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A new metric to calculate the opportunity for selection on quantitative characters

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ABSTRACT

Background: Evolutionary changes in natural populations can occur on ecological time scales. Investigators have become very interested in characterizing short-term fluctuations in selection pressure, in identifying the circumstances under which the opportunity for selection is greatest, and in determining whether this opportunity is realized.

Aims: Introduce a new metric to explore how the opportunity for selection on the mean of a phenotypic character varies with time. Using data from two long-term studies of marked individuals, examine how the opportunity for and the selection on a character mean and variance covary with population growth.

Metrics: The traditional opportunity for selection metric (OS) is defined as the variance in relative fitness or the variation in absolute fitness divided by the square of the mean absolute fitness. This metric might not be appropriate to evaluate the maximum selection acting on a quantitative character because individual variation in both quantitative characters and in fitness underpins evolution by natural selection. We therefore develop a new metric, the opportunity for selection on a quantitative character (OSM), which considers variation in both character and fitness distributions.

Methods: Determine selection, OS, and OSM, in both simulated and empirical data. Compare the results for the traditional OS metric with the new OSM.

Results: The classical measure of the OS correlates with the OSM when calculated on simulated data but their association was curvilinear for non-normally distributed fitness components. Similar results were found for empirical data but their correlations were lower. Selection is strongest in declining populations and is greatest when the OSM is large, as in harsh environments.

Conclusions: Because most fitness components are non-normally distributed, OS will only approximately capture the maximum possible selection differential on phenotypic characters over a time step. The OSM should be a more useful metric for determining how selection will alter the distribution of characters.

Keywords: fitness, opportunity for selection, population dynamics, survival, vertebrates.

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INTRODUCTION

Investigating how the opportunity for selection on phenotypic characters fluctuates with the environment is not a trivial task because it requires estimating the maximum strength of selection acting on quantitative characters. The maximum upper rate of micro-evolutionary change on a quantitative character will be a function of variation in fitness (Fisher, 1930). If there is no variation in fitness among individuals, there can be no selection on the character and therefore no evolution. Typically, researchers have used the opportunity for selection as a proxy for the maximum possible strength of selection. The opportunity for selection, defined as the variance in relative fitness or the variation in absolute fitness divided by the square of the mean absolute fitness (Crow, 1958; Arnold and Wade, 1984a), is a measure used to quantify the maximum possible rate of evolution for fitness. Although the opportunity for selection is an appropriate measure to use when examining the evolution of fitness (Arnold and Wade, 1984a), several researchers have questioned its usefulness for measuring the opportunity for selection on phenotypic characters (Downhower *et al.*, 1987; Fairbairn and Wilby, 2001; Klug *et al.*, 2010), primarily because selection for a given phenotypic character is not always strongest when the opportunity for selection is greatest (Fitze and Le Galliard, 2011; Jennions *et al.*, 2012). This 'failure' of the opportunity for selection occurs, at least partially, because selection on a phenotypic character requires variation in fitness, variation in the character, and an association between the character and fitness. The opportunity for selection quantifies only the first of these (Krakauer *et al.*, 2011). To understand how selection varies with time, it is necessary to understand how variation in relative fitness, phenotypic variance, and the association between the character and fitness vary with time. In addition, to understand whether the proportion of possible selection a character experiences varies with time, it is useful to quantify the opportunity for selection on the character mean.

Individual variation in both quantitative characters and in fitness underpins evolution by natural selection. Understanding the causes and consequences of individual variation in natural populations is consequently central to progress in evolutionary ecology. There is a growing body of evidence that suggests that selection on phenotypic characters varies over time in natural populations (Kingsolver *et al.*, 2001; Siepielski *et al.*, 2009, 2011; but see Kingsolver *et al.*, 2012; Morrissey and Hadfield, 2012). In long-lived species, selection on quantitative characters can vary within an individual's life span as the environment fluctuates (for an example, see Grant and Grant, 2002). This realization has led evolutionary ecologists to ask whether selection is strongest in harsh or favourable environments (Both *et al.*, 2006; Wilson *et al.*, 2006); whether the strength of selection consistently varies across different phenotypic characters (Kingsolver *et al.*, 2012), whether selection operates primarily via survival or recruitment (Siepielski *et al.*, 2011; Morrissey and Hadfield, 2012), and how these processes combine to influence the overall strength of selection in age-structured populations living in variable environments (Coulson *et al.*, 2003; Pelletier *et al.*, 2007). The answers to these questions are fundamental for understanding the temporal dynamics of phenotypic selection on quantitative characters under natural conditions.

The main objective of this article is to explore how the opportunity for selection on a character's mean varies with time in populations living in the wild. To do this, we first had to develop a new metric that integrates information on the variation in relative fitness, the phenotypic variance, and the associated covariance between the character and fitness, which are essential to adequately measure the opportunity for selection on quantitative characters. We refer to this quantity as the opportunity for selection on a character mean (OSM).

