Current Biology 18, 751–757, May 20, 2008 ©2008 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2008.04.059

Report

Environmental Heterogeneity Generates Fluctuating Selection on a Secondary Sexual Trait

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Summary

In any population in which resources are limiting, the allocation of resources toward increased reproductive success may generate costs to survival [1–8]. The relationship between a sexually selected trait and fitness will therefore represent a balance between its relative associations with fecundity versus viability [3, 6, 7]. Because the risk of mortality in a population is likely to be heavily determined by ecological conditions, survival costs may vary as a function of the prevailing environment [7]. As a result, for populations experiencing heterogeneous ecological conditions, there may not be a single optimal level of allocation toward reproduction versus survival [9]. Here, we show that early viability and fecundity selection act in opposing directions on a secondary sexual trait and that their relative magnitude depends upon ecological conditions, generating fluctuating selection. In a wild population of Soay sheep (*Ovis aries*), phenotypic and genetic associations between male horn growth and lifetime reproductive success were positive under good environmental conditions (because of increased breeding success) and negative under poor environmental conditions (because of reduced survival). In an unpredictable environment, high allocation to early horn growth is a gamble that will only pay off if ensuing conditions are favorable. Such fluctuating selection may play an important role in preventing the erosion of genetic variance in secondary sexual traits.

Results and Discussion

Our aim in this study was to assess the genetic architecture of, and the selection pressures on, a male sexually selected trait across changing environmental conditions in a population experiencing natural environmental heterogeneity. We did so by examining the covariance (and correlation) between male horn growth and three measures of fitness (average fecundity, longevity, and lifetime breeding success) in a feral population of Soay sheep that live on the Scottish island of Hirta, St. Kilda, UK, and that have been studied over a 17 year period [10]. The phenotypic covariance between a trait and fitness (equivalent to the selection pressure on the trait [11]) can be broken down into genetic and environmental components. In this way, we estimated the phenotypic, genetic, and environmental covariance (and correlations) between horn growth and lifetime fitness in male Soay sheep that experienced different environmental conditions during the year of their birth. This study population is ideal for this purpose as weather conditions, population density, and consequently resource availability fluctuate from year to year, providing substantial differences between individuals in the environmental quality of their birth year and thus their survival rates (Figure 1) [10, 12, 13].

We first examined the genetic and environmental basis of variation in male horn growth between the ages of 1 and 5 years, when ~92% of horn growth occurs. Using a random-regression animal model [13, 14], we combined pedigree and phenotypic data to partition the phenotypic variance of horn growth at each age into a genetic component, an environmental component specific to the year of growth (short-term environmental variance), and a residual (which includes long-term environmental effects) component. The genetic component of horn growth was modeled as a polynomial function of age [15], and statistically, the best model fit was a second-order function (compared to first order: $\chi^2_3 = 9.34$; $p = 0.025$) indicating significant additive genetic variance, which decreased with age (Figure 2A). The 95% confidence intervals indicate that significant additive genetic variance was only present for horn growth in the first two years of life (Figure 2A), and coefficients of additive genetic variance indicate the same trends (Table 1). Additive genetic correlations between horn growth at each age were also estimated from the model and were found to be uniformly positive and close to one (Figure 2B). The strength of these correlations suggests that variation in horn growth involved the same (or closely linked) loci at all ages and that individuals showed consistency in their relative genetic merit for horn growth across ages. The environmental effect of the year of growth was also modeled as a function of age, to test for differences between ages in the effects of prevailing environmental conditions on the amount of horn growth in a given year. Variance in the horn growth of later years was mostly attributable to environmental factors (Table 1), a first-order function for changes in effects of year of growth with age gave the best model fit (compared to zero order: $\chi^2_2 = 8.22$; $p = 0.016$), and coefficients of residual and year of growth variance generally increased with age.

