

ST. KILDA SOAY SHEEP PROJECT: ANNUAL REPORT 2006

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POPULATION OVERVIEW

The sheep population on Hirta entered 2006 at a moderately high level and, as a result there was a slightly higher level of mortality than normal in a non-crash year. 59 sheep, of which 57 were tagged, were found dead within the study area between March and May of 2006. Lambing recruitment began on the 28rd of March with 80.5% of lambs born surviving (Fig.1).

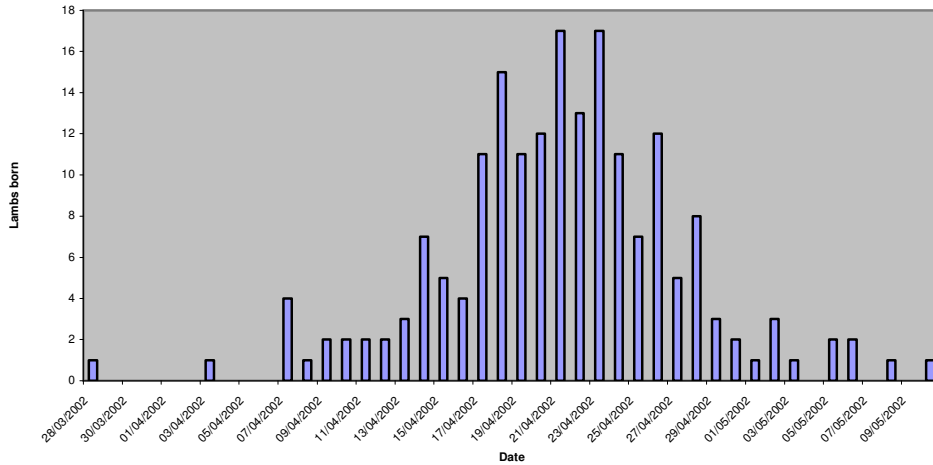


Figure 1. The temporal distribution of lamb births during 2006.

In December 2006, 636 tagged sheep were believed to be alive on Hirta, of which 467 regularly used the study area, a total increase of 15% using the study area since the previous year. The age distribution of the population is shown in Fig. 2 and changes in sheep numbers in the study area over time are shown in Fig. 3.

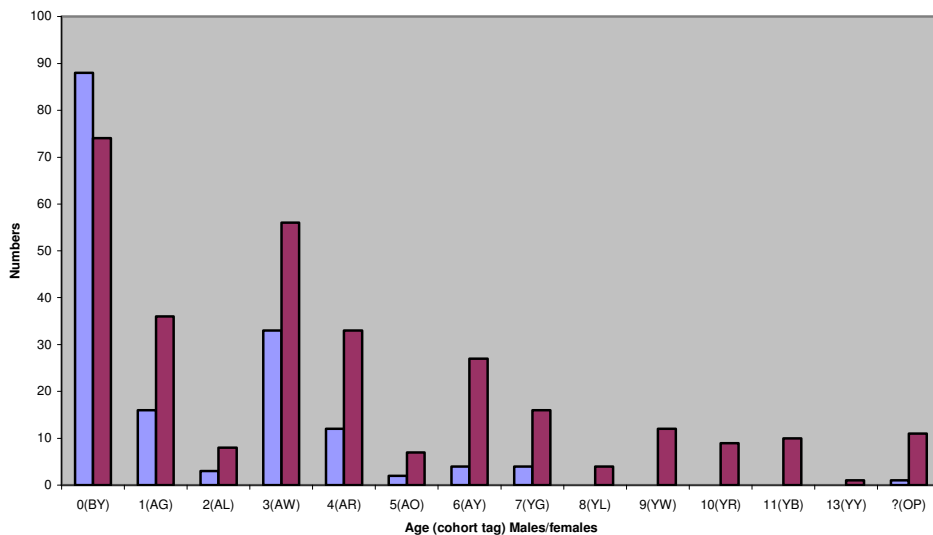


Figure 2. Age distribution of tagged Soay sheep presumed to be alive at the end of 2006.

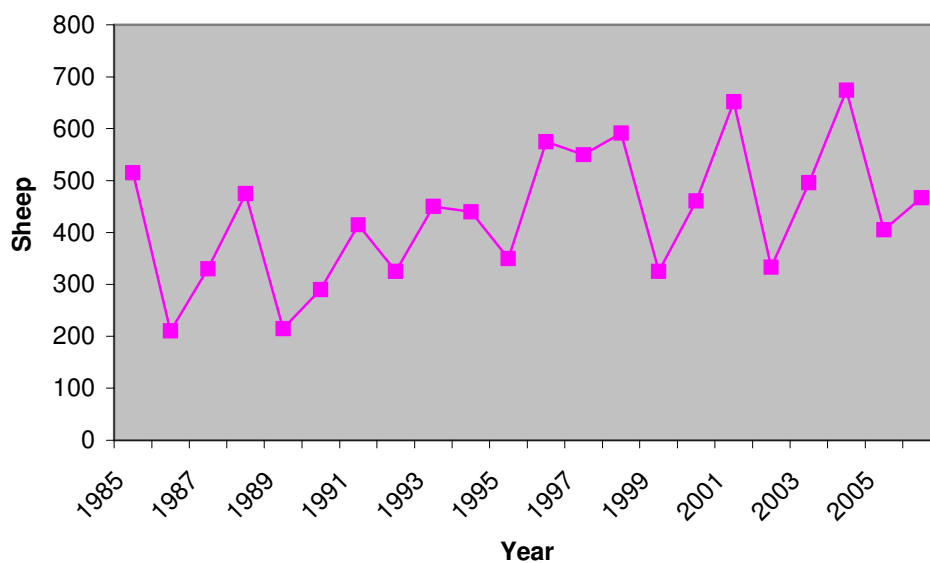


Figure 3. The number of tagged sheep regularly using the study area since 1985.

One whole-island count yielded 1794 tagged and untagged sheep, with the details displayed in Table 1. The total population had increased by almost 32% since summer 2005, when it was at 1362. This gives a Δ (calculated as $\ln(N_{t+1}/N_t)$) of +0.28.

Table 1. Demographic and geographic distribution of sheep observed during the count of *Hirta* on August 14th 2006. Coat colours are DW = dark wild, DS = dark self, LW = light wild, and LS = light self.

Location	Females				Males				Lambs	Total
	DW	DS	LW	LS	DW	DS	LW	LS		
Conachair/Oiseval	198	12	70	2	46	1	17	0	126	472
Mullach Bi/Cambir	223	13	95	4	71	1	12	0	266	685
Ruaival/Village	230	13	93	3	50	1	15	0	232	637
Total	651	38	258	9	167	3	44	0	624	1794

REPORTS ON COMPONENT STUDIES

Vegetation.

Mick Crawley.

The outstanding feature of the 2005-06 season was the amount of grass growth as measured inside the sheep-proof pyramids. The mean over-winter grass growth, measured for the in-bye grasslands over the period September 2005 to March 2006 was 4.51 tonnes/hectare, which is higher than many of the *summer* productivities measured in other years. The summer grass production, measured over the period April to August 2006 was the highest we have ever seen (8.75 tonnes/hectare). Thus, the total food production available for the sheep in the year August 2005 to August 2006 inside the Head Dyke was more than 13 tonnes/hectare, easily the highest we have ever measured. This suggests that density dependent mortality is unlikely to be severe (despite the fact that there were 1794 animals in the whole-island count in August 2006), so we do not expect to observe a crash in sheep population in February-March 2007.