To calculate this quantity, we work through the population growth rate. Second, we use simulations to investigate the conditions under which the classical measure of the opportunity for selection [OS (Crow, 1958)], calculated through survival and recruitment, correlates with the OSM. Third, to illustrate the application of our metric, we ask whether a decline in population growth always leads to higher opportunity for and greater selection on our phenotype of interest. We reconstruct time series of the opportunity for selection on the character mean as well as selection on juvenile body size in two well-characterized species: the red deer (*Cervus elaphus*) of the island of Rum and the St. Kilda Soay sheep (*Ovies aries*). Given the increasing number of wild populations that are facing new environmental conditions, understanding whether selection systematically varies with population dynamics should yield insights on the joint dynamics of ecological and evolutionary processes.

MATERIALS AND METHODS

In the first part of this section, we explain the rationale for suggesting a metric to estimate the opportunity for selection on a character mean by using information on the variance in fitness, on the variance in the character, and their association. Based on this theory, we had *a priori* expectations that selection should be strongest when populations are declining. The second part of this section presents the data and the analyses conducted to test this expectation in natural settings and to evaluate when the opportunity for selection, the opportunity for selection on a character, and selection itself are correlated.

The measurement of selection over a time step

The selection differential on a character is the difference in mean character value between selected individuals and the population prior to selection. It can be calculated as the covariance between the character (z) and (absolute) fitness (w) divided by mean (absolute) fitness (Arnold and Wade, 1984b): $S = \mathrm{cov}(z, w)/\bar{w}$. The mean of annual individual fitness over a time step, $\bar{w}$, is the population growth rate (N_{t+1}/N_t) and, in seasonal environments where survival (s) and recruitment (r) occur in pulses, can be written as the sum of mean survival and mean recruitment $\bar{w} = \bar{s} + \bar{r}$. There is no analytical reason that the covariance between a character and individual fitness should vary with population size, but this does not preclude biological processes generating a correlation (Svanbäck and Bolnick, 2007). Consequently, the key to understanding how selection operates in fluctuating populations is undertaking an empirical examination of how the covariance between a character and fitness varies with the population growth rate. In this article, we use two long-term datasets of marked ungulates to explore how the covariance between a character and fitness changes with population growth under field conditions.

The opportunity for selection via survival and recruitment over a time step

Classically, the opportunity for selection defined for fitness is:

$$I = \frac{\sigma^2(w)}{\bar{w}^2}, \tag{1}$$

where σ^2 is the variance of w. Rewriting $w = s + r$ and assuming a single pulse of survival and recruitment during a given year, we can define the opportunity for selection over a time step as:

$$\begin{aligned} I &= \frac{\sigma^2(s_i + r_i)}{(\bar{s} + \bar{r})^2} \\ &= \frac{\sigma^2(s_i) + \sigma^2(r_i) + 2\mathrm{cov}(s_i, r_i)}{\bar{w}^2}. \end{aligned} \tag{2}$$

The calculation of these quantities from field data can be achieved using data on individual survival over a time step (dead or alive) and individual recruitment over a time step (0 . . . n, where n is maximum litter size). These expressions could, of course, be calculated from frequencies (Falconer and Mackay, 1996), but for the purposes of this article we work with individual fitness.

For many distributions the variance is related to the mean. This means that the opportunity for selection may be dependent on mean survival or recruitment, especially because individual survival and recruitment are usually not normally distributed. Individual survival over a time step is binomially distributed (dead, alive). The variance of the binomial distribution is defined as $p(1 - p)$, where p is a parameter representing the probability of success in a binomial draw. The opportunity for selection for survival is therefore $p(1 - p)/p^2 = 1/p - 1$. Individual recruitment is often assumed to be Poisson distributed (Fairbairn and Wilby, 2001). This means that the opportunity for selection for a Poisson distributed fitness component is $p/p^2 = 1/p$, where p is a parameter representing the mean of the Poisson distribution. Similar derivations can easily be calculated for any distribution for which the mean and variance are defined (see Fig. 1, below).

Measuring the maximum achievable selection differential over a time step

One simple way to estimate the maximum possible linear selection differential on a phenotypic character is to calculate the selection differential having independently ranked fitness and character values from highest to lowest values:

$$P = \frac{\mathrm{cov}(rank(z), rank(w))}{\bar{w}}. \tag{3}$$

We refer to P as the opportunity for selection on a character mean. It is worth noting that when fitness and trait are both normally distributed, the maximum covariation between them is defined as the variance of z times the variance of w. However, fitness and fitness components are very rarely normally distributed, which means that Crow's insight is of more statistical than biological value. There is no equivalent identity when fitness (or character) is non-normally distributed. For this reason, we develop a new approach.

