

LIVE FAST, DIE YOUNG: TRADE-OFFS BETWEEN FITNESS COMPONENTS AND SEXUALLY ANTAGONISTIC SELECTION ON WEAPONRY IN SOAY SHEEP

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Abstract.—Males are predicted to compete for reproductive opportunities, with sexual selection driving the evolution of large body size and weaponry through the advantage they confer for access to females. Few studies have explored potential trade-offs of investment in secondary sexual traits between different components of fitness or tested for sexually antagonistic selection pressures. These factors may provide explanations for observed polymorphisms in both form and quality of secondary sexual traits. We report here an analysis of selection on horn phenotype in a feral population of Soay sheep (*Ovis aries*) on the island of Hirta, St. Kilda, Scotland. Soay sheep display a phenotypic polymorphism for horn type with males growing either normal or reduced (scurred) horns, and females growing either normal, scurred, or no (polled) horns; further variation in size exists within horn morphs. We show that horn phenotype and the size of the trait displayed is subject to different selection pressures in males and females, generating sexually antagonistic selection. Furthermore, there was evidence of a trade-off between breeding success and longevity in normal-horned males, with both the normal horn type and larger horn size being associated with greater annual breeding success but reduced longevity. Therefore, selection through lifetime breeding success was not found to act upon horn phenotype in males. In females, a negative association of annual breeding success within the normal-horned phenotype did not result in a significant difference in lifetime fitness when compared to scurred individuals, as no significant difference in longevity was found. However, increased horn size within this group was negatively associated with breeding success and longevity. Females without horns (polled) suffered reduced longevity and thus reduced lifetime breeding success relative to the other horn morphs. Our results therefore suggest that trade-offs between different components of fitness and antagonistic selection between the sexes may maintain genetic variation for secondary sexual traits within a population.

Key words.—Horns, polymorphism, sexual antagonism, sexual selection, trade-off, weapons.

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Natural and sexual selection will act upon a trait if there are differences in fitness between individuals with different phenotypic values of that trait (Falconer and Mackay 1996). When males compete for reproductive opportunity, sexual selection may drive the evolution of exaggerated male weaponry such as horns and antlers, through the advantage they confer in male contests for access to receptive females (Darwin 1871; Clutton-Brock et al. 1992; Andersson 1994). However, if selection acts continuously upon a trait it will presumably favor certain genotypes at the expense of others and hence result in the depletion of genetic variation underlying that trait (Fisher 1958; Falconer and Mackay 1996). The abundant genetic variation underlying many sexually selected traits that has been observed in natural populations (Pomiankowski and Møller 1995; Rowe and Houle 1996; Tomkins et al. 2004) therefore presents a paradox.

Various explanations have been proposed to account for variation in the form and size of secondary sexual traits, but relatively little testing of these hypotheses has been conducted, particularly in wild populations. First, there may be trade-offs between different components of fitness, with fecundity versus viability selection favoring different genotypes so that no single genotype is optimal. Trade-offs are a major topic of interest in evolutionary biology with several studies focusing on the trade-off between reproduction and survival (Stearns 1989; Roff 1992, 2000; Gustafsson et al. 1994; Roff et al. 2002). A number of studies of sexually selected traits have demonstrated an association between trait size and reproductive success within a given year (Coltman

et al. 1999, 2002; Preston et al. 2003) but data on lifetime breeding success are necessary to appreciate potential trade-offs with longevity. To our knowledge, only one study to date has shown that male weaponry increases lifetime breeding success in a wild mammal population, but it did not explicitly contrast viability and fecundity selection (Kruuk et al. 2002; see also Coltman et al. 2005).

Second, there may be contrasting or antagonistic selection pressures acting on the same genotype when expressed in the two sexes (Rice 1992; Chippindale et al. 2001). If two traits are positively correlated in males and females each sex will be constrained from adopting a separate evolutionary pathway (Falconer and Mackay 1996; Merilä et al. 1998; Jensen et al. 2003). More notably, recent *Drosophila* studies have shown negative correlations between the fitness of a particular genotype in males versus in females (Linder and Rice 2005; Rice and Holland 2005). To date, there has been little opportunity to explore the effects of the expression of phenotypic traits that are known to be under sexual selection in males but whose function is not understood in females, and hence to test for sexually antagonistic selection pressures.

Finally, selection may vary with temporal or spatial environmental variation (Via and Lande 1985; Greenfield and Rodriguez 2004). The strength of selection acting on phenotype may therefore alter in different environments or different phenotypes may be favored in different environmental conditions (Rose et al. 1998). This latter scenario can lead to a balancing effect, giving equal mean fitness of different phenotypes in the long term (Shuster and Wade 1991). Al-

ternatively, phenotypic variation may also be maintained by frequency-dependent selection, in which one phenotype is most advantageous when rare, and thus may be maintained at relatively low numbers within a population (Maynard Smith 1982).

To quantify the magnitude of selection pressure, the covariances between measures of different components of fitness and phenotype are required (Endler 1986). In this paper we examine patterns of selection on the different horn morphologies and horn sizes of males and females in a free-living population of Soay sheep (*Ovis aries*) on the Island of Hirta, St. Kilda, Scotland. By examining lifetime breeding success and two component traits, annual breeding success and longevity, we are able to show trade-offs within, and test for antagonistic selection between, the sexes. Soay sheep have a polymorphism for horn development with males growing either a full horn (normal horned) or a reduced horn known as a scur (scurred). Females develop smaller horns, and may be either normal horned, scurred, or show no horn growth (polled). Horn type is heritable, and a single-locus three-allele model is the most parsimonious explanation of inheritance in the Hirta population (Coltman and Pemberton 2004). Within normal and scurred horn types, there is also considerable variation in horn size. Horn length in normal-horned males has been shown to be associated with annual breeding success, independent of body size within a given year (Preston et al. 2003), but has not been shown to influence lifetime breeding success. However, prior studies have shown evidence of positive selection through survival, fecundity, and lifetime breeding success on body size (hind limb length) in Soay males (Coltman et al. 1999).

Results from previous studies of the St. Kilda Soay sheep population suggest the potential for differences in fitness between the different horn types. First, males of different horn type show different mating strategies. Scurred males avoid conflict with other males by mating with females only when they are not guarded by another male (Preston et al. 2003; Stevenson et al. 2004). Although scurred males always gain fewer paternities within a given year, they appear to increase their percentage of mating gained when their frequency in the population is low, and thus it is speculated that the horn polymorphism may be maintained via frequency dependence (Stevenson et al. 2004). Second, scurred males also show a greater overwinter survival rate (Moorcroft et al. 1996). Therefore, as scurred males appear to gain a lower number of paternities per year, this could potentially be balanced by greater longevity generating equal fitness in both groups. Furthermore, scurred females have been shown to have on average higher conception, weaning rates, and overwinter survival, relative to a combined class of normal and polled females (Clutton-Brock et al. 1997). This suggests that antagonistic selection may also be maintaining the phenotypic polymorphism, with the advantage of scurring in females opposing the selective forces acting against scurring in males (Moorcroft et al. 1996; Clutton-Brock et al. 1997; Milner et al. 2004). However, although we therefore have evidence of several associations between horn phenotype and different components of fitness in either sex, a full comparison of selection on horn phenotype acting through lifetime breeding

success in this long-lived species has not previously been conducted.

The long-term data available on the Soay sheep population also provide the opportunity to quantify changes in selection in relation to environmental conditions. Population density has been shown to alter the selection pressures acting on many phenotypic traits within this population (Moorcroft et al. 1996; Clutton-Brock et al. 1997; Coltman et al. 1999; Milner et al. 2004). In particular, cohort-specific effects such as density in the year of birth are known to influence the breeding success of males (Coltman et al. 1999; Stevenson et al. 2004), and the fitness differences between the horn morphs in females have also been shown to increase with population density (Clutton-Brock et al. 1997). We extend these analyses here to consider the environmental dependence of selection acting through lifetime breeding success.

In this paper we explore selection pressures on the form and size of the secondary sexual trait of horns in both males and females of the St. Kilda Soay sheep. We consider the effects of selection on horn type and then horn size in both sexes, acting via lifetime breeding success and its two components, annual breeding success and longevity. This allows us to test for potential trade-offs between different components of fitness and antagonistic selection within and between the sexes.