We then investigated whether selection pressures on horn growth were dependent upon the environmental conditions experienced during the first year of life. We used first-year measures of horn growth because average lifetime values may be influenced by longevity and additive genetic effects (although highly correlated) varied over ontogeny. We used an indirect measure of environmental quality (*E*) of an individual's birth year defined as the proportion of lambs that

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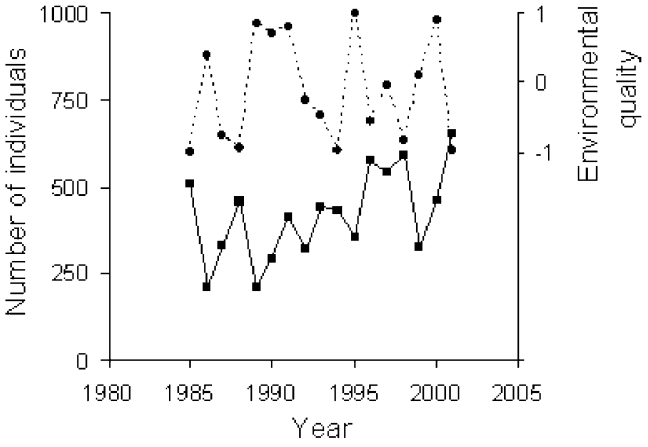

Figure 1. Counts of Soay Sheep in the Hirta Village Bay Study Population and Measures of Environmental Quality from 1985–2001

Counts of Soay sheep are shown by black squares and solid line, and measures of environmental quality are shown by black circles and dotted line. Environmental quality is estimated as the proportion of live-born lambs that survived to one year of age, standardized to −1 to 1.

survived their first winter (proportion surviving ranged from 0.05–0.86, with a mean of 0.41), with low survival indicating a poor environment and high survival indicating a good-quality environment (Figure 1; for an analogous method, see [13]). First, we used bivariate linear models to estimate the phenotypic correlations between first-year horn growth and fitness within four birth-year groups, corresponding to the quartiles of the distribution of *E*. Second, beecause phenotypic associations between a trait and fitness may be environmentally driven [11] as well as having a genetic basis, we extended the models to bivariate random-regression animal models to break down phenotypic associations between horn growth and fitness into genetic and environmental correlations. We did this three times, one for each measure of fitness, calculating an individual's lifetime breeding success (LBS) as the sum of offspring sired over lifespan; fecundity (FEC) as the average age-corrected number of offspring sired per year of life; and longevity (LG) as the total number of years alive. Because relatives are born into different environments, the genetic component of both traits and the genetic correlation between traits were modeled as a linear function of the continuous variate *E*. However, because any given individual is only born into one environment, the residual (environmental) components of each trait and the correlation between them were estimated within each of four environmental-quality groups (see Experimental Procedures). We first tested for significant phenotypic relationships between horn growth and fitness, by comparing the original models to ones in which the covariance is constrained to be zero (no relationship). We then tested whether the phenotypic relationships were constant across environments, by comparing the original models to ones with constant covariance (constant relationship). In this way, we can determine whether the relationships are (1) significantly different from zero and (2) significantly different across environments. We then break down phenotypic relationships and test for significant genetic and environmental covariance (see Experimental Procedures).

At the phenotypic level, selection on horn growth via lifetime breeding success was positive under good environmental conditions and negative under poor environmental conditions (Figure 3A; compared to a model of zero covariance: χ^2_4 = 55.70; $p < 0.001$; compared to a model of constant covariance: χ^2_3 = 25.58; $p < 0.001$). This relationship was driven by the opposing selection pressures on horn growth through fecundity and longevity across environmental conditions. High rates of first-year horn growth were generally associated with increased fecundity (Figure 3B; compared to a model of zero covariance: χ^2_4 = 10.87; $p = 0.028$), and this relationship was constant across environments (compared to a model of constant covariance: χ^2_3 = 2.06; $p = 0.560$). In contrast, high rates of first-year horn growth were negatively associated with longevity (Figure 3C; compared to a model of zero covariance: χ^2_4 = 41.02; $p < 0.001$), and this relationship varied over environments (compared to a model of constant covariance: χ^2_3 = 9.04; $p = 0.029$), with trends suggesting increased effects in more stressful environments.