Given the observed selection differential on the character,

$$S = \frac{\mathrm{cov}(z, w)}{\bar{w}}, \tag{4}$$

the proportion of maximum possible selection that is realized is:

$$Q = \frac{S}{P}. \tag{5}$$

When the absolute value of Q is close to one, most of the opportunity for selection on the character is realized; when it is close to zero, little is realized. The sign of Q describes the direction in which selection operates.

In many cases, it may be informative to work out these quantities for survival or recruitment, possibly within an age-class for a time step. This is because variation in w and in z can vary with age and demographic rate (Coulson *et al.*, 2006). Given w can be divided into survival and recruitment components (see above), then $\mathrm{cov}(z, w) = \mathrm{cov}(z, (s + r)) = \mathrm{cov}(z, s) + \mathrm{cov}(z, r)$ and

$$S = \frac{\mathrm{cov}(z, s)}{\bar{w}} + \frac{\mathrm{cov}(z, r)}{\bar{w}}. \tag{6}$$

Denoting demographic classes as a and the proportion of the population in each class as c_a, the following equations apply for a structured population:

$$S = \frac{1}{\bar{w}} \sum_{a=1}^{N} c_a(\mathrm{cov}(z_a, s_a) + \mathrm{cov}(z_a, r_a)) \tag{7}$$

and

$$P = \frac{1}{\bar{w}} \sum_{a=1}^{N} c_a(\mathrm{cov}(rank(z_a), rank(s_a)) + \mathrm{cov}(rank(z_a), rank(r_a))). \tag{8}$$

Q can now be calculated for each demographic class and for each rate if desired.

Until now, we have only considered a univariate character. Similar logic can be used for multivariate characters. For example, to calculate the maximum possible strength of selection on two correlated characters, rank both characters and fitness and calculate P.

In the following sections, we empirically examine the associations between mean survival, the covariation between survival and juvenile body size, selection differentials, the OS and the OSM. We also build time series of OSM to explore when selection on juvenile body size is strongest in the wild. We focus on selection on body size via juvenile survival (viability selection) because weight and fitness data are available for both populations. Previous studies have shown that juvenile body size in Soay sheep and red deer is under directional selection (Coulson *et al.*, 2003; Pelletier *et al.*, 2007), so we use the equation for the OSM (equation 3) to analyse these data.

Are the OS and the OSM correlated?

The OS is a function of the distribution of fitness, while the OSM is dependent on both the character and fitness distributions. We used simulation to examine the association between the OS and OSM. We did this for both normally and log-normally distributed characters and for normal, Poisson, binomially, negatively binomially, and gamma distributed fitness. Character values and fitness values were drawn from random uncorrelated distributions; the mean of the random fitness distribution was itself a random number. For the normal distribution, the mean was sampled randomly but the variance was fixed. The gamma distribution is a two-parameter distribution (shape and rate). For our simulation, the values for both the shape and the rate parameters were drawn from random uncorrelated distributions. These data were used to calculate the OS and OSM and we then investigated their correlation.

Building time series of OS and OSM

We use data from two longitudinal studies of marked animals where animals have been monitored from birth to death. We investigate patterns in viability selection on juvenile measures of body size in red deer and Soay sheep.

Red deer

The red deer population of the North Block of the island of Rum, Scotland, has been the subject of a detailed long-term study since 1971 (Clutton-Brock *et al.*, 1982). Most calves are captured and marked within 2–3 days of birth and more than 95% of individuals present in the study area each year are individually recognizable with artificial marks or natural phenotypic characteristics (Clutton-Brock *et al.*, 1982). Censuses are conducted over the entire study area four times each month for 10 months each year and mortality searches are made daily during winter. We analysed calf survival (0, 1) using these data. In our analyses, we considered calf survival from birth to one year of age. The probability of sighting an animal in the population if it is alive is close to 1, thus an animal not seen in censuses but that has not been found dead is considered dead (Catchpole *et al.*, 2004; Moyes *et al.*, 2006). We used calf birth weight as a measure of body size for our investigations of patterns of selection. As there is variation in the time at which newborn calves are caught and weighed, we used a regression of capture mass against capture age to adjust calf mass at birth. [For more details on the methodology and the study population, see Clutton-Brock *et al.* (1982).]

Soay sheep

Intensive monitoring of the Soay sheep population on the island of Hirta in the St. Kilda Archipelago, Scotland, started in 1985. Since 1986, over 95% of individuals seen in censuses are individually recognizable in all years (Catchpole *et al.*, 2001). Survival is determined via repeated observation of marked sheep. Around 30 censuses of the study area population are conducted in each year (Clutton-Brock and Pemberton, 2004) and 79% of dead animals are recovered during winter mortality searches. We define first year lamb survival as survival (0 or 1) from birth to one year of age. Birth body mass (kg) is measured soon after birth and has been adjusted for capture age [for details on the Soay sheep study, see Clutton-Brock and Pemberton (2004)]. In this article, we used data on birth weight and lamb survival collected from 1986 to 2005; note that no data on birth weight were collected in 2001 because the UK outbreak of foot and mouth disease precluded lamb capture.

