\[ \text{mass}_i = \mu_4 + b_{4,2} \cdot \text{m60}_i + g_{\text{line}_i}(\text{mass}) + e_{\epsilon,i}(\text{mass}), \]  

\[ \text{dtf}_i = \mu_3 + b_{3,2} \cdot \text{m60}_i + g_{\text{line}_i}(\text{dtf}) + e_{\epsilon,i}(\text{dtf}), \]  

\[ \text{m60}_i = \mu_2 + b_{2,1} \cdot \text{dgerm}_i + g_{\text{line}_i}(\text{m60}) + e_{\epsilon,i}(\text{m60}), \]  

\[ \text{dgerm}_i = \mu_1 + g_{\text{line}_i}(\text{dgerm}) + e_{\epsilon,i}(\text{dgerm}), \]  

where the traits are (numerical indices for model term subscripts in brackets): (1) days to germination, \( \text{dgerm} \), (2) mass on day 60, \( \text{m60} \), in grams, (3) days to first flower, \( \text{dtf} \), (4) final total mass, \( \text{mass} \), in grams, (5) number of reproductive tillers, \( \text{rpt} \), (6) combined mass of reproductive tillers, \( \text{mrt} \), in grams, and (7) relative fitness, \( w \). I obtained relative fitness by dividing the number of seed spikes (each spike contains two seeds) by the mean number of spikes. For consistency with Latta and McCain (2009), I standardized each trait observation by subtracting block averages (the experimental rearing was conducted in three blocks) prior to the mixed model analyses. \( \mu \) are intercepts, and \( b_{jk} \) values are partial regression coefficients, where \( j \) indexes response variables and \( k \) indexes predictors. \( g_{\text{line}_i}(k) \) are the trait \( (k) \)-specific exogenous genetic values of each line, and are assumed to be drawn from normal distributions with estimated variances \( g_{\text{line}_i}(k) \sim N(0, \sigma^2_{g,k}) \). Where \( N(0, \sigma^2) \) represents a normal probability distribution with mean 0 and variance \( \sigma^2 \). \( g \), for genetic value, replaces \( a \), for breeding value, above, in the typical notation of the genetic effects, simply because the estimated parameters, given the inbred line-based experiment, are broad-sense (exogenous) genetic values rather than additive genetic effects. Similarly, \( e_{\epsilon,i}(k) \) are residuals, drawn from normal distributions with trait-specific estimated variances, i.e., \( e_{\epsilon,i}(k) \sim N(0, \sigma^2_{e,k}) \). As for equation 5, I evaluated each multiple
regression mixed model specified by equation 6 separately using MCMCglmm (Hadfield, 2010).

Conditional on the structure of the path model defined by equation 6, the estimates of \( b \) and \( \Phi \) are given in table 3. The genetic and residual variance-covariance matrices (and ultimately the phenotypic variance-covariance matrix, their sum), obtained using equation 3, and equivalently, \( R = \Phi R, \Phi^T \) are given in supplemental table S2. These estimated variance-covariance matrices generally match previously-reported genetic parameters from this experiment (Gardner and Latta, 2008), as well as a mixed model-based estimate of the genetic variances and covariances made without any assumptions (i.e., without the path model; supplemental table S3), using a multi-response mixed model-based analysis to estimate the covariance matrix associated with line and the residual covariance matrix, using MCMCglmm. However, the path analysis-based estimates of the matrices generally contained estimates of individual covariance components that are smaller in magnitude than the unconstrained estimates, for variances and covariances involving mass, number of reproductive tillers, mass of reproductive tillers, and relative fitness.

I obtained extended selection gradient estimates by application of equation 2 to the estimate of \( b \) from equation 6, and obtained credible intervals by integrating this analysis over the posterior distribution of the solution to equation 6. Path model-based inference of direct and extended selection gradients revealed negative total effects of the two phenological traits on fitness, and positive total effects of the vegetative and reproductive traits. Trivially, the path-based estimate of the direct effects of number and mass of reproductive tillers on fitness were also positive, because \( \eta \) and \( \beta \) are identical for these traits, given the path model (figure 3, equation 6). The direct effect of mass on fitness is negative.