At the genetic level, we found significant genotype-by-environment interactions for lifetime breeding success (χ^2_2 = 6.79; $p = 0.034$), and longevity (χ^2_2 = 7.96; $p = 0.019$), but not for fecundity (χ^2_2 = 1.74; $p = 0.419$) or first-year horn growth (χ^2_2 = 2.96; $p = 0.174$). This indicated that within this population, different genes may contribute to longevity and thus lifetime breeding success in different environments. For fecundity and horn growth, we found no evidence that genetic effects changed with environmental conditions, suggesting that the allocation of a given genotype is the same in all environments. From the same model, we also examined the genetic correlations between horn growth and fitness and found the same pattern as the phenotypic correlations (Figure 3). Genetic correlations between horn growth and lifetime breeding success showed a reversal from negative to positive across the gradient of environmental quality, suggesting that no single

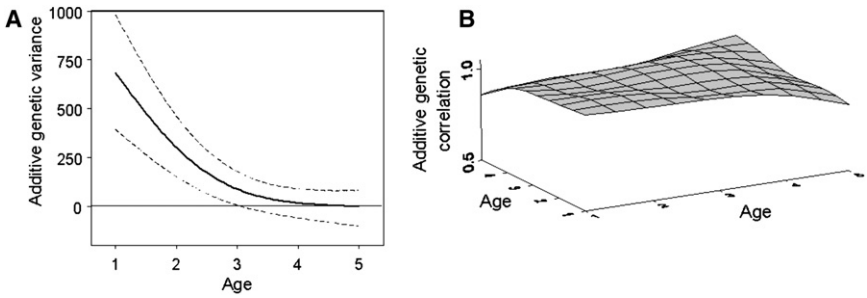

Figure 2. Quantitative Genetic Parameters for Male Horn Growth from a Random-Regression Animal Model

(A) shows additive genetic variance with age (in years), and (B) shows genetic correlation between ages. The additive genetic component of horn growth (mm) was modeled as a second-order quadratic function of age, giving estimates of additive genetic variance at each age; these estimates are shown as the solid line in (A) (dashed lines indicate 95% confidence interval). The analysis produced a genetic covariance matrix for horn growth at each age, which was converted into the matrix of genetic correlations shown in B. There is significant additive genetic variance for first and second year horn growth and strong positive genetic correlations between all ages.

Table 1. Age-Specific Quantitative Genetic Parameters for Horn Growth, in Millimeters, in Normal-Horned Males, with Standard Error

Age (year)	N	Mean ± SD	V_P	V_A	V_{YR}	V_R	CV_A	CV_{YR}	CV_R	h^2
1	854	178.06 ± 39.27	1690.92 ± 75.18	784.22 ± 167.95	125.50 ± 33.19	781.20 ± 135.70	15.73	6.29	15.70	0.464
2	497	113.69 ± 33.55	1068.43± 69.80	180.26 ± 47.76	91.36 ± 33.42	796.44 ± 72.40	11.81	8.41	24.82	0.169
3	327	75.53 ± 21.61	476.90 ± 38.80	73.42 ± 46.61	62.53 ± 33.93	378.58 ± 58.56	11.34	10.47	25.76	0.143
4	195	57.93 ± 16.23	284.50 ± 29.87	42.80 ± 35.15	39.02 ± 36.02	204.72 ± 48.74	11.29	10.78	24.70	0.149
5	135	36.72 ± 12.62	162.91 ± 20.85	3.41 ± 53.62	20.83 ± 42.78	158.65 ± 49.18	5.03	12.43	34.30	0.019

Estimates are from a random-regression animal model, with second-order genetic effects, first-order year-of-growth effects, and an age-specific residual variance structure. Mean age-specific horn growth with standard deviation (SD) in normal-horned male Soay sheep is shown. Quantitative genetic parameters of phenotypic (V_P), additive genetic (V_A), year of growth (V_{YR}), and residual (V_R) variance were converted into coefficients of variance (CV_A, CV_{YR}, and CV_R), and estimates of heritability (h^2) are shown. N gives the number of records at each age.

genotype for horn growth is optimal in all environments (Figure 3A; compared to a model with zero genetic covariance: $\chi^2_4 = 11.16$; p = 0.025). The fecundity benefits were generally greater for individuals of higher genetic merit for horn growth (Figure 3B; compared to a model with zero genetic covariance: $\chi^2_4 = 9.53$; p = 0.049). In contrast, the survival costs of investment appeared to be greater for individuals of high genetic merit for horn growth, with negative correlations between longevity and first-year horn growth (Figure 3C; compared to a model with zero genetic covariance: $\chi^2_4 = 10.44$; p = 0.034).

