

Density-Dependent Variation in Lifetime Breeding Success and Natural and Sexual Selection in Soay Rams

D. W. Coltman,^{1,*} J. A. Smith,² D. R. Bancroft,² J. Pilkington,¹ A. D. C. MacColl,³ T. H. Clutton-Brock,³ and J. M. Pemberton¹

¹Institute of Cell, Animal, and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, United Kingdom;

²Department of Genetics, University of Cambridge, Cambridge CB2 3EH, United Kingdom;

³Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom

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ABSTRACT: Variation in male lifetime breeding success (LBS) is central to understanding selection, yet it has rarely been measured in natural populations of large mammals. Here, we first describe variation in the opportunity for selection in cohorts of Soay rams (*Ovis aries*) on the archipelago of St. Kilda, Scotland, that were born during years of varying population density. Variation in LBS is closely coupled with demography, as rams born in years of low density following population crashes enjoy greater LBS than do those born in high-density years. Paradoxically, the opportunity for selection was greatest in the largest cohorts, those born in years of high population density, owing to low juvenile breeding success and overwinter survival. Variation in longevity and the contribution of nonbreeders were the most important components of the total variance in LBS in cohorts born in years of high density, while variation in fecundity was more important in cohorts born in low-density years. The opportunity for sexual selection is thus stronger in cohorts born in low-density years, as many rams in these cohorts survive to compete for mates as adults in subsequent ruts. Variation in population density in the year of birth also influenced the intensity of selection. Individuals born in years of high population density underwent strong natural selection in favor of longer hindlimbs over their first winter. In contrast, in cohorts born in low-density years, there was no natural selection on hindlimb in the first year of life. Longer hindlimbs were associated with increased fecundity over the entire lifetime of individuals born in low-density years. Natural and sexual selection thus act on the same trait in the same direction at different life-history stages in Soay rams, depending on the population density experienced in the year of birth.

* To whom correspondence should be addressed; e-mail: David.Coltman@ed.ac.uk.

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Quantifying variation in the lifetime reproductive success of individuals is essential for the measurement of the potential for natural and sexual selection (Crow 1958; Arnold and Wade 1984a, 1984b; Brown 1988; Clutton-Brock 1988) and for the estimation of effective population size (Hill 1972; Nunney 1993; Caballero 1994). So far, however, relatively few studies of natural mammalian populations have measured the reproductive success of marked individuals of both sexes throughout their life span (exceptions include Clutton-Brock et al. 1982, 1988; Altmann et al. 1988, 1996; Cheney et al. 1988; Le Boeuf and Reiter 1988; Packer et al. 1988). Only one study has been conducted over a sufficiently long time span to examine systematic differences between cohorts in male lifetime breeding success (Rose et al. 1998). In many polygynous mammals, the growth, survival, and lifetime reproductive success of males may be more strongly affected by adverse environmental conditions experienced early in life than those of females (Clutton-Brock et al. 1982; Rose et al. 1998). Cohort-specific effects, such as density in the year of birth, may therefore have profound effects on the opportunity and action of natural and sexual selection in male mammals. Empirical data are scant, however.

This may be largely because it is easier to measure lifetime reproductive success in females, owing to the difficulties in ascertaining paternity in the field for most mammals. This is particularly true for populations with polygynous mating systems and is especially true when females are promiscuous or in species with cryptic or nocturnal mating behavior. For this reason, most published studies of lifetime reproductive success in natural populations consider only females (e.g., Alados and Escos 1991; Sugiyama 1994; Festa-Bianchet et al. 1995; Ransome 1995; Wauters and Dhondt 1995; Pusey et al. 1997; Kelly et al. 1998). Even when associations between individuals can be monitored by census techniques, estimates of male reproductive output based on observed copulations or domi-

nance rank may be prone to bias and inaccurately reflect paternity (Hughes 1998). The application of genetic markers has provided many insights in this regard. In some cases, behavior underestimates the true variance in breeding success among males (e.g., Pemberton et al. 1992), yet in others, success is more evenly distributed among males than observed behavior would suggest (e.g., Amos et al. 1993). For these reasons, lifetime male breeding success may be most accurately measured using genetic methods to assign paternity. However, most published paternity studies consider only a few breeding seasons.

In this study, we investigate variation in the lifetime breeding success (LBS) of Soay rams (*Ovis aries*) on the island of Hirta in the St. Kilda archipelago, Scotland, using molecular methods to determine paternity. The mating system of Soay sheep is characterized by extreme promiscuity in both sexes. Rams do not attempt to maintain harems; rather, they associate with individual receptive ewes and mate with them repeatedly before attempting to locate the next estrous ewe (Grubb 1974). Ewes may mate with many males during a single estrus (Grubb and Jewell 1973). Paternity analysis indicates that observed copulations inaccurately reflect paternity and therefore provide a very crude measure of male breeding success, necessitating the use of molecular methods (Coltman et al. 1999a).

In this investigation, we seek to characterize the effects of variation in population density in the year of birth on the opportunity and action of natural and sexual selection. The Hirta population shows marked instability in population size. Dramatic changes in population density are caused by periodic episodes of high overwinter mortality caused by starvation or "crashes," during which over 70% of the population may die (Clutton-Brock et al. 1991, 1992; Grenfell et al. 1992, 1998). This instability is thought to be caused by the consistently high fecundity associated with abundant food in the summer (Clutton-Brock et al. 1991). These factors allow the population to pass through winter at a level close to carrying capacity, then to increase by up to 50% in the subsequent summer and to enter the next winter at a level higher than the island can support. High overwinter mortality only occurs during years of high population density, and crashes typically occur in years of heavy rainfall and strong gales in March (Grenfell et al. 1998). Overwinter mortality is biased toward males and juveniles (Clutton-Brock et al. 1991, 1992). As a result, the ratio of adult (aged 1 yr or greater) males to females varies systematically with population size (from 1986 to 1996, $r = 0.91$; see also Pemberton et al. 1996). The level of competition between rams is thus lowest during ruts in years of low population density. All rams have greater breeding success during low-density rut years, including juveniles (i.e., ram lambs born earlier that year) and year-

ling rams (Pemberton et al. 1996, 1999). For these reasons, we expect the population density in the year of birth to have a profound effect on lifetime breeding success.

Individuals born in years of low density are likely to sire more offspring as juveniles and will usually survive to breed again in subsequent seasons. Therefore, most rams born in these years will survive to breed, and much of the variation within low-density cohorts may be in the number of offspring sired over multiple ruts. Conversely, in cohorts born in high-density years, we expect a large proportion of rams to have zero breeding success, and a smaller proportion breeding as adults, as many rams will not survive their first winter. We therefore expect a higher standardized variance in the LBS of cohorts born in years of high population density. Such systematic variation in male breeding success also has implications for the effective population size of the Hirta population, as effective population size is inversely related to the variance in male breeding success (Hill 1972; Nunney 1993).

The variance in male LBS sets the upper limit on the opportunity for selection (Arnold and Wade 1984a, 1984b). We hoped to gain a better understanding of how the opportunity for natural and sexual selection varies with demographic fluctuations in the Hirta population by partitioning the variance in LBS into sexually and naturally selected components. These components are the variance in LBS within cohorts due to nonbreeders (individuals with LBS = 0) and, within breeders, variation in life span (ruts survived), fecundity (breeding success per rut), and their covariance. We hypothesize that the contributions of nonbreeders and variation in life span account for more of the total variation in LBS in cohorts born in high-density years because of high juvenile overwinter mortality. In cohorts born in low-density years, we expect more of the variation to be attributed to variation between rams in fecundity and covariance between life span and fecundity.

