Quantification and decomposition of environment-selection relationships

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Abstract

8

9   In nature, selection varies across time in most environments, but we lack an understanding of how

10   specific ecological changes drive this variation. Ecological factors can alter phenotypic selection coef-

11   ficients through changes in trait distributions or individual mean fitness, even when the trait-absolute

12   fitness relationship remains constant. We apply and extend a regression-based approach in a population

13   of Soay sheep (*Ovis aries*) and suggest metrics of environment-selection relationships that can be com-

14   pared across studies. We then introduce a novel method which constructs an environmentally-structured

15   fitness function. This allows calculation of full (as in existing approaches) and partial (acting separately

16   through the absolute fitness function slope, mean fitness, and phenotype distribution) sensitivities of

17   selection to an ecological variable. Both approaches show positive overall effects of density on viability

18   selection of lamb mass. However, the second approach demonstrates that this relationship is largely

19   driven by effects of density on mean fitness, rather than on the trait-fitness relationship slope. If such

20   mechanisms of environmental dependence of selection are common, this could have important implica-

21   tions regarding the frequency of fluctuating selection, and how previous selection inferences relate to

22   longer-term evolutionary dynamics.

Introduction

Variation in selection is key to understanding the dynamics of adaptive evolution (Bell, 2010; Uyeda *et al.*, 2011; Chevin & Haller, 2014; Estes & Arnold, 2007; Hadfield, 2016). If variation in selection occurs, any estimate from a single episode of selection, or over short timescales, will be insufficient, or potentially misleading, for predicting how that trait will evolve. While the existence and some aspects of variation in selection have been documented (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2013), relating selection to environmental variables is likely to provide a much more complete picture of how and why selection varies and the likely effects on the evolutionary timescales involved (Wade & Kalisz, 1990; MacColl, 2011). However, until recently, despite many studies describing selection in natural populations (Endler, 1986; Kingsolver *et al.*, 2001), little progress has been made in understanding the ecological causes of selection (MacColl, 2011). Temporal replication provides information on how selection fluctuates over time (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2009) and as a consequence provides the opportunity to investigate the importance of particular ecological factors.

Any description of selection is a representation of some aspects of a fitness landscape. This landscape relates different phenotypic or genetic combinations to population mean fitness in a given environment (Wright, 1932; Arnold, 2003). For quantitative traits, this idea can be visualised as a (potentially multi-dimensional) surface relating phenotype to fitness (Lande, 1979). The idea of a fitness landscape allows visualisation of the concept but can potentially lead to an over simplified view. For example, fitness landscapes may change as a function of environmental conditions. This has led to suggestions that the idea of a fitness landscape can be enhanced by adding extra dimensions for relevant environmental variables (Chevin *et al.*, 2010; MacColl, 2011). Key information about the fitness landscape that a population is experiencing can be gained through the calculation of fitness functions which relate individual fitness to genotype or phenotype (Arnold, 2003). Although fitness functions are central to many theoretical approaches (Geroldinger & Bürger, 2015; Slatkin, 1978), visualisations of fitness functions, or how they change in relation to changing environmental conditions are surprisingly rarely used in empirical studies (but see for e.g. Chevin *et al.*, 2015; Grant, 2002; Sinervo *et al.*, 2000).

Phenotypic selection coefficients, i.e. selection differentials (Lush, 1937; Robertson, 1966) and gradients (Lande, 1979; Lande & Arnold, 1983), provide information on the strength, shape and direction of selection on a particular trait (Phillips & Arnold, 1989) by linking relative fitness to trait values. Consequently, they have been widely used to characterise selection (Kingsolver *et al.*, 2001) and variation in selection (Morrissey & Hadfield, 2012; Siepielski *et al.*, 2013). The use of selection gradients was popularised by Lande & Arnold in their paper published in 1983 where they laid out a quantitative genetic framework for multivariate

55 selection analysis. In conjunction with standardising phenotype in units of standard deviations (Lande &
56 Arnold, 1983), or less often in units of means (Hereford *et al.*, 2004), the concept of selection gradients
57 has been critical in allowing comparisons to be made across traits, taxonomic groups etc. Specifically, this
58 comparison is possible because phenotypic selection coefficients express the direction and strength of selection
59 in forms that relate quantitatively to phenotypic and genetic variation, and to evolution (via the breeder's
60 equation for differentials, and the Lande equation for gradients). These estimates provide information on the
61 fundamental process underlying evolution by natural selection since both selection gradients and selection
62 differentials are related to how the mean of a phenotypic trait changes due to a period of selection per unit
63 of genetic variance (Wade & Kalisz, 1990). While phenotypic selection coefficients provide a powerful link
64 for empirical studies of selection to evolutionary theory, the standardisations of phenotype and fitness (i.e.
65 relative vs absolute fitness) inherent to their use, definition and comparison, makes them potentially quite
66 distantly related to fitness functions which relate absolute fitness to unstandardised phenotypes. Many of
67 the questions we may wish to ask about variation in selection pertain to fitness functions. Therefore, simply
68 relating coefficients to the environment may generate incomplete representations of how the environment
69 interacts with the trait-fitness relationships.

70   The fact that phenotypic selection coefficients link traits to relative rather than absolute fitness is im-
71 portant for the ecological interpretation of variation in selection. Whenever an estimate of relative fitness is
72 used, it is assumed there is an underlying absolute fitness function which relates each individual's absolute
73 fitness to its trait value in a given environment. Critically, the values of phenotypic selection coefficients are
74 not just determined by the mean slope of this absolute fitness function. Consider selection occurring under
75 two different sets of environmental conditions. A possible scenario is that the resulting fitness functions have
76 the same slope in both cases, but a different mean fitness (Figure 1A). Quantification by phenotypic selec-
77 tion coefficients would demonstrate different trait-relative fitness relationships exist despite a very important
78 aspect of the trait-fitness relationship (i.e., the slope) remaining constant. In fact the same may also be true
79 for changes in the mean or variance of the trait distribution which can also affect phenotypic selection coeffi-
80 cients under some fitness functions. Thus, while variation in these selection coefficients alone can begin to tell
81 us about important ways that selection varies, focussing only on phenotypic selection coefficients, without
82 consideration of the properties of fitness functions, could obscure many ecologically important ways in which
83 selection can vary. To this end, Chevin *et al.* (2015) constructed log-linear and Gaussian models of a fitness
84 function and its dependence on an environmental variable. These models, based on fitting a Gaussian fitness
85 peak, have useful and direct relationships between the model coefficients and selection gradients. However,
86 this is a specific model and more general approaches are desirable. We hope that an additional benefit of
87 our approach is to provide a more flexible way of modelling variation in the fitness function.

88   Here, we first present a simple mathematical example demonstrating that there are four different path-
89   ways through which the environment can alter phenotypic selection coefficients under a linear fitness function.
90   We review and clarify that a change in trait mean, trait variance, mean fitness, or the relationship between
91   the trait and fitness all can result in an altered selection differential. Variation in any (combination) of these
92   effects could generate variation in selection. Each of these sources of variation would have very different
93   ecological implications, which cannot be distinguished by considering variation in phenotypic selection co-
94   efficients alone, or by considering their relationship with environmental variables. Thus, no firm ecological
95   conclusions can be drawn solely from establishing relationships between phenotypic selection coefficients and
96   environmental variables. Standardisations of the traits and fitness required for the calculation of phenotypic
97   selection coefficients necessarily obscure information about how environmental variables may influence fit-
98   ness functions. We then develop and apply two different ways that selection in natural populations can be
99   analysed in relation to environmental variables. Our demonstration analyses use data from an intensively
100 studied wild population of Soay sheep (*Ovis aries*) on St Kilda, Outer Hebrides.

101   Our first type of analysis mirrors that which has been carried out by several other authors, where selection
102 differentials are regressed on an environmental covariate of interest (Campbell & Powers, 2015; Husby *et al.*,
103 2011; Visser *et al.*, 2015) as was suggested by Wade & Kalisz (1990). This analysis introduces an important
104 potential benefit of such an approach: the opportunity for a standardised way to quantify the effects of an
105 environmental variable on selection that is comparable across studies, which is currently missing from the
106 literature. Despite interest in how much selection is explained by particular aspects of ecology (e.g. McAdam
107 & Boutin, 2003; Steele *et al.*, 2011) little has been published using a convention that would allow meaningful
108 comparisons between studies. We suggest that a solution is to calculate the proportion of the variance seen
109 in selection that is attributable to an environmental variable, and suggest how this can be estimated robustly
110 in practice. In the Soay sheep, we find that a substantial amount of the variation in selection on lamb mass
111 in August can be attributed to changes in the population size.

112   Next, we develop an approach based on direct estimation of an environmentally-structured fitness function
113 i.e., the relationship between unstandardised phenotype, an environmental variable and expected absolute
114 fitness. We also estimate the effect of an environmental variable on mean phenotype and phenotypic variance.
115 We use these estimated functions to calculate relative fitness based selection differentials for which we can
116 derive the total sensitivity to the environment, as well as the components of this total relationship that act
117 through the trait-fitness relationship, mean fitness, and environment-dependent changes in the distribution
118 of phenotype. In Soay sheep, we find that much of the dependence of selection of lamb mass on population
119 size acts through changes in mean fitness, and that the slope of the fitness function is actually relatively
120 constant.

121 Components of selection differentials

122 In this section the aim is to express the selection differential, S, in a way that includes the components of the

123 underlying absolute fitness function and the trait distribution. We do this for a very simple scenario using

124 a linear fitness function, to demonstrate the principle. This exercise highlights different pathways through

125 which the environment can alter selection estimates and provides key information required to develop analyses

126 assessing the individual importance of each component.