To compare the path-based estimate of \( \beta \) with unconstrained estimates, I estimated \( \beta \) by multiple regression of spike number on the other six traits. For this I fitted a model directly analogous to equation 6a, but including partial regressions of relative fitness on all other traits, and without the estimate of the among-line variance of relative fitness. For the traits with non-zero \( \beta \) as defined by the path model, the path-based and unconstrained
estimates of $\beta$ are similar. Unconstrained inference of $\beta$ suggests a negative direct effect of days to first flower on fitness (table 3).

As in the Soay sheep example, differences between $\beta$ and $\eta$ in the wild oats illustrate important ways in which formalization the path-analysis perspective into evolutionary quantitative genetic inferences yields insight into selective mechanisms. For mass at day 60 and days to first flower, $\eta$, suggests much more substantial selection than does $\beta$. Selection of mass is particularly interesting, as the two types of selection gradients have different estimated signs. Except insofar as individuals with greater mass may have greater mass of reproductive organs, total vegetative mass is (trivially) not itself a component of fecundity. Since fecundity variation is the only source of fitness variation in this greenhouse-based experimental system, the portion of the effect of mass on fitness that is independent of effects acting via fecundity is unlikely to be positive. Because non-reproductive structures must be maintained, they must be costly in-and-of themselves, and so the direct selection gradient of mass is negative. However, individuals with greater total mass also have greater reproductive capacity, and so the extended selection gradient of mass, i.e., the total causal effect of mass on fitness, is positive.

To compare evolutionary predictions based on extended selection gradients with alternative approaches to evolutionary prediction, I made predictions of microevolution based on application of the Lande equation $\Delta \tilde{z} = G \beta$ (Lande, 1979), and on the secondary theorem of selection, whereby expected evolutionary change is the genetic covariance of each trait with relative fitness $\Delta \tilde{z} = \sigma_a^2(z, w)$ (Morrissey et al., 2010; Robertson, 1966). I estimated $G$ (broad-sense genetic variances and covariances) as the among-line covariance matrix using a multi-response mixed model treating the six traits other than fitness (for the Lande equation) or all seven traits (for the secondary theorem of selection) as dependent variables.

All three systems of evolutionary prediction yield qualitatively similar results (figure 4). Based on all three systems of prediction, little evolution of days to germination and mass at day 60 is expected, days to first flower is expected to advance, a modest increase
in total mass is expected, and finally, substantial evolution of greater number and mass of reproductive tillers is expected. In general, the predictions based on the Lande equation and the secondary theorem of selection are greater in magnitude than those based on the path analysis of extended selection gradients (figure 4). The smaller predictions of evolutionary change based on the path model seem to be due to lower path model-based (co)variance estimates (supplemental tables S2 and S3), rather than any substantial differences in trait-fitness relationships (table 3).

Discussion

Extended selection gradients provide a means of quantitatively summarizing selection that reflects the concept of “selection for” (Endler, 1986; Sober, 1984), i.e., they reflect the total dependence of relative fitness on variation in a trait. The example analyses of Soay sheep and wild oat data illustrate scenarios where total and direct effects of traits on fitness differ in important ways. The inferred effect of sheep birth mass on fitness might be relegated to indirect selection of a mere correlated trait, if only $\beta$ was considered. Similarly, the positive covariance of oat plant mass and fitness might also be relegated to a case of indirect selection where the positive relationship is an indirect result of selection for reproductive traits. Such conclusions would represent, at best, incomplete interpretations of the selective consequences of variation in Soay sheep birth weight and wild oat plant mass.