Despite the high plant productivity, it was not an outstanding year for flowers, presumably because the grazing pressure was still high enough to inhibit flower production. Most of the main species produced flower counts close to their long-term averages (*Holcus lanatus*, *Lolium perenne*, *Potentilla erecta*, *Ranunculus acris*, etc.) while one species (*Plantago lanceolata*) produced an unusually high flower crop, and four species (*Anthoxanthum odoratum*, *Cerastium fontanum*, *Leontodon autumnalis* and *Trifolium repens*) produced lower than average flower densities.

The amount of dead organic matter in the sward in August is a useful index of grazing pressure. This is because DOM derives from uneaten live matter, and hence summer DOM is negatively correlated with sheep numbers per unit live grass biomass. The figure for summer 2006 was more than twice as high as in 2005 (2.71g vs 1.05g DOM averaged over all sampling locations), for an almost identical total mass (19.60g total plant dry mass in 2006 vs 20.26g in 2005), indicating that grazing pressure was unusually low in 2006 despite relatively high sheep numbers.

Linking ecological and evolutionary processes: trait variation and population growth in Soay sheep.

Fanie Pelletier and Tim Coulson.

Ecological and evolutionary processes have traditionally been considered to operate at such different time scales that ecologists could ignore evolutionary dynamics while evolutionary biologists could overlook ecological processes. Population dynamics and evolutionary change, however, are intimately linked by the fundamental biological processes of birth and death. This means that population growth may correlate with the strength of selection, while evolutionary change may leave an ecological signature. Recently there has been considerable interest in marrying ecological and evolutionary processes. For example, recent studies have illustrated that genetic variation at one

allozyme locus influences population dynamics in a metapopulation of Glanville fritillary butterfly and that evolutionary change in body and beak size has contributed more to population growth in a Darwin's finch population than ecological processes. In parallel to these ecological observations, evolutionary biologists have demonstrated that selection can fluctuate with ecological processes and that this can generate evolutionary change. For example, in Darwin's finches inhabiting the Galapagos islands, it has been demonstrated that ecological conditions in different decades impacted on the strength, direction and outcome of selection. Given that ecological and evolutionary processes are intertwined, it is necessary to develop methods that permit ecological and evolutionary processes to be married. We develop a method to decompose population growth in an age-structured population into contributions from variation in a quantitative trait such as body weight. Then, we apply the method and ask i) how quantitative trait variation impacts population growth in Soay sheep, and ii) how the strength of selection varies with population growth?

We link ecological and evolutionary dynamics in Soay sheep by describing the population dynamics as a function of the dynamics of a heritable quantitative trait with strong associations to fitness. The approach is simple: we estimate individual contribution to population growth as the difference between observed population growth and population growth calculated with the contribution of a focal individual removed over a one year time step. Then, we look at the association between a quantitative character (here body weight) and individual contribution. We found that variation in body weight in Soay sheep explains up to 18% of population growth (Fig. 4a), while additive genetic variation underlying body size explains, on average, 0.88%. Both the association between the trait value and population growth and selection on the trait vary substantially according to year (Fig. 4a and b). The general decrease in both total selection and trait contribution to population growth overtime correspond to a period when the winter North Atlantic Oscillation (NAO) was low and winter weather was good for sheep, being relatively dry and storm-free (mean NAO 1985-1994=2.348 versus 0.039 from 1995 to 2002). We therefore found that NAO was significantly correlated with the contribution of variation in body weight to population growth ($r^2=0.23$, $t=2.13$, $p=0.049$, $n=16$ years). Consequently, environmental variation does appear to influence the magnitude of the contribution of variation in quantitative traits to population growth.

The results from the contribution and selection analyses are similar (Fig. 4a and b) – as the strength of selection increases so too does the contribution of trait variation to population growth (Fig. 4c). This result is not surprising as, in a linear framework, the proportion of variation explained (the r^2 value) and the regression slope differ only by a scaling factor – the variation in the independent variable. This demonstrates the intimate link between the ecological consequences of evolutionary change in a trait value and the strength of selection on the trait.

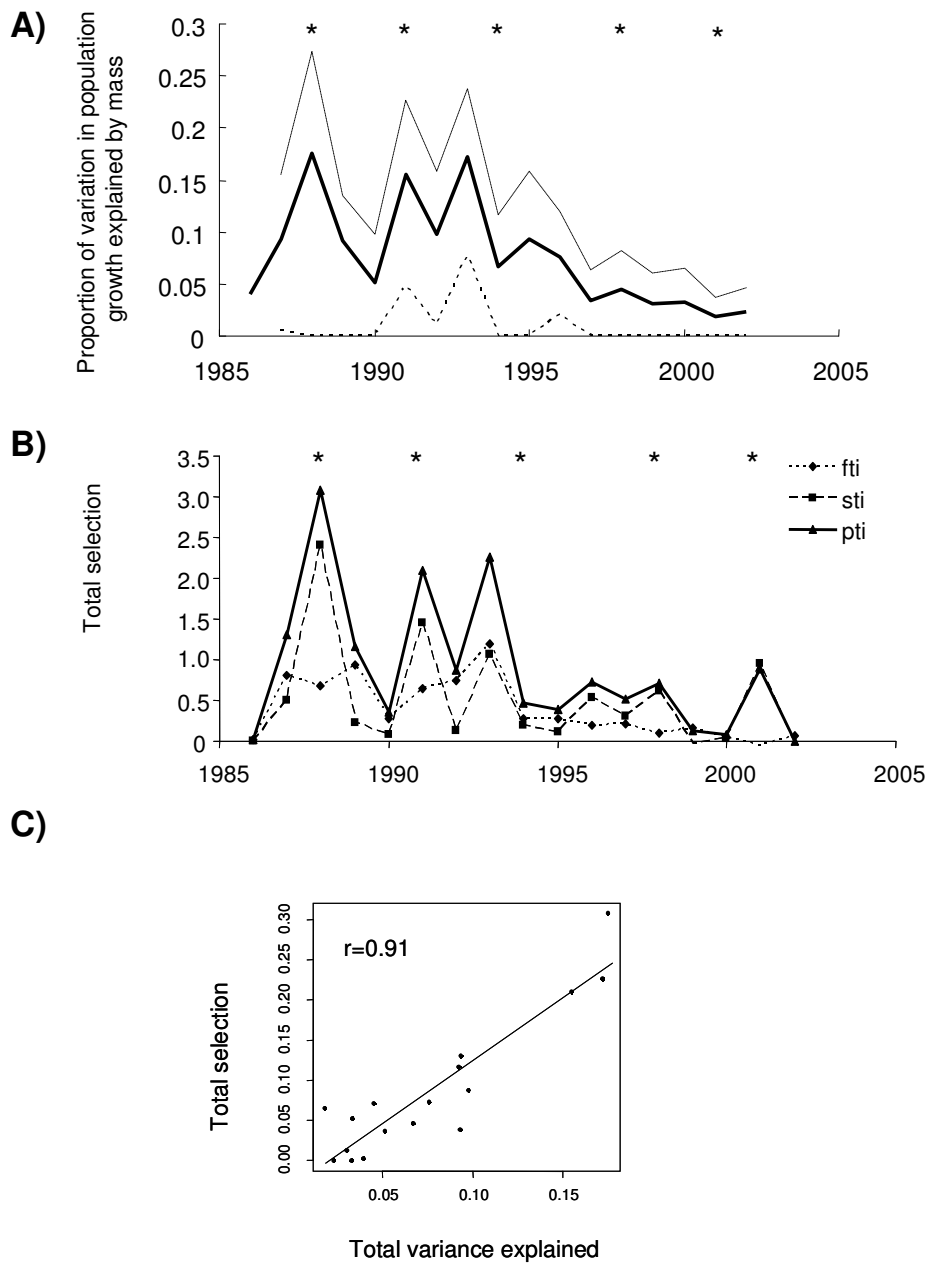


Figure 4. (A) Contributions of body weight to population growth between 1985 and 2002. Dotted lines represent 95% confidence intervals. Stars (*) represent crash years (B) Estimates of the overall strength ($\times 10^{-4}$) of selection on body size (solid line) and via survival ($S_{t(i)}$ dashed line) and recruitment ($F_{t(i)}$ dotted line). (C) Association between total selection and trait contribution to population growth.