Quantifying the variation in LBS provides a measure of the potential for selection to act; however, if variation in LBS is unrelated to phenotype, then the opportunity for selection measures only the opportunity for gene or phenotypic change to occur through drift. We therefore examined phenotypic selection on body size at two life-history stages in relation to population density in the year of birth. Previous studies on St. Kilda have demonstrated selection of morphometric characters (Illius et al. 1995), density-dependent selection of coat color and horn type (Moorcroft et al. 1996; Clutton-Brock et al. 1997a), and body size (Milner et al. 1999), based on differential overwinter survival of both sexes. Here, we examine selection on body size resulting from differential first winter survival and selection on body size later in life caused by variation in fecundity and longevity. On the basis of previous anal-

yses (Milner et al. 1999), we expected to see selection in favor of increased body size owing to differential survival in first winter in cohorts born in high-density years (natural selection). We also hypothesized that large body size confers a mating advantage to rams born in low-density years throughout their lifetime (sexual selection). Large body size may be advantageous for males in direct competition for mates, as well as because of energetic reasons favoring endurance (Andersson 1994).

This article describes significant cohort variation in male LBS in an 11-yr study of Soay sheep on the island of Hirta. We address several main questions: Do cohorts show significant variation in juvenile overwinter survival and LBS, and is this variation related to changes in population density in the year of birth? How does variation in the components of LBS (fecundity and longevity) and the opportunity for natural and sexual selection vary between cohorts in relation to population density in the year of birth? Is variation in the intensity of selection on morphometric traits between cohorts related to population density in the year of birth? Is this variation consistent with the variation in the opportunity for selection between cohorts?

Material and Methods

Study Site and Population

Soay sheep on St. Kilda have been the focus of biological research since the early 1960s (Jewell et al. 1974; Clutton-Brock et al. 1991, 1992). An unmanaged population has existed on the island of Hirta (638 ha), the largest island in the St. Kilda group (57°49'N, 8°34'W), since their introduction in 1932 from the adjacent island of Soay (99 ha), where they have existed for centuries. The analyses described in this article are based on individually marked animals that reside in a 170-ha study area centered on the Village Bay. The Village Bay population makes up approximately 30% of the island total. Since 1985, over 95% of lambs born in the study area have been sampled for genetic analyses shortly after birth. Genetic samples have also been obtained by catching sheep resident in the Village Bay area each August. All individuals sampled for genetic analyses have been marked with ear tags for permanent identification.

Since 1985, survival has been monitored by systematic searches of the Village Bay for corpses in early spring each year, combined with regular censuses of the study area during three periods of the year: April, August, and the rut (mid-October to the end of November). A small number of individuals have unknown fates, as they disappear from the study area and are not seen again, nor are their corpses found. For the purpose of this study, rams that

had not been seen for at least 2 yr (i.e., over six consecutive census periods) were considered to have died following the last rut in which they were known to have been alive.

Each August, over one-half of the study area population was caught, allowing body measurements to be taken. A smaller number of rams were also caught during the rut (October–November). Hindlimb length was measured at each capture. From 1985 to 1988 inclusively, a “round” hindlimb length measurement was taken to the nearest millimeter by laying a measuring tape along the posterior surface of the hindlimb from the tubercalcis of the fibular tarsal bone to the posterior edge of the hoof. Since 1988, a “linear” hindlimb length has been measured to the nearest millimeter from the tubercalcis of the fibular tarsal bone to the distal end of the metatarsus, using calipers. Round lengths collected in 1986 and 1987 were converted to linear lengths from regression equations derived from the data collected in 1988 on similarly aged animals. We interpret linear hindlimb length as a linear index of body size.

We used hindlimb length data collected from August to November for rams caught as lambs and as yearlings in two separate analyses of phenotypic selection. As there was considerable variation in catch date and individuals were caught during a period in which they may have experienced considerable growth, we used general linear models to account for variation in the date and year of measurement for lambs and yearlings separately. The residuals, standardized by the standard deviation, were then used in subsequent analyses of selection.

Paternity Analysis

We analyzed the paternity of 1,480 lambs born from 1986 to 1997, using single-locus genetic markers, listed in table 1. From 1986 until 1994, all sampled lambs, their mothers, and candidate rams were typed at five protein and 10 microsatellite DNA loci. Cohorts born from 1995 to 1997 were typed at 11 more variable microsatellite loci. The methods used to screen these polymorphisms and the genetic characteristics of these loci are described in detail elsewhere (Bancroft 1993; Bancroft et al. 1995; Smith 1996; Coltman et al. 1999*b*; Pemberton et al. 1999). All loci are autosomal, with the exception of MAF45, which is located on the pseudoautosomal region of the X chromosome and segregates as an autosomal locus. No locus showed significant genotypic disequilibrium, nor was there evidence for allelic disequilibrium between any pair of loci (tests implemented in Genepop 3.0 [Raymond and Rousset 1995]; data not shown). The combined average exclusion probability of the genetic system for cohorts born between 1986 and 1994 was 0.970 and 0.987 for cohorts born

Table 1: Microsatellite and protein loci used in the analysis of paternity in Soay sheep born from 1986 to 1997

Locus name	Cohorts typed	Number of alleles	Observed heterozygosity	Exclusion probability
Microsatellites:				
BM 1314	1995–1997 ^a	8	.82	.448
BM 203	1995–1997 ^a	11	.75	.414
INRA 5	1995–1997 ^a	9	.73	.302
TGLA 13	1995–1997 ^a	6	.74	.312
TGLA 263	1995–1997 ^a	7	.79	.409
MAF 18	1986–1994 ^b	3	.57	.147
RBP	1986–1994 ^b	3	.64	.189
RM 106	1986–1994 ^b	4	.45	.110
DRB 3	1986–1997 ^{a,b}	8	.79	.473
OarFCB 304	1986–1997 ^{a,b}	4	.59	.196
MAF 35	1986–1997 ^{a,b}	4	.57	.159
MAF 45	1986–1997 ^{a,b}	6	.76	.340
MAF 65	1986–1994 ^b	4	.52	.122
OarCP 26	1986–1997 ^{a,b}	5	.71	.295
OarVH 34	1986–1997 ^{a,b}	6	.56	.174
Proteins:				
Adenosine deaminase	1986–1994 ^b	2	.37	.073
Glutamate oxaloacetate deaminase	1986–1994 ^b	2	.35	.053
Hemoglobin	1986–1994 ^b	2	.53	.124
Isocitrate dehydrogenase	1986–1994 ^b	3	.50	.123
Transferrin	1986–1994 ^b	7	.78	.398

^a Used in paternity analysis of cohorts born 1995–1997.

^b Used in paternity analysis of cohorts born 1986–1994.

1995–1997 (calculated assuming no knowledge of the maternal genotype according to formulas in Marshall et al. 1998).

We assigned paternity using a likelihood-based approach described in Marshall et al. (1998). The simulation program within CERVUS 1.0 (Marshall et al. 1998) was used to estimate the critical difference in log-likelihood scores between the most likely and second most likely candidate male for assignment of paternity at a level of 80% confidence in each rut separately. Although we may expect one in five assignments to be incorrect at this confidence level, incorrect assignments are unlikely to be biased in relation to the assigned ram's age class or year of birth.

For each rut, all sampled rams known to be alive at the time of the rut, including juveniles born in the spring preceding the rut, were considered as equally likely candidate fathers. For the paternity simulation, we assumed that 80% of candidate males were sampled, 95% of loci were typed, and a 1% rate of typing error existed. Throughout the rest of this article, we refer to the number of paternities assigned to a ram as lifetime breeding success (LBS).