Direct integration of an hypothesis about the mechanism of selection into the statistical mechanics of the estimation of genetic and phenotypic variances and covariances has several potential benefits, but also necessitates careful interpretation and explicit consideration of the associated assumptions. First, two potential misconceptions must be addressed. Extension of a causal model of phenotypic covariance among traits to the genetic level does not require any additional assumptions beyond those that are involved in application of path analysis at the phenotypic level. If trait $A$ causes variation in trait $B$, then the partial
genetic and phenotypic regressions of $B$ on $A$ are the same (see Hadfield 2008; Morrissey et al. 2010; Queller 1992; Robertson 1966 for further discussion of the manifestation of causation as equivalent genotypic and phenotypic partial regressions). Note that this is only true for the partial regressions - the action of other traits or of environmental variation might make the total genetic and phenotypic regressions different, and failure to account for all the contributors to covariances among traits may result in erroneous estimation of any focal partial regression parameters, just as in any selection analysis (Hadfield, 2008; Morrissey et al., 2010; Rausher, 1992; Robertson, 1966).

Second, equivalence of phenotypic and genetic partial regressions does not imply equivalence, or even common signs, of phenotypic and genetic covariances and correlations. The magnitudes and signs of phenotypic and genetic correlations are determined jointly by the partial regressions and the relative magnitudes of the genetic and non-genetic components of the exogenous (co)variances of traits. Consider, for example, a situation in which a trade-off occurs between two heritable traits (perhaps a trade-off between life history traits). This could be manifested as a negative partial regression of one trait on the other. However, if the values of the two traits are both partially determined by a third trait (perhaps resource availability or acquisition rate; this generates a model very similar to de Jong and van Noordwijk’s (1992) model of resource acquisition and allocation), then they may covary positively despite the inherent trade-off. In a situation where the third trait is highly variable but not heritable, it could cause a positive overall phenotypic covariance between the first two traits while they could covary negatively at the genetic level, even though the phenotypic and genetic partial regressions among all the traits are equal.

Path-analytic estimates of genetic variance-covariance matrices will generally be (statistically) more precise than unconstrained estimates of genetic parameters. Consequently, evolutionary predictions based on $\eta$ will be estimable with less sampling variance (i.e., smaller standard errors). This effect may generally be dramatic, because path-based estimation of $G$ uses information about the partial regressions of traits on one another, obtained from phenotypic data in conjunction with an a priori causal model of trait co-
variance. The extent to which the statistical precision of path-based estimation of $G$ is justified depends on the validity of the path model. Essentially, statistical uncertainty is traded against the validity of assumptions. Under the assumption that the wild oat path model (figure 3, equation 6) represents a valid causal explanation of the covariances among the traits, the standard deviations of the posterior distributions (interpretable as similar to standard errors) of the elements of $G$ (supplemental table S2a) are about half of what they are based on unconstrained estimation of $G$ (supplemental table S3), and uncertainty in evolutionary predictions based on $\eta$ is correspondingly smaller as well (figure 4).

Incorporation of path analysis into evolutionary quantitative genetic theory generates a new system of evolutionary prediction that is statistically and philosophically distinct from the breeder’s and Lande equations (Lande, 1979; Lush, 1937), and from the secondary theorem of selection (Robertson, 1966). Path analysis-based evolutionary prediction relies most heavily on a priori assumptions of the causal nature of phenotype-fitness covariance.

Evolutionary prediction based on the breeder’s equation assumes that all traits directly responsible for multivariate phenotype-fitness covariances are identified, meaningfully measured, and adequately modelled, but makes no assumptions about the causal structure of phenotypic and genetic relationships among traits. Finally, evolutionary prediction based on the secondary theorem of selection (Etterson and Shaw, 2001; Morrissey et al., 2010, 2012; Price, 1970; Robertson, 1966, 1968) does not require that all, or indeed any, causal sources of trait-fitness covariance are identified, nor does it make any assumptions about the causal structure of phenotypic or genetic covariation among traits or between traits and fitness.

The three systems for evolutionary prediction (ordered as above, i.e., path, breeders/Lande, and secondary theorem) vary in three more practical aspects: (1) This order represents decreasing statistical precision of evolutionary predictions when all the assumptions of each system are met. (2) This order represents decreasing risk of erroneous predictions when the assumptions are not met. And (3), this order represents decreasing level of insight into the mechanisms of natural selection. In fact, the secondary theorem
of selection provides a prediction of evolutionary change, but yields almost no insight into natural selection: genetic covariances of a trait and fitness may be due to selection of those traits, selection of other genetically correlated traits (measured or not), or may be due to drift, population structure, or variation in accumulated mutation (in the last two cases the covariation of traits with fitness may nonetheless be reasonably characterized as selection). Robertson’s theorem could be considered a primary quantitative genetic theorem of evolution, neither necessarily nor specifically of selection.