The environmental covariance between horn growth and lifetime breeding success showed the same trends as the genetic covariance, with a reversal from negative to positive (Figure 3A; compared to a model with zero residual covariance: $\chi^2_4 = 12.86$; p = 0.012). There was some evidence of positive environmental covariance between horn length and fecundity (Figure 3B; although this was nonsignificant when compared to a model with zero residual covariance: $\chi^2_4 = 8.16$; p = 0.086). There was also a negative environmental correlation between horn growth and longevity in the worst environmental conditions, implying a trade-off in resource allocation between survival and horn growth (Figure 3C; compared to a model with zero residual covariance: $\chi^2_4 = 10.84$; p = 0.028). Therefore in an unpredictable environment, high allocation to early horn growth is a gamble, the pay-offs of which depend on the environmental conditions an individual encounters during its first year of life.

Sexually selected traits often show allometric scaling [16, 17], and thus we attempted to disentangle selection on first-year horn growth from selection on overall body growth. When first-year weight was included as a fixed effect into our models to gain a measure of allocation to horn growth relative to body size, we found that the phenotypic patterns described above increased in strength (Figure 4). This suggests that the negative relationship with longevity was driven by associations with horn growth rather than a potentially confounding factor of body size. Furthermore, previous work has shown consistently positive selection on body weight in poor environments [13]. The mechanisms generating reduced longevity in males with high rates of first-year horn growth are not clear, and we also found no evidence of any relationship between longevity and horn growth for males who survive their first year ($F_{1,326} = 1.946$; p = 0.169). It may be that males who grow larger horns also show increased mating effort within their first year, thereby exposing themselves to the risk associated with conflicts in the rut. Previous studies have suggested that environmental parameters may influence the relative fitness of male mating tactics [18–20]. We found no immediate evidence that this is the case, because excluding males who successfully sired at least one lamb within their first year did not alter the results that we present here, but behavioral observations would be required in order to fully disentangle these effects.

We have shown that the relationship between a male secondary sexual trait and fitness is dependent upon ecological conditions and can change from positive to negative if environmental conditions are significantly variable. This relationship presumably reflects a balance between the relative associations of the trait with fecundity versus viability [3, 6, 7]; our results indicate that in populations experiencing heterogeneous ecological conditions, there may not be a single optimal trait value. Such fluctuating selection is an intuitively appealing explanation for the maintenance of genetic diversity in secondary sexual traits [7], although to date it has received surprisingly little empirical support, with the notable exception of a wild population of Darwin's finches [21, 22]. Our study furthermore demonstrates that environmental heterogeneity generates fluctuating selection at both the phenotypic and genotypic level. At present, the role of fluctuating selection in maintaining genetic variation is under debate, with some studies supporting the hypothesis [23–25], some finding limited evidence [26, 27], and some finding population-specific effects [28]. In the St Kilda Soay sheep population, a combination of overlapping generations and unpredictable environmental conditions may be sufficient for fluctuating selection to prevent the erosion of genetic variance by selection pressures [9], although quantitative predictions of their effect may be difficult due to differences between cohorts in their contribution to future generations [29].

In this study, we determined the effects of environmental heterogeneity on the evolutionary potential of a trait, by simultaneously examining both the expression of the trait and the selection pressures acting across a gradient of environmental conditions, and demonstrated that high genetic merit for a secondary sexual trait does not convey increased fitness across all environments encountered. Only by examining fitness through both viability and fecundity, and by accounting for the fluctuating environmental conditions that wild populations experience, can we accurately assess the relationship between a secondary sexual trait and fitness. In the wild, allocation to secondary sexual traits is a trade-off between survival versus fecundity, and our results indicate that in unpredictable environments, no single strategy may be optimal.

Experimental Procedures

Study Population and Data Structure

Soay sheep (*Ovis aries*) were introduced onto the island archipelago of St. Kilda, NW Scotland in the North Atlantic (57°49′N, 08°34′W) during the Bronze Age [10]. The unmanaged study population of Village Bay, Hirta, was founded in 1932 [10] and currently fluctuates around an average size of 432 individuals (Figure 1). The population has been the subject of intensive individual-level study since 1985, yielding morphological and life-history data for 6387 pedigreed individuals, including 3626 maternal links