Estimating the Opportunity for Selection and Partitioning the Variance in LBS

We examined variation in LBS with population density, using the standardized variance as a measure of variation in male breeding success (variance/mean²). This ratio, denoted I_{LBS} , is a measure of the opportunity for selection (Crow 1958; Arnold and Wade 1984a, 1984b) and describes the upper limit on changes in phenotype that may be caused by selection or variation in fitness. We also calculated I for all rams known to be alive in each breeding season (I_{SBS}) to compare cross-sectional and longitudinal estimates.

The ratio I_{LBS} reflects the total opportunity for selection over the lifetime; however, the total variance in LBS can be partitioned into naturally and sexually selected components if these components are defined so that their product gives total breeding success or fitness (Arnold and Wade 1984a, 1984b; Brown 1988). Here, we use Arnold and Wade's (1984a) definitions of natural and sexual selection to define two multiplicative components of LBS. We consider variation in lifetime fecundity, calculated as LBS/number of ruts survived (L_r), as part of the oppor-

tunity for sexual selection. Variation in longevity, taken as the number of ruts survived (L_L), then represents part of the opportunity for natural selection as it arises from variation in fitness components other than breeding success. Brown (1988) provides formulas for estimating the contribution of nonbreeders to the total variance in LBS:

$$\% \text{ contribution} = 100[p(1 - p)(\bar{x}_{LBS_{breeders}})], \quad (1)$$

where p is the proportion of individuals that sired at least one offspring (breeders), and $\bar{x}_{LBS_{breeders}}$ represents the mean in the LBS of rams that sired at least one lamb ($LBS_{breeders}$). For partitioning the variation in $LBS_{breeders}$ to its multiplicative components and their joint variation (Q_{LF}), we solved

$$V_{LBS_{breeders}} = (\bar{x}_{L_{breeders}})^2(V_{F_{breeders}}) + (\bar{x}_{F_{breeders}})^2(V_{L_{breeders}}) + Q_{LF}, \quad (2)$$

for Q_{LF} , where $\bar{x}_{L_{breeders}}$ and $V_{L_{breeders}}$ represent the mean and variance in the number of ruts survived in successful breeders, and $\bar{x}_{F_{breeders}}$ and $V_{F_{breeders}}$ describe the mean and variance in the fecundity of successful breeders (Brown 1988). The term Q_{LF} is complex, involving covariance in both terms and the covariance of the squares of the deviation of $L_{L_{breeders}}$ and $L_{F_{breeders}}$ from their means. It can be interpreted as a joint variation term that indicates the extent to which the components of LBS vary independently. A negative Q_{LF} , for example, indicates that the variance in the product of L and F is less than would be expected if they were independent. Equation (2) was solved in a simplified form:

$$V(LBS_{breeders}/\bar{x}_{L_{breeders}}\bar{x}_{F_{breeders}}) = V(F_{breeders}/\bar{x}_{F_{breeders}}) + V(L_{breeders}/\bar{x}_{L_{breeders}}) + Q(F_{breeders}/\bar{x}_{F_{breeders}}, L_{breeders}/\bar{x}_{L_{breeders}}), \quad (3)$$

in which the terms are standardized by their means (Brown 1988). We calculated these parameters for each cohort separately and for all cohorts combined.

Measuring Natural and Sexual Selection on Phenotype in Cohorts Born in High- and Low-Density Years

Selection differentials on hindlimb length were measured at two life-history stages in two different ways. First, the standardized selection differential, i (Falconer and Mackay 1996), was used to investigate natural selection on hind-

limb length caused by overwinter mortality in the first year of life (e.g., Milner et al. 1999). This was calculated as the change in trait mean before (\bar{x}_b) and after (\bar{x}_a) selection:

$$i = (\bar{x}_a - \bar{x}_b)/SD_b, \quad (4)$$

where SD_b is the standard deviation in the trait before selection. The significance of i was determined by t -tests comparing the trait means of survivors with nonsurvivors (Endler 1986; Milner et al. 1999). We calculated i separately for high- and low-density cohorts pooled (cohorts born in years of greater than or less than the median population size) using hindlimb measured as a juvenile at age 4–8 mo (i.e., from August to November in the first year of life).

Second, we measured i on body size using linear regression of LBS and its components (F and L) on body size measured at age 1 yr. The covariance of relative fecundity and longevity (standardized by the sample mean) and trait value is equivalent to the shift in mean trait value induced within a generation by directional selection (Arnold and Wade 1984b). This parameter represents the standardized selection differential over the life cycle following survival to breed at age 1 yr, and we also calculated it separately for rams born in low- and high-density years.

Results

Variation in LBS and the Opportunity for Selection

We estimated the breeding success of 699 rams of known age born in 11 cohorts since 1986, using paternity analysis (table 2). We assigned the paternity of 945 of the 1,480 sampled lambs born between 1986 and 1997 (63.9%). We restricted our analyses to sampled individuals that reached breeding age (i.e., those that survived to rut as a juvenile in their first year). Paternity of 731 of the 945 lambs of known paternity was assigned to rams in this sample, the remainder assigned to older rams or those of unknown age. Of the known-age rams, 257 (36.8%) were still alive at the end of the 1996 rut (table 2). There was systematic variation in the mean seasonal breeding success of juveniles and older rams with population density in the rut year (fig. 1).

Differences in mean seasonal breeding success between adults and juveniles in relation to population density were analyzed by ANCOVA (weighted by sample size), in which age class (factor: juveniles vs. adult rams) and population size (covariate) and their interaction were tested. Breeding success declined with increasing population density ($F = 14.84$, $df = 1, 18$, $P < .001$) and differed between age classes ($F = 9.18$, $df = 1, 18$, $P = .007$); however, the effect of den-

sity did not differ significantly between age classes (age class : density interaction, $F = 4.35$, $df = 1, 18$, $P = .052$).

Population density in the year of birth and LBS varied greatly between cohorts (fig. 2A, 2B). However, many rams born in later cohorts were still alive at the time of analysis (table 2). Restricting the data to individuals that have died introduces a downward bias in LBS (fig. 2B). However, considering only the cohorts born before 1992, for which the data are almost complete, there was a significant negative relationship between mean LBS and population density in the year of birth. Figure 3 illustrates the increasing relationship between LBS and the number of ruts survived. Age-specific breeding success averaged across all cohorts and, including individuals that were still alive at the end of the 1996 rut, increased from 0 to 5 yr of age, then suggested a decline at ages 6 and 7 (fig. 4).

Subsequent analyses of LBS were restricted to data from the cohorts born between 1986 and 1991. Complete data were available for >92% of these individuals (26 of 340 rams survived past the 1996 rut). Although a few surviving individuals were thus included in subsequent analyses, their omission did not qualitatively influence the results (data not shown).