MATERIALS AND METHODS

Study Population

The present study focuses on the unmanaged population of Soay sheep (*Ovis aries*) which reside in Village Bay on the island of Hirta within the St. Kilda archipelago in the North Atlantic (57°49'N, 08°34'W). The population of sheep on Hirta fluctuates between 600 and 2000 individuals as a result of periodic population crashes, with almost all deaths occurring during late winter as a consequence of starvation (Clutton-Brock and Pemberton 2004). The population has been the subject of ecological study since the 1960s, and from 1985 about 95% of lambs born within the study site have been ear tagged, giving intensive sampling of individual level data.

Lambs are ear tagged shortly after birth in April or May, sampled for genetic analysis and weighed. Lambs are born as either twins or singletons. The population is monitored by census 30 times per year, with individual positions recorded, and by performing systematic searches for corpses in early spring. Soay sheep have a promiscuous mating system in which the onset of the rut is marked by increasing male aggression as rams roam and search for estrous females. Once located, males fight to gain access to estrous females, which often involves butting the flanks of rivals and engaging in head-on clashes (Preston et al. 2003).

Pedigree Determination

The pedigree structure of the Village Bay population has been inferred by both behavioral observation and genetic analysis. From 1985, daily observations were made from March to May on lambing females, with maternal identities assigned with greater than 99% accuracy when tested by ge-

netic analysis (Pemberton et al. 1999; Overall et al. 2005). Paternities were assigned from genotypic data via the maximum-likelihood method implemented in CERVUS (Marshall et al. 1998) using 18 microsatellite loci (Pemberton et al. 1999). The pedigree structure contains all known maternal links from 1987 to 2004, and all known paternities from 1987 to 2002 in which the latter were assigned at a confidence level of 80% or greater with the additional restriction of not more than one locus mismatching between offspring and candidate sire. Since not all lambs were assigned a father, male breeding success was therefore underrepresented, but this bias should not vary between males. The complete pedigree structure contained 5999 individual records with 3536 maternal links, and 1668 paternal links (from 806 distinct dams and 527 distinct sires, respectively).

Components of Fitness

Annual breeding success (ABS) was defined as the number of lambs sired by a male, or as the number of live lambs born to a female, in a given year. Longevity (LG; in years) was defined as an individual's age at death for animals with a known death date. Lifetime breeding success (LBS) was defined as the sum of annual breeding successes across an individual's lifetime. Therefore selection analyses were divided into short-term annual events (ABS) and long-term life-history traits, such as LG and LBS. All data from all available individuals were included in the analysis. For females, analyses were also repeated using a measure of the number of offspring that survived their first winter, rather than the number of live offspring produced, to incorporate the effects of any potential differences in maternal care. This different measure of ABS and subsequently LBS yielded identical conclusions to analyses based on the original measure of ABS, thus we do not present the results here.

Phenotypic Traits

The analysis of ABS used morphometric and environmental covariates recorded during the year in which the lambs were conceived. Morphometric measurements were recorded during a two-week period in August, in which 49–67% of the study area population are rounded up each year. Live weight, hind-leg length and horn length values were therefore taken from measurements made in the August immediately prior to the breeding season. Horn size was measured as the length of the horn (in mm) from the base along the outer curvature of the spiral to the tip. Hind-leg length was taken as the distance between the tubercle of the fibular tarsal bone to the distal end of the metatarsus (in mm). Fecal egg counts of five nematode gut parasites collectively termed strongyles and 13 small intestinal protozoa termed coccidia were collected over the course of a year. Counts were averaged to provide a yearly estimate of parasite burden, which is unbiased of any temporal trends. Strongyle counts were recorded from 1986 onward and Coccidia counts from 1991 onward.

Horn type was recorded either during the two-week catch period in August, during census observations, or at death. It should be noted that reclassification of horn type in females from polled to scurred may occur over an individual's life-

time, because distinguishing scurred and polled horns during early development may be difficult. However, the probability of an individual being reclassified is only 9% and there is no change in this value over the study period or with age. Furthermore, we found no significant difference in fitness of reclassified compared to scurred females, when repeating the analyses of LBS described below. It is therefore unlikely that error, generated by inclusion of individuals who would never be reclassified because they die young, will affect the associations presented here. Therefore, reclassification is unlikely to affect the conclusions presented here.

The analysis of selection acting through LG or LBS used phenotypic measurements recorded at death. We focused on the traits of horn type and then horn size (measured at death) within each horn type. To compare the relative contributions of different physical attributes to fitness, other phenotypic trait values were incorporated into analyses. Skeletal body size was estimated from a measure of hind-leg length at death. Both body size and horn size were age adjusted by standardizing the means across all age groups for males and females independently. This avoids the detection of significant associations of body size and horn size with LG and LBS simply because of the confounding effects of age. A standardized age-adjusted measure was calculated by dividing individuals into age groups of 1, 2, 3, 4, and 5+ years and standardizing to a mean of zero and a variance of one within each group. These measures provide a conservative method of comparing the associations of horn and body size with LG and LBS across individuals who survived to different ages. Using this method, two individuals who survived to age four and five with large horns for their age can both have age-adjusted horn size values of 1, and thus no relationship will be observed between LG and horn size. However, if values of horn size were age adjusted without standardizing the variance, fluctuations in sample sizes with older age may inflate horn values, thus biasing the relationship between LG and horn size. Birth weights (in kg) were defined operationally as the residuals from a linear regression of capture weight on days since birth (Robertson et al. 1992), since individuals could not be weighed immediately after birth.

Environmental Variables

Each year, from 1985 to 2003, the Village Bay population density was estimated on October 1 as the total number of individuals observed from census or caught before this date and the number of lambs born that year (excluding those known to have died by October 1). Estimates of this population density ranged from 211 to 594. For analyses of ABS, the value used was the density recorded during the year in which the lambs were conceived, and for LG and LBS measures recorded in the year of birth were used, to test for long-term effects of the environmental conditions experienced during early development. Heft was also included in the analysis of ABS: the study site is divided into three sections or hefts (Coulson et al. 1999). Individuals were assigned to a particular heft based upon the average census position recorded over the year.

Selection through Annual Breeding Success

A series of analyses was used to build a complete picture of the selective pressures on horn type and then horn size in both males and females. First, we considered the relative effect of horn type and then horn size in a given year on the breeding success in that year for males and females, while also taking into account both associated selection through other phenotypic traits and environmental factors. All individuals who were either sighted or caught within the year of the rut were included in the analysis.

Selection analyses were conducted for males and females separately, because the distributions of ABS differed greatly between males and females and to allow comparison with earlier results. Male ABS followed a negative binomial distribution, so a generalized linear mixed model (GLMM) with a negative binomial error structure and logarithmic link was used to test for associations between horn phenotype and ABS. Female ABS took the values of 0, 1, or 2 and thus did not follow a standard statistical distribution; we therefore adopted an assumption of normal errors and analyzed ABS using a linear mixed model with ABS as the dependent variable. Although this assumption of normality is clearly an approximation, a binomial model of bred/not bred within a given year yielded identical conclusions for female ABS as the model with normal errors. Horn type, hind-leg length, weight, Village Bay population size (density), and the heft within which the individual resided were fitted as fixed effects. Analysis of female ABS also included age and a quadratic term of age. Neither measure of parasite burden (strongyle and coccidia counts) was shown to have a significant effect on ABS in either sex (males: coccidia Wald statistic = 1.44, $P = 0.230$; strongyle Wald statistic = 0.81, $P = 0.367$; females: coccidia Wald statistic = 0.08, $P = 0.771$; strongyle Wald statistic = 0.75, $P = 0.690$; $df = 1$ for all parameters). We therefore excluded the parasite measures from further analyses. Scurred and normal-horned males employ different reproductive strategies (Preston et al. 2003); thus, in males, the effects of density and age (divided into three groups) on ABS were nested within the effects of horn type. Nesting allows effects to be quantified independently within each of the horn types. Density dependence in selection pressures was tested for in both models of ABS by including a nested term for males and an interaction term for females of horn type and population density in the year of conception.