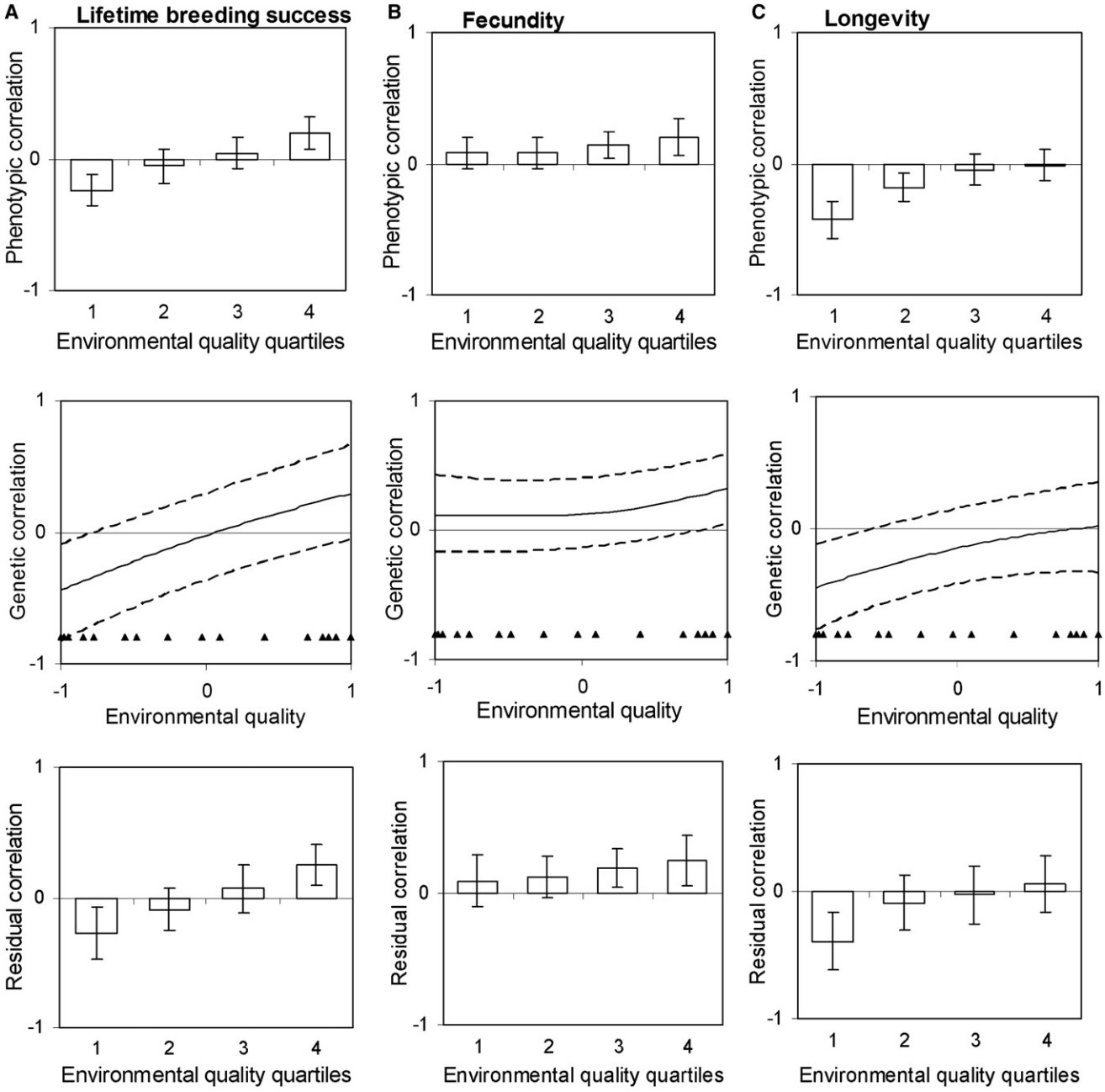

Figure 3. Phenotypic, Genetic, and Residual Correlations between First-Year Horn Growth and Lifetime Breeding Success, Average Age-Adjusted Fecundity, and Longevity

An estimate of environmental quality was gained for each year of birth from 1985–2001 with triangles on the middle panels indicating their distribution. Estimates of the genetic correlation and 95% confidence interval (dashed line) between horn growth and each fitness measure (A–C) were generated from random-regression animal models allowing additive genetic effects to change as a function of environmental quality. For phenotypic and residual correlations, birth years were grouped on the basis of the quartiles of the distribution of environmental quality. Estimates of phenotypic and residual correlations were made within each of these four groups, and error bars show 95% confidence intervals for the correlations.

and 1699 paternal links (from 807 distinct dams and 495 distinct sires). Maternal identity is known from field observations, and paternity is inferred by microsatellite-based paternity analysis at a pedigree-wide confidence level of $\geq$80%, allowing no more than one allelic mismatch between offspring and putative sire, with maximum likelihood methodology implemented in CERVUS [30].