The trick of dying young as late as possible.

Alastair Wilson.

Senescence may be defined as a decline in fitness, (measured as survival, reproductive success, or both), with increasing age. While senescence is commonly observed in many organisms, it presents an apparent conundrum for evolutionary biologists. Since senescence must (by definition) involve a decrease in fitness, how has it evolved and how is it maintained in the face of natural selection? Alternate hypotheses for the origin and maintenance of senescence give rise to predictions that can be tested using quantitative genetic analysis.

Estimates of annual fitness (p_{ii}), a composite of annual survival (s_{ii}) and reproductive success (f_{ii}) for female Soay sheep (*Ovis aries*), show a clear pattern of senescence in the population (Fig. 5). Mean annual fitness declines with age (after initially increasing to a maximum at age 4), and contributions from survival and reproduction show similar patterns.

Quantitative genetic analyses support the presence of a genotype-by-age interaction, consistent with theoretical predictions. Estimates of genetic variance for annual fitness (p_{ii}) increase with age (Fig. 6), a finding expected under the so-called “mutation accumulation hypothesis” which states that senescence is a consequence of the accumulation of deleterious mutations that act late in life. However, increasing genetic variance is also predicted by the “antagonistic pleiotropy hypothesis” which asserts that selection will favour alleles that have a positive effect on early fitness, even if they cause deleterious effects later in life. This latter hypothesis also predicts negative genetic correlations (r_G) between early and late fitness, and in Soays estimates of r_G between ages support this (Table 2). While this does not rule out mutation accumulation (the two mechanisms not being mutually exclusive), these results demonstrate that senescence seen in Soay sheep most likely involves antagonistic genetic effects on early and late fitness traits.

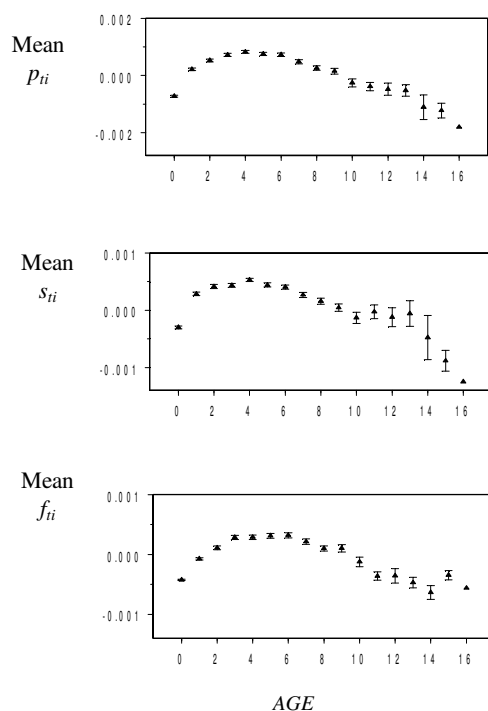


Figure 5. Mean annual fitness (p_{ii}) of female Soay sheep by age (years). Also shown are average contributions to annual fitness from survival (s_{ii}) and reproduction (f_{ii}). Error bars denote standard errors.

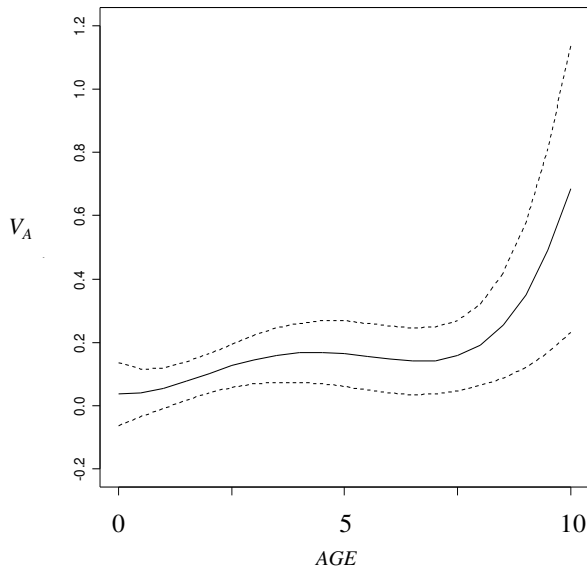


Figure 6. Estimated additive genetic variance (V_A) for annual fitness of female Soay sheep as a function of age. Dotted lines indicate approximate 95% confidence intervals.

Table 2. Estimated genetic correlations (r_G) between age specific fitness traits (p_i) for female Soay sheep between ages 0 to 10 years. Note how correlations between adjacent ages are generally high, but they decline and even go negative as the age classes set further apart.

	AGE									
	0	1	2	3	4	5	6	7	8	9
1	0.710									
2	0.453	0.948								
3	0.330	0.893	0.989							
4	0.268	0.850	0.966	0.993						
5	0.238	0.798	0.922	0.961	0.987					
6	0.225	0.699	0.813	0.864	0.914	0.967				
7	0.210	0.482	0.558	0.616	0.693	0.799	0.925			
8	0.172	0.151	0.161	0.214	0.307	0.452	0.663	0.897		
9	0.126	-0.137	-0.184	-0.146	-0.056	0.099	0.347	0.677	0.932	
10	0.092	-0.313	-0.397	-0.372	-0.290	-0.140	0.113	0.481	0.819	0.971

Heritable variation for horn size and growth.

Matthew Robinson & Loeske Kruuk

Soay sheep have a polymorphism for horn type with males and females growing either a normal-horn or a reduced horn known as a scur. Females may also show no horn development (polled). The horns of normal-horned males are of interest because they are used in the rut, with males fighting for access to females in order to reproduce. There is substantial variation between individuals in the length of horn that is grown each year, which may be related to the genes they possess or the environment they have encountered.

We know that the environment influences horn length in normal-horned males but we know little of its inheritance from one generation to the next.

Horns are grown incrementally - growth stops over winter forming a growth ring or annulus. We are therefore able to measure both an individual's total horn length at a given age, and the amount of horn grown at each age (horn increment length). Using data on horn size of normal-horned males and the “animal model” we found significant heritability for both total horn length ($h^2 = 0.379 \pm 0.086$, shown as V_A in Fig. 7A) and horn increment length ($h^2 = 0.120 \pm 0.026$, shown as V_A in Fig. 7B). Environmental conditions significantly influenced the variance of both total horn length and horn increment length (V_E : Fig. 7A and B). There was evidence that the total horn length reached at a given age is influenced by previous growth (V_{PE} : Fig. 7A) but that the length of increments in different years may not be related (V_{PE} : Fig. 7B). There was also some evidence that on average the horn lengths of Soay sheep may be decreasing over time (V_{BYR} : Fig. 7A and B). There was no indication of any maternal effects on either total horn length or horn increment length (V_M : Fig. 7A and B).