Estimating selection differentials, OS, and OSM

As the sheep and the deer are temperate ungulates with one main episode of selection (in winter), we use an annual time-scale to calculate selection, OS, and OSM. For species experiencing several selective events within a year, these quantities can be computed for time steps shorter than a year. In our study, mean annual survival, $\bar{s}$, was estimated as the number of individuals that survive from year t to year $t + 1$ divided by the number of individuals present at time t. Because individual survival is binomially distributed, the variance in annual survival, $\sigma^2(S)$, was calculated as $\bar{s}(1 - \bar{s})$. The OS via survival was calculated as $1/p - 1$, where p is mean survival. The OSM on body size was calculated using equation (3) (individuals are given either rank 0 or 1 for survival). Selection differentials for red deer and Soay sheep juvenile body size were calculated using equation (4). The significance of selection differentials was obtained using generalized linear models with a binomial error structure. Generalized additive models [GAMs (Wood, 2006)] were used to investigate the form of the relationships between mean survival, the covariation between survival and quantitative characters, viability selection differentials, the OS and the OSM for body size for both species. Predictions from the GAMs are displayed. Slopes are reported with their standard error (S.E.). We use the absolute values of selection differentials because we were only interested in variation in the strength of selection and not in its direction. Studies investigating fluctuating selection on juvenile body size in the two species have previously been published (Milner *et al.*, 1999; Coulson *et al.*, 2003; Pelletier *et al.*, 2007) and we used these data to illustrate how our approach can provide insight on selection in the wild. All analyses and simulations have been conducted in R v.2.12.0 for Windows (R Development Core Team, 2011).

RESULTS

Associations between OS and OSM for simulated data

Simulations showed that for a normally distributed character, the OS correlated linearly with the OSM only when fitness was normally distributed (Fig. 1A). When fitness was non-normally distributed, the association between the OSM and OS was curvilinear (Fig. 1). For a log-normally distributed character, the association between the opportunity for selection and the opportunity for selection on a character was also curvilinear (Fig. 1B). Because most fitness components are non-normally distributed, the OS will

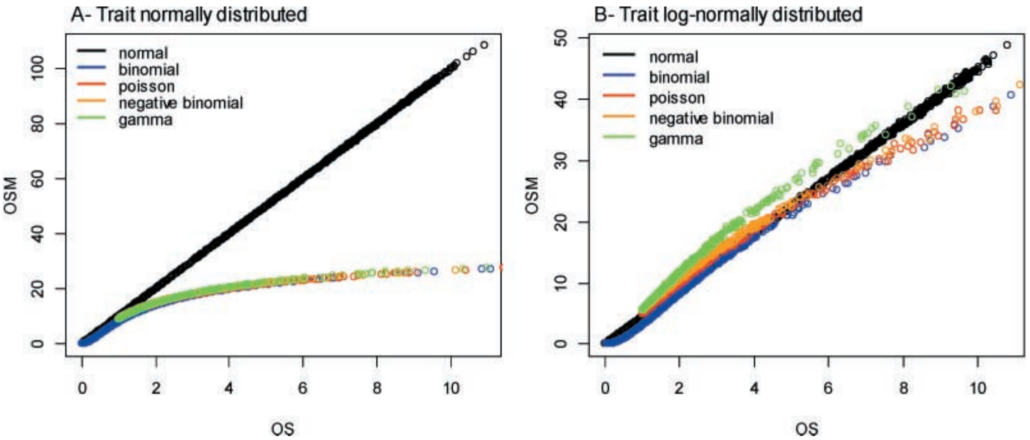

Fig. 1. Associations between the opportunity for selection (OS) and the opportunity for selection on a character mean (OSM) for a case that is (A) normally distributed and (B) log-normally distributed for a range of different fitness distributions. The OS and the OSM are non-linearly associated for most fitness and character distributions.