Soay sheep have a distinct polymorphism for horn type producing either a full (normal) horn (86% of males; 32% of females), a reduced horn (14% of males; 28% of females), or no horn at all (40% of females only). We consider only males who grew full horns because this is the only group in which horn size is associated with sexual selection [31]. The horns of sheep grow cumulatively over life, with annual increments being apparent when horn growth stops over winter, forming an annulus. Horn increment measures were made later in life while the animal was alive (in the years following growth) or after death. Therefore, measures of first-year horn growth were available regardless of whether an individual survived its first winter or not.

Random-Regression Model of Horn Growth over Ontogeny

Age-specific quantitative genetic parameters for horn growth were estimated with random-regression animal models [13, 32] to partition

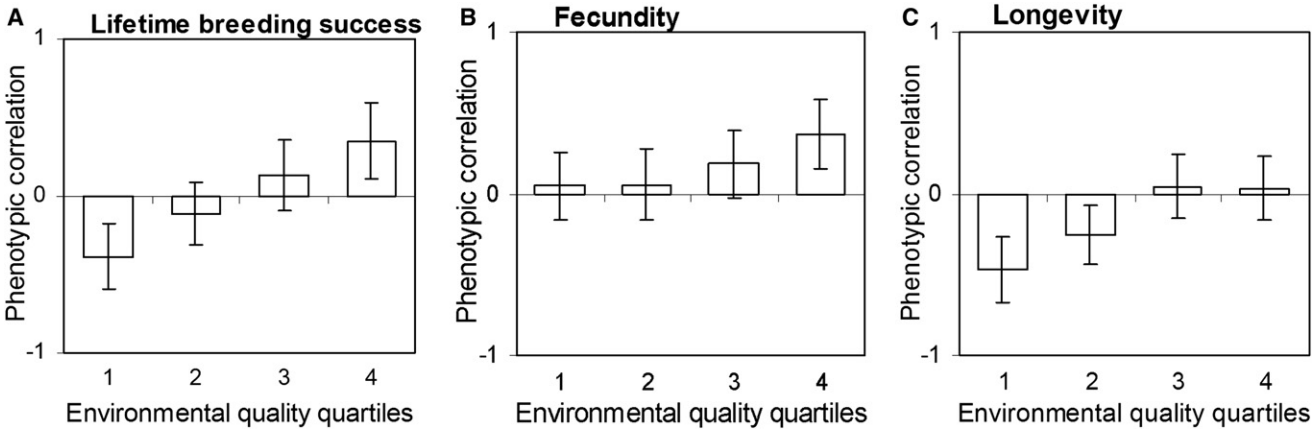

Figure 4. Phenotypic Correlations between First-Year Allocation to Horn Growth Relative to Body Weight and Lifetime Reproductive Success, Average Age-Adjusted Fecundity, and Longevity

Correlations to lifetime reproductive success are shown in (A), to average age-adjusted fecundity in (B), and to longevity in (C). Estimates were gained from Equation 3 (see Experimental Procedures) with the inclusion of first-year body weight as a fixed effect to gain a measure of allocation to horn growth relative to body weight. The genetic models did not converge because of reduced sample size of only 489 first-year body-weight measures, and thus we only present the phenotypic correlations. Error bars show 95% confidence intervals for the correlations.