Mixed models were used to allow for the repeated measures in the dataset. Individual identity was fitted as a random effect to account for multiple measures on the same individual, and year as a random effect to account for multiple measures on the same year, accounting for any unmeasured environmental variation attributable to the year of measurement. The significance of the fixed effects was assessed using Wald statistics, on their associated degrees of freedom when fitted last in the model. The models were then repeated, adding horn size nested within horn type to test the effects of horn size within each horn type.

Selection through Longevity and Lifetime Breeding Success

Selection through LBS depends on the sum of ABS values over an individual's lifetime and thus will also depend upon

longevity (LG). The same generalized linear model (GLM) framework was used for analyses of LG and LBS as dependent variables in both sexes, using a negative binomial error structure with a logarithmic link. A GLM approach was used because it enables appropriate significance testing of the associations of a trait with LBS and LG, while including other factors and their associations. Hind-leg length (adjusted by age at death), horn type, population density in year of birth, birth weight, and whether the individual was born as a twin or a singleton were fitted as independent variables. A density-by-horn type interaction was also added to the models as a fixed effect to test whether the effect of density on LBS and LG differed between individuals of different horn types, but significant associations were not found in either males or females; thus for clarity the interactions were removed from the models shown. The significance of the fixed effects was assessed using F -statistics, on their associated degrees of freedom when fitted last in the model. The models were then repeated, adding horn size nested within horn type to test the effects of the size of horn grown over an individual's lifetime within each horn type.

Having established the statistical significance of any associations between fitness and horn phenotype, using appropriate error structures and significance testing, formal analyses of selection were conducted to gain selection coefficients and gradients. Standardized measures of the selection on horn type through LBS were estimated using selection coefficients, defined as the difference in mean relative fitness between two groups. For males, we therefore estimated the difference between normal-horned and scurred males in relative LBS (estimated as LBS divided by average male LBS); for females, with their three horn types, we estimated the difference between normal-horned and scurred, normal-horned and polled, and then between scurred and polled, in relative LBS. Standardized hind-leg was included in all calculations of selection coefficients to estimate direct selection independent of size, thus accounting for any subtle confounding effects with other factors.

Standardized measures of the total and the direct selection on horn size, through LBS, were then estimated using selection gradients from least-squares regressions (Arnold and Wade 1984). Total selection was estimated by regressing relative LBS on age-standardized horn size at death (age standardized as above) for each sex and horn type separately. Direct selection on horn size independent of body size was then assessed from standardized selection gradients obtained from a multiple regression including an age-standardized measure of hind-leg length at death (Lande and Arnold 1983).

To formally test whether selection through LBS on horn traits differed between males and females, selection coefficients and gradients were estimated using the same structure described above, with the addition of sex as a factor and a sex by horn trait as an interaction. Partial F -tests were then used to compare the unexplained sums of squares from models with and without the interaction term (for details of model building procedure see Chenoweth and Blows 2005), thus testing whether direct linear selection on horn type and size differed between the sexes.

All models were carried out using Genstat (VSN International Ltd., Hemel Hempstead, U.K.), S-Plus 2000 Profes-

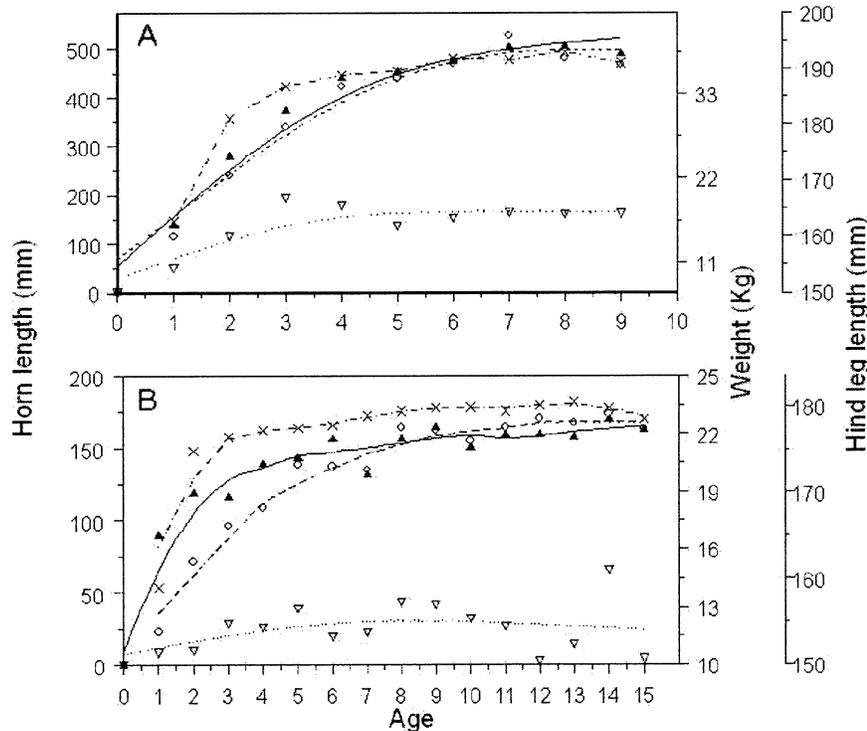


FIG. 1. Changes with age in mean August live weight, hind-leg length, and horn size in (A) males and (B) females. Crosses: hind-leg length with Gompertz growth curve shown by dotted-dashed line; filled triangles: horn length for individuals with normal-horns, with Gompertz curve shown by solid line; open circles: weight, with Gompertz growth curve shown by dashed line; open triangles: horn length for individuals with scurred horns, with Gompertz curve shown by dotted line.

sional Release 2 (Insightful, Seattle, WA) and R version 2.1.1 (R Development Team; <http://www.r-project.org>).

RESULTS

Variation in Morphology

Horn size in normal-horned individuals showed substantial variation with age, and followed a similar pattern of increase as live body weight, with both measures asymptoting at age seven in males and females (Fig. 1). In contrast, horn size in scurred individuals increased in smaller amounts each year, with substantial variation in females surviving to older ages due to smaller sample sizes (Fig. 1). A skeletal measure of body size (hind-leg length) reached its maximum by the age of three years in both sexes and thus followed a steeper rate of increase during the first few years of life than in later years (Fig. 1). No significant differences were found in body size (age-adjusted hind-leg length) or birth weight between the horn types in either sex.

The number of males known to be present within the population fluctuated between 120 and 381, with the proportion of scurred males varying 18–42% between years (Fig. 2). The density of normal-horned males appeared to fluctuate more widely than that of scurred males and thus the total population density depended more upon the density of normal-horned males than scurred males (Pearson's correlation with overall density: normal-horned males $t = 114.74$, $df = 19$, $P < 0.001$; scurred males $t = 3.53$, $df = 19$, $P = 0.06$). In females, there were no differences between horn types in fluctuations in density (Fig. 2).

Annual Breeding Success

Annual breeding success (ABS) was greatest in normal-horned males, between the ages of three and six years (Fig. 3A). Average ABS in scurred males was less variable with age, increasing slightly until four years of age, and then decreasing (Fig. 3A). As a result of these observations, selection acting upon horn type was tested at three different age groups: a zero-to-two-year group (A1); a three-to-six-year group (A2); and seven years and above (A3).

Selection was found to act upon the horn type of males through ABS, with normal-horned males showing significantly higher ABS when compared to scurred males (Table 1). This association appears to be driven by normal-horned males having significantly greater ABS between the ages of three and six, when compared to either scurred males or normal-horned males of other ages (Table 1). The associations with age class were maintained when the analysis was repeated considering only males that had lived to at least seven years of age, suggesting that this trend was not driven by the selective appearance or disappearance of successful breeders from the older age classes (results not presented here). Body weight was also positively associated with ABS, but no significant association was found for hind-leg length (Table 1). ABS was lower at high population density for normal-horned males, but there was no significant association for scurred males (Table 1). The addition of horn size nested within horn type showed that horn size was significantly positively related to ABS in normal-horned males but had no effect in scurred males (Fig. 4; Table 1).