127 Phenotypic selection coefficients relate relative fitness, w, to a trait value, z. Relative fitness is calculated

128 as individual absolute fitness (i.e., the response variable in a fitness function), W, divided by the mean

129 absolute fitness,

$$w = \frac{W}{\overline{W}}. \tag{1}$$

130 The selection differential, S, is the change in population mean after a period of selection, $\overline{z}' - \overline{z}$. It can also

131 be expressed as the covariance of relative fitness with the trait values (Robertson, 1966; Lande & Arnold,

132 1983; Lynch & Walsh, 1998),

$$S = \text{cov}(w, z). \tag{2}$$

133 Expressing this selection coefficient in terms of an (absolute) fitness function, $W(z)$, gives

$$S = \overline{W}^{-1} \text{cov}(W(z), z). \tag{3}$$

134 The selection differential takes into account all selection, both direct and indirect, acting on the trait (Lande

135 & Arnold, 1983).

136 The direct selection gradient, β, is the average derivative of relative fitness with respect to phenotype.

137 In multivariate analyses there is an important distinction that the selection gradient is a measure only of

138 selection acting directly on the trait. However, in univariate form,

$$\beta = E\left[\frac{dw}{dz}\right] = \frac{\text{cov}(w, z)}{\text{var}(z)}. \tag{4}$$

139 Therefore, the difference between the two selection coefficients for univariate analyses, as we are working

140 with here, is only in regards to scaling. The commonly used variance standardised selection gradient, β_σ,

141 (Hereford *et al.*, 2004) is equivalent to variance standardisation of the selection differential, S/σ_z. The use

142 and interpretation of the direct selection gradients requires more consideration when multiple traits are being

143 considered simultaneously (Morrissey, 2014). Therefore, selection differentials are used here as we believe

144 this is a better general starting point if the methods are to later be extended to allow multivariate analysis.

145   Consider a very simple absolute fitness function, a linear function with an intercept (a) and slope (b) i.e.

$$E\left[W\right]_i = W(z) = a + bz_i. \tag{5}$$

146 Mean absolute fitness is,

$$\overline{W} = \int_{-\infty}^{+\infty} W(z)_i p(z) dz = \int_{-\infty}^{+\infty} a + bz p(z) dz = a + b \int_{-\infty}^{+\infty} z p(z) dz,$$

147 where the last term, $\int_{-\infty}^{+\infty} z p(z) dz$, is the mean phenotype, $\overline{z}$, therefore in our simple model

$$\overline{W} = a + b\overline{z}, \tag{6}$$

148 because equation (5) is a linear function.

149   The covariance of absolute fitness with the trait can be expressed as a function of the trait variance and

150 the slope of the absolute fitness function,

$$\mathrm{cov}(W, z) = b\left(E\left[z^2\right] - (E\left[z\right])^2\right) = \sigma_z^2 b. \tag{7}$$

151 Combining equations (3), (6) and (7), the selection differential can be expressed as

$$S = \frac{\sigma_z^2 b}{a + b\overline{z}}. \tag{8}$$

152 This formula for the selection differential in terms of the parameters of a linear fitness function is useful

153 for elucidating four ways in which ecological changes could alter selection differentials and other phenotypic

154 selection coefficients. Each variable and distribution of phenotype in equation (8) represents a way through

155 which ecology can alter selection differentials. The term $b\overline{z}$ in the denominator of (8) accounts for the

156 fact that a change in mean phenotype changes mean fitness, and so ultimately S, if the fitness function is

157 sloped ($b \neq 0$). Thus, any effect of $\overline{z}$ on selection may act through changes in mean fitness, independent

158 of perturbation of a (which independently controls mean fitness). The effect of $\overline{z}$ on selection coefficients

159 is thus equivalent to the ultimate effect of one variable ($\overline{z}$) on another (S) in a path analysis, where the

160 effect is mediated by an intermediate quantity (in this case, the component of mean fitness controlled by

161 $b\overline{z}$). This pathway is distinct from, but no less ecologically relevant than, a change in a while all other

162 components remain constant. There have been implications in the literature that differences in selection

163 gradients (for instance among temporal or spatial replicates) attributed to environmental variables are a

164 result of changes in trait-fitness relationships (Wade & Kalisz, 1990; MacColl, 2011). Such interpretations

165 effectively assume all change occurs through parameter b. Almost certainly this is not the understanding

166 of the authors themselves but it has likely led to wider belief that difference in selection gradients can be

167 largely or solely attributed to changes in the trait fitness relationship. We hope to clarify that in fact a wider

168 range of possible explanations exists for any change seen in a selection differential estimate and each may

169 lead to very different ecological interpretations.

170 Taking the derivatives of S with respect to each of the parameters illustrates how each will change the

171 selection differential, under this linear fitness function, when all other factors are constant. These derivatives

172 are listed in Table (1) and depicted graphically in Figure (1). As an example, in Figure (1), doubling mean

173 fitness from 0.4 to 0.8, while all other parameters are held constant, does not alter the absolute fitness

174 function slope but halves the resulting variance-standardised selection gradient from 0.2 to 0.1. If only these

175 selection gradients were reported, which is commonly the case, the information would not be available to

176 establish that mean fitness was driving the change which could result in erroneous ecological interpretations.

177 The exact relationships between selection coefficients and parameters of fitness functions and phenotypic

178 distributions will change with the nature of the fitness function and the distribution of phenotype. This may

179 include additional pathways and higher moments, especially if fitness functions are curved (Bonamour *et*

180 *al.*, 2017). However, the principles illustrated in this section should be quite general. For example, consider

181 another simple fitness function $W(z) = a \exp(bz)$. It is well known that the selection gradient is equal to b,

182 for this kind of fitness function, and does not depend on the value of a (Lande, 1983; Chevin *et al.*, 2015).

183 In a situation where some ecological variable affected a, that variable would certainly be relevant to the

184 fitness of individual organisms. Organisms experiencing high values of a would have both higher fitness, and

185 a steeper relationship between their absolute fitness and the trait z. For this specific fitness function, these

186 two affects cancel each other exactly i.e. an increase in a leads to a steeper relationship between z and W,

187 this potential change in the strength of directional selection is exactly cancelled out by mean fitness itself

188 being higher due to the increase in a. So, while S or β do not vary with a, it is certainly not true that all

189 aspects of natural selection are inert with respect to variation in a. In some circumstances understanding

190 these multiple effects of a variable on selection may be required to fully understand why selection does (or

191 does not) vary.

Methods

Study system, data selection and handling

The Soay sheep (*Ovis aries*) of St Kilda, in the Outer Hebrides, have been the subject of an intensive individual-based long-term study since 1984 (Clutton-Brock & Pemberton, 2004). The majority of lambs within the main study area are born, caught and tagged during April each year. Each August, a large portion of the sheep, of all ages, in the study area are caught and weighed. Dates of mortality are known with high precision for the majority of individuals that use the study area through population monitoring involving 30 censuses per year, daily mortality searches of the study area during periods of high mortality (late winter), and occasional surveys of the entire island. This ensures that the lifespan of most individuals can be determined with high precision. These censuses also yield highly precise estimates of the numbers of individuals using the study area each year. Mortality, which is at least partly density-dependent, can vary dramatically between years, which results in the population size falling to very low numbers at irregular periods (Grenfell *et al.*, 1992; Clutton-Brock & Pemberton, 2004).

We investigate selection of August mass via first year survival, in relation to population size. The analyses consider the two sexes separately unless otherwise stated and use lambs which survived until the August of their first year and that were caught and measured during that August.

First year survival, our measure of absolute fitness (W), was based on census, death and capture data. Lambs were assigned as having survived the winter if they were still alive at the end of April the year after their birth. Individuals whose survival over their first winter was uncertain, 122 (10.646%) females and 188 (18.431%) males, were removed from the data set. These individuals are either known to be dead but it is not known whether or not they died prior to the end April or they have not been recorded dead but do not appear in censuses after their first winter. An alternative data set where these lambs were included and assumed to have died during their first winter was also compiled. All subsequent analyses were performed on both data sets, the results from the alternative dataset are included as a supplemental analysis (S3), but the main results reported were unchanged by the inclusion of these additional individuals.

The phenotype (z) used in the analyses was live body mass in August, measured to the nearest 0.1 kg and mean centred across all years. In cases where an individual had been captured more than once in August the entry on the day closest to the mean capture day across all 29 years, the 14th, was kept. To account for growth that occurred when individuals were caught on different days throughout August the mean centred mass (z_i) was modelled against the day of August capture (Day), including year as a random effect (b_t) with

222   error, ϵ_i;

$$z_i = \alpha_g + b_g \text{Day} + b_t + \epsilon_i. \tag{9}$$

223   Males increase in mass by 0.200 kg each day during August while females gained 0.158 kg each day. These

224   estimates were used to correct each individual's mass to that predicted for mean day of capture (the 14th)

225   in August over the 29 years. This corrects for differing capture days without removing annual differences in

226   mass. These corrected mass estimates were used as the trait values in the following selection analyses.

227   The population size (E) used is representative of the core study population on the 1st of October each

228   year, it includes all females and males seen in censuses or caught in that year and all males seen or caught

229   before the 1st of October i.e. it does not include males who only visit the study area for the rut. All lambs

230   that were born in the study area and not subsequently recorded as dead before this date are also included

231   in the total.

232   The final dataset used in the analyses included sheep born in 29 years, from 1985 to 2013. It contained

233   1146 female individuals and 1020 male individuals. Over this time the size of the population ranged from

234   211 to 672 individuals.