Figure 5A illustrates the relationship between density in year of birth and I_{LBS} for these cohorts. The opportunity for selection increased steeply and significantly with population density in the year of birth ($P < .01$) and varied as much as tenfold between cohorts. This was not the case if this analysis were restricted to individuals that successfully bred (fig. 5B). We also calculated I for each breeding season over all rams known to be alive in that year (I_{SBS}) and found that I_{SBS} showed a weak increasing trend with population density (fig. 5C). This term varied as much as 2.4-fold between seasons (e.g., 1988 = 2.91; 1989 = 6.92); however, it fell within a much narrower range of values than I_{LBS} (I_{LBS} range: 0.63–10.54). Combining the cohorts

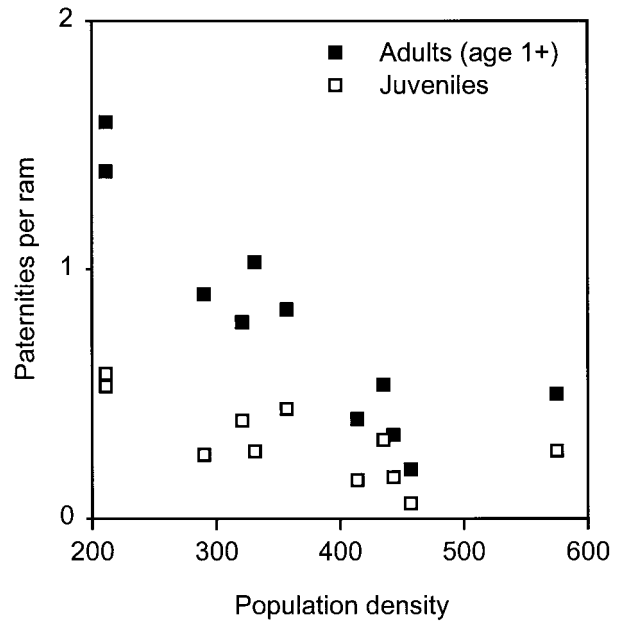


Figure 1: Mean seasonal breeding success of adult (age 1 yr or greater) and juvenile Soay rams for ruts 1986–1996 in relation to population density.

born between 1986 and 1991, the I_{LBS} calculated for rams that successfully bred was less than one-third of I_{LBS} estimated for all rams including nonbreeders (1.11 vs. 3.46) and did not vary significantly with density in year of birth (fig. 5B).

Up to 74.3% of the variance in LBS could be attributed to rams that failed to breed (table 3), and this was usually greater in cohorts born in high-density years (fig. 6). In contrast, for cohorts born in low-density years, the fecundity component of LBS was the most important single

Table 2: Sampled rams born since 1986 that have survived to rut in their first year

Year of birth	Village Bay population size	Number of rams considered	Percentage surviving first winter	Percentage surviving to rut at age 2	Percentage alive in 1996 rut	Mean number of ruts survived (\pm SE)
1986	211	36	100	86.1	0	2.92 \pm .08
1987	331	61	91.8	14.8	0	2.56 \pm .23
1988	457	63	4.8	3.2	0	1.09 \pm .06
1989	211	40	87.5	77.5	10.0	3.68 \pm .33
1990	290	66	89.4	60.6	22.7	3.94 \pm .26
1991	414	74	25.7	23.0	9.5	1.85 \pm .19
1992	321	54	81.5	64.8	44.4	3.35 \pm .22
1993	443	76	43.4	31.6	31.6	2.07 \pm .16
1994	435	52	13.5	13.5	13.5	1.27 \pm .10
1995	357	70	98.6	NA	98.6	1.98 \pm .01
1996	575	107	NA	NA	100	1.00

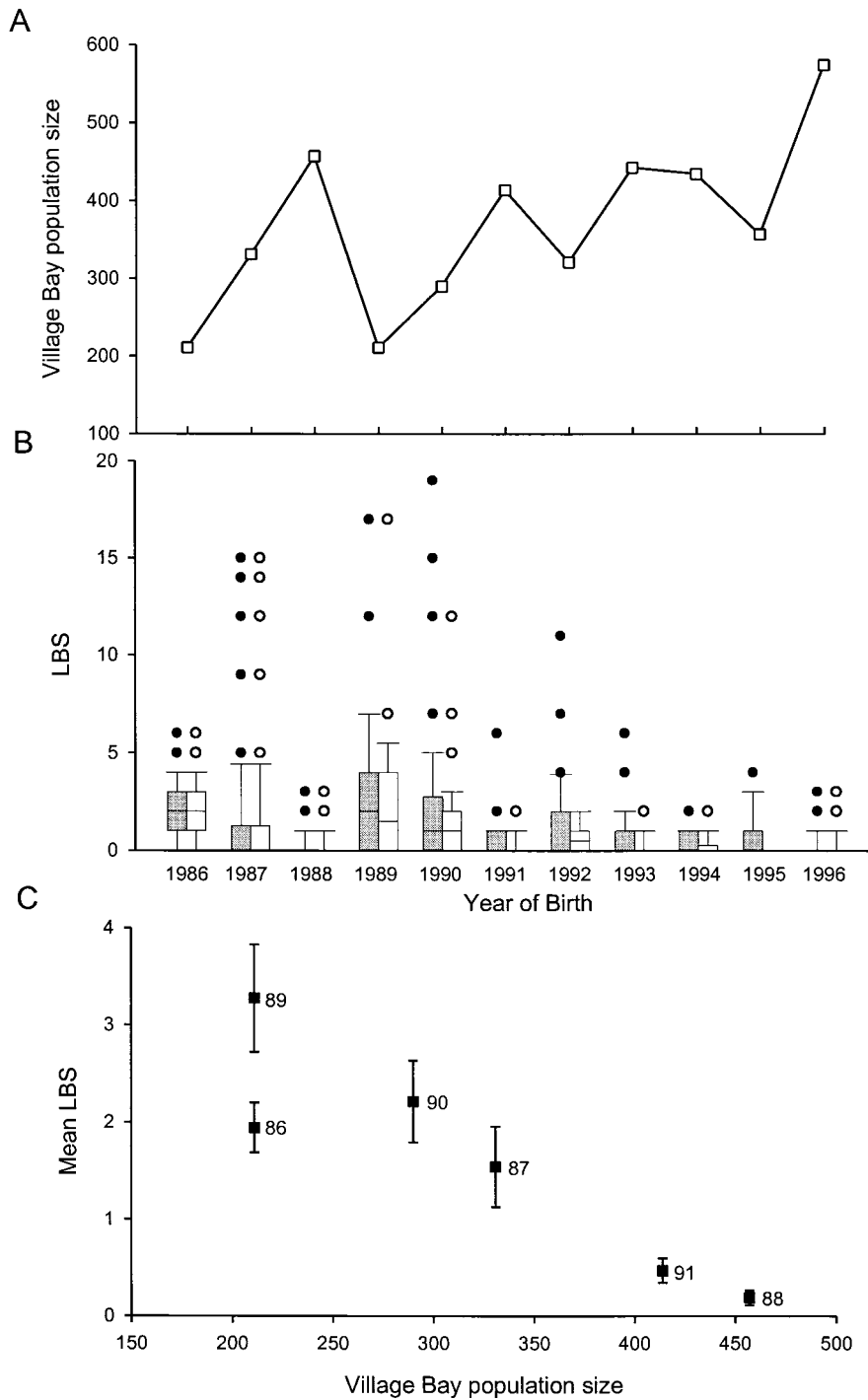


Figure 2: A, Village Bay population size from 1986 to 1996. B, Box plot of Soay ram lifetime breeding success (LBS) for cohorts born since 1986. Data are for all sampled individuals (*filled boxes*) and restricted to individuals that are known to have died (*open boxes*). Bars represent the 95th percentile, boxes encompass the second and third quartiles, the horizontal line gives the median, and circles indicate points outside the 95th percentile. C, Mean (\pm SE) LBS of Soay rams for cohorts born between 1986 and 1991. Data from these cohorts are >92% complete.