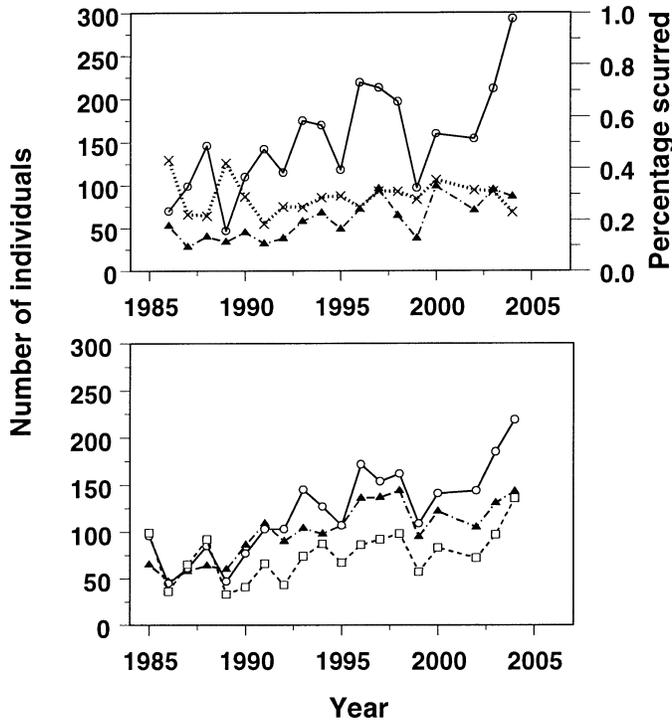


FIG. 2. Changes in numbers of horn types in males (top) and females (bottom) with year. Normal-horned individuals are depicted by open circles and solid lines; scurred individuals by solid triangles and dotted-dashed line; polled individuals by open squares and dashed line. The proportion of scurred amongst all males is also shown by crosses and dashed line.

The percentage of females conceiving increased with age until the age of eight, when senescence appeared to reduce the percentage reproducing in older age groups (Fig. 3B). Although no apparent differences were observed across horn types in the percentage of females reproducing with age (Fig.

3B), once other variables had been corrected for in the full model, normal-horned females showed reduced average ABS across all ages (Table 2). Weight and hind-leg length were significantly positively related to ABS in females (Table 2), indicating that, as with males, larger individuals were more likely to reproduce in a given year. Population density was also associated with ABS in females, with no significant differences found between the horn types (Table 2). Heft was not related to ABS in either sex (Tables 1 and 2). Both linear and quadratic associations of ABS with age were found in females (Table 2), confirming the pattern identified in Figure 3.

Horn size nested within horn type was negatively associated with ABS for normal-horned females (Table 2), indicating that increased horn growth may be costly; however, the coefficients were extremely small (Table 2). No significant association was found between horn size and ABS in scurred females (Table 2).

Longevity

In males, viability selection acting through longevity favored scurred individuals, with negative coefficients observed for normal-horned males indicating a survival cost associated with their phenotype (Table 3A; Fig. 5A). Population density at birth was significantly related to longevity in males and explained the greatest proportion of model deviance, with negative coefficients suggesting that individuals born at low population densities survived for greater periods of time (Table 3A). Age-adjusted hind-leg length was positively associated with longevity in males (Table 3A). Natural selection favors males born as singletons, as shown by the significant negative association between twin status and longevity; but no association with birth weight was found, probably due to the effect being removed by the association with twin status (Table 3A).

Longevity was negatively associated with horn size in nor-

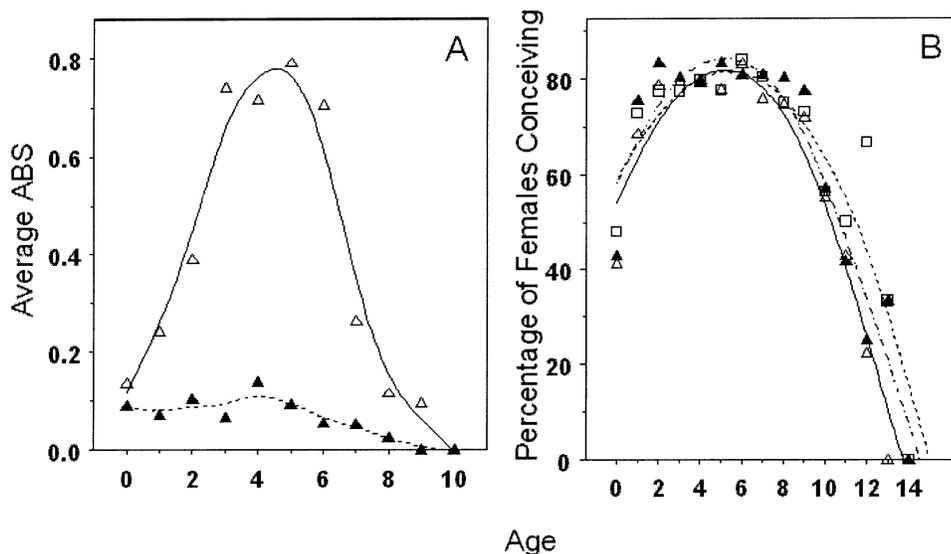


FIG. 3. Changes in annual breeding success (ABS) (A) in males and (B) the percentage of females conceiving each year, with age (in years). Normal-horned individuals are depicted by open triangles and solid lines; scurred individuals by solid triangles and dotted-dashed line; polled females by open squares and dashed line. Lines are fitted using a cubic spline function.

TABLE 1. Analysis of selection through annual breeding success in males (ABS). Results are from a generalized linear mixed model with male ABS as dependent variable, negative binomial error structure, and logarithmic link function. Individual identity and year were fitted as random effects. Significance of terms was calculated using Wald statistics and indicated by *P* based upon the term fitted last in the model. *n* denotes the number of observations based upon number of individuals. Nested effects of age groups (A1: 0–2 years; A2: 3–6 years; A3: 7+ years) within horn type are compared to those individuals within the first age group. The model was then repeated with horn size nested within horn type. The addition of horn size had a negligible effect on the random effects.

Male ABS	Parameter estimate (SE)	df	Wald statistic	<i>P</i>
Heft		2	0.43	0.782
northwest	−0.032 (0.190)			
southwest	−0.036 (0.226)			
Hind-leg length	0.002 (0.003)	1	0.67	0.415
Weight	0.031 (0.007)	1	20.67	<0.001
Horn type		1	15.67	<0.001
normal horned	0.175 (0.041)			
Horn type: Age		4	82.99	<0.001
scurred: A2	0.061 (0.057)			
scurred: A3	−0.094 (0.074)			
normal horned: A2	0.396 (0.044)			
normal horned: A3	−0.089 (0.066)			
Horn type: density		2	37.87	<0.001
scurred: density	−0.005 (0.003)			
normal horned: density	−0.013 (0.002)			
Random effects	Variance component		SE	
Individual	0.107		0.011	
Year	0.003		0.002	
Residual	0.426		0.013	
			<i>n</i> = 986 observations (637 individuals)	
Horn type: horn size		2	31.24	<0.001
scurred horn	−0.002 (0.001)			
normal horn	0.015 (0.005)			
			<i>n</i> = 946 observations (621 individuals)	

mal-horned males (Table 3A; Fig. 6A), but there was no significant relationship in scurred males (Table 3A; Fig. 6B).

In females, viability selection favored scurred and normal horned individuals as opposed to those who were polled, with a negative coefficient observed for polled females (Table 3B; Fig. 5B). As for males, population density at birth was significantly negatively related to longevity in females, and explained the greatest proportion of model deviance, with negative coefficients indicating that females born at low population densities survived for greater periods of time (Table 3B). Age-adjusted hind-leg length was associated with in-

creased longevity in females, thus confirming positive selection on body size in both sexes (Table 3B). Birth weight was not associated with longevity in females, but females born as singletons had greater longevity than those born as twins, as shown by the significant negative association between twin status and longevity (Table 3B).