Issues pertaining to fundamental meaning, as opposed to the inference, of causal mechanisms of selection must be kept distinct. First, understanding the mechanistic, i.e., causal, basis of natural selection can bring an understanding of natural selection that statistical quantification of trait fitness relationships cannot provide alone. Whether one is interested in direct selection gradients (direct causal effects), extended selection gradients (total causal effects), or selection differentials (covariance arising from selective processes), each of these parameters is in some way a reflection of a causal process (Godfrey-Smith, 2007; Sober, 1984). Inference of selection gradients relies on the existence of a correct causal model of the mechanism underlying trait-fitness covariance. For direct selection gradients, this model of direct effects of traits on fitness is implicit in the concept of partial derivatives of relative fitness with respect to phenotype, which in practice is normally assessed by multiple regression. Failure to include traits that covary with focal traits, and that cause fitness variation amounts to applying an incorrect model of direct effects of traits on fitness. This type of ‘wrong model’ problem, arising from missing traits, is well discussed (Hadfield, 2008; Kruuk et al., 2003; Morrissey et al., 2010; Rausher, 1992; Robertson, 1966).

Inference of extended selection gradients similarly requires that all factors that ultimately cause focal traits to covary with fitness be measured, and additionally, requires that a valid scheme by which to relate their causal effect on one another and on fitness is available. It must be kept in mind that the fit of observational data to a causal model of any kind (whether it be a multiple regression model, or a more complex causal hypothesis) provides only the weakest kind of inference about the validity of the model. Wright (1934) describes
“In considering the reliability of path coefficients there are two questions which must be kept distinct. First is the adequacy of the qualitative scheme to which the path coefficients apply and the second is the reliability of the coefficients, if one accepts the scheme as representing a valid point of view. The setting up of a qualitative scheme depends primarily on information outside of the numerical data and the judgement as to its validity must rest primarily on this outside information. One may determine from standard errors whether the observed correlations are compatible with the scheme and thus whether it is a possible one, but not whether it correctly represents the causal relation.”

The current work (i) highlights why the causal structure of trait-fitness relationships matters for making inferences about natural selection, and (ii) derives the statistical quantitative genetic mechanics that relate causal schemes to selection, genetic variation, and evolutionary change. The current work does not provide any recipe for determining the causal structure of trait-fitness relationships. Inferences of $\eta$ in any given application will vary with different assumed causal structures, but this does not mean that $\eta$ is in any way arbitrary: there will be a correct causal structure that yields correct inference of extended selection gradients. As Wright points out (quote above), observational data such as that typically used for quantitative genetic inference of selection provides only the weakest kind of test of the adequacy of causal hypotheses. However, the necessity of understanding the causal structure of trait-fitness covariance could indeed benefit from a range of different kinds of information about causal relationships. Logical decisions based on chronology, natural history, existing theory, and experiment could all in principle be brought to bear. For example, in the sheep example, I considered all relationships among traits plausible; some effects may be small, but rather than exclude them a priori, I allowed them to be estimated as small values. As such the sheep analysis can be seen as a contrivance to exploit the least restrictive possible path model, guided only by a linear view of time and
It is unlikely that relationships among measured variables in any study system will ever completely reflect all causes of covariance. With careful consideration of the biology of any given study system, it is plausible that relationships among measured variables could often reflect the major causes of covariance, but in general, unmeasured traits and aspects of the environment will generally also cause covariance among measured quantities. The consequences of this simple and realistic view of empirical data have profound implications for what can be achieved using the many existing procedures in the path analysis literature for assessing the fit of different models to the same dataset. In particular, in the presence of modest effects of unmeasured variables, essentially correct causal structures (among measured quantities) may appear to be preferred when modest amounts of data are available, but with increasing data, there will be a tendency for indices of statistical fit to lead to preference of more complicated models, i.e., models that contain effects that do not exist, but reflect spurious associations due to unmeasured quantities. This principle, where data-driven analytical decisions, especially in frequentist analytical frameworks, will generally result in preference for overly complex and wrong models, applies to statistical modelling in general, not just to path analysis.