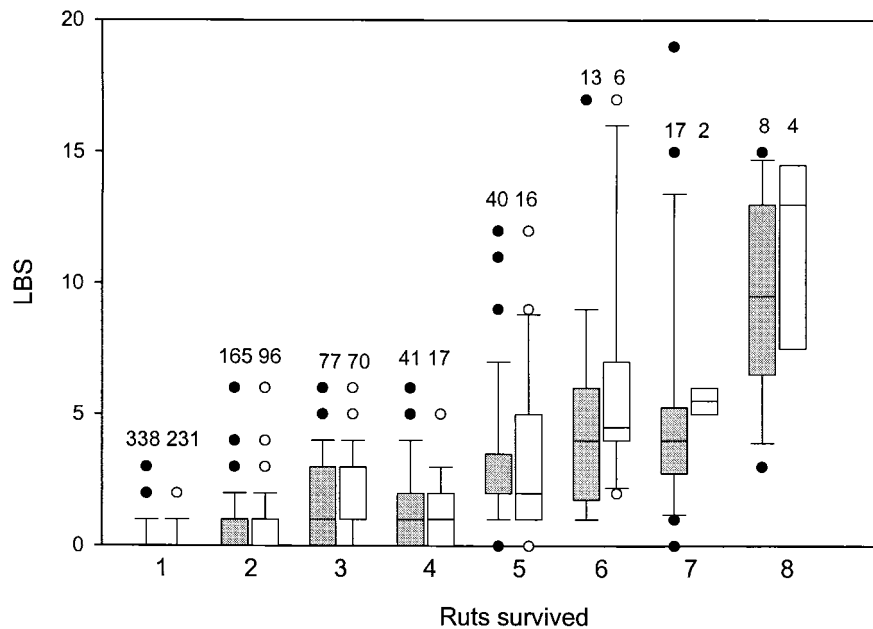


Figure 3: Box plot of Soay ram lifetime breeding success by number of ruts survived. Data are for all sampled individuals (*filled boxes*) and restricted to individuals that are known to have died (*open boxes*). Bars represent the 95th percentile, boxes encompass the second and third quartiles, and the horizontal line gives the median. Circles indicate points outside the 95th percentile. Numbers at the top of the boxes give sample size.

source of variation (e.g., 1986, 1989, and 1990; table 4; fig. 6). Within cohorts, variation in longevity accounted for 6.0%–35.7%, and the joint variation term ranged from –16.0% to 28.2% of the total V_{LBS} . Over all cohorts combined, the contributions of nonbreeders (32.1%) and the fecundity component of $LBS_{breeders}$ (27.2%) were the most important sources of V_{LBS} . The positive joint variation term over all cohorts combined (21.7%) may be partly because of the nonindependence of L and F and their positive covariance (0.406), which may be explained by age-specific variation in seasonal breeding success (fig. 4).

Phenotypic Selection

In cohorts born in years of high population density, lambs that survived their first winter had significantly longer hindlimbs than those that died ($t = 2.30$, $n = 108$, $P < .05$; table 4). This was not observed in cohorts born in years of low population density ($t = -0.40$, $n = 33$, $P > .50$; table 4). In the latter case, the test lacks power because of the small number of individuals that died. However, these observations are wholly consistent with the findings of Milner et al. (1999), which were based on measurements from more years. Overwinter survival differences suggest that there is selection favoring longer hindlimbs in male lambs born in years of high population density, resulting in a shift in mean residual hindlimb length by +0.25 SD

(2.7 mm) in a single episode of selection. This represents a change of approximately 1.6% (mean hindlimb length = 165.6 ± 1.0 mm, $n = 108$) in these cohorts.

Among animals that survived to age 1 yr, hindlimb length measured at 1 yr of age did not vary significantly with longevity, fecundity, or LBS in cohorts born in years of high population density (fig. 7A–7C). In low-density cohorts, hindlimb length measured at age 1 yr varied positively with fecundity ($P < .01$) and LBS ($P < .005$) but not with the number of ruts survived (fig. 7D–7F). This resulted in significant selection differential on hindlimb length of +0.317 SD (2.2 mm) in cohorts born in years of low population density (table 5). This represents a change of approximately 1.2% (mean hindlimb length measured at age 1 = 184.3 ± 0.8 mm, $n = 74$).

Discussion

The Importance of Density in Year of Birth to LBS

Our data clearly demonstrate the importance of density in year of birth to variation between cohorts in Soay ram LBS. Individuals born in low-density years have a long-term reproductive advantage (table 2). This advantage may be mostly because of their higher probability of survival during their first year of life (table 2) and hence participation in ruts as adults later in life. Many rams born in

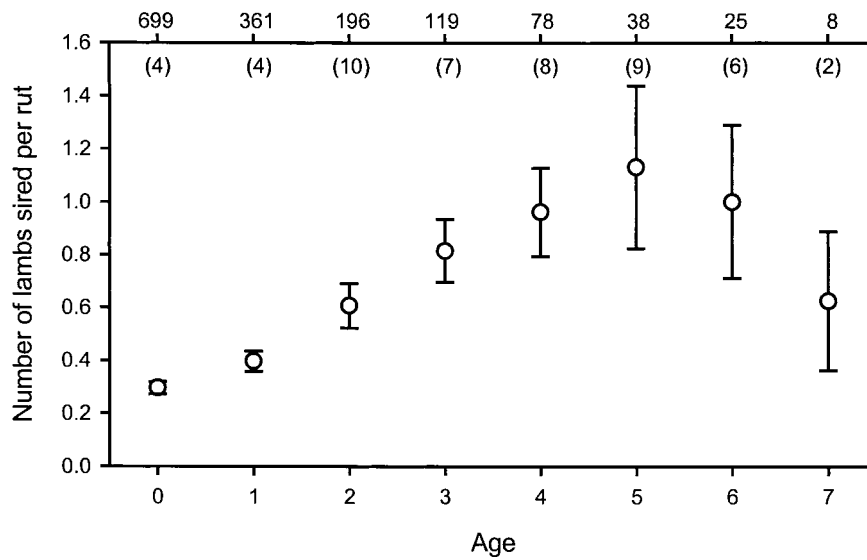


Figure 4: Age-specific breeding success of Soay rams. Data are mean (\pm SD) number of paternities assigned per ram per rut by age for all rams born since 1986. Numbers in parentheses give the maximum age-specific breeding success, and numbers along the top X-axis give sample size represented by that point.

high-density years will only survive to rut in their first year as a juvenile, and cohorts born in high-density years have a high proportion of rams that fail to sire lambs (table 3). To make matters worse for these cohorts, the breeding success rate for juveniles is lowest in high-density ruts owing to the level of competition with adult rams (fig. 1; Pemberton et al. 1996, 1999). The opportunity for selection thus increases with population density in the year of birth because of the effect of nonbreeders on the standardized variance (table 3; fig. 5A). If we were to omit nonbreeders from the calculation of the total opportunity for selection, this would cause a downward bias in the estimate for most cohorts (table 3; fig. 5B). The apparent relationship between the opportunity for selection and density in year of birth between cohorts would therefore be obscured in the absence of knowledge of the survival of full cohorts.

The partition of the variance in LBS revealed the extent to which natural and sexual selection may act on traits in different cohorts. Variation in fecundity among breeders accounted for most of the total variance in LBS in cohorts born in low-density years (table 3; fig. 6). With most rams surviving to compete in ruts at age 2 and beyond when born in years of low population density (table 2), much of the variation between males will therefore be in their success rate in competition for mates, and sexual selection has great opportunity to act on traits that enhance fecundity or mating success.