As for males, horn size in normal-horned females was negatively associated with longevity, with negative coefficients suggesting normal-horned individuals with increased horn length were significantly more likely to die at an earlier age than normal-horned individuals with shorter horns (Table 3;

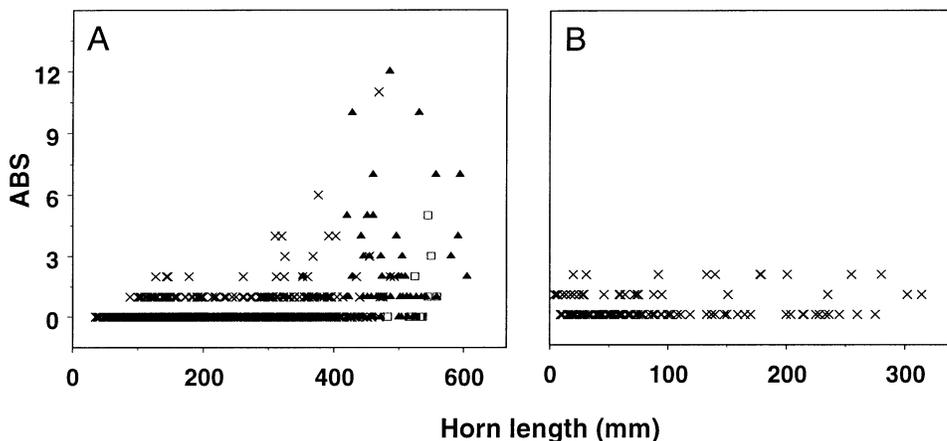


FIG. 4. Changes in annual breeding success (ABS) with horn length in (A) normal-horned and (B) scurred males. Normal-horned males are divided into three age categories; crosses: age one to three years; triangles: three to seven years; open squares: seven years and above.

TABLE 2. Analysis of selection through annual breeding success (ABS) in females. Results are from a linear mixed model for female ABS. Individual identity and year were fitted as random effects. Significance of terms was calculated using Wald statistics and indicated by *P* based upon the term fitted last in the model. *n* denotes the number of observations based upon number of individuals. The model was then repeated with horn size nested within horn type (note that polled females are necessarily excluded from the final analysis). The addition of horn size had a negligible effect on the random effects.

Female ABS	Parameter estimate (SE)	df	Wald statistic	<i>P</i>
Age	0.151 (0.014)	1	670.10	<0.001
Age ²	-0.016 (0.001)	1	517.76	<0.001
Heft		2	0.20	0.907
northwest	-0.042 (0.028)			
southwest	-0.001 (0.032)			
Hind-leg length	0.005 (0.002)	1	24.12	<0.001
Density	-0.001 (3.0×10^{-4})	1	26.78	<0.001
Weight	0.017 (0.008)	1	8.65	0.001
Horn type		2	6.80	0.010
polled	0.031 (0.036)			
scurred	0.000			
normal horned	-0.142 (0.056)			
Horn type: density		2	0.99	0.611
scurred: density	0.000			
normal horned: density	-0.005 (0.003)			
polled: density	0.003 (0.003)			
Random effects	Variance component		SE	
Individual	0.083		0.009	
Year	0.017		0.006	
Residual	0.232		0.006	
			n = 2936 observations (1307 individuals)	
Horn type: horn size		2	22.49	<0.001
polled	NA			
scurred horn	-4.5×10^{-4} (4.5×10^{-4})			
normal horn	-0.001 (4.5×10^{-4})			
			n = 1734 observations (864 individuals)	

Fig. 6B). No relationship was observed between longevity and horn size in scurred females (Table 3; Fig. 6B).

Lifetime Breeding Success

Selection pressure acting through lifetime breeding success (LBS) did not differ between horn types in males, suggesting no difference in overall fitness between the two phenotypes (Table 4A; Fig. 5C). Population density at birth had the greatest influence on LBS in males, with negative coefficients suggesting that individuals born at low density produced more offspring. Age-adjusted hind-leg length was significantly positively associated with LBS in males, suggesting that larger individuals also produced more offspring. Birth weight and being born a twin or a singleton were not associated with LBS in males (Table 4A).

There was no association between horn size and LBS in males (Table 4A; Fig. 6C). The positive association of horn size with ABS thus appeared to be masked by the negative association with longevity (Table 4A; Fig. 6A).

Polled females were shown to have reduced LBS, with negative coefficients suggesting a reduction in lifetime fitness (Table 4B; Fig. 5D). Although normal-horned females were shown to have reduced annual breeding success, no difference in LBS was found between scurred and normal-horned females using GLM analysis (Table 4B; Fig. 5D). Population density at birth had the greatest influence on LBS in females, and similar to males, negative coefficients suggested that individuals born at low population density did, on average, produce more offspring (Table 4B). Age-adjusted hind-leg

length was positively associated with LBS in females, with positive coefficients confirming results gained from the analyses of ABS and longevity that larger individuals had greater lifetime breeding success (Table 4B). Birth weight was also positively associated with LBS in females, a result not found in males (Table 4B). In females, being born a singleton was also significantly associated with LBS (Table 4B). It therefore appears that the circumstances of birth affect lifetime fitness in females to a greater degree than in males.

In normal-horned females there was a significant negative association between horn size and LBS (Table 4B; Fig. 6D). No significant association of horn size and LBS was found in scurred females (Table 4B; Fig. 6D).

Selection Coefficients and Gradients

Selection coefficients revealed associations between horn type and lifetime breeding success similar to those gained from the GLM for longevity and LBS. In males, selection coefficients for horn type indicated a nonsignificant reduction in relative LBS of scurred as compared to normal-horned individuals (Table 5). In females, selection coefficients for horn type indicated no significant difference between scurred and normal-horned individuals and a lower relative lifetime breeding success for polled individuals when compared to either group (Table 5). When directly compared, linear selection on scurred compared to normal-horned individuals differed significantly between the sexes, with the inclusion of a sex-by-horn type interaction significantly decreasing model deviance (Table 6).

TABLE 3. Analysis of selection through longevity in (A) males and (B) females. Coefficients (with SE) for terms in an analysis of longevity in males and females with a negative binomial error structure and logarithmic link. Significance of departures from zero was estimated using F statistics indicated by P . All terms have one degree of freedom with the exception of horn type (2 df), and both residual deviance and degrees of freedom are given. For analysis of horn type, three horn phenotypes are present in females: polled (no horns), scurred (reduced horn), and normal horned; and two in males: scurred and normal-horned. All effects are compared to scurred individuals. The model was then repeated with horn size (recorded at death and age corrected) nested within horn type (2 df). The direction of coefficients remained the same and thus only the effects of the additional terms are shown.

	(A) Males			(B) Females		
	Coefficient (SE)	F	P	Coefficient (SE)	F	P
Birth weight	0.004 (0.061)	0.003	0.950	0.103 (0.056)	2.524	0.080
Hind-leg length	0.011 (0.005)	5.955	0.010	0.017 (0.005)	12.946	<0.001
Horn type		3.629	0.035		8.266	<0.001
polled	NA			-0.267 (0.086)		
scurred horn	0.000			0.000		
normal horn	-0.183 (0.094)			0.102 (0.081)		
Density	-0.004 (0.001)	154.888	<0.001	-0.004 (3.3×10^{-4})	227.488	<0.001
Twin	-0.217 (0.085)	6.691	0.010	-0.299 (0.086)	11.263	<0.001
Residual deviance = 687.68				Residual deviance = 829.94		
Residual df = 856				Residual df = 1090		
Horn type: Horn size		3.921	0.020		3.636	0.030
polled	NA			NA		
scurred horn	-0.048 (0.088)		0.586	0.069 (0.192)		0.721
normal horn	-0.147 (0.053)		0.006	-0.347 (0.126)		0.006
Residual deviance = 660.47				Residual deviance = 735.33		
Residual df = 840				Residual df = 876		

Calculating selection gradients on horn size for each horn type revealed a contrasting pattern in the relationship between horn size and LBS for normal-horned males and females, with nonsignificant positive coefficients for males but significant negative coefficients for females (Table 5). This sup-

ports the negative associations of fitness and horn size in normal-horned females that were found within all of our analyses. There was no evidence for selection on horn size in scurs of either sex (Table 5). Estimates of direct selection on horn size after taking into account selection on body size