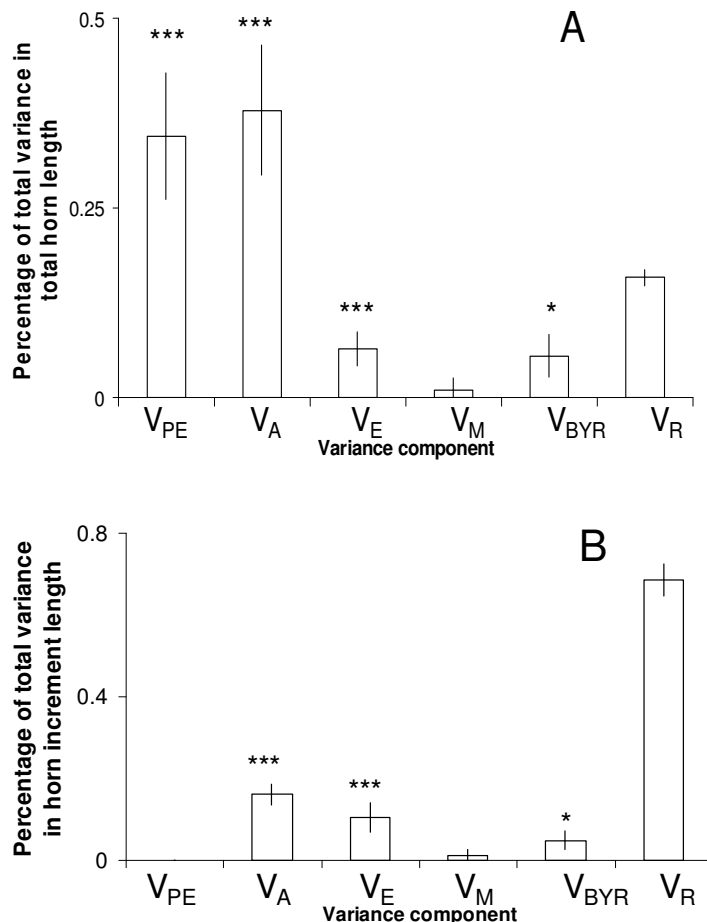


Figure 7. Estimates of the variance components for (A) total horn length; (B) horn increment length. V_{PE} , permanent environment effect variance; V_A , additive genetic variance; V_E , environmental variance (variance between different years of horn growth); V_M , maternal effect variance; V_{BYR} , variance between different birth years; V_R , residual variance. Significance assessed by changes in log-likelihood when adding the term last to the model: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

A breeding value was estimated for each individual, which can be used as an estimate of an individual's genetic merit for horn increment length. There was no change in average breeding values with time, indicating that there was no evidence of any genetic change for horn length in the population. This was not surprising given previous results which showed that normal-horned males who grew large horns did not have any greater lifetime reproductive success and thus there is no evidence of any selection pressure which may increase horn size. We found evidence that when good environmental conditions allow for larger horn length, individuals also lived longer (Fig. 8A). However, individuals with a high breeding value were more likely to have a shorter lifespan, indicating that genes which positively influence horn length may have a negative influence on longevity (Fig. 8B).

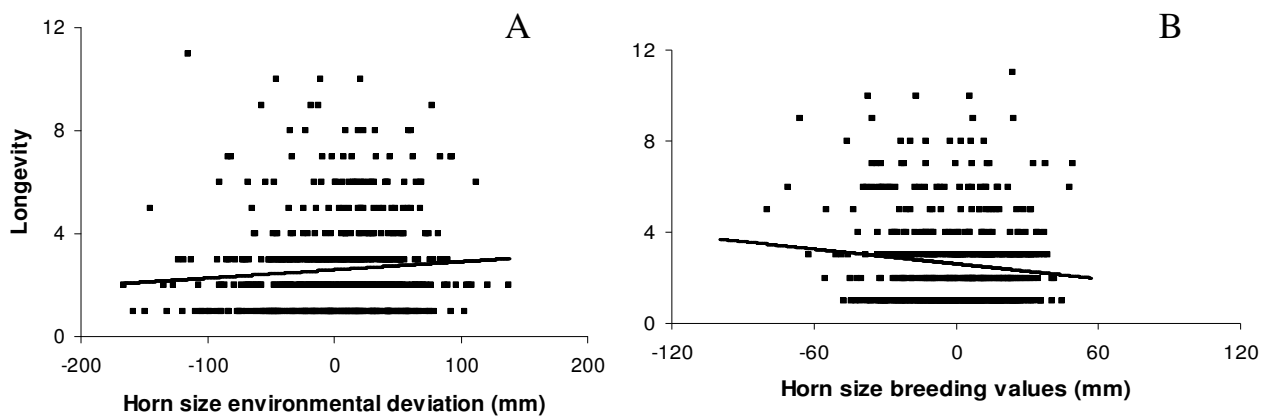


Figure 8. Relationship between longevity and (A) environmentally determined horn increment length; (B) breeding values for horn increment length. Solid lines show least-squares regression between longevity and each variable.

Individuals experience varying environmental conditions and different episodes of genetic expression throughout their lifetime and therefore the expression of additive genetic variance may be age or environment specific. Furthermore, selection may also change strength and direction over an individual's lifetime. Therefore, if we can determine when selection is strongest and when the greatest amount of heritable variation is expressed we can gain a better understanding of how trait variance is maintained and how selection acts. We used a "random regression" to test whether genetic effects of horn increment lengths vary with age or environmental conditions. We found that additive genetic variance decreased with age (Fig. 9A) and increased population density (Fig. 9B), indicating that genetic effects are greatest at the beginning of life and when environmental conditions are good.

Work is still ongoing to determine when selection pressure is greatest but we can conclude that variation in horn size in normal-horned males may be maintained by genetic trade-offs between horn growth and survival and also by varying genetic effects with both age and environmental conditions.

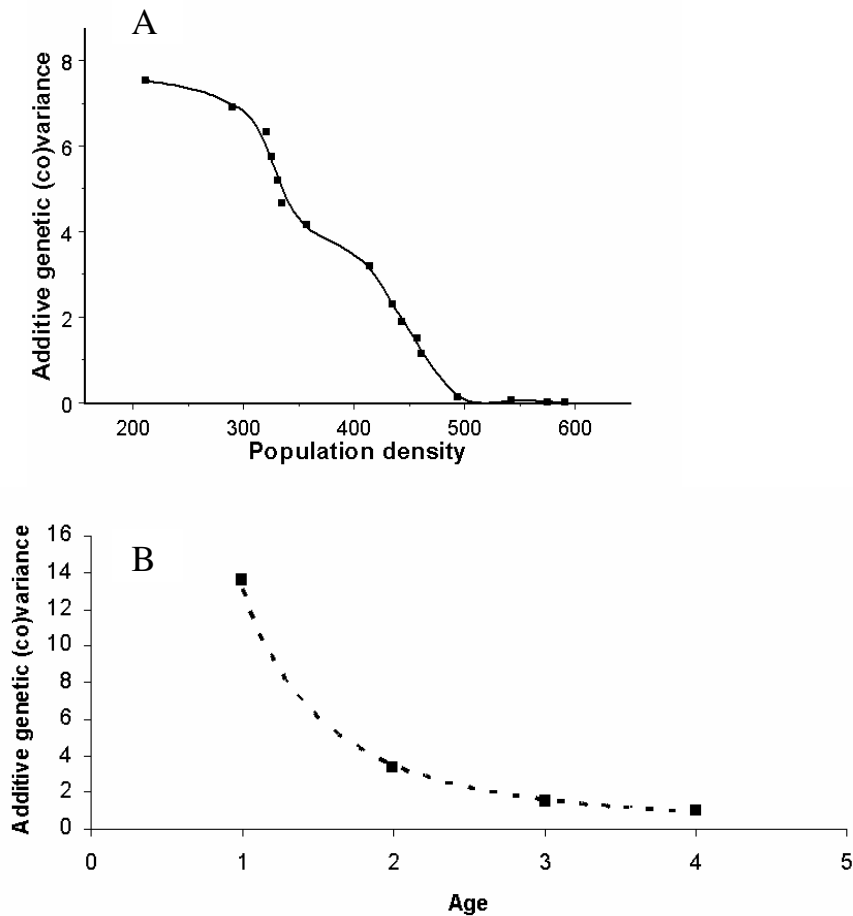


Figure 9. Additive genetic (co)variance of horn increment length with increasing (A) population density; (B) age.