This is not to say that assessing fit is irrelevant. Rather, what one does with information about fit is what matters. Under the assumption that each wild oat plant is independent (it is not, as each belongs to an inbred line), the residual mean squared error of approximation (Steiger, 1990) is 0.109 (90% CI: 0.085-0.133), which by most arbitrary thresholds indicates a marginal fit, and Bentler’s (1990) comparative fit index is 0.966, which is quite good (indices of fit from SEM Fox 2006, based on fitting the model in equation 6, but without accounting for inbred line). The χ² value arising from the difference between the covariance structure implied by the fitted path model, and the observed covariances is 80.0, which on 11 degrees of freedom (the covariance matrix of the seven variables has 28 unique elements, minus the number of free parameters, which include 7 exogenous variances and 10 partial regression coefficients) indicates that a more complex model could provide highly
statistically significantly better fit. Note that assessment of fit in these ways is not relevant to the Soay sheep example, as it is based on a saturated model. Imperfect fit may indicate that there are paths that should be added to the model, or it may indicate the presence of some unmeasured variable. If a path model is well considered, the latter will often be the case. A statistical solution will sometimes be available via fitting latent variables. Latent variables are not directly considered here, but their use is common in path analysis, and the quantitative genetic principles pertaining to systems of causally covarying traits should be relatively easily extended to models that include latent variables. More usefully, imperfect fit could be used to inform future data collection, or could motivate experiments. In the wild oat example, a saturated path model (detailed in the supplemental material), ordered chronologically, yields the extended selection gradients (SD of posterior distribution): dgerm, 0.021 (0.026); m60, 0.351 (0.076); dtf, -0.0232 (0.001); mass, 0.033 (0.005); rpt, 0.033 (0.002); and mrt, 0.086 (0.006). These inferences of selection based on a saturated model, which by definition fits the data perfectly, represent only small quantitative differences from those based on the original model (table 3b and figure 3). The main difference is the slightly more negative selection of days to first flower (see also table 3c, which shows a potential direct component of the effect of dtf on fitness, over and above the effects included in the path model). The addition of such a direct effect to the path model may be justified on the (data-driven, post-hoc) argument that advanced phenology gives more time for optimal allocation of resources to different aspects of reproduction. However, for the present illustrative purposes, I have deferred to the expert opinion that contributed to the original publication of the Avena path model (Latta and McCain, 2009). Inferences of extended selection gradients and associated evolutionary predictions based on another alternative (highly post hoc) path model are presented in the supplemental material, and generate very similar results.

Experimental data may in principle be more powerful for testing causal hypotheses (Fisher, 1935), though experimentalists know that specific causal inference from any kind of data can be difficult! Manipulations of traits, or of the selective context in which traits
are expressed, are under-used approaches to characterizing mechanistic basis of natural sele-
ction. The concept of extended selection gradients may greatly facilitate the experimental
verification of observational inferences about natural selection, especially for approaches
based on trait manipulation. Developmental associations among traits make experimental
verification of $\beta$ notoriously difficult. The basic experiment to verify or quantify a direct
selection gradient requires that a trait be manipulated independently of other traits, to
test whether relative fitness changes by $\beta \cdot \Delta z_{\text{experimental}}$. However, developmental asso-
ciations of traits - which may themselves be part of the casual structure of selection -
generally make independent manipulation of traits difficult if not impossible or irrelevant.
In contrast, experimental verification of extended selection gradients is not in principle
opposed to the existence of developmental relationships among traits. Importantly, exper-
imentation should be seen not only as a means of qualitatively verifying causal hypotheses,
but also of quantitatively parameterizing mechanistic models. The statistical mechanics
presented here for relating extended selection gradients to genetic variation and evolution
are equally applicable using inferences from observational or experimental data, separately
or in combination.