Regression of phenotypic selection coefficients on the environmental covariate

236   Possibly the simplest way that ecology can be incorporated into selection analysis builds on the idea suggested

237   by Wade & Kalisz (1990) to estimate the covariance between, or regression of phenotypic selection coefficients

238   on, environmental variables. By calculating selection coefficient estimates for each year individually and

239   regressing these on the population size we quantify how selection on lamb August mass varies with population

240   size and calculate the proportion of the variation in selection that is attributable to changing population

241   size.

242   We calculated unstandardized annual selection differentials as the difference in mean trait value for

243   individuals alive before and after the period of selection. The standard errors associated with these un-

244   standardized selection differentials was calculated as $\sqrt{\frac{\sigma_{t1}^2}{n_{t1}} + \frac{\sigma_{t2}^2}{n_{t2}} - 2\frac{\sigma_{t2}^2}{n_{t1}}}$, where σ^2 is the variance, n is the

245   number of individuals and the subscripts indicate whether the value is from before ($t1$) or after ($t2$) se-

246   lection. Further details on this approach are provided in the supplementary material(S1). Due to small

247   sample sizes in some years, our attempts to calculate these estimates and standard errors in other ways were

248   unsuccessful. This was particularly true for attempts using bootstrapping to generate the standard errors,

249   with small sample sizes inevitably some of the bootstrap samples have zero survival and therefore undefined

250   selection differentials. This problem was unavoidable for some years when all the individuals included in the

final dataset had the same survival outcome. In these cases either a selection coefficient is undefined, if all individuals die, or the associated error cannot be calculated, if all individuals survive (due to there being no variation in the relative fitness). We therefore did not include these years in the analysis, they were generally years early in the study with very small sample sizes but also included male lambs born in 2001 when none of the 41 individuals included in our dataset survived through the winter. Additionally in some years there was only a single survivor. In these situations calculation of the standard error is complicated and any error that could be estimated would be too large to add useful information to the analysis and so these were also removed. To model the effect that the environment had on the strength of selection in each sex, we carried out regression of the selection differentials against population size taking into consideration uncertainty in the estimates. We used a diffuse inverse-gamma prior on the residual variance, using the parameters (V=1 and ν=0.002; DeVillemereuil, 2012).

$$\hat{S}_t = \mu + be_t + m_t + \epsilon_t, \tag{10}$$

where $\hat{S}_t$ is the selection differential estimate for each replicated period of selection, t, (e.g. year) and e_t is the value of the environmental variable. The measurement error associated with the selection differential estimate is included as m_t with a distribution $m_t \sim N(0, SE_t^2)$ and the residual error, ϵ_t, is distributed as $\epsilon_t \sim N(0, \sigma_\epsilon^2)$.

The variance in selection attributed to the across year variance in the environmental variable, σ_e^2, is $b^2\sigma_e^2$. While the total variance in S is

$$\sigma_S^2 = b^2\sigma_e^2 + \sigma_\epsilon^2. \tag{11}$$

The proportion of the total variation in selection attributed to the environmental component of the model is thus

$$\frac{b^2\sigma_e^2}{b^2\sigma_e^2 + \sigma_\epsilon^2}. \tag{12}$$

We can also calculate the proportion of variance in selection that would have been attributed to the environmental variable had we used a regression model which only included the point estimates of the phenotypic selection coefficients, ignoring any associated estimation error,

$$\frac{b^2\sigma_e^2}{\sigma_{\hat{S}}^2}, \tag{13}$$

where $\sigma_{\hat{S}}^2$ is the variation in the calculated selection differentials, ignoring the associated error.

274 Model-based full and partial sensitivities

275 In this section we describe the estimation of three functions which can be combined to generate model-based
276 predictions of the selection differential, S, in any given environment, e. The sensitivity of the selection
277 differential to changes in the environment (equivalent to the slope of the regression line in the previous
278 section) is quantified and this sensitivity is then split into components acting through the four previously
279 identified pathways: A change in trait mean, trait variance, mean fitness or the relationship between the trait
280 and fitness. In order to implement the ideas demonstrated by equation (8), Table (1) and Figure (1), three
281 functions are needed. First we need to estimate an "environmentally-structured fitness function", $W(z, e)$,
282 linking absolute fitness to trait values, z, and the environmental variable of interest, e. We also need a
283 function relating the mean trait value to the environmental variable, which will be denoted by $\bar{z}(e)$, and
284 finally a function relating the trait variance to the environmental variable, $\sigma_z^2(e)$.

285 In order to obtain a flexible model of the effects of August mass and population density on survival,
286 we fitted a logistic generalised linear mixed model (GLMM; Bolker *et al.*, 2009; Hadfield, 2010) assuming
287 a binomial error distribution, $W \sim B(E[W])$, with linear and quadratic effects of mass and density, plus
288 their interactions. We included a random effect of year. Additionally we modelled effects of sex on all
289 terms, i.e. a main effect of sex on the model intercept, and interactions of sex with all other terms. While
290 we subsequently conduct all analyses separately by sex, this treatment allows us to better interpret sex
291 differences in environment-selection relationships. Specifically this model took the form;

$$
\begin{aligned}
\mathrm{logit}(E[W]) = {} & \alpha_B + B_1 z + B_2 z^2 + B_3 e + B_4 e^2 + B_5 \mathrm{Sex} + B_6 ez + B_7 e\mathrm{Sex} + B_8 e^2 \mathrm{Sex} \\
& + B_9 z\mathrm{Sex} + B_{10} z^2 \mathrm{Sex} + B_{11} ez\mathrm{Sex} + b_t + \epsilon_i.
\end{aligned}
\tag{14}
$$

292 This models how individual absolute survival data is related to the trait value, z, environment, e and sex,
293 Sex, quadratic terms and relevant interactions are also included with residual error, ϵ_i. As temporal variation
294 is being investigated the period between replicated selection events, t, in this case year, was included as a
295 random variable. Since the residual variance is unobservable in a binomial model with a single trail per
296 unit of observation, the residual variance was fixed to one (Morrissey *et al.*, 2014). Using the fixed factor
297 coefficients of equation (14) we can construct a function to estimate absolute fitness of an individual, of
298 either sex, with any trait value for a given environment condition in an average year;

$$
\begin{aligned}
W(z, e) = E\left[W|z, e, \mathrm{Sex}\right] = \int_{-\infty}^{+\infty} g'\Big(& \alpha_B + B_1 z + B_2 z^2 + B_3 e + B_4 e^2 + B_5 \mathrm{Sex} + B_6 ez + eB_7 \mathrm{Sex} \\
& + B_8 e^2 \mathrm{Sex} + B_9 z\mathrm{Sex} + B_{10} z^2 \mathrm{Sex} + B_{11} ez\mathrm{Sex} + \epsilon_i \Big) p(\epsilon) d\epsilon,
\end{aligned}
\tag{15}
$$

299   where g' is an inverse logit function and $p(\epsilon)$ is a standard normal density function corresponding to the

300   fixed overdispersion term evaluated at ϵ.

301   The dependence of mass on population size was modelled, again with year as a random variable, as

$$z_i = \alpha_C + C_1 e + C_2 \text{Sex} + C_3 e \text{Sex} + b_t + \epsilon_i. \tag{16}$$

302   Using the coefficients from this model we can construct a function predicting population mean mass from

303   population size as

$$\overline{z}(e) = E[z|e, \text{Sex}] = \alpha_C + C_1 e + C_2 \text{Sex} + C_3 e \text{Sex}. \tag{17}$$

304   This allows the prediction of the mean trait value in any given environment. Finally we estimated the log

305   of the trait variance and the standard error of that log variance individually for each year. We estimated

306   the standard error of the estimates of the phenotype variance as $\hat{\sigma}^2_{zt}\sqrt{\frac{2}{N_t-1}}$ where N_t is the number of

307   individuals of a given sex in a given year, this comes from the chi-square distribution of $S^2(n-1)/\sigma^2_{zt}$ with

308    $n-1$ degrees of freedom. We obtained corresponding standard errors of log variances by the delta method

309   (see e.g. Appendix 1 of Lynch & Walsh, 1998). These values were used to fit a model of how the trait

310   variance changes with the environment, taking account of the errors in the variance estimates;

$$\log\left(\hat{\sigma}^2_{zt}\right) = \alpha_D + D_1 e_t + D_2 \text{Sex} + D_3 e \text{Sex} + m_t + \epsilon_t. \tag{18}$$

311   The measurement error associated with the log of the estimate of trait variance is included as m_t with

312   a distribution $m_t \sim N(0, SE_t^2)$ and the residual error, ϵ_t, is distributed as $\epsilon_t \sim N(0, \sigma_t^2)$. The resulting

313   coefficients can be used to construct a function for predicting $\sigma_z^2(e)$;

$$\sigma_z^2(e) = E\left[\sigma_z^2|e, \text{Sex}\right] = e^{(\alpha_D + D_1 e_t + D_2 \text{Sex} + D_3 e \text{Sex})}. \tag{19}$$

314   This allows prediction of the trait variance in a given environment.

315   Using the equations (15), (17) and (19), the mean fitness in a given environment can be calculated as

316   the integral of absolute fitness as a function of the trait, z, and environment, e, $W(z, e)$, multiplied by the

317   weighted probability density function of the trait in that environment, $p(z; e)$,

$$\overline{W}(e) = \int_{-\infty}^{+\infty} W(z, e) p(z; e) dz, \tag{20}$$

318   where $p(z; e)$ is a normal probability density function with the mean and variance determined by the envi-

319   ronment according to

$$p\left(z;e\right) = N\left(z; \overline{z}\left(e\right), \sigma_z^2\left(e\right)\right), \tag{21}$$

320   with $N(z; \overline{z}(e), \sigma_z^2(e))$ representing the density of a normal distribution with mean, $\overline{z}(e)$, and variance, $\sigma_z^2(e)$,

321   evaluated at z.