Coat colour and body size in Soay sheep.

Jake Gratten, Allan McRae, Alastair Wilson, Peter Visscher, Dario Beraldi, Josephine Pemberton and Jon Slate.

Previous studies of selection on coat colour in the population have demonstrated that dark-coated individuals have higher survival than light-coated individuals in winters when selection is strongest. However, in some years light-coated individuals have had significantly higher survival, and overall there does not appear to have been a change in coat colour phenotype frequency over the >20 year lifetime of the study. In order to understand selection for coat colour it would be informative to know *why* dark-coated individuals have better over-winter survival than light-coated individuals. There is evidence that dark-coated animals are heavier than light-coated ones, but a formal quantitative genetic investigation of this question is lacking. In particular, it is unknown whether there is a genetic association between coat colour and size, or whether coat colour somehow modulates sheep behaviour, which in turn could influence size. Dark sheep may be heaviest because the gene determining coat colour is also associated with

body size, either directly (a process known as pleiotropy) or because it is in close chromosomal proximity (linkage) to another gene that affects body size. Alternatively, dark sheep may be able to invest more time in feeding rather than sheltering during bad weather as dark coats have lower reflectance and therefore should result in better ability to maintain body temperature.

In previous Annual Reports (2004, 2005) we have described how we have identified the gene and mutation responsible for the dark/light coat colour polymorphism in the population. Two genetic variants (alleles) termed G and T in the tyrosinase related protein 1 gene (*TYRP1*) on chromosome 2 are responsible for coat colour variation. Animals with two T alleles (genotype TT) have light coats, while animals with genotype GT or GG have dark coats (i.e. the G allele is dominant to the T allele). We have now genotyped all of the animals (~2500) in our DNA archives at the coat colour gene. This means that we can now distinguish dark-coated animals that are GG from those that are GT. Therefore, we are in a better position to understand if and how selection has maintained this polymorphism. If there is a genetic association between coat colour and size, then one might expect to be able to detect the association at birth. Conversely, if coat colour modulates feeding behaviour, such that dark-coated sheep grow to be largest, the association should be absent in newborn lambs. Furthermore, if coat colour is genetically associated with body size, it should be possible to detect genetic linkage to body size in the same chromosomal location as the coat colour gene. Here we describe a series of models that test whether the region of the genome containing the coat colour gene is associated with body size at birth.

Birth weight has previously been investigated in the population by Alastair Wilson (Edinburgh) using an 'animal model' approach. This method is able to account for the various environmental (e.g. population density, climate, maternal age) and developmental (e.g. sex, natal litter size) factors known to influence early life-history traits in Soay sheep. In the present study, we first fitted a model identical to Wilson, and then added coat colour genotype as an additional explanatory variable. This analysis indicated that coat colour genotype explains a significant proportion of the variance for birth weight ($p \approx 0.0002$), and that sheep with the TT genotype (light coats) are significantly smaller at birth than dark animals with genotype GG or GT (by 109 ± 29 g and 82 ± 22 g respectively; Fig.10). This represents an effect size of ~4-5% of mean corrected birth weight, which was 2.158Kg. Animals with genotype GG are largest, but they are not significantly larger than animals with genotype GT (27 ± 25 g smaller). This suggests that the G allele is at least partially dominant over T with respect to birth weight.

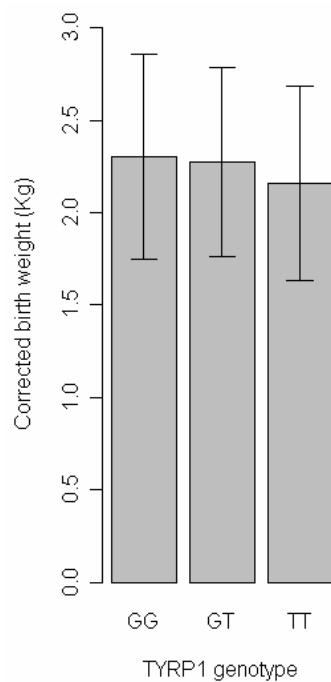


Figure 10. Mean and standard deviation of corrected birth weight (i.e. after removal of effects due to sex, natal litter size, capture age and birth year) for each of the three *TYRP1* genotypes ($N=365$, 887 and 505 for *GG*, *GT* and *TT*, respectively)

A well-recognised weakness of association studies such as that described above is that spurious associations can arise in the presence of undetected population structure. Although this is unlikely in the Village Bay population, given that the genetic distinctions between hefts are very minor, we used a Transmission Disequilibrium Test (TDT) to confirm the presence of linkage between coat colour gene and a quantitative trait locus (QTL) for birth weight. The TDT partitions the overall association into a within-family component (TD), due to linkage, and a population component (PD), due to population structure, all within an animal model framework. This analysis demonstrated that the association between coat colour genotype and birth weight is due to linkage (TD $p=0.0244$), rather than population structure (PD $p=0.1175$).

We can draw two conclusions on the basis of these results. First, there is a genetic association between coat colour genotype and body size that is detectable at birth. Consequently, the idea that dark-coated sheep grow to be largest solely due to an improved capacity to forage in poor weather can be discounted. Second, the TDT analysis indicates that a birth weight QTL exists in the vicinity of the coat colour gene *TYRP1* on chromosome 2. At this stage we do not know if *TYRP1* has pleiotropic effects on birth weight, or if it is linked to another gene affecting body size. We favour the latter explanation because *TYRP1* has no known pleiotropic effects on body size in mice or humans, and an obvious candidate gene for birth weight (*VLDLR*) is located close to *TYRP1* in cattle (the most closely related species with available genomic information).

What insight can these findings give us into selection on coat colour and the mechanisms by which genetic variation at the coat colour locus is maintained in the population? We know from previous studies that birth weight, and body size in general, is under positive

directional selection in the population. We would therefore expect the T allele at the coat colour locus, which is associated with reduced body size, to be eliminated from the population by selection. The fact that this has not occurred (the T allele is currently at a frequency of 0.52) suggests one of a number of explanations. First, it has been shown that a negative correlation exists between the proportion of variance in birth weight explained by additive genetic effects (i.e. the heritability) and the strength of selection on birth weight. Consequently, the potential for evolution of larger body size may be constrained by either a lack of heritable genetic variation (in years with high mortality) or a lack of selection (in years with low mortality). Under this scenario it is possible that the T allele at the coat colour gene has simply drifted to high frequency. Alternatively, a negative genetic correlation may exist between birth weight and another fitness-related trait, such that there is a trade-off between selection for increased birth weight (G allele) and selection for the other trait (T allele). Analyses of both fitness traits and fitness-related traits and the genetic correlations between these traits and birth weight is ongoing. It is hoped that these analyses will provide further insight into selection on coat colour in the population.

Linkage mapping in Soay sheep: a summary.

Dario Beraldi, Jake Gratten, Allan McRae, Peter Visscher, Jon Slate, Josephine Pemberton.

One of the purposes of the Soay sheep project is to investigate of how natural selection works and, consequently, how evolution takes place. Since genetic variation among individuals in a population is the raw material for the progress of evolution, the understanding of how genetic variation is maintained and shaped by selection is of primary importance. Typically, it is assumed that a trait is determined by several genes of small effect. This assumption makes the study of the genetic component more tractable in terms of theoretical analysis. However, it may fail to detect interactions between specific genes and environment that could be relevant for the evolution and dynamics of natural populations.