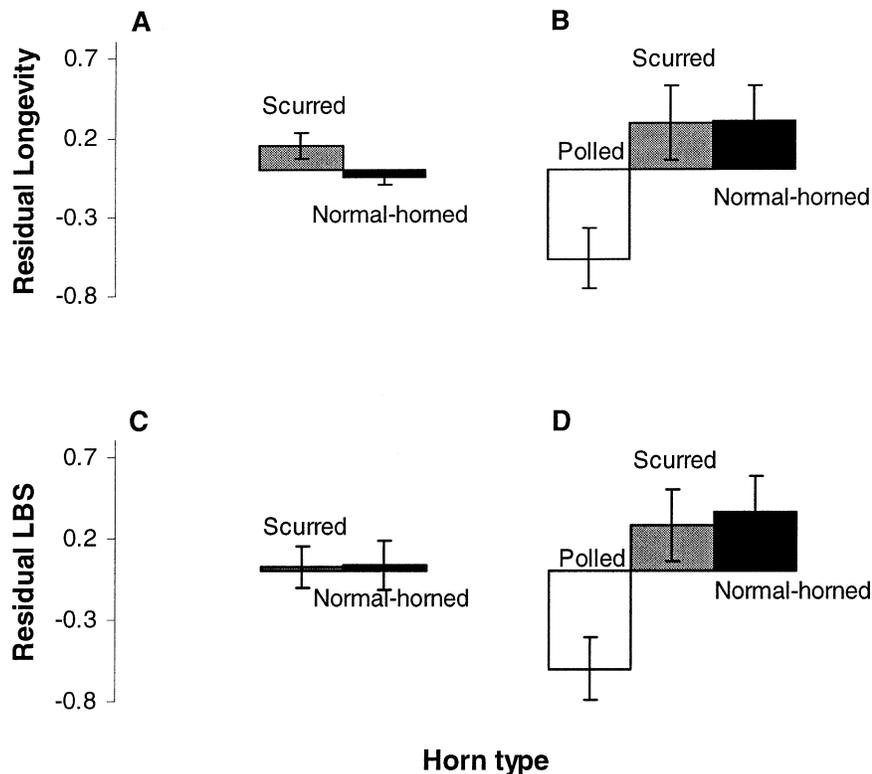


FIG. 5. Bar charts (with SE) showing average residual longevity and lifetime breeding success (LBS) for males (A, C) and females (B, D) within each horn type. Residuals were gained from models of longevity and LBS containing birth weight, density in year of birth, twin, and age-adjusted hind-leg length.

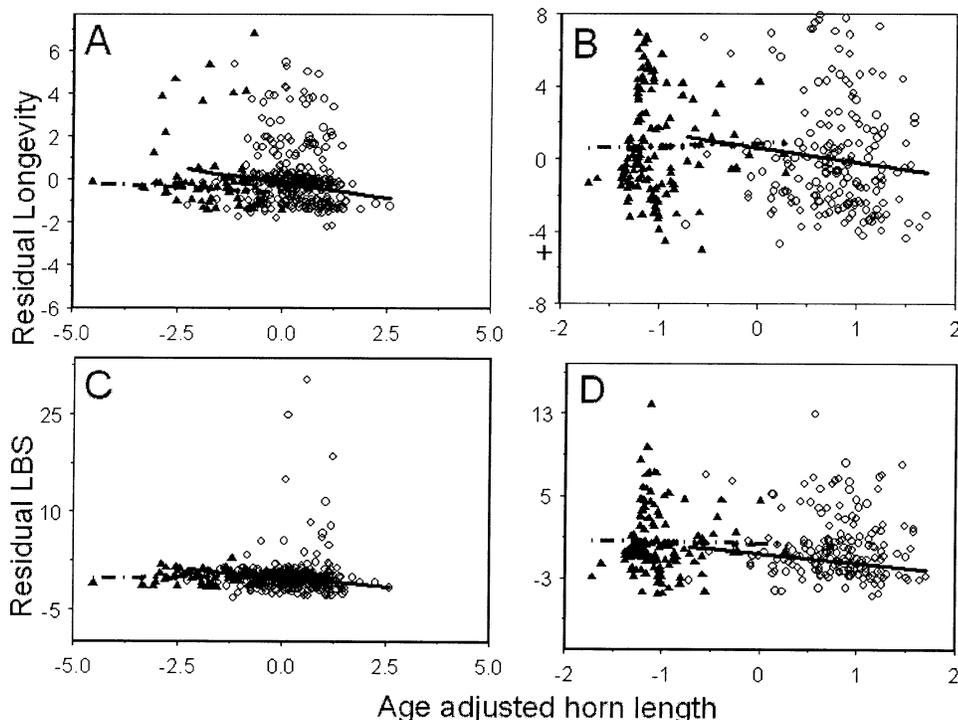


FIG. 6. Changes in residual longevity and lifetime breeding success (LBS) with age-adjusted horn size in males (A, C) and females (B, D). Residuals gained from a model of hind leg (age adjusted), density at year of birth, twin, and horn type on fitness variables longevity and lifetime breeding success. Horn size is age standardized for age at death (see Materials and Methods). Scurred individuals: solid triangles and dotted-dashed line; normal-horned individuals: solid line. Lines show linear regression between two variables.

through hind-leg length were generally lower than those for total selection (Table 5). There was evidence of significant antagonistic selection on horn size between normal-horned males and females, with the inclusion of the interaction term sex-by-horn size significantly reducing model deviance (Table 6).

DISCUSSION

We have shown that when a polymorphic trait is displayed in both males and females it may be subject to different selective pressures depending upon the phenotypic type and the sex of the individual. In this population of Soay sheep, differences in selection pressures between the sexes generated sexually antagonistic effects. Furthermore, there was evidence of a trade-off between annual breeding success and longevity in males, with both the normal horn type and (in normal-horned males) larger horn size associated with greater annual breeding success but reduced longevity. As a result, selection through lifetime breeding success was not found to act on horn phenotype in males. When combined, these factors will presumably contribute to the maintenance of the present phenotypic polymorphism for both horn type and size observed in this population.

Trade-Offs between Components of Fitness

The cost of breeding may be the most important control of a mating system, with trade-offs occurring between reproductive success and survival in many systems (Brooks 2000; Liker and Szekely 2005). If investment in sexual traits

does not vary in relation to the ability to bear the costs, then a functional trade-off will occur with a negative relationship between male longevity and the expression of sexual traits (Jennions et al. 2001). In this population, the reproductive strategy of male-to-male conflict, typical of normal-horned males, may be more costly than that of the courting or sneak mating tactics used by scurred males (Stevenson et al. 2004), given the likely costs of fighting as well as of greater investment in weaponry. The fitness of normal-horned males may be maximized by balancing investment in weaponry as they mature with their survival each year (Hansen and Price 1995). However, the results presented here may reflect a survival cost of investment in weaponry (in both sexes), and hence support the suggestion that individuals may not be able to sufficiently regulate their horn growth during periods of harsh conditions.

Several studies have reported associations between a secondary sexual trait and breeding success within a given year, independent of body size (Coltman et al. 2002; Preston et al. 2003). However, in this population variance in longevity was sufficient to neutralize any breeding advantages of normal-horned males, with selection through longevity favoring scurred males who on average gain a lower number of paternities each year. This is likely to be the reason why no difference in lifetime breeding success was evident between scurred and normal-horned males. Selective forces can act in opposing directions at different stages of life history (Schluter et al. 1991), and this study provides further illustration of the need to consider lifetime breeding success and its component factors rather than short-term measures of breeding success.

TABLE 4. Analysis of selection through lifetime breeding success in (A) males and (B) females. Coefficients (with SE) for terms in an analysis of lifetime breeding success in males and females with a negative binomial error structure and logarithmic link. Significance of departures from zero was estimated using *F*-statistics indicated by *P*. All independent terms have one degree of freedom, and both residual deviance and residual degrees of freedom (df) are given. Three horn phenotypes are present in females, polled (no horns), scurred (reduced horn), and normal horned; and two in males, scurred and normal horned. All effects are compared to individuals who are scurred. The model was then repeated with horn size (recorded at death and age corrected) nested within horn type.