In contrast, much of the variance in the LBS of rams in high-density cohorts can be attributed to nonbreeders and variation in longevity or survival among breeders (table 3). Traits related to survival will be under natural selection, and many phenotypic and genetic factors are known to be associated with overwinter survival in Soay sheep. In some cases, this results in directional natural selection owing to differential survival in years of high population density in both sexes. For example, increasing overwinter survival probability has been associated with dark coat color and scurred horn morph (Moorcroft et al. 1996), increasing birth weight (Clutton-Brock et al. 1992), increasing summer body weight (Clutton-Brock et al. 1992; Milner et al. 1999), decreasing parasite resistance (Gulland 1992; Gulland et al. 1993; Illius et al. 1995; Coltman et al. 1999b), and increasing multilocus heterozygosity (Coltman et al. 1999b). In some cases, these associations suggest reinforcing selection pressures (e.g., birth weight is positively associated with neonatal survival, and summer weight is positively associated with overwinter survival; Clutton-Brock et al. 1996). In other cases, there may be countervailing selection in other fitness components in either sex, and countervailing selection pressures may explain the persistence of polymorphic traits such as coat and horn morph. The scurred horn polymorphism may be maintained in the population because of conflicting sexual selection favoring normal horns in males (Clutton-Brock et al. 1997a). The results of this analysis indicate

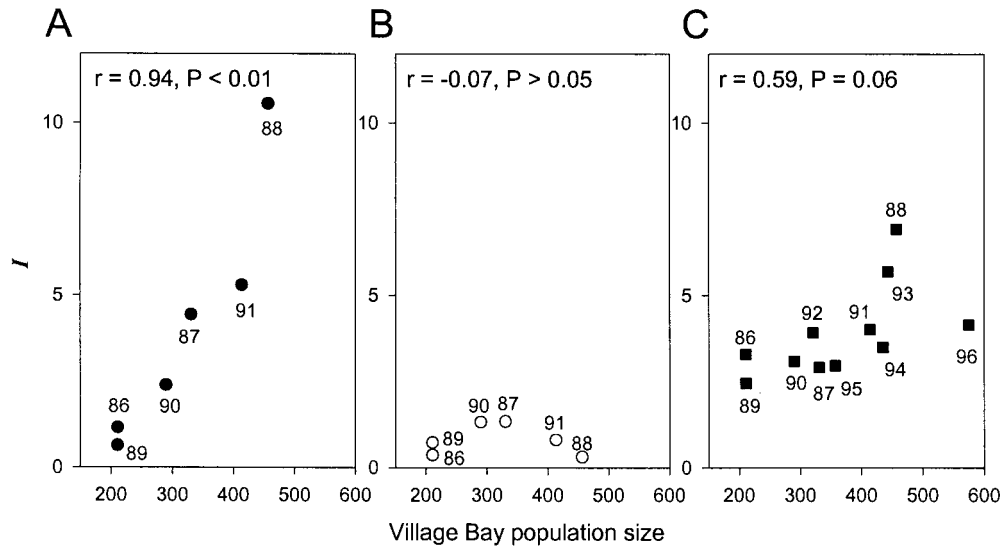


Figure 5: Variation in lifetime breeding success for all sampled rams (A), among successful breeders only (B), and variation in seasonal breeding success expressed as the ratio of the variance to the mean² (C). Numbers adjacent to points give either year of birth for lifetime data (A and B) or rut year for seasonal data (C).

that the opportunity for sexual selection through differential fecundity or seasonal mating success in cohorts born in years of low population density is of sufficient magnitude to either counteract or reinforce directional natural selection (table 3).

Natural and Sexual Selection on Hindlimb Length

As has been found previously (Milner et al. 1999), there was significant positive directional natural selection on hindlimb length (or correlated characters) caused by differences in overwinter survival of lambs born in years of high population density. The results of this study show that greater hindlimb length was also selected for in cohorts born in years of low population density because of differential LBS, which can be attributed to a fecundity advantage (fig. 7E, 7F). There was no evidence for sexual selection on hindlimb length in cohorts born in years of high population density (fig. 7B, 7C). This may be because the individuals that survive their first year in these cohorts already have already undergone natural selection on hindlimb, or the relevant correlated character, in their first winter. These results are concordant with the results of the analysis of the opportunity for selection (fig. 6). The intensity of selection, here measured as the standardized selection differential (+0.25), was significant in a single episode of natural selection in cohorts born in high-density years. For cohorts born in low-density years, only the in-

tensity of sexual selection on hindlimb length caused by differential fecundity (+0.249) was significant. Natural and sexual selection therefore act in a reinforcing manner with similar magnitude on hindlimb length.

So far, we have interpreted the results of our phenotypic selection analyses as selection on the specific trait hindlimb length. It is possible that neither sexual nor natural selection is actually acting on this trait; selection instead may be acting on correlated traits such as general body size, growth rate, or maternal performance. It is also possible that natural and sexual selection may be acting on different correlated traits (e.g., natural selection on maternal performance in lambs vs. sexual selection on horn size, growth rate, or competitive ability in rams). Using multiple regression, Milner et al. (1999) found that apparent natural selection on hindlimb length in Soay ewes acted on the correlated character body weight. Of course, it is possible that body weight was not the true target of selection in Milner et al.'s (1999) analysis and that the true target of selection is yet another unmeasured correlated variable. We chose to analyze hindlimb length in this study because it has higher repeatability within and between seasons than body weight (J. Milner, unpublished data). Similar patterns were observed using body weight in both selection analyses (data not shown). Both body weight and hindlimb length at age 1 yr explained similar levels of variation in fecundity, but they could not be fitted in the same model because

Table 3: Contribution of nonbreeders and partition of the variance in lifetime breeding success to its components in six cohorts of Soay rams

Cohort	Proportion of nonbreeding rams (LBS = 0)	I_{LBS}	$I_{LBS_{breeders}}$	V_{LBS} because of nonbreeders (%)	V_{LBS} because of $V_{L_{breeders}}$ (%)	V_{LBS} because of $V_{F_{breeders}}$ (%)	V_{LBS} because of joint variation in $V_{L_{breeders}}$ and $V_{F_{breeders}}$
1986	.167	.63	.36	31.70	6.00	73.65	-11.35
1987	.574	4.43	1.34	30.06	25.11	16.67	28.16
1988	.889	10.54	.31	74.28	35.71	6.04	-16.04
1989	.200	1.15	1.72	21.81	32.34	40.82	5.02
1990	.318	2.38	1.31	19.55	10.65	42.86	26.94
1991	.716	5.29	.80	47.14	30.00	20.06	2.80
All	.473	3.46	1.11	32.12	19.07	27.15	21.66

of their high correlation (in lambs, $r = 0.86$; in yearlings, $r = 0.56$).

Our finding that low- and high-density cohorts encounter similar strengths of directional selection on the same trait by different mechanisms contrasts with many other studies that show that variation in density can lead to stabilizing or disrupting selection. For example, sexual selection generally favors large body size and snout length in male coho salmon (*Oncorhynchus kisutch*). However, the ability of large males to control spawning females declines with increasing density, and the relative success of smaller, sneakier males increases, which may ultimately be responsible for the evolution of alternate reproductive tactics (Fleming and Gross 1994). Similarly, density-dependent sexual selection for body size in fireflies (*Photinus pyralis*) is also disruptive. Female fireflies are attracted to the displays of large males when density is low; however, during high-density scramble competition, small males are more able to reach and to inseminate females (Vencl and Carlson 1998). In other systems, sexual selection may act in the same direction yet vary in intensity with population density (Conner 1989).

Our results indicate the natural and sexual selection reinforce directional selection favoring large body size in males, yet studies have commonly reported stabilizing selection on body size from the opposition of natural and sexual selective pressures in different fitness components. For example, fecundity selection favors long-bodied female waterstriders (*Aquarius remigis*); however, short-bodied waterstriders have greater longevity, leading to balancing selection on female body size (Preziosi and Fairbairn 1997). Similarly, mortality increases equally with body size in both sexes of marine iguanas (*Amblyrhynchus cristatus*). This natural selection pressure is countered by sexual selection favoring large body size in both sexes. However, the fecundity advantage caused by large size is much greater in males, leading to the evolution of approximately twofold sexual size dimorphism (Wikelski and Trillmich 1997).