The selection differential (equation 3) in any given environment can then be expressed as

$$S\left(e\right) = \frac{1}{\overline{W}\left(e\right)} E\left[zW\left(z,e\right)\right] - E\left[z\right] E\left[W\left(z,e\right)\right] = W^{-1}\mathrm{cov}\left(z,W\right)$$

322   and therefore,

$$S\left(e\right) = \frac{1}{\overline{W}\left(e\right)} \int_{-\infty}^{+\infty} zW\left(z,e\right) p\left(z,e\right) dz - \overline{z}\left(e\right)\overline{W}\left(e\right). \tag{22}$$

323   **Calculating sensitivities**

324   In a given environment, the sensitivity of the selection differential to the environmental variable is given by

$$\frac{dS\left(e\right)}{de} = \lim_{h \to 0} \frac{S\left(e+h\right) - S\left(e\right)}{h}. \tag{23}$$

325   In practice, setting h to a small number, relative to the range of the environmental variable, allows the

326   sensitivity of the selection differential to the environment to be accurately evaluated numerically. The

327   average sensitivity of selection can be calculated as the sensitivity averaged over all observed values of e.

328   For the Soay sheep data, we calculated the sensitivity of the selection differentials to population size for

329   the population size recorded each year with h set as 1. To quantify error associated with each estimate we

330   repeated the analysis integrating over 1000 samples of the posterior distribution of the models specified by

331   equations (14), (16) and (18), to generate posterior distributions of the average sensitivity of S to e.

332   **Partial sensitivities**

333   In order to establish how sensitive selection is to each of the four paths we have identified through which the

334   environment can alter selection (Table 1, Figure 1), we can perturb the model defined by equations (22) and

335   (23) according to the effects acting through each path. This requires that the perturbation, h in equation

336   (23), can be broken down into the components relating to each path. We re-define h (see equation 23) as a

337   vector,

$$\mathbf{h} = [h_\mu, h_{\sigma^2}, h_a, h_b], \tag{24}$$

338   where the four vector components relate to the four paths:

339   h_μ - a change in trait mean,

340   h_{σ^2} - a change in trait variance,

341   h_a- a change in mean fitness, and

342   h_b- a change in the relationship between the trait and fitness.

Equations (15), (17) and (19) can be altered to include this $\mathbf{h}$ vector. With resulting set of equations we can predict the mean absolute fitness in any given environment while allowing manipulation of one of the four vector component pathways at a time, holding the others constant:

$$W(z, e) = E\left[W^*|z, e, \text{Sex}, \mathbf{h}\right] = \int_{-\infty}^{+\infty} g'\Big(\alpha_B + B_1 z + B_2 z^2 + (B_3 + B_7 \text{Sex})(e + h_a) + (B_4 + B_8 \text{Sex})(e + h_a)^2$$

$$+ B_5 \text{Sex} + (B_6 + B_{11} \text{Sex})(z(e + h_b)) + B_9 z \text{Sex} + B_{10} z^2 \text{Sex}$$

$$- (B_6 + B_{11} \text{Sex})(\mu_c h_b) + \epsilon\Big) p(\epsilon) d\epsilon. \tag{25a}$$

$$\overline{z}(e) = E\left[\overline{z}^*|e, \text{Sex}, \mathbf{h}\right] = \alpha_C + C_1(e + h_\mu) + C_2 \text{Sex} + C_3(e + h_\mu)\,\text{Sex} \tag{25b}$$

$$\sigma_z^2(e) = E\left[\sigma_z^{2*}|e, \text{Sex}, \mathbf{h}\right] = e^{\left(\alpha_D + D_1\left(e + h_{\sigma_z^2}\right) + D_2 \text{Sex} + D_3\left(e + h_{\sigma_z^2}\right)\text{Sex}\right)} \tag{25c}$$

343   The subtraction of $B_6(\mu_c h_b)$ from equation (25a) is an adjustment to correct for changes in the mean fitness

344   that are a consequence of a change in the fitness function slope rather than a direct change, where μ_c is the

345   result of equation (25b) when $h_\mu = 0$. The selection differential can then be calculated as

$$S^*(e, \mathbf{h}) = \frac{1}{\overline{W}(e)} \int_{-\infty}^{+\infty} z W(z, e, \mathbf{h}) p(z; e, \mathbf{h}) dz - \overline{z}^*(e, \mathbf{h}) \overline{W}(e), \tag{26}$$

346   where

$$p(z; e, \mathbf{h}) = N\left(z; z^*(e, \mathbf{h}), \sigma_z^{2*}(e, \mathbf{h})\right). \tag{27}$$

347   The partial sensitivities are then

$$\frac{\partial S^*(e)}{\partial e} = \lim_{h_j \to 0} \frac{S^*(e) - S(e)}{h_j}, \tag{28}$$

348   where h_j is the component of the $\mathbf{h}$ vector that is non-zero.

349   We averaged the partial sensitivities calculated at the observed population size each year over the observed

350   population sizes to allow calculation of the average proportion of the total sensitivity that can be attributed

351   to each of the fours components. As for the full sensitivities we integrated this analysis over the posterior

352   distribution of the models specified by equations (14), (16) and (18), to generate posterior distributions of

353   each of the average partial sensitivities of S to e.

354   All analyses were carried out using the R statistical package (R Core Team, 2013) and all mixed models

355   (equations 9, 10, 14, 16 and 18) were fitted using the MCMCglmm package (Hadfield, 2010).

Results

Regression of phenotypic selection coefficients on the environmental covariate

358   Estimated annual selection differentials of lamb August body mass are predominantly positive. For females

359   the estimated selection differentials range from -0.397 $\pm$ 0.397 kg (estimate $\pm$ SE) in a year with a population

360   size of 211 (1989) to 2.738 $\pm$ 0.426 kg where the population size was 671 (2004). In males the lowest estimated

361   selection differential is -1.542 $\pm$ 1.542 kg at a population size of 211 (1989) rising to 2.187 $\pm$ 0.482 kg at a

362   population size of 575 (1996) (Table 3). The selection differentials covary positively with population size in

363   both sexes with strongest selection in years with higher numbers of individuals (Figure 2). The estimated

364   regression slope is 0.004 kg sheep^{-1} (95% credible interval 0.003 - 0.006) for females and 0.006 kg sheep^{-1}

365   (95% C.I. 0.003 - 0.008) for males.

366   The variance in selection attributable to variance in the population size is 0.488 (95% C.I. 0.153 to 0.831)

367   for males and 0.274 (95% C.I. 0.097 to 0.497) for females. This means that the proportion of variance in

368   selection explained by population size is 0.787 (95% C.I. 0.560 to 0.972) for males and 0.644 (95% C.I. 0.385

369   to 0.881) in females.

370   In contrast, if we had not accounted for the error in the selection coefficient estimates we would only

371   have been able to attribute a proportion of 0.442 (95% C.I. 0.139 to 0.753) in the variation seen in selection

372   in males to changes in population size and similarly only a proportion of 0.489 (95% C.I. 0.173 to 0.886) in

373   females.

Model based full and partial sensitivities

375   Environmentally structured fitness functions for both sexes are depicted in Figure (3) modelled by equation

376   (14); the coefficients from this model are shown in Table (2). In both sexes, lambs with a higher August

377   mass have a better chance of survival. Individuals with low August mass have a greater likelihood of winter

378   survival when born into a low population size than they would in high population years. Overall, female

379   lambs (Figure 3B) are more likely to survive their first winter than males (Figure 3A). Their August mass

380   has a greater influence on their winter survival than males, with lighter males showing less variation in

381   survival across population sizes. The effect of mass on survival is more pronounced at large population sizes

382 in males, while at low population sizes (below 300) males survive well regardless of their phenotypes.

383 The relationship between mean lamb mass in August and population size modelled by equation (16) is

384 shown in Figure (4). Mean August lamb mass is higher in years of low population size, with the difference

385 being more apparent in males with a regression slope of -0.004 kg sheep^{-1} (95% C.I. -0.007 to -0.001) compared

386 to -0.002 kg sheep^{-1} (95% C.I. 7.992×10^{-4} to -0.004) in females.

387 The relationship between the variance in lamb mass in August and population size is shown in Figure (5)

388 modelled by equation (18). Variance in August lamb mass is slightly higher in years of high population size,

389 with males having a regression slope of 2.009×10^{-4} kg^2 sheep^{-1} (95% C.I. -3.658×10^{-4} to 9.217×10^{-4})

390 and the slope for females being 2.371×10^{-4} kg^2 sheep^{-1} (95% C.I. -5.098×10^{-4} to 8.698×10^{-4}).

391 Mean absolute fitness ranges from 0.108 in years with high population size to 0.961 in years of low

392 population size for males. Mean absolute fitness in females is consistently higher than in males ranging from

393 0.198 to 0.951 with the greatest differences between the sexes seen in years of high population size. The

394 estimated mean absolute fitness for each population size observed in the data set are plotted in Figure (6).

395 The predicted environment-specific selection differentials for males range from -0.046 kg at the largest

396 observed population size to 2.773 kg at the lowest population size. In females the range is from 0.041 kg to

397 1.902 kg. The estimated selection differential for each observed population size are plotted in Figure (7).

398 The average full sensitivity of selection to population size for males is 0.007 kg sheep^{-1} (95% C.I. 0.003

399 to 0.011) and 0.004 kg sheep^{-1} (95% C.I. 0.001 to 0.008) for females, indicating that the selection differential

400 may be more sensitive to a change in population size for males than females. In females changes in the

401 selection differential are largely driven by changes in mean fitness, with the partial sensitivity relating to

402 mean fitness being 0.003 kg sheep^{-1} (95% C.I. 3.169×10^{-4} to 0.006). In males, this change is influenced by

403 both the mean fitness, 0.003 kg sheep^{-1} (95% credibility interval 2.733×10^{-4} to 0.006) and the relationship

404 between the trait and fitness, 0.003 kg sheep^{-1} (95% C.I. 0.002 to 0.005). The average full sensitivities and

405 partial sensitives for both males and females are plotted in Figure (8).