	(A) Males			(B) Females		
	Coefficient (SE)	<i>F</i>	<i>P</i>	Coefficient (SE)	<i>F</i>	<i>P</i>
Birth weight	0.129 (0.189)	0.489	0.480	0.304 (0.114)	4.367	0.030
Hind-leg length	0.049 (0.015)	8.967	0.001	0.043 (0.010)	18.894	<0.001
Horn type		0.019	0.891		5.720	0.001
polled	NA			-0.478 (0.177)		
scurred	0.000			0.000		
normal horn	0.044 (0.322)			0.136 (0.166)		
Density	-0.011 (0.001)	111.809	<0.001	-0.009 (0.001)	160.842	<0.001
Twin	-0.309 (0.268)	1.331	0.250	-0.636 (0.180)	12.275	0.001
Residual deviance = 678.39				Residual deviance = 744.07		
Residual df = 856				Residual df = 986		
Horn type: Horn size		0.726	0.480		3.304	0.037
polled	NA		NA			
scurred horn	-0.083 (0.301)		0.782	0.126 (0.378)		0.739
normal horn	0.222 (0.172)		0.198	-0.656 (0.245)		0.008
Residual deviance = 666.73				Residual deviance = 502.29		
Residual df = 840				Residual df = 878		

TABLE 5. Selection coefficients and standardized selection gradients for lifetime breeding success in (A) males and (B) females. (1) Selection coefficients for horn type in males (normal horned relative to scurred; *n* = 1815) and females (normal horned relative to scurred *n* = 2571; normal horned relative to polled *n* = 2730; scurred relative to polled *n* = 2395), corrected for body size (positive coefficients were found for hind leg in all comparisons and thus are not presented here). (2) Selection gradients for horn size in males and females: (a) total selection; (b) direct selection correcting for body size. The effects of horn size were first tested for all individuals and then for (3) scurred males (*n* = 174) and females (*n* = 516); (4) normal horned males (*n* = 1643) and females (*n* = 749) separately.

Variable	(A) Males (SE)	(B) Females (SE)
(1) Selection coefficients for horn type:		
(a) As compared to normal-horned individuals:		
scurred	-0.218 (0.148)	-0.069 (0.128)
polled	NA	-0.824 (0.014)
(b) As compared to scurred individuals:		
polled	NA	-0.789 (0.012)
(2) Selection gradients for horn size:		
(a) Horn size	0.393 (0.171)	-0.009 (0.187)
(b) Horn size	0.151 (0.174)	-0.103 (0.181)
Hind leg	0.991 (0.176)	1.160 (0.191)
(3) Selection gradients for horn size in scurred individuals:		
(a) Horn size	-0.135 (0.154)	0.412 (0.778)
(b) Horn size	-0.175 (0.158)	0.290 (0.768)
Hind leg	0.263 (0.136)	1.136 (0.328)
(4) Selection gradients for horn size in normal-horned individuals:		
(a) Horn size	0.555 (0.279)	-0.143 (0.087)
(b) Horn size	0.071 (0.291)	-0.044 (0.079)
Hind leg	1.156 (0.210)	1.084 (0.249)

TABLE 6. Selection coefficients and standardized selection gradients for lifetime breeding success (LBS) across the sexes. Note that, because all offspring are not assigned a sire, male breeding success is underrepresented, generating the apparent significant differences in average LBS between the sexes; however, this will not be biased across males. Partial *F*-statistics represent the comparison of the unexplained sums of squares from the regression with and without the interaction term to test whether selection differed between the sexes. **P* < 0.05; ***P* < 0.01; ****P* < 0.001. Polled females were excluded from the analysis in section (1).

Variable	Regression coefficient (SE)	Partial <i>F</i> -statistic
(1) Selection coefficients for horn type (<i>n</i> = 2581)		
Sex		
male compared to female	-1.548 (0.265)	
Hind leg	0.718 (0.088)	
Horn type		
scurred compared to normal horned	0.473 (0.173)	
Sex × horn type	-0.869 (0.330)	15.72***
(2) Selection gradients for horn size in scurred individuals (<i>n</i> = 325)		
Sex		
male compared to female	-2.225 (0.703)	
Hind leg	0.869 (0.323)	
Horn size	0.177 (0.358)	
Sex × horn size	-0.693 (0.458)	1.02
(3) Selection gradients for horn size in normal-horned individuals (<i>n</i> = 901)		
Sex		
male compared to female	-2.253 (0.565)	
Hind leg	1.267 (0.156)	
Horn size	-0.783 (0.126)	
Sex × horn size	0.783 (0.128)	38.96***

Further evidence for the need to consider long-term measures of breeding success is demonstrated in females, in which there were no apparent differences in fitness between scurred and normal-horned females when analyzed using a GLM incorporating a range of other variables. Although normal-horned females showed reduced average annual breeding success (Table 2), there was no evidence of a significant reduction in longevity (Table 3), thus neutralizing any associations with lifetime breeding success in the GLM.

Sexually Antagonistic Selection

Sexually antagonistic associations have received relatively little attention within the literature (but see Rice and Chippendale 2001). Previous studies have shown that when selection acts differently on different components of a trait and between the sexes, sexually antagonistic phenotypic selection will occur (Endler 1980; Forsman 1995). We found differences in the patterns of selection acting on horn phenotype in males and females, with significantly contrasting linear selection on scurred compared to normal-horned individuals between the sexes (Table 6). Furthermore, there was evidence of antagonistic selection in the associations of horn size with LBS in normal-horned individuals (Table 6). This supports previous studies that have also shown antagonistic selection to be consistent with the direction of a sexual size dimorphism (e.g., Preziosi and Fairbairn 2000; Schulte-Hostedde et al. 2002). Our results suggest that sexually antagonistic selection may therefore contribute to the polymorphism for horn phenotype and variation observed in trait size.

The most significant association in our results was that of polled females with reduced lifetime breeding success. It would therefore be expected that selection would serve to remove alleles generating this phenotype from the population. However, although polled females are the least frequently occurring class, there is no evidence of any decline in frequency over the study period (linear regression of percentage of polled females over 20-year study period $b = 0.002$ (0.001), $F_{1,19} = 2.28$, $P = 0.157$). Previous work has suggested that the inheritance of horn type can be described with a model containing three alleles with sex-specific effects (Coltman and Pemberton 2004), but reanalysis of larger sample sizes suggests a less acceptable fit of this model to the data (M. Robinson, unpubl. data). The genetic basis of horn phenotype in the St. Kilda Soay sheep is the subject of ongoing research, and once a reliable model has been established it will be possible to explore the contribution of the phenotypic selection pressures described here to the maintenance of genetic polymorphism.

Selection on body size was clearly evident in both sexes and all horn types, with larger individuals having greater breeding success, supporting previous results gained for this population (Clutton-Brock et al. 1996, 1997; Coltman et al. 1999; Milner et al. 1999) and another ungulate species (Festa-Bianchet et al. 1997, 1998; Realè et al. 1999; Coltman et al. 2002).

Selection and the Environment

In the wild, variable environments can lead to fluctuating selection pressures, which have been shown to maintain var-

iation in many traits ranging from behavior (e.g., Dingemose et al. 2004) to reproduction (e.g., Visser et al. 1998). In this study, population density was shown to be associated with fitness, density during the rut associated with ABS, and the density at which an individual is born associated with both LG and LBS. This confirms previous results of cohort-specific effects in wild ungulate populations (Coltman et al. 1999), with the deviance of models of LG and LBS being most affected by population density in the year of an individual's birth. However, contrary to previous results (Clutton-Brock et al. 1997), there was no evidence that selection pressure on the horn type of either sex differed in differing environments. However, in males, population size was associated with ABS in normal-horned but not scurred males. This is likely to be a result of the mating strategy of normal-horned males, where competition for mates will increase with increasing population density.

Future Directions

The causal mechanisms underlying the correlations between fitness components and horn type and size in this population may take several forms but are not yet fully understood. Speculation as to the costs and benefits of horns in both males and females has persisted since work by Geist (1971). Currently, there is no explanation as to how female mammals use weaponry or whether there are any benefits to growing horns that could counteract the negative associations with fitness demonstrated here. A behavioral analysis of horn use in males detailing the relative importance of size and shape would also be beneficial, to determine more proximate mechanisms of horn use within this population. Furthermore, an analysis of the ecological determinants of horn size and how males and females respond to the environment may also shed further light on the relative costs and benefits of displaying the phenotypes described.

Conclusions

In summary, we found evidence for selection acting upon horn type and size within both male and female Soay sheep, independent of skeletal body size. This polymorphic trait was subject to different selection pressures depending on the phenotype displayed and the sex of the individual, thus generating sexually antagonistic selection for both horn type and horn size. Furthermore, estimates of phenotypic selection were dependent on the specific component of fitness measured, with a balance between the effects of selection through annual breeding success versus through longevity. As a result, there were no differences in lifetime fitness between scurred and normal-horned males who adopt different mating strategies. Our results illustrate the contrasting conclusions that may be drawn when different components of fitness are used in selection analyses, and underline the need to use as comprehensive an estimate of fitness as possible for a full representation of evolutionary processes.