Despite evidence for directional selection on hindlimb or a correlated trait, Soay sheep show no evidence of increasing body weight (Milner et al. 1999) or hindlimb length (D. W. Coltman, unpublished data) in either sex since detailed measurements started to be collected in 1985. We might fail to detect a response to selection for several reasons. First, while statistically significant, heritability of hindlimb length in male Soay sheep is not high ($h^2 = 0.32 \pm 0.09$, estimated using restricted maximum likelihood; J. Milner, unpublished data). Coupled with a relatively weak selection differential (0.25 SD), we may have insufficient power to detect a subtle response to selection over the duration of this study. Second, there may be yet unidentified countervailing selection pressures arising from variation in other fitness components on correlated traits, and we have yet to investigate the components of lifetime reproductive success in females because data from most cohorts are still incomplete.

Sources of Bias and Comparison with Other Mammalian Systems

There are few empirical estimates of male LBS in large mammals in the literature for comparison, and comparisons between studies are difficult because of differences in methods and criteria that may cause bias. For example, this study employed molecular methods to determine paternity at a level of confidence from which we expect one in five assignments to be incorrect. Because the variance in LBS exceeds the mean, this approach means that relatively less successful rams will more frequently be assigned false paternities at the expense of successful rams (Marshall 1998). As a result, the true opportunity for selection is underestimated. However, this bias should affect all cohorts equally, meaning that it does not invalidate the conclusions drawn from this study. It should be kept in mind when making comparisons across studies, however.

Perhaps the best mammalian study population for com-

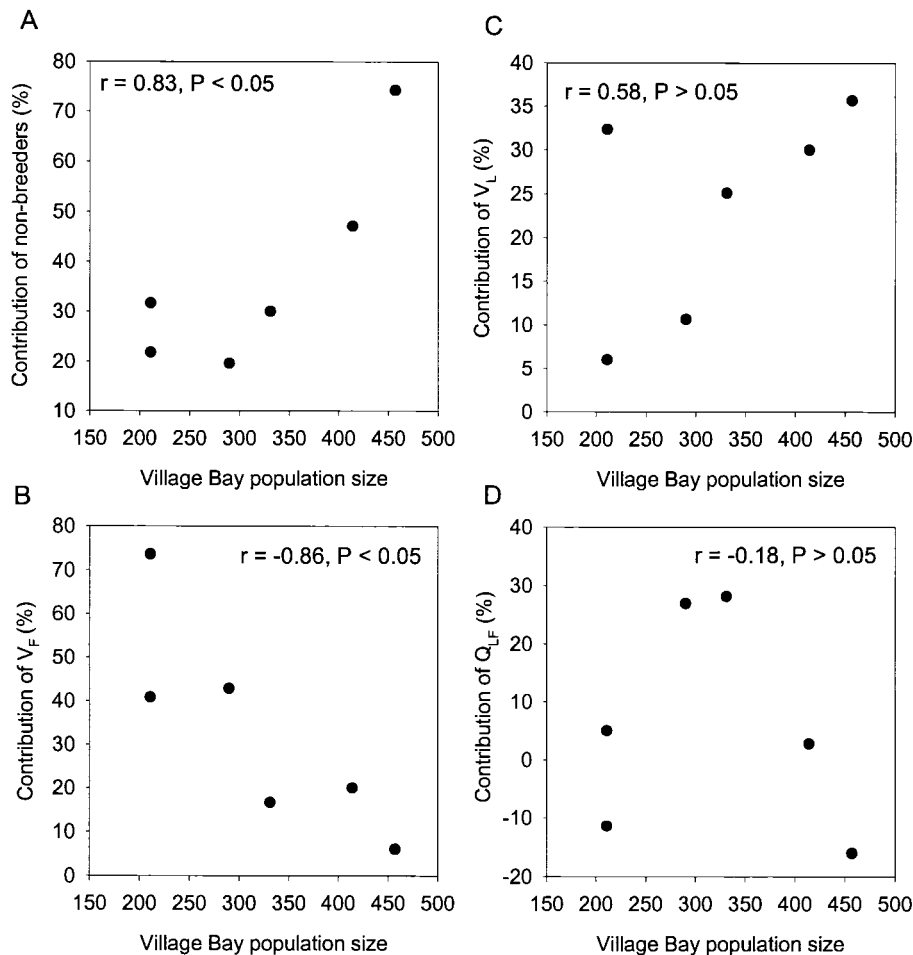


Figure 6: Contributions of nonbreeders (A), variance in the fecundity of breeders (B), variance in the longevity of breeders (C), and joint variation in fecundity and longevity (D) to the variance in lifetime breeding success in relation to population density in the year of birth for six cohorts of Soay rams.

parison, in terms of similar methodology and sample size, is the red deer (*Cervus elaphus*) of Rum. Variation in seasonal breeding success of red deer stags appears to decline with increasing female-biased sex ratio or level of competition in the rut (Clutton-Brock et al. 1997b). This resembles the situation in years of low density on St. Kilda, in which all age classes have greater breeding success as the sex ratio becomes more female biased (fig. 1). The difference between the systems is that, at high density, there is a greater female-biased ratio and reduced mate competition in the red deer (Clutton-Brock et al. 1997b). For Soay rams, the variation in SBS increases with population density (fig. 6), which in turn reflects the relative density of males and increasing level of mate competition. This pattern of an increasing opportunity for selection with population density or intensity of mate competition has

similarly been reported in many other organisms (e.g., Wade 1980; McLain et al. 1993; Fleming and Gross 1994).

The I_{LBS} of red deer stags, including nonbreeders, has been estimated to be 2.51 in cohorts based on paternities inferred from behavioral observation (Clutton-Brock et al. 1988). Since behavioral observation tends to underestimate the true success of dominant stags and overestimate the contribution of low-ranking stags (Pemberton et al. 1992), this may be an underestimate. Furthermore, this estimate included the survival of offspring as a component of stag reproductive success and thus is not strictly comparable to LBS estimated here. Recently, Marshall (1998) estimated I_{LBS} in red deer stags using both behavioral and genetic measures of paternity. Estimated from harem holding in five cohorts, I_{LBS} was 9.08, while that estimated from paternities assigned at 80% confidence I_{LBS} was lower, 5.97.

Table 4: Comparison of hindlimb lengths of ram lambs born in high- (1987, 1988, 1991) and low-density years (1986, 1989, 1990) that died with those that survived their first winter

	High-density cohorts		Low-density cohorts	
	Survived	Died	Survived	Died
Residual hindlimb length (mm)	2.1 ± 1.6	-2.5 ± 1.3	-.2 ± 1.2	1.1 ± 3.5
<i>N</i>	46	62	28	5
Selection differential	.2503	...

Note: Data are shown as residuals corrected for catch date and year, ±SE.

Like the Soay rams, I_{LBS} among stags that successfully bred (0.88) was considerably lower than the estimate for all stags, as 73% of sampled stags did not survive to reproductive age. These results highlight the importance of following entire cohorts, as nonbreeders make a significant contribution to the total opportunity for selection. Unfortunately, Marshall (1998) could not estimate the variation in the opportunity for selection within cohorts because of small sample sizes in some years. Rose et al. (1998) examined cohort variation in LBS and survival in red deer. Like Soay rams, stags in cohorts born in years of high population density experienced low first-winter survival. Furthermore, LBS was influenced by environmental variation in the year of birth, with cohorts born in years with abundant rainfall in spring having greater mean LBS.