Perhaps the most important conceptual contribution in Arnold’s (1983) paper is the
demonstration of how to link theoretical and empirical perspectives on relationships among
traits and relationships among traits and fitness in a quantitative framework. To date,
applications of path analysis in studies of natural selection have relied almost entirely
on observational data. In some cases, this includes complete life history data, which
entirely determines fitness. Analyses are then conducted treating fitness as a (statistically)
independently observed variable, when in fact it is derived entirely from other observed life
history variables; van Tienderen (2000)’s methods provide the mathematical machinery to
combine evolutionary demographic theory with path analytic approaches, but the method
has been surprisingly little used (but see Coulson et al. 2003). The generalization of
evolutionary demographic theory of quantitative traits provided by integral projection
models (Coulson et al., 2010; Ellner and Rees, 2006) should provide a general means of
integrating demographic perspectives on fitness variation into path analysis and empirical studies of selection. Integration of path analytic approaches to characterizing natural selection into integral projection models will provide the analytical tools to model the consequences of non-linear causal effects of traits on one another and on fitness, and to rigorously model non-normal distributions of traits. Also, Rice (2002, 2004) provides a complimentary set of theoretical principles by which a more comprehensive quantitative genetic theory of the selection, genetics, and evolution of non-normal and non-linearly causally-covarying traits could be developed. By these approaches, more theoretically and statistically-sound inference of causal relationships, and corresponding path coefficients and extended and direct selection gradients, among traits and fitness could be obtained directly from life history theory. In this context, life history and demographic theory can also be exploited to provide robust inference of path coefficients when traits interact multiplicatively.

Summary

Given a priori assumptions about causal relationships among traits and between traits and fitness, path analysis can provide inference of the total causal effects of traits on fitness. Formalization of such characterizations of selection as extended selection gradients, and consideration of how these coefficients relate to quantitative genetic variation and evolutionary change, provides the basis for incorporation of path analysis into the theoretical and empirical evolutionary quantitative genetics tool box. In particular, extended selection gradients may prove to be particularly useful for comparisons of selection across studies. While traditional, direct selection gradients provide entirely valid evolutionary predictions when used with their associated statistical quantitative genetic machinery (Lande, 1979), their biological interpretation is hindered by the fact that they do not describe the total

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3The direct application of path rules to squared deviations of trait values from population means (e.g., as advocated by Scheiner et al. 2000) does not generally yield quantitatively or qualitatively correct inference of non-linear selection. It is not clear whether or not general analytical expressions for path-based inference of non-linear selection will be tractable, except in very simple restrictive cases. Outside of an integral project model framework, path-based inference of compound non-linear selection gradients could be obtained by numerical techniques.
causal effects of traits on fitness, and that their (correct) values vary arbitrarily as functions of what traits are studied. This statistical, rather than biological, definition can lead to trivialization of the mechanism of selection. In particular, evolution of traits that cause fitness variation indirectly, and traits that are incidentally correlated with selected traits, are both treated as cases of evolution due to genetic correlations in microevolutionary studies based only on direct selection gradients. Empirical extended selection gradient-based inferences of microevolutionary processes rely heavily on a priori assumptions about causation, or in other words, on additional information about the mechanism of selection, but perhaps only slightly more so than the use of direct selection gradients (Morrissey et al., 2010). The validity of such assumptions cannot be comprehensively assessed with observational data (Wright, 1934) alone, such as that with which path-based studies of natural selection are typically parameterized. However, a priori biological knowledge can be used to construct plausible causal schemes. Furthermore, the clarification provided herein of how hypotheses about the organismal biology underlying trait-fitness relationships relate to selection gradients in a formal quantitative genetic sense should motivate and facilitate further use of experimental approaches to understanding selective mechanisms. Path model-based thinking about natural selection should provide the means for formally linking observational, theoretical, and experimental inferences (Arnold, 1983), and this will greatly complement application of the statistical quantitative genetic principles pertaining to extended selection gradients.