Discussion

407 The absolute fitness function i.e. the relationship between unstandardised measures of phenotype and ex-

408 pected absolute fitness, is surprisingly rarely considered in studies of natural selection in the wild. When

409 selection is characterised primarily via the relationship of traits with relative fitness (i.e. phenotypic selec-

410 tion coefficients) substantial information regarding variation in the selection may be lost. Consequently, any

411 observed change seen when calculating multiple phenotypic selection coefficients is likely to be attributed to

412 differences in the relationship between trait and fitness. However, this lost ecological can be retained if we

413 study fitness functions and distributions of phenotype in conjunction with the measures of natural selection

414 that are justified in evolutionary quantitative genetic theory.

415 The purpose of our illustrative example of these relationships (Table 1, Figure 1) is twofold. First, we

416 wish to make it clearer and more widely known that there is a much richer range of paths through which

417 biological variables could potentially explain any pattern observed in phenotypic selection coefficients. In

418 fact, not only are there explanations that are typically ignored, but these explanations can act simultaneously.

419 Two comparable replicates of selection could have the same values for selection differentials and gradients

420 (i.e. selection has the same evolutionary effect) but there still be differences in the nature of the selection

421 acting on the trait. For example, one replicate could have both a stronger trait-(absolute) fitness relationship,

422 and higher fitness. In this case consideration of only the selection gradients would fail to reveal interesting

423 aspects of the evolutionary ecology of the study system. Second, by putting these principles into a formal

424 mathematical structure, the theoretical component of our work points the way to implementing estimates of

425 fitness functions as part of formal methods for inference of selection. Previously known partial determinants

426 of phenotypic selection coefficients including a population's mean fitness (Wade & Kalisz, 1990) and the

427 distribution of phenotype (Wade & Kalisz, 1990; Steele *et al.*, 2011; Haller & Hendry, 2014; Chevin &

428 Haller, 2014) have not, until now, been incorporated into approaches designed to increase understanding of

429 variation in selection.

430 It is important to note that the fact that changes in mean fitness, and in the distribution of phenotype,

431 can influence the values of selection gradients and differentials in no way invalidates the quantitative genetic

432 theory by which selection gradients are justified. A change in the intercept of a linear fitness function, in

433 the absence of changes in other relevant variables such as its slope and the distribution of phenotype, does

434 cause relative differences in fitness among individuals to be less than they otherwise would. Correspondingly,

435 we would expect the evolutionary consequences, e.g., predictions of the breeders (Lush, 1937; Falconer &

436 Mackay, 1996) or Lande (Lande, 1979; Lande & Arnold, 1983) equations, of this lesser selection coefficient to

437 be smaller than usually estimated. There has been substantial discussion of the importance of understanding

438 the effects of ecological variables on the form of natural selection in the wild. However, the key point is that

439 ways of establishing the consequences of these effects have not been fully integrated into theory, methods,

440 and empirical studies of the variation of natural selection. Accordingly, methods have not previously been

441 developed to study the pathways by which ecological variables might affect fitness variation.

442 From an ecological perspective, having an understanding of variation in absolute fitness (e.g. survival

443 probability or reproductive success) under a fluctuating environment is crucial. Under a linear fitness func-

444 tion, as shown in Figure (1), when observed changes in selection are driven by an altered trait distribution

445 the survival probability of an individual of a particular phenotype is not going to change with the environ-

446   mental variable. Therefore, knowing what is driving changes observed in selection differentials, and correctly

447   interpreting the consequences that this will have under the fitness model being used, provides an important

448   link between the fields of ecology, evolution and demography. By deriving information about variation in

449   selection from models of absolute fitness dependence on phenotype and environment, we are able to say more

450   about how population level metrics are affecting changes in selection. This type of information is highly

451   relevant to those studying demography in wild populations.

452   Our analyses were conducted using unstandardised phenotype values (apart from mean-centring across

453   the whole study) so as not to obscure any paths by which the environment may ultimately affect selection.

454   The principle of multiple pathways affecting phenotypic selection coefficients will hold for other coefficients,

455   including both gradients and differentials, under different standardisations. Therefore, the basic principle

456   that phenotypic selection coefficients can be affected by the environment via the four paths identified (Figure

457   1, Table 1) should hold regardless of the kind of selection coefficient or standardisation (with the exception

458   that an unstandardised selection gradient will be unaffected by changes in the trait variance, when a fitness

459   function is linear). However, this list of pathways is only exhaustive for cases of linear absolute fitness

460   functions and when the traits analysed are normally distributed.

461   Using the calculation of the proportion of selection explained by the environment in the regression-

462   based analysis (Figure 2) demonstrates a relatively easy way to produce a quantitative measure that can be

463   compared across studies. Use of a measure such as this could support meta-analysis of the environmental

464   dependence of selection that allow investigation of commonalities in links between environmental variables

465   and selection across study systems. In particular, the proportion of variation in selection explained by

466   the environment, when accounting for statistical noise in phenotypic selection coefficients estimates, will be

467   particularly useful. Other approaches will underestimate the strength of environment-selection relationships.

468   The proportion of variation in selection explained by the environment rises from 0.442 to 0.787 in males and

469   from 0.489 to 0.644 in females when the associated errors are considered.

470   Our model-based approach (equations 15, 17 and 19) to analysing the components of the total effects of

471   an environmental variable, population size, on viability selection of summer lamb mass in male and female

472   Soay sheep (Figure 8) revealed total effects of density similar to regression-based methods (Figure 2) that

473   characterise only the total effect. Selection of mass in both sexes is predominantly positive, and increases in

474   both sexes with population size. The model-based average sensitivity of selection to population size, 0.007

475   kg sheep^{-1} in males and 0.004 kg sheep^{-1} in females, matches reasonably well to the closely-related parameter

476   of the slopes of the linear regressions of selection differentials on population size, 0.006 kg sheep^{-1} and 0.004

477   kg sheep^{-1}, respectively. Changes in the mean (Figure 4) and variance (Figure 5) of mass in response to

478   population size are modest in both sexes. Consequently, effects of density on selection do not act through

479 these descriptors of the trait distribution (Figure 8). However, population size does substantially affect mean

480 fitness (Figure 6, Table 2), and consequently, mean fitness is the main variable through which density affects

481 selection in females (Figure 8), and a major contributor in males (Figure 8).

482 An important methodological consideration for studies of variation in selection based on inferences of

483 environmentally-structured fitness functions, and effects of the environment on distributions of phenotype,

484 is the nature of the component models (equations 25a, 25b & 25c in our analysis) in any such analysis.

485 In particular, any component model predicting absolute fitness from values of phenotype and ecological

486 variables will have to be sufficiently flexible. Main effects and interactions of phenotype and environment

487 will generally be necessary while additional terms may add realism. If a study seeks to extend the basic

488 analysis to understanding variation in quadratic selection, it will be necessary to include interactions of

489 the environmental variable with non-linear terms pertaining to phenotype. Our choice of a generalised

490 (specifically, using a binomial distribution) function for fitness was probably not necessary. In fact, in some

491 situations, a linear model (i.e., not a generalised analysis) of trait-environment-fitness relationships could be

492 most useful. The non-linear link functions used in generalised model induce a certain amount of dependence

493 between the intercept and slope of fitness functions on the data (as opposed to the latent) scale. In our case,

494 there will be little dependence, on average, because values of expected fitness take a large range and the

495 dependence of the mean and slope on the intercept have opposite signs when expected fitness is above and

496 below 0.5. When our analyses is carried out using a linear mixed model instead of the generalised fitness

497 function (S2 in Supplementary Material) the results obtained are broadly similar. In other situations, this

498 dependence could be problematic. For example, if a log-link model were used, there would be no direct

499 dependence of selection on the model intercept (Morrissey & Goudie, 2016). This would not invalidate

500 the approach, but further developments, or use of linear models to characterise fitness functions, would be

501 necessary.

502 Analyses such as those we have implemented here, to separate the effects of a driver of selection acting

503 through trait-fitness relationships, mean fitness, and the distribution of phenotype, are potentially applicable

504 in a wide range of study systems. It would be particularly interesting if mean fitness proved to be a major

505 contributor to variation in selection of a range of traits in different study systems. While changes in mean

506 fitness, which may be driven by environmental stochasticity, can effect variation in selection, they cannot

507 in themselves change the sign of selection. A lot of interest in variation in selection arises from a desire to

508 characterise the prevalence of fluctuating selection (e.g. as an explanation for stasis, Bell 2010; Uyeda *et al.*

509 2011; Chevin & Haller 2014; Estes & Arnold 2007), any generality in the finding that mean fitness is a major

510 driver of variation in selection could imply that fluctuations in selection in the wild are even rarer than the

511 most recent analyses (i.e., Morrissey & Hadfield 2012) have indicated. Further work on the dependence of

512 selection on density could be particularly valuable. It seems likely that different pathways through which

513 ecology could alter the dependence of selection on population density could have different eco-evolutionary

514 consequences (Sæther *et al.*, 2016; Engen *et al.*, 2017).