phenotypic variance into genetic and environmental (residual) components. Animal models are a form of linear mixed model implemented in ASReml (VSN International Ltd) with restricted maximum likelihood, and these models are able to accommodate unbalanced data sets and complex pedigrees [14], and random-regression animal models allow different random effects to be modeled as functions of a continuous variable. Fixed effects of age (factor 1–5) and birth year (factor 1985–2001) were included. We included birth year to remove effects of conditions at birth on mean horn growth and to remove temporal trends in mean values. We then included random effects to model both the additive genetic effects and the year of growth effects as polynomial functions of age. The residual error structure was partitioned to gain age-specific estimates of residual (or environment) variance. At the individual level, horn-growth phenotype (HG_{AGE}) of individual *i*:

$$HG_{i,\,AGE} \sim (AGE + BIRTHYEAR)_i + f(\alpha_i, n, AGE_{SD}) + f(YR, n, AGE_{SD}) + e_{i,\,AGE} \quad (1)$$

where $f(\alpha_i, n, AGE_{SD})$ is the random-regression function of orthogonal polynomials of standardized age (age in years standardized to the interval $-1 \leq AGE_{SD} \geq 1$) with order *n*, of additive genetic merit α_i (or breeding value) of individuals obtained from the pedigree structure; $f(YR, n, AGE_{SD})$ is the random-regression function for the year of growth YR, and e_{iAGE} is the age-specific error for individual *i*.

The error term was modeled with a 5 × 5 unstructured matrix allowing residual errors to be correlated across ages within individuals and thereby removed the need for a permanent environment effect. Adding mother's identity as a random effect did not improve model fit ($\chi^2_1 = 0.96$; p = 0.327), and so we do not model maternal effects. Models were fitted wity polynomial functions of increasing order, and these functions were compared statistically with log-likelihood ratio tests. Model convergence was not achieved for n > 3. The variance-covariance matrix of the random-regression parameters obtained for the additive genetic effect [matrix **Q** with dimensions (n +1) × (n +1)] was used for derivation of age-specific genetic parameters (**G** for HG_{AGE}) and their approximate standard errors [33].

Bivariate Random-Regression Model of Horn Growth and Fitness

We then modeled the phenotypic, genetic, and residual covariance between horn growth and fitness over fluctuating environmental quality. To do this we used bivariate random-regression models, with both fitness (*W*) and first-year horn growth (*HG1*) as response variables and ran one model for each of three fitness measures: average age-adjusted lifetime fecundity (FEC), longevity (LG), and lifetime breeding success (LBS), with data available for 1691 normal-horned males, after removing animals known to be still alive. Environmental quality (*E*) was defined as the proportion of live-born lambs that survived the first winter following their birth year (standardized to the interval $-1 \leq E \geq 1$ [13]).

We first estimated the phenotypic correlations between *W* and *HG1* within different environmental conditions by fitting a model without any random effects such that all phenotypic variance in both traits was allocated to a residual structure. We standardized both the fitness measure and the horn-growth value of each birth year to a zero mean and a unit variance, thus placing both on the same scale. As a result, converting the phenotypic covariance into correlations produced standardized selection differentials for first-year horn growth. Thus, for each individual (*i*) we fitted a model:

$$HG1_i\, W_i \sim (EG)_i + e_{iEG} \quad (2)$$

where the fixed effect of *EG* is a four-level factor (1: very poor, 2: poor, 3: good, and 4: very good) produced by grouping birth years on the basis of the 25% quartiles of the distribution of *E*, and the residual error structure e_{iEG} was partitioned into four EG groups. This gave an estimate of the phenotypic variance of each trait and the phenotypic covariance (converted into a correlation) between the traits within each of the four EG groups. The residual structure was divided to provide approximately equal sample sizes across environments, thus maximizing the accuracy of the estimates and reducing the number of variance components to be estimated. We first tested the significance of the phenotypic correlations by rerunning the model with the phenotypic covariance between the traits constrained to zero within each EG group and comparing the models with log-likelihood ratio tests with four degrees of freedom. We then tested whether these relationships were constant across environments, by rerunning the model with the phenotypic covariance between traits constrained to be constant across EG groups, and compared models with log-likelihood ratio tests with three degrees of freedom.

We then extended model two to partition the phenotypic covariance between *W* and *HG1* into genetic and environmental components over fluctuating environmental quality, testing for significant genetic and environmental relationships. To model the genetic covariance between *W* and *HG1*, we included a random effect that estimates the additive genetic variance of each trait and the genetic covariance between them as a polynomial function of environmental quality. Thus for each individual (*i*), we fitted the random-regression model:

$$HG1_i\, W_i \sim (EG)_i + f(\alpha_i, n, E) + e_{iEG} \quad (3)$$

where $f(\alpha_i, n, E)$ is the random-regression function on an orthogonal polynomial of *E*, with order *n*, of the additive genetic merit values α_i of individuals for both fitness and first-year horn growth, and e_{iEG} is the environment specific residual error for individual *i*.