Acknowledgements

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The data were provided by Bob Latta, who also developed the recombinant inbred lines with funding from NSERC, and contributed invaluable comments on an earlier draft of this manuscript. Bill Hill, Bruce Walsh, Jarrod Hadfield, Graeme Ruxton, Charles Goodnight, Kerry Johnson, Tom Meagher, Steve Frank, Sam Scheiner, Tim Coulson, Mike Ritchie, and Diane Byers provided valuable discussions and comments.

References


Coulson, T., S. Tuljiaipurkar, and D. Z. Childs. 2010. Using evolutionary demography to


Table 1: Variances (diagonal), covariances (below diagonal) and correlations (above diagonal) of lamb traits and relative fitness (based on first year over-winter survival) in female Soay sheep. Traits are Julian birth date \textit{bdy}, twin status \textit{twn}, birth weight \textit{bwt} (kg), weight in August \textit{awt} (kg), and relative fitness is denoted \(w\) (first year survival scored as 0 and 1, divided by annual mean survival). Values are the modes of the posterior distribution of the (co)variances or correlations and bracketed values are standard deviations of the posterior distribution, interpretable similarly to standard errors.

<table>
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<tr>
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<th>bwt</th>
<th>awt</th>
<th>w</th>
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Table 2: Standardized (a) path coefficients, and (b) compound path coefficients, i.e., \(\eta_{ij}\) based on the fitted path model relating sheep neonatal and lamb traits to relative fitness during the first year of life. The bottom row of (a) are equivalent to direct selection gradients, and the bottom row of (b) are path model-based extended selection gradients. Units are: birth day, days; twin status \(\in [0,1]\), birth and August weights, kg. Values are the modes of the posterior distribution estimates and bracketed values are standard deviations of the posterior distribution, interpretable similarly to standard errors.

(a) path coefficients \(b\), bottom row are path-based \(\beta\)

<table>
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<tr>
<th></th>
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<th>August weight</th>
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<tr>
<td>birth weight</td>
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<td>August weight</td>
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<td>w</td>
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<td>0.033 (0.021)</td>
<td>0.174 (0.021)</td>
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(b) compound path coefficients \(\Phi\), bottom row are \(\eta\)

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<th>twin status</th>
<th>birth weight</th>
<th>August weight</th>
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<tbody>
<tr>
<td>birth weight</td>
<td>0.126 (0.026)</td>
<td>-0.396 (0.026)</td>
<td></td>
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</tr>
<tr>
<td>August weight</td>
<td>-0.100 (0.027)</td>
<td>-0.254 (0.028)</td>
<td>0.363 (0.027)</td>
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<tr>
<td>w</td>
<td>0.022 (0.019)</td>
<td>-0.092 (0.020)</td>
<td>0.096 (0.021)</td>
<td>0.174 (0.021)</td>
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Table 3: Unstandardized (a) path coefficients, (b) compound path coefficients, i.e., $\eta_{ij}$ based on the fitted path model, and (c) unstandardized, unconstrained direct selection differentials, of phenological, vegetative, and reproductive traits in a greenhouse experiment with a population of recombinant inbred lines of wild oat *Avena barbata* derived from contrasting ecotypes. Traits are days to germination $d_{germ}$, mass at day 60 $m_{60}$ (g), days to first flower $dtf$, total final mass $mass$ (g), number of reproductive tillers $rpt$, mass of reproductive tillers $mrt$ (g), and relative fitness $w$. The bottom row of (a) are path model-based direct selection gradients, and the bottom row of (b) are path model-based extended selection gradients. The unconstrained direct selection gradients in (c) are obtained by the multiple regression of relative fitness on all six traits. Values are the modes of the posterior distribution estimates and bracketed values are standard deviations of the posterior distribution, interpretable similarly to standard errors.