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Table 1: Derivatives for the selection differential with respect each parameter which can alter its estimation

Absolute Fitness Component	Derivative of S with respect to the absolute fitness component	Change in parameter required to decrease S_σ or β_σ as depicted in Figure (1)(plot)
Mean Fitness, $\frac{dS}{da}$	$\frac{-\sigma_z^2 b}{(a+b\bar{z})^2}$	Increase(a)
Trait/Fitness Relationships, $\frac{dS}{db}$	$\frac{\sigma_z^2 a}{(a+b\bar{z})^2}$	Decrease(b)
Trait Mean, $\frac{dS}{d\bar{z}}$	$\frac{-\sigma_z^2 b^2}{(a+b\bar{z})^2}$	Increase(c)
Trait Variance, $\frac{dS}{d\sigma^2}$	$\frac{b}{(a+b\bar{z})}$	Decrease(d)

Table 2: Coefficients from the individual mean fitness model

	Regression Coefficients	95% Credible Interval		p-value
(A) Fixed				
Intercept	-0.889	$(-1.736,$	$-0.103)$	0.030
Mass	0.311	$(\ 0.218,$	$0.404)$	0.001
Mass^2	-0.005	$(-0.027,$	$0.017)$	0.634
Sex	1.107	$(\ 0.717,$	$1.577)$	0.001
Population Size	-0.016	$(-0.022,$	$-0.010)$	0.001
Population Size^2	0.000	$(\ 0.000,$	$0.000)$	0.494
Mass·Population Size	0.002	$(\ 0.001,$	$0.002)$	0.001
Sex·Population Size	0.005	$(\ 0.002,$	$0.008)$	0.002
Sex·Mass	0.195	$(\ 0.057,$	$0.350)$	0.008
Sex·Population Size^2	0.000	$(\ 0.000,$	$0.000)$	0.584
Sex·Mass^2	0.025	$(-0.011,$	$0.061)$	0.172
Sex·Population Size·Mass	-0.001	$(-0.002,$	$0.000)$	0.152
(B) Random				
Year(variance)	2.362	$(\ 1.111,$	$3.973)$	*NA*

Table 3: Selection differentials and standard errors for first year survival for each sex in each cohort of lambs born. When all individuals survive the selection differential is 0 and no associated standard error can be calculated. Where an NA is shown for the selection differential all individuals with a known August mass died that year. Other instances of NA are in years when there was only one survivor and no associated error could be estimated. None of these cases were included in the regression analysis