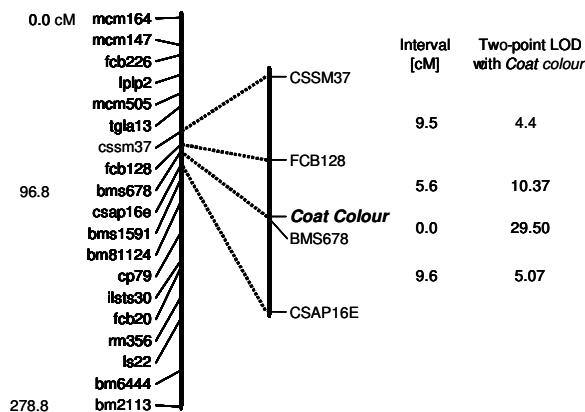
If we think about the genetic make-up of an organism as a DNA sequence of genes (and non-genes), linkage mapping attempts to locate the genetic regions responsible for a given trait on this ideal DNA string. Once these positions have been identified, it becomes possible to track their inheritance across different generations and families in order detect if and how evolution and selection are acting on them. The Soay sheep population offers a rare opportunity to achieve this goal since it has the requisites necessary for this so called “linkage mapping”: measurements on many individuals have been collected for different traits of evolutionary importance, an extended pedigree has been reconstructed, and many DNA markers have been mapped.

A number of morphological and physiological traits differing in their relationship to total fitness and for their genetic architecture were analysed through linkage mapping. Three traits known to be encoded by one or a few genes have been successfully mapped (Fig. 11, see also St Kilda Annual Report 2005 and Gratten *et al* (this report)). These traits were the coat colour (dark or light), coat pattern (uniform colour of the body or contrast between belly and coat), and horn type (normal, polled or scurred (deformed) horns).

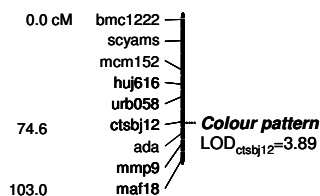
Most of the characters of an organism, however, are better described by a metric or continuous scale rather than by discrete categories, and they are probably encoded by several regions, usually referred to as QTL (quantitative trait loci), instead of by one or a few genes. Therefore, we focused our attention on detecting regions affecting different aspects of body size, timing of birth, and parasite resistance. Seven regions showed evidence that they contain genes responsible for these traits. Some of these regions have been described in our previous report. In particular, one region on chromosome 11 and one on chromosome 15 are likely to determine part of the variation in jaw length and hind leg length respectively (Fig. 12). Due to the nature of the statistical procedure employed to perform the analyses, the possibility that these map positions are false positives cannot be rejected.

Currently, we are working to confirm the QTL detected on chromosome 11 and 15 by typing additional markers and additional families. The future aim of this work will be to include the knowledge of the genotype of sheep at genes known to affect traits into ecological studies in order to understand selection and maintenance of genetic variation in the population.

A) Chr 2 – Coat colour



B) Chr 13 – Colour pattern



C) Chr 10 – Horn type

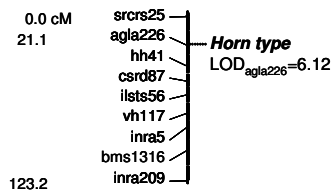


Figure 11. Map positions of the genes responsible for coat colour (dark/light), colour pattern (wild type/self), and horn type (normal/scurred/polled). Chromosomes are represented by bars with the positions of the markers mapped on them. cM is a measure of genetic distance, i.e. of how frequently adjacent markers are inherited together. LOD is a measure of the strength of evidence for the gene position shown.

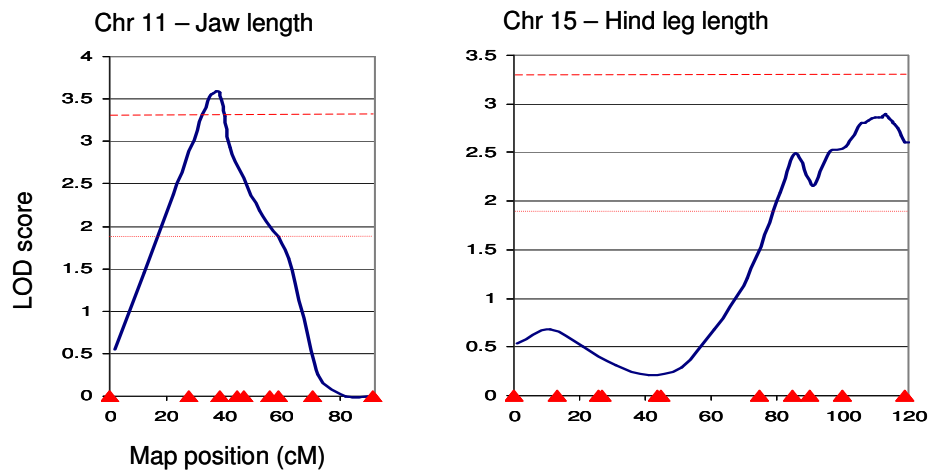


Figure 12. Map position of the putative *QTL* for jaw length and hind leg length. Here, the position is shown as a probability of having a *QTL* at a given position against the probability of no *QTL* in that position (LOD score). Chromosomes are represented on the *x*-axes with markers shown as triangles. The lower dotted line marks the threshold probability of having one false *QTL* per experiment (suggestive evidence) whereas the upper dotted line is probability of having one false *QTL* every 20 experiments (significant evidence).

Comparison of *Teladorsagia* and *Trichostrongylus* spp. burdens of sheep from the last three population crashes.

Barbara Craig, Jill Pilkington and Josephine Pemberton

We have previously reported that two genera of parasitic nematodes are important pathogens in St. Kilda Soay sheep, and that their patterns of intensity with host age occur in opposite directions. In order to test for temporal variation between crashes, we compared intensity data from a subset of sheep sampled post mortem from 1999, 2002 and 2005 ($n=55, 69$ and 39 respectively). Intensity data for *Teladorsagia circumcincta* and *Trichostrongylus axei* (both dwelling in the abomasum) and *Trichostrongylus vitrinus* (from the small intestine) were analysed using a general linear models with negative binomial error structure and host age, sex and year as explanatory variables (Fig. 13).