<table>
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<tr>
<th>(a) path coefficients ($b$, bottom row are path-based $\beta$)</th>
<th>$d_{germ}$</th>
<th>$m_{60}$</th>
<th>$dtf$</th>
<th>$mass$</th>
<th>$rpt$</th>
<th>$mrt$</th>
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<td>$m_{60}$</td>
<td>-0.004 (0.014)</td>
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<tr>
<td>$dtf$</td>
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<td>-12.707 (2.174)</td>
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<tr>
<td>$mass$</td>
<td></td>
<td></td>
<td>3.966 (0.517)</td>
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<tr>
<td>$rpt$</td>
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<td></td>
<td>-0.265 (0.018)</td>
<td>0.303 (0.075)</td>
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<tr>
<td>$mrt$</td>
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<td></td>
<td>-0.125 (0.006)</td>
<td>0.401 (0.023)</td>
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<tr>
<td>$w$</td>
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<td>-0.014 (0.004)</td>
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<th>(b) compound path coefficients ($\Phi$, bottom row are $\eta$)</th>
<th>$d_{germ}$</th>
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<th>$dtf$</th>
<th>$mass$</th>
<th>$rpt$</th>
<th>$mrt$</th>
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<tr>
<td>$m_{60}$</td>
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<td>$mass$</td>
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<td>3.966 (0.517)</td>
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<td>$rpt$</td>
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<tbody>
<tr>
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<td>0.032 (0.043)</td>
<td>-0.0033 (0.0011)</td>
<td>-0.012 (0.0045)</td>
<td>0.027 (0.002)</td>
<td>0.086 (0.0064)</td>
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Figure 1: A hypothetical relationship between a morphological trait \( (m) \), and aspect of organismal performance \( (p) \), and fitness \( (w) \). Arrows indicate hypothesized causal relationships. Path coefficients, \( b_{pm} \) and \( b_{wp} \) are the regression coefficients of performance on morphology, and relative fitness on performance, respectively. \( \sigma^2 \) are exogenous variances, i.e., variation in endogenous variables beyond that attributable to causal effects in the path model.

Figure 2: Parameterized path diagram representing relationships among lamb traits, and among lamb traits and relative fitness \( (w, \) based on first year over-winter survival), in female Soay sheep. Traits are Julian birth date \( bdy \), twin status \( twn \), birth weight \( bwt \), weight in August \( awt \). Path coefficients among traits are standardized, i.e., they represent partial correlations, and path coefficients between traits and relative fitness represent unit variance-standardized partial regression coefficients. The thickness of arrows represents the strength of the corresponding path coefficients. Solid arrows represent positive relationships and dashed arrows represent negative relationships. Exogenous inputs of variance are omitted for clarity.
Figure 3: Parameterized path diagram representing relationships among phenological, vegetative, and reproductive traits in a population of recombinant inbred lines derived from contrasting ecotypes and raised under greenhouse conditions. The traits are days to germination \( d_{germ} \), mass at day 60 \( m_{60} \), days to first flower \( dt_{f} \), final total mass \( mass \), mass of reproductive tillers \( m_{rt} \), number of reproductive tillers \( r_{pt} \), and relative fitness \( w \), as assessed via variation in fecundity. Path coefficients among traits are standardized, i.e., they represent partial correlations, and path coefficients between traits and relative fitness represent unit variance-standardized partial regression coefficients. The thickness of arrows represents the strength of the corresponding path coefficients. Solid arrows represent positive relationships and dashed arrows represent negative relationships. Exogenous inputs of variance are omitted for clarity.
Figure 4: Evolutionary prediction for vegetative and reproductive traits from a laboratory experiment on a population of recombinant inbred lines of wild oat *Avena barbata* using extended selection gradient-based evolutionary prediction, the breeder's equation (specifically, Lande's formulation based on direct selection gradients, $\beta$), and the secondary theorem of selection, i.e., the genetic covariance of each trait with relative fitness, $\sigma_g(z, w)$. Traits are (a) days to germination, (b) mass at day 60, (c) days to first flower, (d) final total mass, (e) number of reproductive tillers, and (f) total mass of reproductive tillers. Points are mean values of the posterior distribution of the evolutionary prediction based on each predictive framework (path-based extended selection gradients: $\eta$, multiple regression-based application of the Lande equation: $\beta$, and application of the secondary theorem of selection: $\sigma_g(z, w)$), and the error bars denote 95% credible intervals.