| Birth Year	Population Size	n	Males Surviving Individuals	Males Selection Differential(kg)	Males Standard Error	n	Females Surviving Individuals	Females Selection Differential(kg)	Females Standard Error
1985	509	4	1	-5.97	NA	5	0	NA	NA
1986	211	4	4	0.00	NA	3	3	0.00	NA
1987	331	39	37	0.12	0.09	39	32	0.30	0.20
1988	457	22	2	-1.23	2.69	23	9	1.56	0.56
1989	211	4	3	-1.54	1.54	7	6	-0.40	0.40
1990	290	21	18	-0.47	0.28	32	29	0.27	0.15
1991	414	40	16	1.61	0.51	61	21	1.80	0.41
1992	321	32	26	-0.31	0.24	29	25	-0.01	0.16
1993	443	40	18	1.36	0.47	54	28	1.10	0.33
1994	435	25	1	-0.99	NA	34	9	0.97	0.39
1995	357	31	30	0.01	0.01	47	42	0.07	0.05
1996	575	68	19	2.19	0.48	54	25	1.22	0.40
1997	542	47	14	1.62	0.55	39	16	1.07	0.40
1998	591	44	1	1.54	NA	50	8	0.90	0.43
1999	325	42	34	0.14	0.23	43	41	0.01	0.01
2000	461	29	26	0.33	0.20	34	27	0.06	0.14
2001	651	42	0	NA	NA	52	6	1.90	0.66
2002	335	36	35	-0.05	0.05	32	30	-0.08	0.06
2003	494	47	42	0.13	0.14	60	55	0.08	0.10
2004	671	46	3	2.13	2.53	47	2	2.74	0.43
2005	405	18	9	0.43	0.51	28	17	0.30	0.34
2006	467	33	6	1.20	0.95	23	12	1.09	0.39
2007	447	50	28	0.93	0.32	56	34	0.86	0.27
2008	567	56	28	0.26	0.36	57	32	0.59	0.23
2009	617	52	20	1.63	0.38	48	27	0.84	0.29
2010	672	37	11	1.93	0.58	66	26	1.21	0.31
2011	649	41	1	2.67	NA	41	5	1.84	0.63
2012	362	23	22	0.03	0.03	32	30	0.16	0.12
2013	545	47	8	1.86	0.54	50	13	0.83	0.72
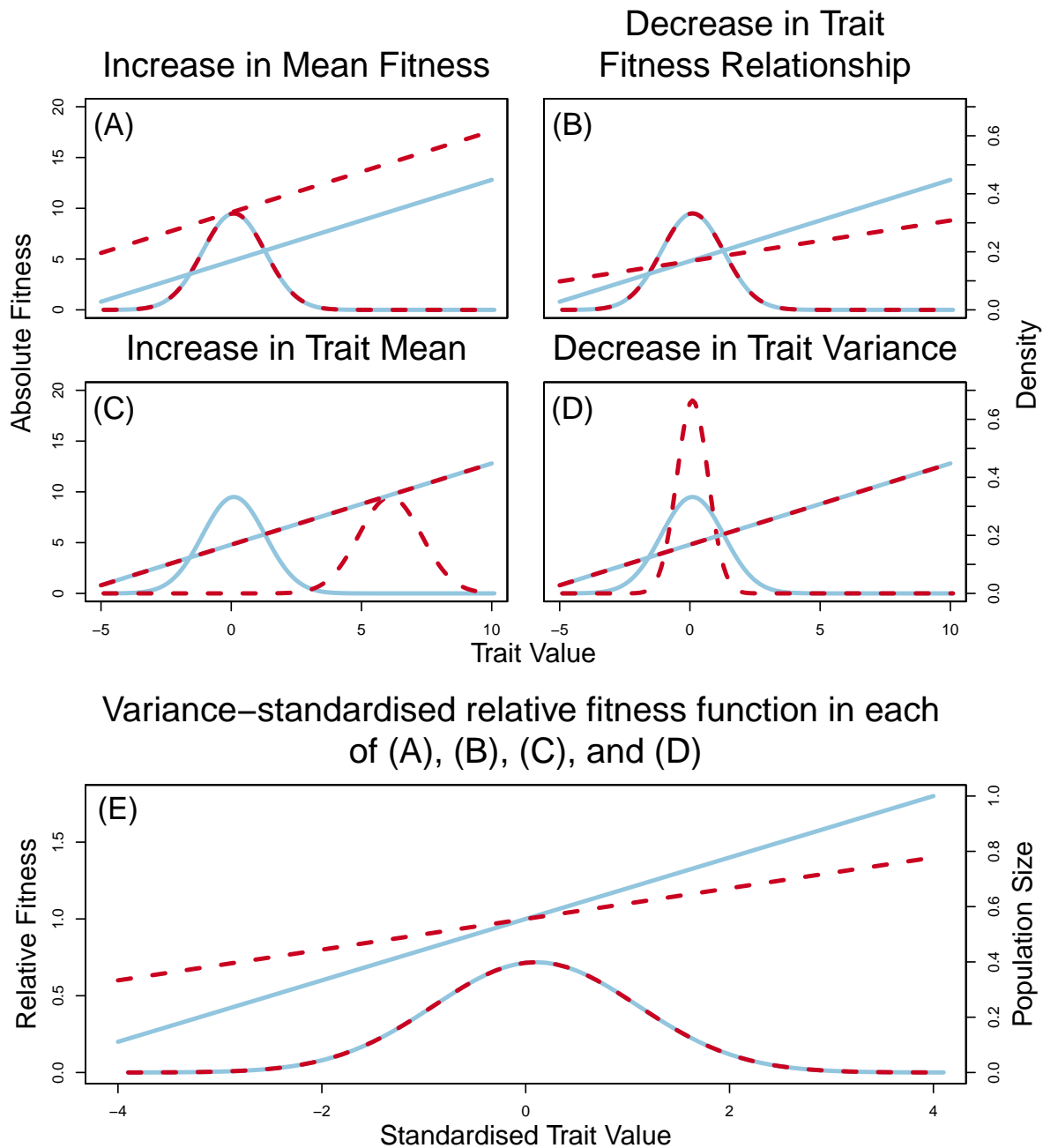
Figure 1: Graphs illustrating the fitness function change when only a single parameter of the trait to absolute fitness relationship, or distribution of phenotype, is altered. The trait values are related to absolute fitness using a linear fitness function. The resulting absolute fitness function is shown in the top four panels. In each case the solid blue line shows the same trait distribution and absolute fitness function while the dashed red line shows the effect of changing only the single parameter indicated above each graph. The bottom plot shows the resulting relative fitness function change when the trait values are mean centred and variance standardised. Importantly in each case illustrated in the top four plots the change in the variance-standardised selection slope, β, is the same despite very different underlying causes.
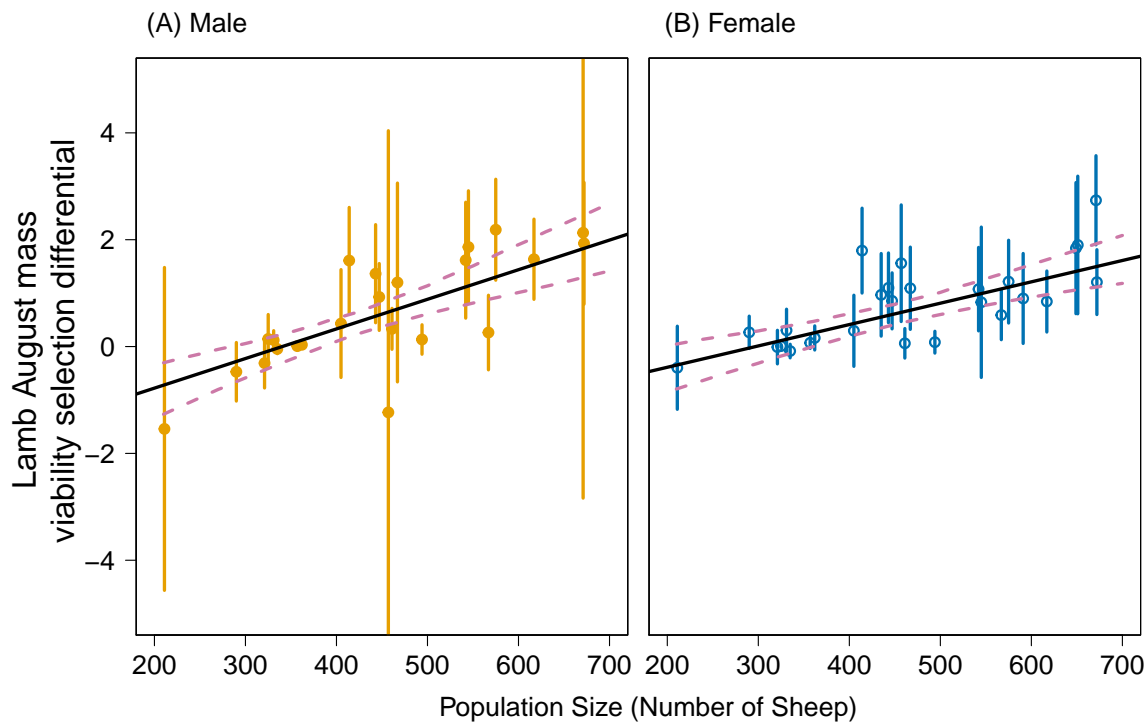
Figure 2: Regression of selection differentials on population size. Graphs showing the change in selection differentials for lamb mass in August with population size. The calculated selection differentials for male (A) and female (B) sheep are shown at different population sizes. The regression lines are calculated using a MCMCglmm model taking into account error in the estimates using their standard errors. The error bars show 95% confidence intervals assuming a normal distribution. The dashed lines show the 95% credibility regions for the regression lines. The slopes for males and females were not significantly different from one another.