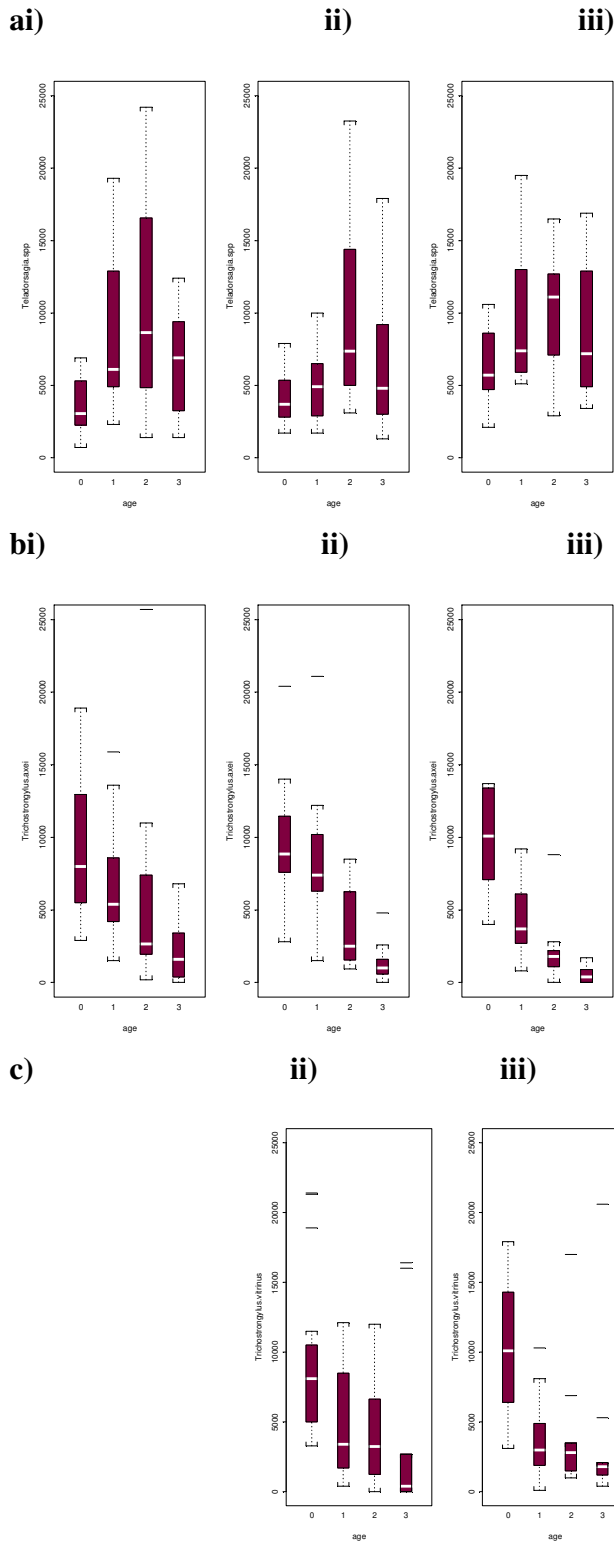


Figure 13. Box-plots showing burdens of **a)** *Teladorsagia circumcincta* **b)** *Trichostrongylus axei* and **c)** *Trichostrongylus vitrinus* in *i)*1999, *ii)*2002 and *iii)* 2005. Age classes were lambs (0), yearlings (1), two year olds (2) and older (3). No small intestine samples were collected in 1999.

Our results confirm our previous findings that *Teladorsagia circumcincta* increases in hosts until the age of two years before decreasing. With three years of data, we were able to fit both age and age² terms and each explained deviance at $P < 0.0001$. There were no differences between host sexes. In addition, whereas previously we found no differences in *T. circumcincta* burden between the 1999 and 2002 samples, the addition of 2005 data introduced an association with year at $P = 0.0055$; *T. circumcincta* was generally more abundant in 2005.

Our results also confirm a strongly contrasting pattern in *Trichostrongylus axei* in which intensity decreases sharply with host age ($P < 0.0001$) and a weak effect of host sex in which males have more worms ($P = 0.047$). No differences were detected between the three years of study. Finally, in the two years of data now available, *Trichostrongylus vitrinus* intensity also declines with age ($P = 0.012$) but no effects of host sex or year were detected.

These results provide important underpinning information for the interpretation of strongyle faecal egg count data from living sheep on St. Kilda, since the eggs of these three main species of strongyle nematode cannot be distinguished.

Metazoan-protozoan parasite co-infections and host fitness in St. Kilda Soay sheep.

Barbara Craig, Louisa-Jayne Tempest, Jill Pilkington and Josephine Pemberton.

Until recently the Soay sheep host-parasite system had been considered to be a relatively simple one. However, we now know the situation is complex, with no one nematode species achieving a monopoly throughout the lifetime of the host and with a significant component of the parasite community comprised of a diverse array of protozoa. In young Soay sheep, the predominant parasite taxa are *Trichostrongylus* worms (*T. axei* and *T. vitrinus*), *Eimeria* protozoans (11 species) and keds (*Melophagus ovinus*), while in older animals, the worm *Teladorsagia circumcincta* predominates (see preceding report).

Few studies have attempted to elucidate the nature and evolutionary consequences of complex co-infections in the wild. Using data from August catches 1989-2005, we conducted non-parametric tests of associations in abundance between the different helminth egg types 'strongyle' (includes the three species mentioned above and two others), *Nematodirus*, *Capillaria*, *Trichuris* and *Moniezia* (presence/absence), coccidian oocysts and *Melophagus ovinus* (keds) in the population. To explore the role of co-infection in determining host fitness, we investigated whether different parasite species intensities have independent effects on host weight in lambs, yearlings and adults (aged two years and older).

In general, many parasite taxa showed positive correlations across hosts, but very few such relationships were significant. In lambs, strongyle eggs and *Nematodirus* spp. eggs were significantly correlated ($r_s = 0.35$, $P < 0.0001$). In yearlings and adults, strongyle eggs and coccidia oocysts were significantly correlated (yearlings $r_s = 0.18$, $P < 0.001$;

adults $r_s = 0.299$, $P < 0.0001$). Because these observations are correlational, we cannot determine causality.

Analysis of host weight revealed one novel association between parasite intensity and weight. We used generalised linear models and fitted a variety of other individual variables known to affect weight (e.g. sex); the model for adults was a mixed model to account for multiple August weights for the same individual. In lambs and yearlings, of all the parasite measures tested, only strongyle eggs were significantly (and negatively) associated with host weight (at $P < 0.001$ and $P < 0.0001$ respectively). This is in accordance with previous published results. However, in adults, both strongyle eggs and coccidia oocysts were independently associated with host weight (both at $P < 0.0001$); in both cases higher counts were associated with lower weights.

Taken together, these results suggest a role for multiple parasite species in shaping the fitness and evolutionary trajectory of Soay sheep. In young Soay sheep, the worm genus *Trichostrongylus* is most abundant (see preceding report), although there may be synergistic effects of the emerging *Teladorsagia* infection with age, and these species are probably responsible for the detrimental association with weight. In older sheep, strongyle eggs are produced predominantly by *Teladorsagia circumcincta*, and both eggs from this species and coccidia oocysts are associated with host weight. Since August weight is associated with the probability of over winter survival, these results imply that at least three genera of parasite are likely to be exerting selection in the population, and for the first time suggest that intracellular (protozoa) as well as extracellular (strongyle) parasites are involved.

The bewildering array of exceedingly exciting elasticities.

Thomas Ezzard and Tim Coulson.

Any change in population size over time is the result of various predictable and random processes. Survival and reproduction rates determine population dynamics; the link between the two is important for evolutionary calculations and identification of potential conservation targets. Many approaches have been developed to analyse the link between demographic processes and population dynamics, and consequently determine key factors for population changes.

Many approaches are based on perturbation analysis on the female part of the population. Elasticity analyses, which assess the proportional effect of small changes in each demographic rate on population growth rate, have frequently been applied. The prospective case, which is based upon perturbing average survival and reproduction rates, continues to be employed despite the acceptance that it happily and quite correctly gives results of changes that are biologically impossible. Incorporating observed variation (retrospective analysis) in demographic rates over multiple years is one method of incorporating variation observed in the natural world: the similarity between analyses with (retrospective) and without (prospective) observed variation is moderate (Fig. 14).