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LITERATURE CITED

- Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.
- Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. *Evolution* 38:709–719.
- Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. *Nature* 406:67–70.
- Chenoweth, S. F., and M. W. Blows. 2005. Contrasting mutual sexual selection on homologous signal traits in *Drosophila serrata*. *Am. Nat.* 165:281–289.
- Chippindale, A. K., J. R. Gibson, and W. R. Rice. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Natl. Acad. Sci. USA* 98:1671–1675.
- Clutton-Brock, T. H., and J. M. Pemberton. 2004. Soay sheep: dynamics and selection in an island population. Cambridge Univ. Press, Cambridge, U.K.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* 61:381–396.
- Clutton-Brock, T. H., I. R. Stevenson, P. Marrow, A. D. MacColl, A. I. Houston, and J. M. McNamara. 1996. Population fluctuations, reproductive costs and life history tactics in female Soay sheep. *J. Anim. Ecol.* 65:675–689.
- Clutton-Brock, T. H., K. Wilson, and I. R. Stevenson. 1997. Density-dependent selection on horn phenotype in Soay sheep. *Philos. Trans. R. Soc. Lond. B* 352:839–850.
- Coltman, D. W., and J. M. Pemberton. 2004. Inheritance of coat colour and horn type in Hirta Soay sheep. Pp. 321–377 in T. H. Clutton-Brock and J. M. Pemberton, eds. *Soay sheep: dynamics and selection in an island population*. Cambridge Univ. Press, Cambridge, U.K.
- Coltman, D. W., J. A. Smith, D. R. Bancroft, J. Pilkington, A. D. C. MacColl, T. H. Clutton-Brock, and J. M. Pemberton. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am. Nat.* 154:730–746.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B* 269:165–172.
- Coltman, D. W., P. O'Donoghue, J. T. Hogg, and M. Festa-Bianchet. 2005. Selection and genetic (co)variance in bighorn sheep. *Evolution* 59:1372–1382.
- Coulson, T., S. Albon, J. Pilkington, and T. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *J. Anim. Ecol.* 68:658–671.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. John Murray, London.
- Dingemose, N. J., C. Both, P. J. Drent, and J. M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. B* 271:847–852.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91.
- . 1986. *Natural selection in the wild*. Princeton Univ. Press, Princeton, NJ.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. Longman, Essex, U.K.
- Festa-Bianchet, M., J. T. Jorgenson, C. H. Berube, C. Portier, and W. D. Wishart. 1997. Body mass and survival of bighorn sheep. *Can. J. Zool.* 75:1372–1379.
- Festa-Bianchet, M., J. M. Gaillard, and J. T. Jorgenson. 1998. Mass and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* 152:367–379.
- Fisher, R. A. 1958. Polymorphism and natural selection. *J. Ecol.* 46:289–293.
- Forsman, A. 1995. Opposing fitness consequences of colons patterns in male and female snakes. *J. Evol. Biol.* 8:53–70.
- Geist, V. 1971. *Mountain sheep: a study in behavior and evolution*. Univ. of Chicago Press, Chicago.
- Greenfield, M. D., and R. L. Rodriguez. 2004. Genotype-environment interaction and the reliability of mating signals. *Anim. Behav.* 68:1461–1468.
- Gustafsson, L., D. Nordling, M. S. Andersson, B. C. Sheldon, and A. Qvarnstrom. 1994. Infectious-diseases, reproductive effort and the cost of reproduction in birds. *Philos. Trans. R. Soc. Lond. B* 346:323–331.
- Hansen, T. F., and D. K. Price. 1995. Good genes and old age: Do old mates provide superior genes? *J. Evol. Biol.* 8:759–778.
- Jennions, M. D., A. P. Møller, and M. Petrie. 2001. Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* 76:3–36.
- Jensen, H., B. E. Saether, T. H. Ringsby, J. Tufto, S. C. Griffith, and H. Ellegren. 2003. Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). *J. Evol. Biol.* 16:1296–1307.
- Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. E. Guinness, and T. H. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683–1695.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Liker, A., and T. Szekely. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59:890–897.
- Linder, J. E., and W. R. Rice. 2005. Natural selection and genetic variation for female resistance to harm from males. *J. Evol. Biol.* 18:568–575.
- Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* 7:639–655.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge Univ. Press, Cambridge, U.K.
- Merilä, J., B. C. Sheldon, and H. Ellegren. 1998. Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis*. *Evolution* 52:870–876.
- Milner, J. M., S. D. Albon, A. W. Illius, J. M. Pemberton, and T. H. Clutton-Brock. 1999. Repeated selection on morphometric traits in the Soay sheep on St. Kilda. *J. Anim. Ecol.* 68:472–488.
- Milner, J. M., S. D. Albon, L. E. B. Kruuk, and J. M. Pemberton. 2004. Selection on phenotype. Pp. 190–216. in T. H. Clutton-Brock and J. M. Pemberton, eds. *Soay sheep: dynamics and selection in an island population*. Cambridge Univ. Press, Cambridge, U.K.
- Moorcroft, P. R., S. D. Albon, J. M. Pemberton, I. R. Stevenson, and T. H. Clutton-Brock. 1996. Density-dependent selection in a fluctuating ungulate population. *Proc. R. Soc. Lond. B* 263:31–38.
- Overall, A. D. J., K. A. Byrne, J. G. Pilkington, and J. M. Pemberton. 2005. Heterozygosity, inbreeding and neonatal traits in Soay sheep on St. Kilda. *Mol. Ecol.* 14:3383–3393.
- Pemberton, J. M., D. W. Coltman, J. A. Smith, and J. G. Pilkington.

1999. Molecular analysis of a promiscuous, fluctuating mating system. *Biol. J. Linn. Soc.* 68:289–301.
- Pomiankowski, A., and A. P. Møller. 1995. A resolution of the lek paradox. *Proc. R. Soc. Lond. B* 260:21–29.
- Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. R. Soc. Lond. B* 270: 633–640.
- Preziosi, R. F., and D. J. Fairbairn. 2000. Lifetime selection on adult body size and components of body size in a water strider: opposing selection and maintenance of sexual size dimorphism. *Evolution* 54:558–566.
- Realè, D., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity* 83:526–532.
- Rice, W. R. 1992. Sexually antagonistic genes: experimental evidence. *Science* 256:1436–1439.
- Rice, W. R., and A. K. Chippindale. 2001. Intersexual ontogenetic conflict. *J. Evol. Biol.* 14:685–693.
- Rice, W. R., and B. Holland. 2005. Experimentally enforced monogamy: Inadvertent selection, inbreeding, or evidence for sexually antagonistic coevolution? *Evolution* 59:682–685.
- Robertson, A., M. Hiraiwa-Hasegawa, S. D. Albon, and T. H. Clutton-Brock. 1992. Early growth and suckling behaviour of Soay sheep in a fluctuating population. *J. Zool.* 227:661–671.
- Roff, D. A. 1992. *The evolution of life histories: theories and analysis*. Chapman and Hall, London.
- . 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J. Evol. Biol.* 13: 434–445.
- Roff, D. A., S. Mostoway, and D. J. Fairbairn. 2002. The evolution of trade-offs: testing predictions on response to selection and environmental variation. *Evolution* 56:84–95.
- Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. *J. Anim. Ecol.* 67:979–986.
- Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* 263:1415–1421.
- Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressure and life-history trade-offs. *Proc. R. Soc. Lond. B* 246: 11–17.
- Schulte-Hostedde, A. I., J. S. Millar, and H. L. Gibbs. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution* 56:2519–2529.
- Shuster, S. M., and M. J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350: 608–610.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.* 3:259–268.
- Stevenson, I. R., P. Marrow, B. T. Preston, J. M. Pemberton, and K. Wilson. 2004. Adaptive reproductive strategies. Pp. in T. H. Clutton-Brock and J. M. Pemberton, eds. *Soay sheep: dynamics and selection in an island population*. Cambridge Univ. Press, Cambridge, U.K.
- Tomkins, J. L., J. Radwan, J. S. Kotiaho, and T. Tregenza. 2004. Genic capture and resolving the lek paradox. *Trends Ecol. Evol.* 19:323–328.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessels. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* 265:1867–1870.

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