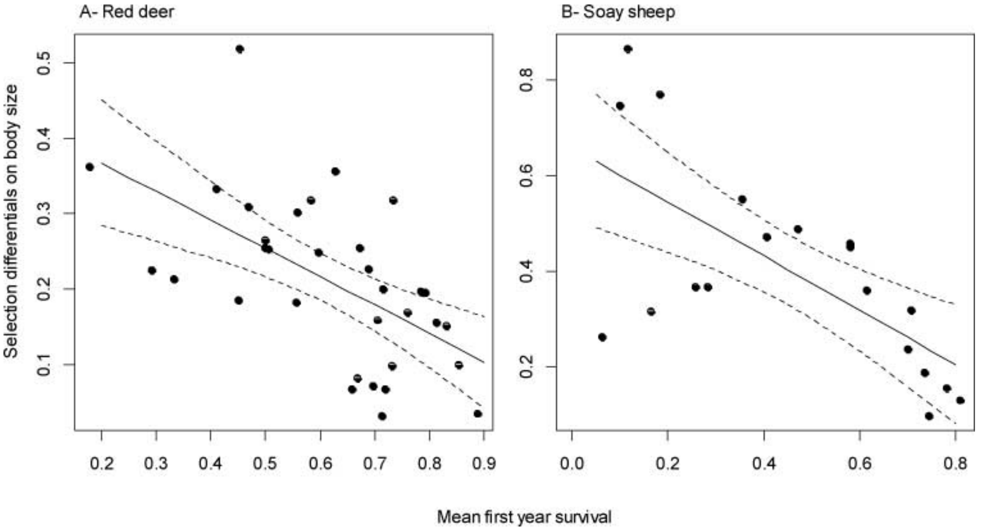

Fig. 2. The association between the strength of selection on body size and mean first year survival for two vertebrate species (see text for interval over which survival was measured). Each dot represents one year. Fitted lines are generalized additive models and dashed lines represent 95% confidence intervals. As predicted, selection decreases as mean survival increases. Note y-axis scale variation.

only approximately capture the maximum possible selection differential on phenotypic characters over a time step.

Is selection stronger in harsh or favourable environments?

The two species showed contrasting patterns of juvenile survival. Red deer and Soay sheep were characterized by variable juvenile survival (annual mean survival ranged between 18% and 89% for red deer and between 6% and 80% for Soay sheep). In the two species, the selection differential on body size increased with decreasing mean survival (Fig. 2). In other words, selection on body size was stronger in years with low juvenile survival. In both red deer and Soay sheep (Fig. 2A, B), these relationships were statistically significant (LM: red deer: slope $= -0.378 \pm 0.095$, $t = -3.99$, $r^2 = 0.34$, $P < 0.001$; Soay sheep: slope $= -0.566 \pm 0.149$, $t = -3.326$, $r^2 = 0.46$, $P = 0.002$). The increase in the strength of selection with decreasing mean survival in red deer, however, was driven through a decrease in mean survival (the denominator of the expression) rather than by an increase in the covariance between juvenile body size and survival (the numerator of the selection function). This is demonstrated by a lack of a relationship between mean survival and the covariance between survival and size-related characters in red deer (Fig. 3A). In Soay sheep, the significant association between the covariance (between body size and survival) and first year survival showed a significant quadratic pattern (LM: mean survival: slope $= 1.213 \pm 0.247$, $t = 4.914$, $P < 0.001$; mean survival^2: -1.224 ± 0.276, $t = -4.437$, $r^2 = 0.64$, $P < 0.001$) (Fig. 3B). The association between the strength of selection and survival was consequently determined by both the numerator and the denominator in equation (4).

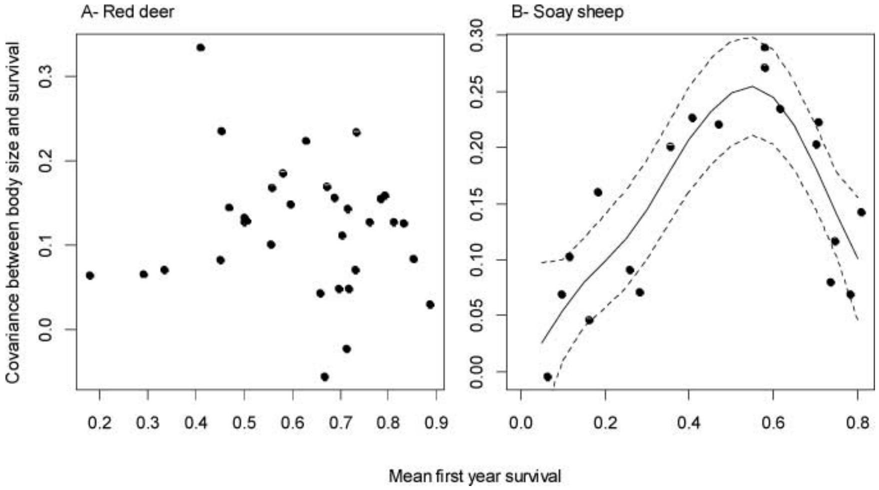

Fig. 3. The association between mean first year survival (see text for interval over which survival was measured) and the covariation between body size and survival in two species of vertebrates. Each dot represents one year. Fitted lines are generalized additive models and dashed lines represent 95% confidence intervals. Note y-axis scale variation.