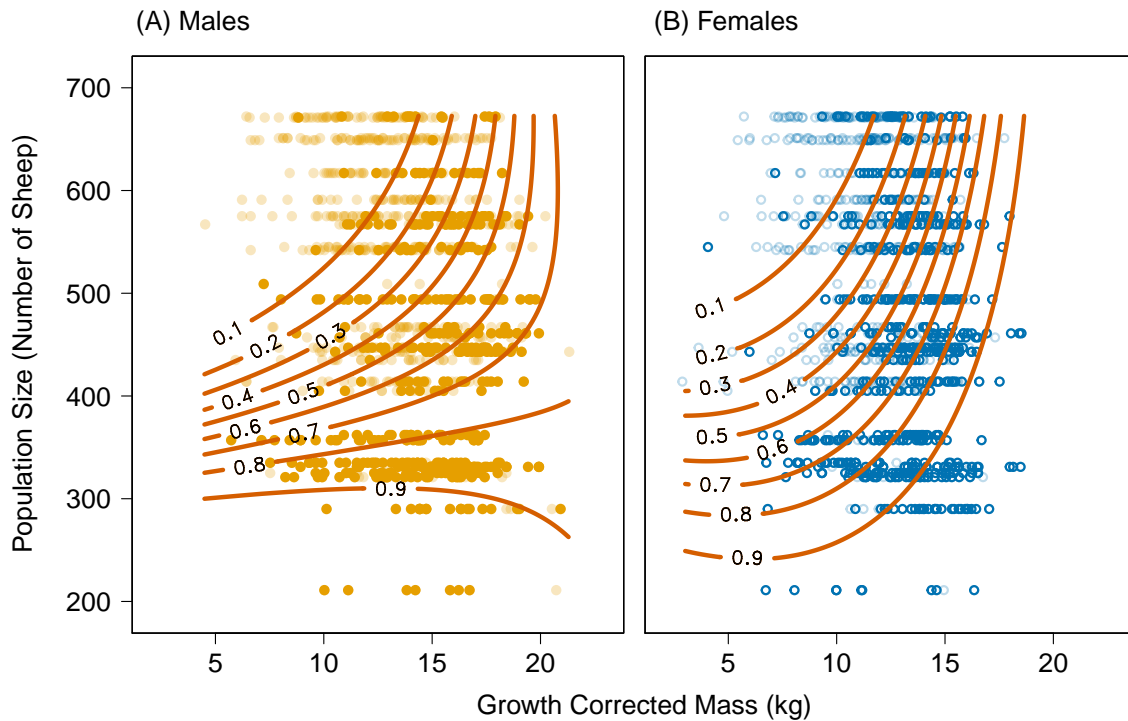
Figure 3: Environmentally Structured Fitness Functions. August mass of male (A) and female (B) sheep are shown at different population sizes. Realised survival is represented using points with higher transparency to represent individuals that did not survive their first winter. Fitness isoclines, showing the survival probabilities, are plotted using the intercepts and fixed factor coefficients shown in Table (1). In both sexes in years of low population size a much larger number of individuals are in the higher area of the fitness function meaning those with lower mass have a better chance of survival than they would in years of large population size. The apparent reduction in fitness at high mass and low population size seen in males compared to less extreme values is almost certainly due to limited data at the extremes of the dataset
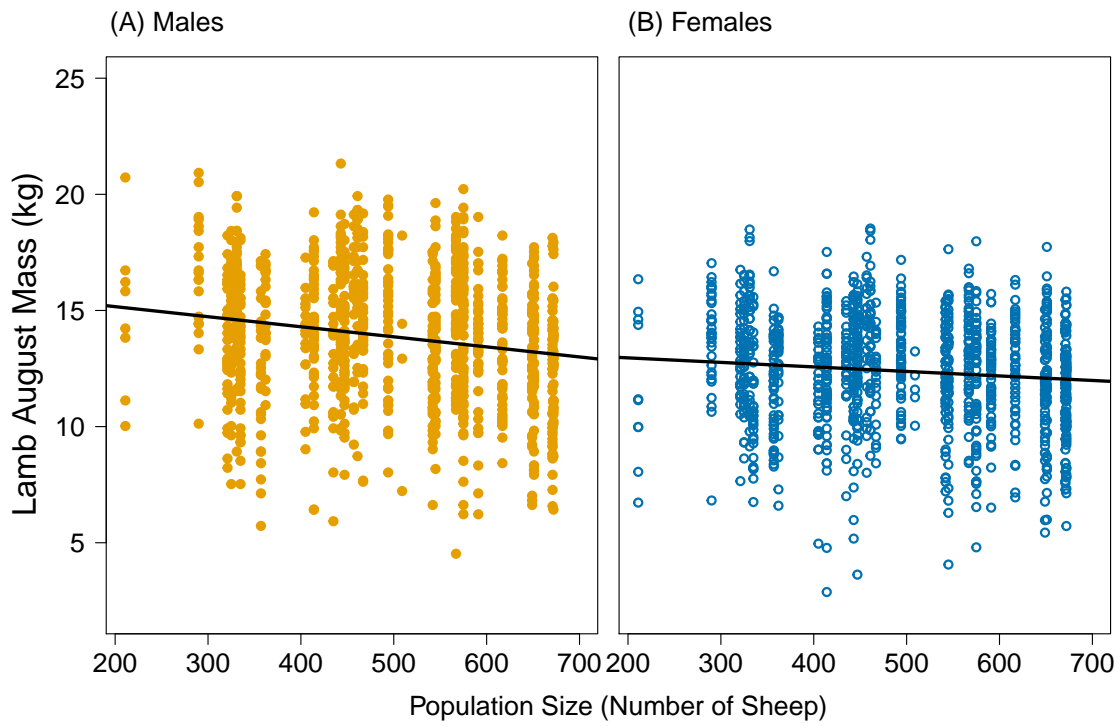
Figure 4: Regression of August mass on population size. August mass of male (A) and female (B) sheep are shown at different population sizes. Regression lines are plotted using the intercept and fixed-effect coefficients from applying equation (16)
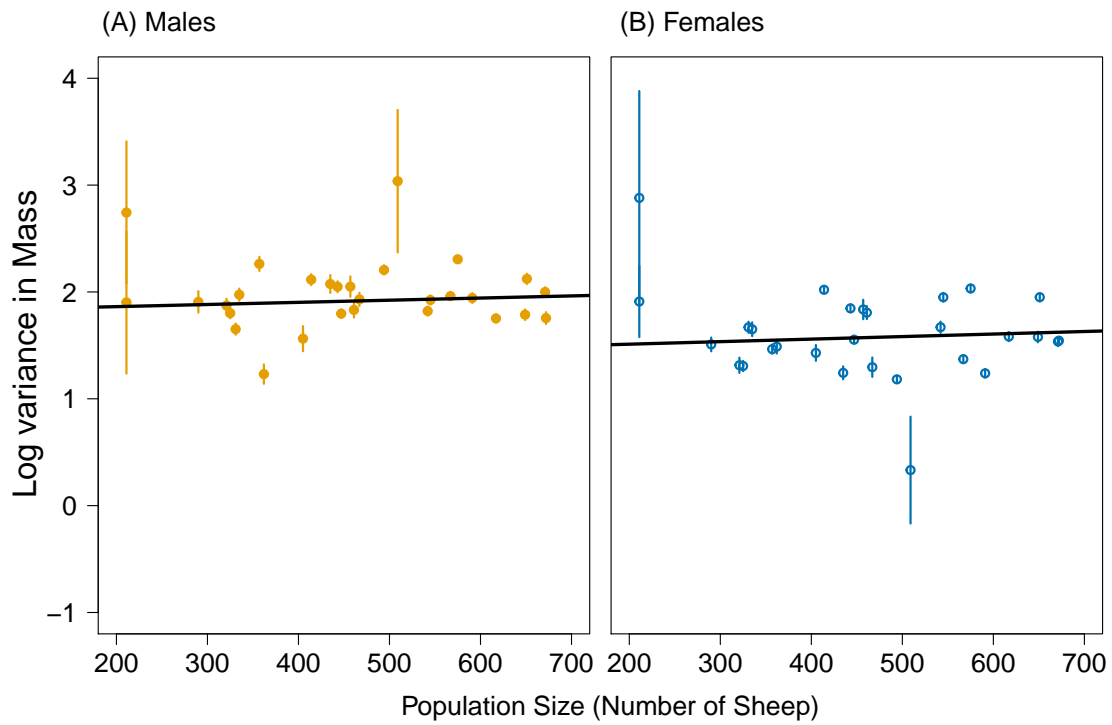
Figure 5: Regression of August mass variance on population size. The variance of August mass in male (A) and female (B) sheep are shown at different population sizes. Regression lines are plotted using the intercept and fixed-effect coefficients from applying equation (18). Error bars show the 95% highest posterior density interval.
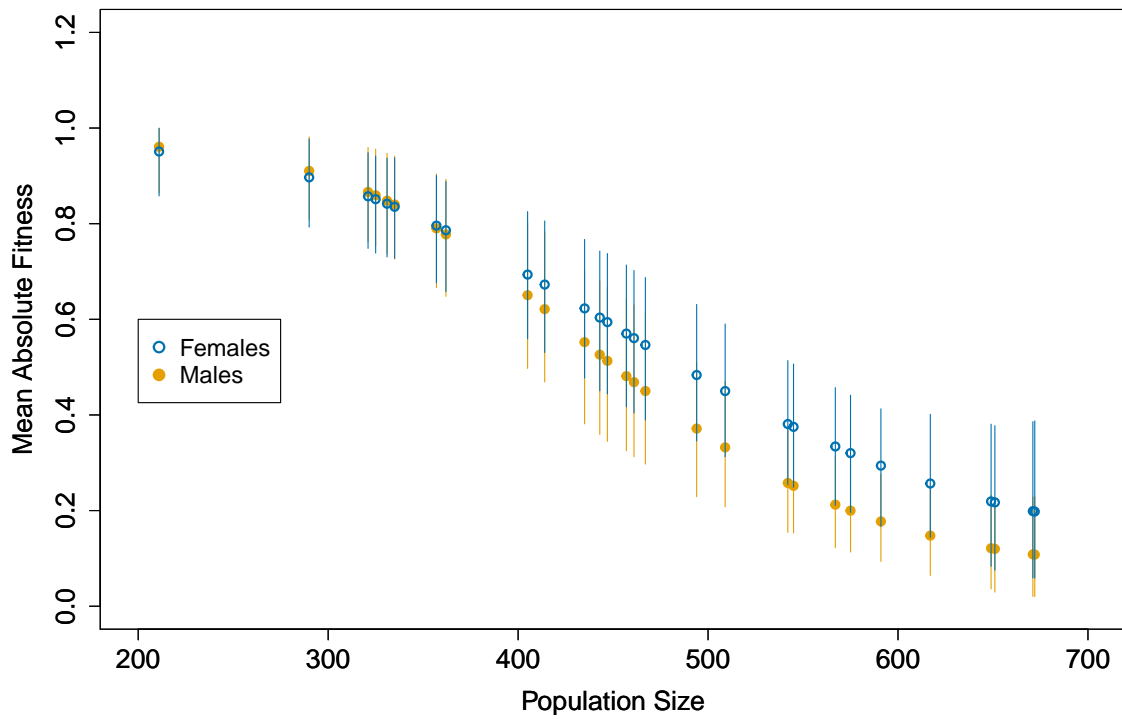
Figure 6: Mean absolute fitness against population size. Mean absolute fitness of male and female sheep are shown at different population sizes as predicted by our environmentally structured fitness function (equation 20)
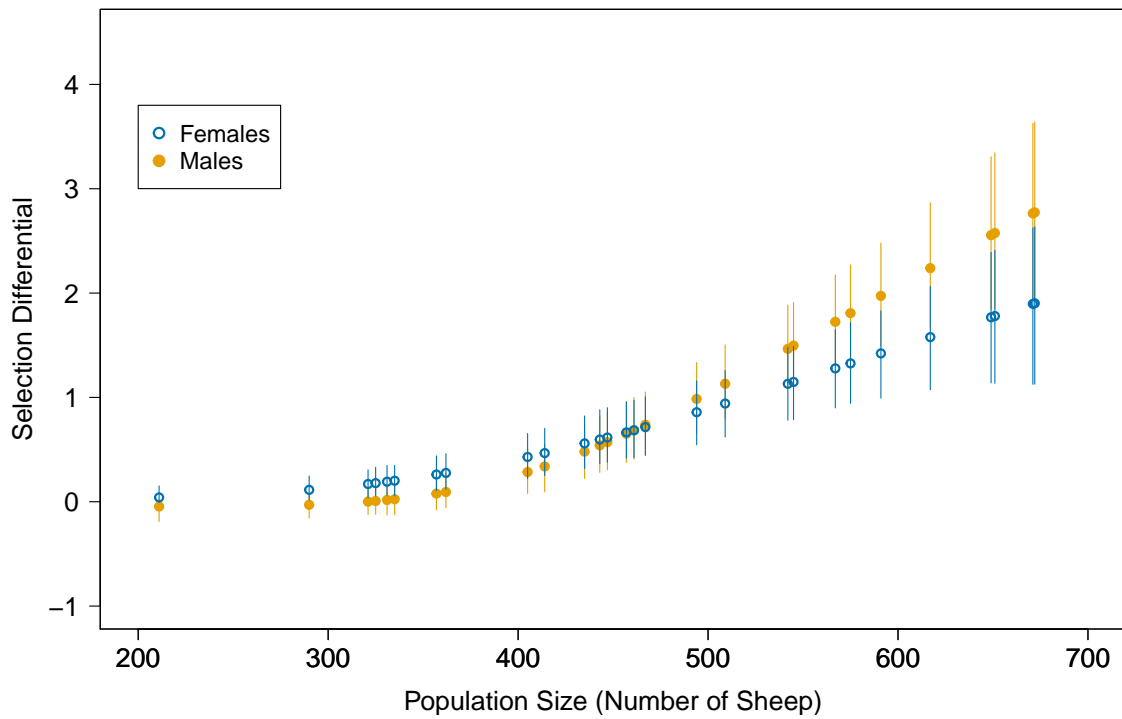
Figure 7: Selection differentials against population size. Selection differentials for male and female sheep are shown at different population sizes as predicted by our environmentally structured fitness function (equation 22)
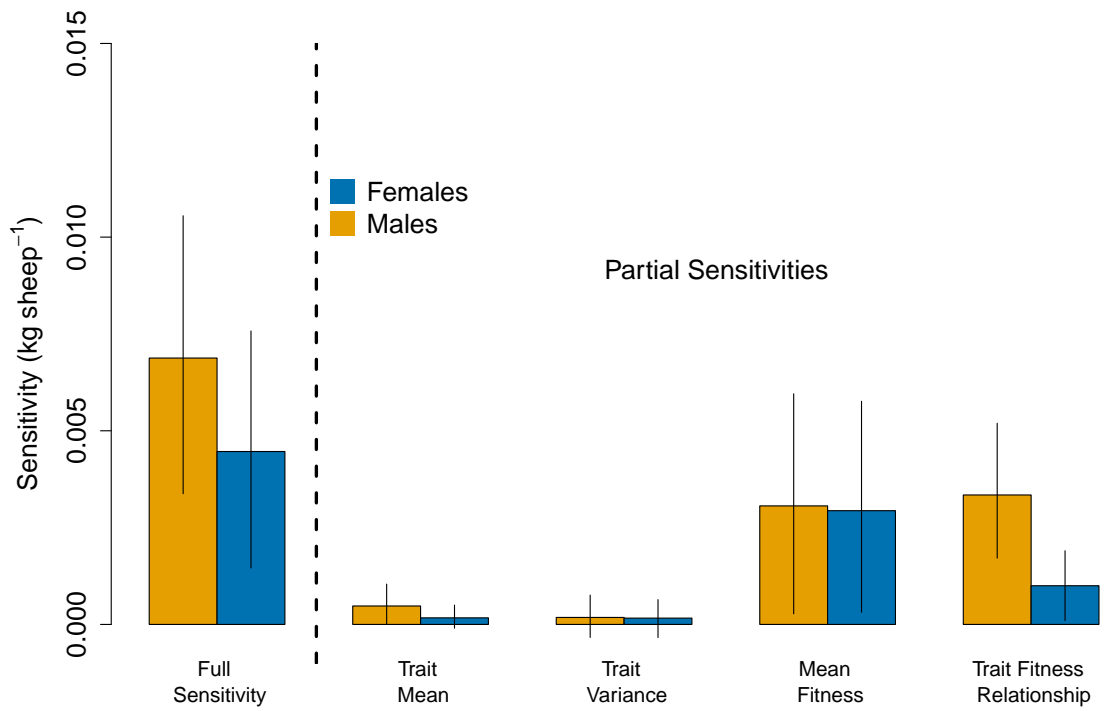.

Figure 8: Full and partial sensitivities. The full and partial sensitivities are shown for male and female sheep. The partial sensitivities show the contribution of each of the four different pathways through which ecology can alter selection estimates.