Individuals only have one year of birth, and thus each individual is only represented once within the data set for Equation 3. However, because an individual's relatives may be born across different environments, the genetic effects for each trait and the covariance between traits can be

estimated as a function of environmental quality. This method represents a more efficient use of the data by avoiding subdivision of records into environment-specific traits [13, 33]. A first-order random-regression term produces a single variance-covariance matrix for the additive genetic effect for both traits [matrix **Q** with dimensions $(2 \times (n+1)) \times (2 \times (n+1))$, where n is the order of the polynomial]. In this case, we did not find support for models of higher order than n = 1 and so consider only the covariance between estimates of intercept and slope of each individual's genetic merit for each trait. We tested for significant genetic covariance between *W* and *HG1* by rerunning the models with all four genetic covariances between the two traits constrained to be zero over environmental quality and comparing the models with log-likelihood ratio tests. This represented a conservative method of testing for a significant genetic association between the traits over *E* [13, 32, 33].

There has to be a dichotomy in the estimation of genetic and residual correlations because residual covariance cannot be estimated across environments. This is because individuals are only born into one environment and thus estimates of the residual (co)variance can only be grouped in some way. We kept our partitioning of the residual error structure into four levels of *EG*, giving both a residual variances term for each trait and the covariance between traits in each of the four environmental groups (i.e., a 2 × 2 matrix within each *EG* group). We attempted to estimate a residual error structure for each of the 17 birth years, but this overparameterized the models, resulting in variance terms that could not be estimated with certainty, and thus we do not present this method. We also ran models with a constant residual error structure, giving a 2 × 2 matrix with a single estimate of residual variance for both terms and a single covariance between. These models were not supported by the data, when compared to models with an error structure divided into the four groups with log-likelihood ratio tests (LBS: $\chi^2_9 = 50.82$; $p < 0.001$; FEC: $\chi^2_9 = 18.97$; $p = 0.025$; and LG: $\chi^2_9 = 40.97$; $p < 0.001$). As a result, the residual correlations between fitness and first-year horn growth represent the associations between the traits that resulted from environmentally determined factors within each *EG* group. We tested the significance of these correlations by rerunning the models with the residual covariances between *W* and *HG1* constrained to zero and compared models with log-likelihood ratio tests.

For the presentation of the results, we used **G** = **Z Q Z'**, where **Z** is the vector of orthogonal polynomials evaluated at the values standardized environmental quality (**Z'** is the transpose of **Z**) and where **G** is a single additive genetic variance-covariance matrix for both traits. The diagonal of the covariance matrix between the additive genetic variance estimates of both traits provides the estimates of the genetic covariance between both traits across *E*. All covariance estimates were rescaled to give the genetic and residual correlations, providing a dimensionless estimate of association between both traits. Both the covariance and correlations revealed the same pattern. An analogous method was used for estimating the approximate standard errors [33], which were converted into ~95% confidence intervals.

Acknowledgments

We thank the National Trust for Scotland and Scottish Natural Heritage for permission to work on St. Kilda, the Royal Artillery Range (Hebrides), and QinetiQ for logistical support. We thank J. Hadfield and A. Wilson for discussion and advice, and thanks to the editors and three anonymous reviewers for comments that greatly improved the manuscript. Thanks to the many previous members of the project (including many volunteers) who have collected field data or have contributed to genotyping and paternity inference. The long-term data collection on St. Kilda has been funded by the Natural Environment Research Council, the Welcome Trust, the Biotechnology and Biological Sciences Research Council, and the Royal Society, through grants to T.H.C.-B., J.M.P., L.E.B.K., B.T. Grenfell, M.J. Crawley, T. Coulson, and S. Albon. The work presented here was funded by a Natural Environment Research Council studentship to M.R.R., supervised by L.E.B.K. who is supported by the Royal Society. J.M.P. and T.H.C.-B. conceived and designed the data collection. M.R.R. and L.E.B.K. conceived the analysis and wrote the paper. M.R.R. analyszed the data. J.G.P. ran the field site and conducted primary data collection.

Received: January 31, 2008
Revised: March 20, 2008
Accepted: April 14, 2008
Published online: May 15, 2008

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