Association between selection on body size, OS, and OSM in the wild

We found evidence that selection on juvenile body size is stronger when the OS and OSM are largest in both species. In red deer, the association between OS and selection was curvilinear and significant (LM for red deer: with outlier: $\text{slope} = 0.163 \pm 0.057$, $t = 2.846$, $I^2 = -0.025 \pm 0.013$, $t = -1.940$, $r^2 = 0.30$, $P = 0.005$; excluding one outlier: $\text{slope} = 0.369 \pm 0.098$, $t = 3.746$, $I^2 = -0.124 \pm 0.420$, $t = -2.978$, $r^2 = 0.38$, $P < 0.001$) (Fig. 4A). For Soay sheep, the relationship was linear (Fig. 4B) and significant (with outlier: $\text{slope} = 0.021 \pm 0.012$, $t = 1.703$, $r^2 = 0.15$, $P = 0.107$; excluding one outlier: $\text{slope} = 0.062 \pm 0.013$, $t = 4.633$, $r^2 = 0.57$, $P < 0.001$). The association between the strength of selection and the OSM in both deer (LM: $\text{slope} = 0.245 \pm 0.063$, $t = 3.912$, $r^2 = 0.34$, $P < 0.001$; Fig. 4C) and sheep (LM: $\text{slope} = 0.302 \pm 0.078$, $t = 3.858$, $r^2 = 0.47$, $P = 0.001$; Fig. 4D) was stronger than the association between selection and OS. The association between selection differential on size and OSM was also less likely to produce outliers compared with the relationship between OS and selection. From the simulations (Fig. 1), we expected the OS and the OSM to be correlated. In both red deer and Soay sheep, their correlations were significant (red deer: $r = 0.91$, $P < 0.001$; Soay sheep: $r = 0.82$, $P < 0.001$) but the associations were curvilinear (Figs. 5A and B).

How does the proportion of realized selection vary?

Given that the OSM was measured on the same scale as the selection differential, we were able to calculate the proportion of realized selection (Q). The mean proportion of variation explained was 0.36 and 0.44 for the deer and sheep, respectively (Figs. 5C and D). Q increased with the strength of the selection differential in both systems (Figs. 5E, F) with a greater proportion of selection being realized when the OSM was largest (red deer:

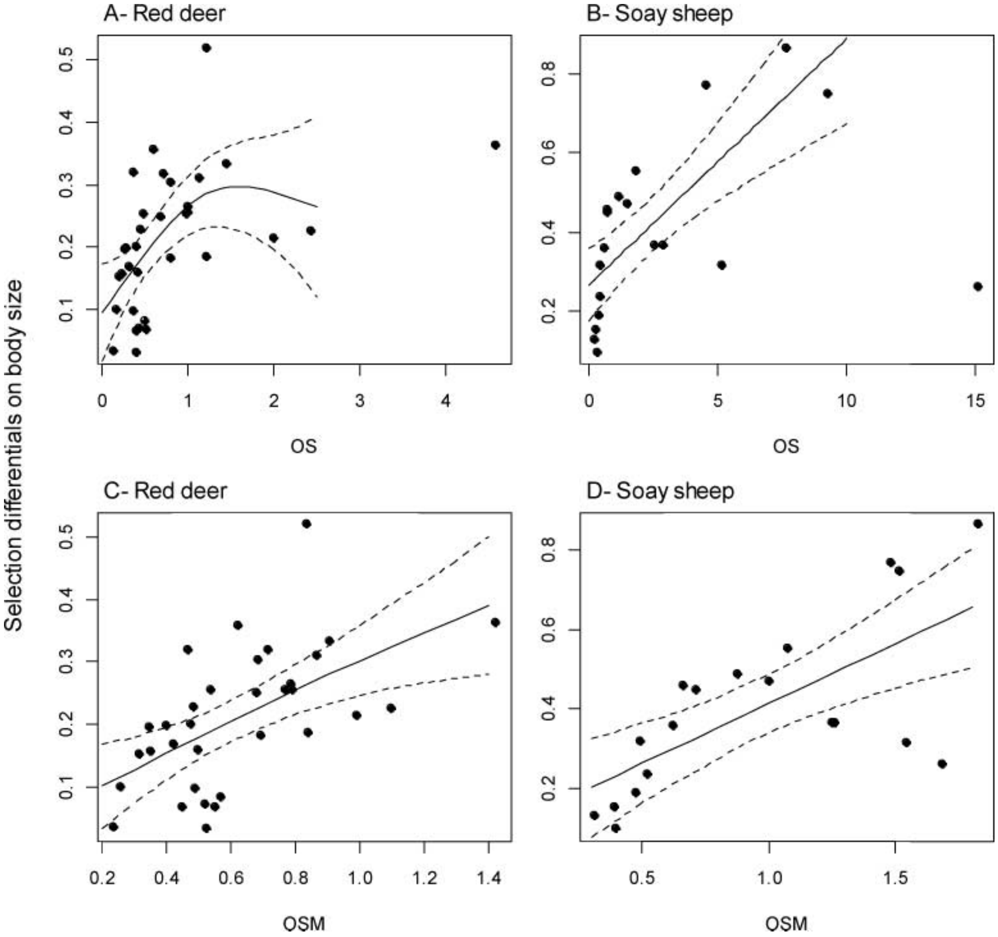

Fig. 4. Relationship between the strength of selection on body size and the OS (A, B) and the OSM (C, D). Each dot represents one year. Fitted lines are generalized additive models and dashed lines represent 95% confidence intervals. Generalized additive models have been fitted excluding one outlier on plots A and B. Note y-axis scale variation.

slope = 1.017 ± 0.199, $t = 5.10$, $r^2 = 0.46$, $P < 0.001$; Soay sheep: slope = 1.413 ± 0.368, $t = 3.838$, selection^2 −1.264 ± 0.461, $t = -2.740$, $r^2 = 0.64$, $P < 0.001$).

DISCUSSION

In this article, we explore associations between the opportunities for selection, selection, and population growth across two populations. We estimate that on average 30–40% of possible selection on juvenile body size was realized in two species for which we have access to detailed information and that the proportion of realized selection increases with an increase in the selection differential. We also found that the OSM and selection on juvenile body size are usually greatest when populations are declining.

One of the questions we wanted to address is whether the OS and OSM are correlated. Using simulations where traits and fitness are simulated and are set to be independent of