Longitudinal versus Seasonal Data

There was a tenfold range in the degree of variation in lifetime breeding success across the cohorts considered in this study. The extent of this variation between cohorts was much higher than the degree of variation between ruts in seasonal breeding success (fig. 5). This is perhaps surprising, given the substantial impact that fluctuations in density have on the seasonal breeding success of rams of all age classes (Pemberton et al. 1996, 1999). From these results, two things are clear. First, it is inadequate to estimate the variance in lifetime breeding success from a single cohort because of cohort-specific effects such as environmental and demographic variation in the year of birth. Second, seasonal or cross-sectional estimates also show considerable interannual variation and thus need to be interpreted with caution if they are to be used in the estimation of effective population size or as a parameter in other demographic models. The paradoxical result here is that the opportunity for genetic variation to be lost through drift or chance variation in reproductive success is greatest in the largest cohorts born in years of high population density.

Implications for Effective Population Size

The extent to which variation in breeding success differs between cohorts has implications for the effective size of the Hirta population. Not only does the census population size vary from year to year in a system with overlapping generations and sex differences in most aspects of survival and reproduction, but also there is interannual variation in the sex ratio and the mean and variance in paternal sibship size. Furthermore, the lifetime breeding success data presented here shows that there are very strong cohort differences in lifetime fecundity and age-specific breeding success in rams. Various formulas have been derived that account for some combinations of these factors (Caballero 1994); however, no single formula yet devised may simultaneously account for all of them (Vucetich et al. 1997). While an estimate of effective population size requires a thorough investigation of female lifetime reproductive success and offspring survival (which we plan to undertake in the future, using the LBS parameters measured here), we can speculate about the relative influence of cohorts born at high and low density.

Cohorts born in low-density years have a higher proportion of individuals that survive to breed (table 2) and thus are better represented in future generations. However, the offspring of cohorts sired in low-density ruts will be more closely related, on average, as low-density ruts result in larger paternal half-sibships (Pemberton et al. 1996). Yet again, this is mitigated by the fact that cohorts born in low-density years were sired in ruts in high-density years and thus are likely to be the sole representative of their father within their cohort (Pemberton et al. 1996) and unlikely to be closely related. The implications of these dynamics for effective population size and the loss of genetic variation caused by drift and inbreeding are therefore more complicated than fluctuations in census population size would suggest. For Soay rams, fluctuations in population size have both repeated effects on breeding success in each rut experienced (fig. 1) and a more profound effect on lifetime breeding success depending on the density in the year of birth (fig. 2).

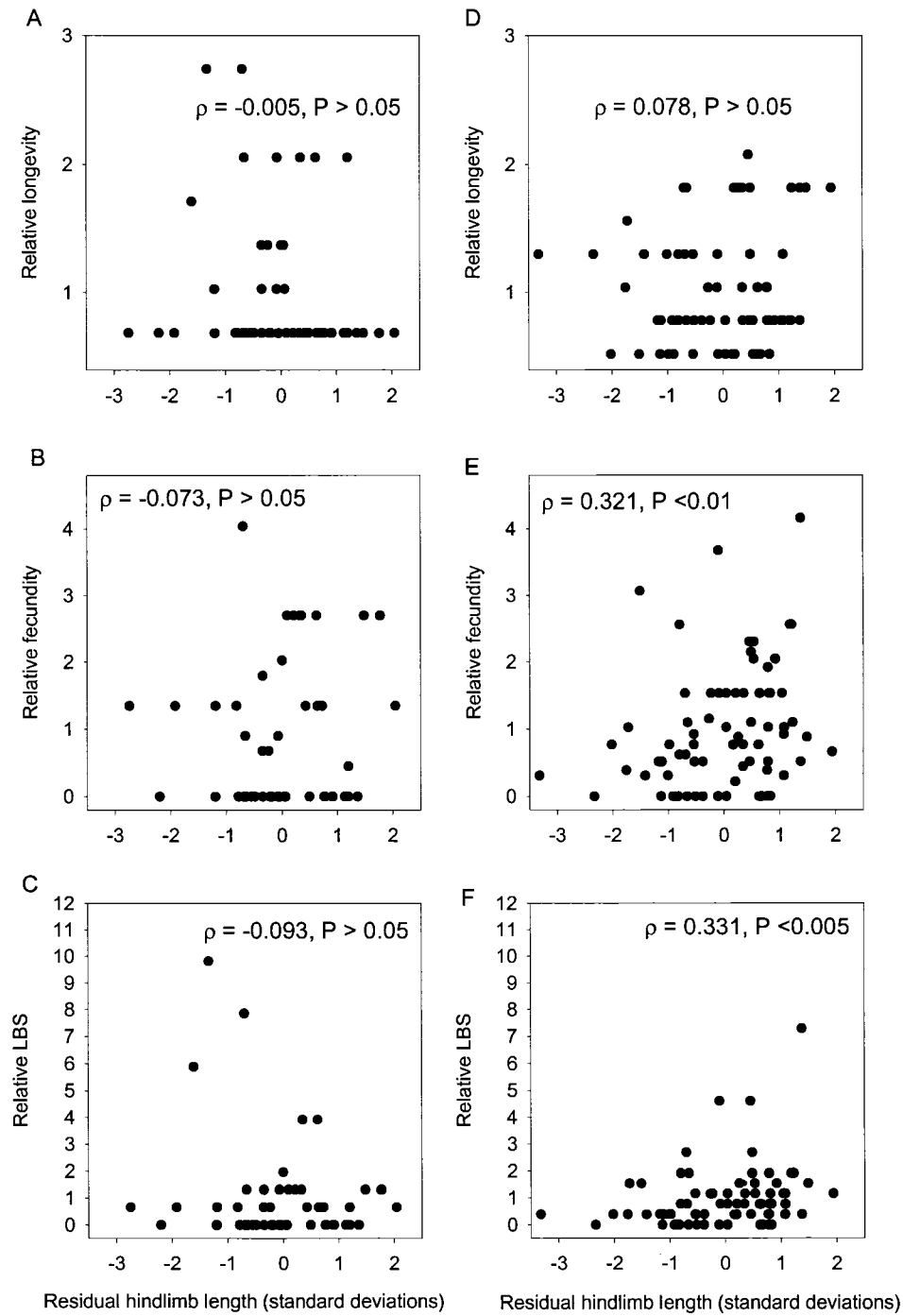


Figure 7: Relationship between lifetime breeding success and its components (expressed relative to the mean) to hindlimb length measured at age 1 yr. Hindlimb length is given as the residual (corrected for date and year of measurement) in units of SDs. Pooled data are shown for cohorts born in years of high (A–C) and low population density (D–F).

Table 5: Covariance of fecundity, longevity, and lifetime breeding success (LBS) with hindlimb lengths of rams born in high- (1987, 1988, 1991) and low-density years (1986, 1989, 1990) that survived to breed at age 1 yr

	High-density cohorts (<i>N</i> = 51)		Low-density cohorts (<i>N</i> = 74)	
	<i>i</i>	<i>P</i>	<i>i</i>	<i>P</i>
Longevity	-.095	>.10	+.037	>.05
Fecundity	-.183	>.50	+.249	<.01
LBS	-.438	>.05	+.317	<.005

Note: The covariance of LBS and its components with hindlimb length measured in units of selection differentials may be interpreted as the standardized selection differential on hindlimb length (*i*). Statistical significance of the selection differential was tested by Spearman's rank correlation.

Periodic population crashes are generally thought to constitute bottlenecks that may result in the loss of genetic variation and a reduced effective population size. However, the standardized variance in LBS for males born in these "bottlenecked" cohorts—the cohorts born in years of low population density following a population crash—is lowest. It therefore seems likely that the negative consequences of population fluctuations and a polygynous mating system for effective population size and the loss of genetic variation in this small island population are minimized by the demographically coupled, systematic changes in the lifetime breeding success of Soay rams.

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