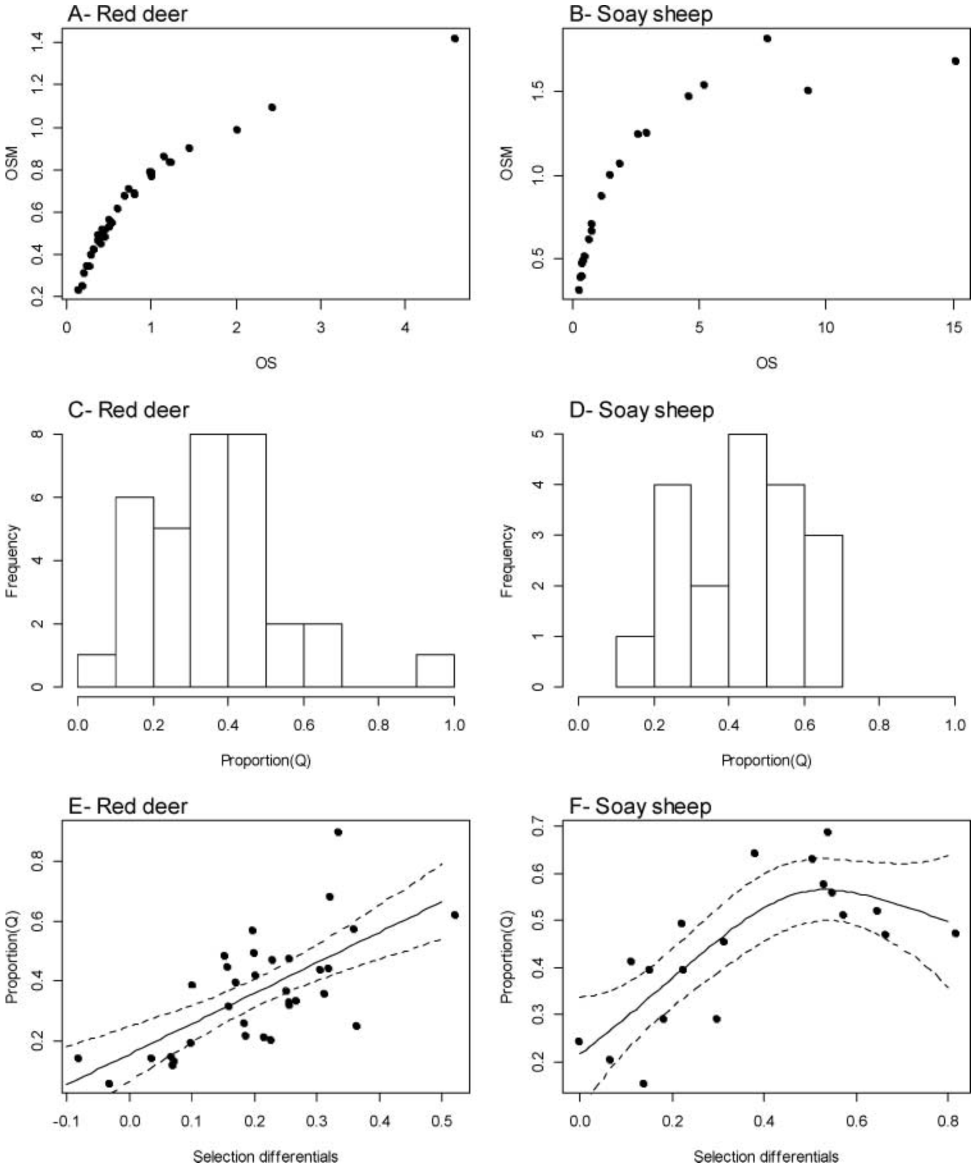

Fig. 5. Association between the OS and the OSM on size (A, B), frequency distribution (number of years) of the proportion of variance in the OSM explained by realized selection in each year for red deer and Soay sheep (C, D), and association between the proportion of variance in the OSM explained by realized selection and the strength of selection on body size for red deer and Soay sheep (E, F). Fitted lines are generalized additive models and dashed lines represent 95% confidence intervals.

each other, we found that the classical measure of the OS correlates with the OSM but their association was curvilinear for non-normally distributed fitness components. As fitness is generally not normally distributed, it is therefore not surprising that previous studies have found a mismatch between the opportunity for selection and the strength of selection (see, for example, Fitze and Le Galliard, 2011). This is primarily because the variance of these fitness component distributions is dependent on the mean – a point already made by Downhower *et al.* (1987). To explore the links between these quantities, one has to consider the variance in fitness but also the variance in the character of interest and the association between this character and fitness. Thus, calculating the OSM using sorted character and fitness data should help researchers identify when the opportunity for selection is likely to be realized (Klug *et al.*, 2010; Krakauer *et al.*, 2011). Another advantage of using a measure on the same scale as that of the selection differential is that the comparison between selection and maximum selection is easier (for example, using Q).

Although some studies have shown that selection and the classical measure of the OS are greatest at high population density (Moorcroft *et al.*, 1996; Coltman *et al.*, 1999; Clutton-Brock and Pemberton, 2004), few previous studies have described the link between population dynamics, the opportunity for selection on different phenotypes, and natural selection. As shown in this article, one advantage of expressing opportunities and selection differentials in terms of fitness components, rather than as a lifetime measure, is that it becomes straightforward to link selection to population growth and environmental conditions (Coulson *et al.*, 2003, 2006; Pelletier *et al.*, 2007; Coulson and Tuljapurkar, 2008). Another advantage of representing selection differentials in the form we propose here is that it is clear that because the population growth rate (mean fitness) appears as the denominator, all other things being equal, the strength of selection will increase as populations decrease in size (equation 4). Our empirical results suggest that selection is strongest in declining populations and is greatest when the opportunity for selection on a character mean is large. All together these results support the contention that selection should be strongest in harsh environments.

As previously mentioned, an interesting advantage of the OSM is to allow for the easy calculation of the ratio between the observed selection differential and OSM, providing a measure of the proportion of achievable selection that is realized (Q). We believe it would be helpful for articles that report selection differentials to also report variance in fitness, and characters, their covariance, and the proportion of selection that is realized. This information will then permit easy comparison across species, habitats, and different demographic classes, providing insight into the conditions when selection is likely to occur and the context in which phenotypic selection is strongest. We found that for the red deer and Soay sheep, the proportion of variance in the opportunity for selection on juvenile body size that is explained by realized selection (Q) is, on average, 36% and 44%, respectively. This means that in these populations, selection on juvenile mass via survival on average attains approximately one-third of its full potential. Here, we only considered one trait, at one stage, and therefore are likely to have underestimated selection on juvenile size. Thus, our estimation is very conservative as it does not integrate selection on this character acting later in life or correlative selection. It also suggests that there may be other characters of equal or greater importance for viability selection in ungulates. By comparing Q values for different characters, it would be possible to quantify their relative importance. The distribution of annual Q values also differed between the species, suggesting that the *modus operandi* of viability selection between these two populations differ. However, for both species, we found that Q was higher when selection was stronger. It would be useful for further comparative work to identify factors that are associated with variation in Q. For example, is more potential selection realized in good or bad environments? Based on our results, selection should be strongest in bad environments.

We believe that identifying contexts in which the OSM is realized might be very helpful in understanding evolutionary processes under wild conditions. For example, populations and species exhibiting substantial opportunities for selection may be more likely to respond to new environmental conditions than populations with smaller opportunities, although the actual response will depend on the genetic architecture of the character. In the current context, where human-driven changes are likely to modify the selective pressures acting on animal populations, the opportunity for selection provides a way to predict which populations or species are most likely to adapt. Our work contributes to a growing literature illustrating how the analysis of annual fitness measures can provide novel insight into the *modus operandi* of phenotypic selection on quantitative characters in stochastic environments.

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