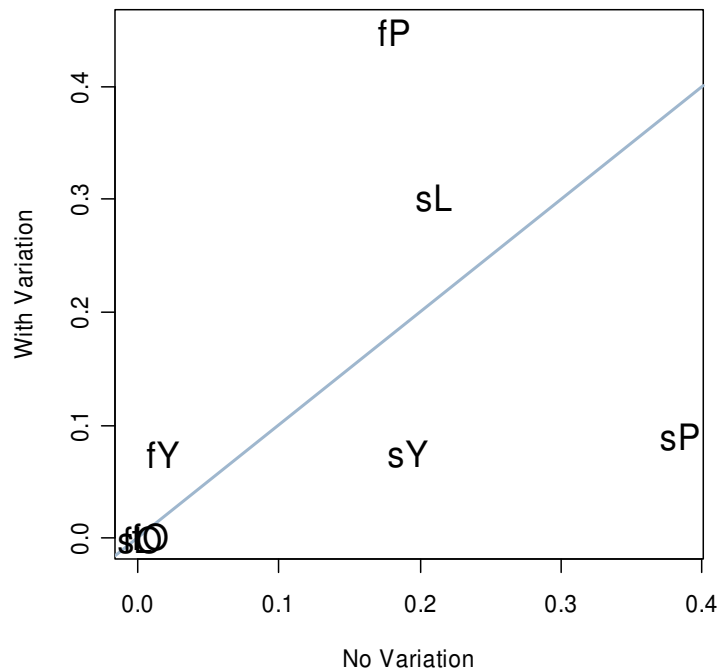


Figure 14. *The similarity between analyses with and without observed variation is moderate. Letter codes of demographic rates: *s* relates to survival; *f*, reproduction; *L*, lambs; *Y*, one-year olds; *P*, prime-aged individuals; *O*, oldest individuals. If all points were on the grey line, the two methods would be identical.*

The real world changes constantly however, and much recent research has focused on changeable (stochastic) rather than fixed (deterministic) environments, which were outlined above. Rather than calculate observed rates, relationships are inferred from statistical relationships between predictable (density) or random (weather) variables and survival and reproduction rates. Stochastic analyses do not necessarily resemble retrospective elasticities, which incorporate observed variation.

It is, however, often not possible to change, say, mean adult survival without changing the variance around this. Recent advances in stochastic demography theory have enabled investigation of perturbations of other moments of distributions. For example, perturbing the variance in rates is predicted to be one response to a changing environment; the tools now exist to examine this in a stochastic framework (Fig. 15).

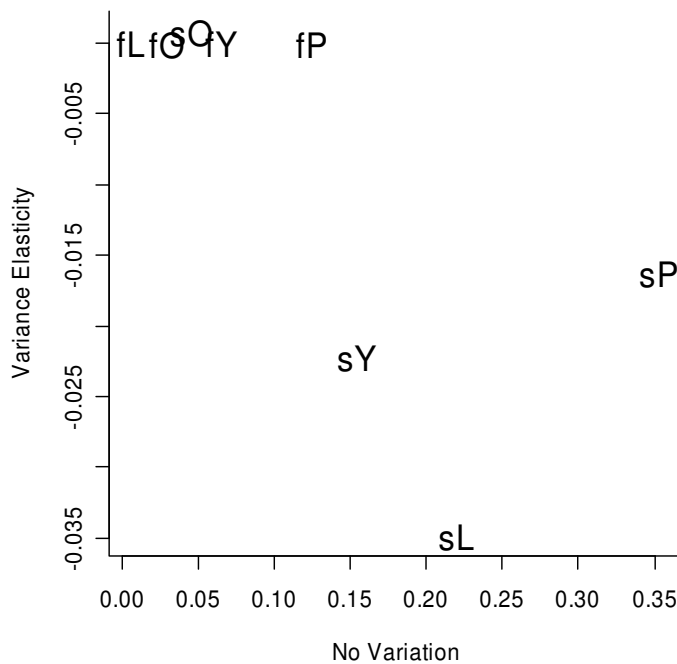


Figure 15. One prediction of a changing environment is greater variation in phenotypic traits and demographic rates. Stochastic demography is now able to analyse changes to different moments of distributions, and therefore potentially increase accuracy of evolutionary predictions. There is little correlation with the traditional method. For rate codes, see Figure 14.

Increasing levels of biological realism in stochastic models have also been the focus of much recent research. These levels include: more frequent disturbance; vegetation changes; the importance of correlated rates; and the importance of correlations in environmental variability.

Work in progress is currently assessing quantitatively the impact of these factors on results of perturbation analyses. Results which incorporate correlations in demographic rates and environments, are likely to in turn increase the predictive power of models and accuracy of predictions of population and evolutionary responses in changing environmental conditions. A review of different methods, of which only a handful is mentioned here, and code to implement these methods in the freeware computer programme R with all associated assumptions and uses, will accompany the comparative results. The aim is to clarify the uncertainty generated by the alternative techniques, and demonstrate where, when and why different measures should be used. Or not.

Using integral projection models and evolutionary game theory to study life-history traits in Soay sheep.

Dylan Childs, Tim Coulson and Mark Rees.

Understanding the enormous diversity of life histories found in the wild remains an open challenge in evolutionary biology. Many important developments in life history theory are based on ideas from evolutionary game theory. This approach places species' ecology firmly at the centre of the research agenda. However, there are very few applications of this technique to study evolution in natural systems. Using the long-term Soay sheep dataset, we aim to develop a suite of empirically derived models of this natural population, and apply evolutionary game theoretic approaches to explore the selective constraints operating on reproductive traits such as litter size and offspring weight. Making sense of such traits in the wild is challenging for a number of well-known reasons:

Natural environments are temporally variable. The environment experienced by a population is unlikely to be constant, leading to fluctuations in key demographic processes. Under these conditions, the fitness consequences and costs of life history decisions can vary enormously between years, and the differences in predictions from constant and variable environment analyses of life histories can be substantial.

Vital rates are density dependent. Density dependence is a central concept in population ecology. In many natural populations such as the Soay sheep density dependent feedbacks may operate in a temporally variable way and influence different individuals in different ways. Despite the presence of a substantial theoretical literature illustrating the need to consider such feedbacks, there are few examples where they have been incorporated into analyses of life histories of natural populations.

Life history components and forces of selection covary. Because multiple individual attributes influence demography and hence the evolution of life history decisions, the interpretation of observational data from the field requires that we study how these attributes interact. Moreover, selection can operate via several pathways simultaneously. For example, there may be fitness advantages to producing large offspring to both mother and offspring, but there may also be costs in terms of reduced future reproduction to the mother.

Matrix models are well-established tools for the study of ecology and evolution. However, their utility is limited by the fact that they are strictly appropriate for systems that are structured by a discrete state such as age. In contrast, the recently developed Integral Projection Model (IPM) is designed to cope with continuous state variables such as weight. We are using this modelling approach to develop population models of the Soay sheep system. The selective constraints operating on the resultant model system can be characterised using invasion analysis (evolutionary game theory), completing the linkage from individual demography to ecological and evolutionary dynamics. Two of us (Childs and Rees) have successfully applied this approach to study reproductive timing in the monocarpic thistle *Carlina vulgaris* under stochastic, density-dependent conditions with age-by-size and size-by-seed structured demography.

In order to illustrate the approach we have developed a simple size-structured constant environment model of the Soay sheep population, assuming density dependent recruitment. We start by characterising the various components of the demography in

terms of individuals' size (Fig. 16). One of the great strengths of the IPM approach is that the resultant population model is a direct translation of these component functions. Since these can be derived using standard regression tools, this makes model construction relatively straightforward. The resultant model performs very well in terms of its predictive properties. For example, the observed and predicted size distributions of individuals are almost identical (Fig. 17, left panel). However, an analysis of the evolutionary dynamics of the model system predicts that the optimal strategy is for females to produce twins every year (Fig. 17, right panel), which is certainly not supported by observations from the field. This mismatch between observation and model predictions is almost certainly due to the fact that the costs of reproduction are not adequately represented in the current model. Reproductive costs are known to vary through time and such variation cannot be adequately captured using a constant environment model. Moreover, certain costs (e.g. gestation) are not included in the current model framework. Our next major task therefore, is to incorporate these missing components of demography into our models.

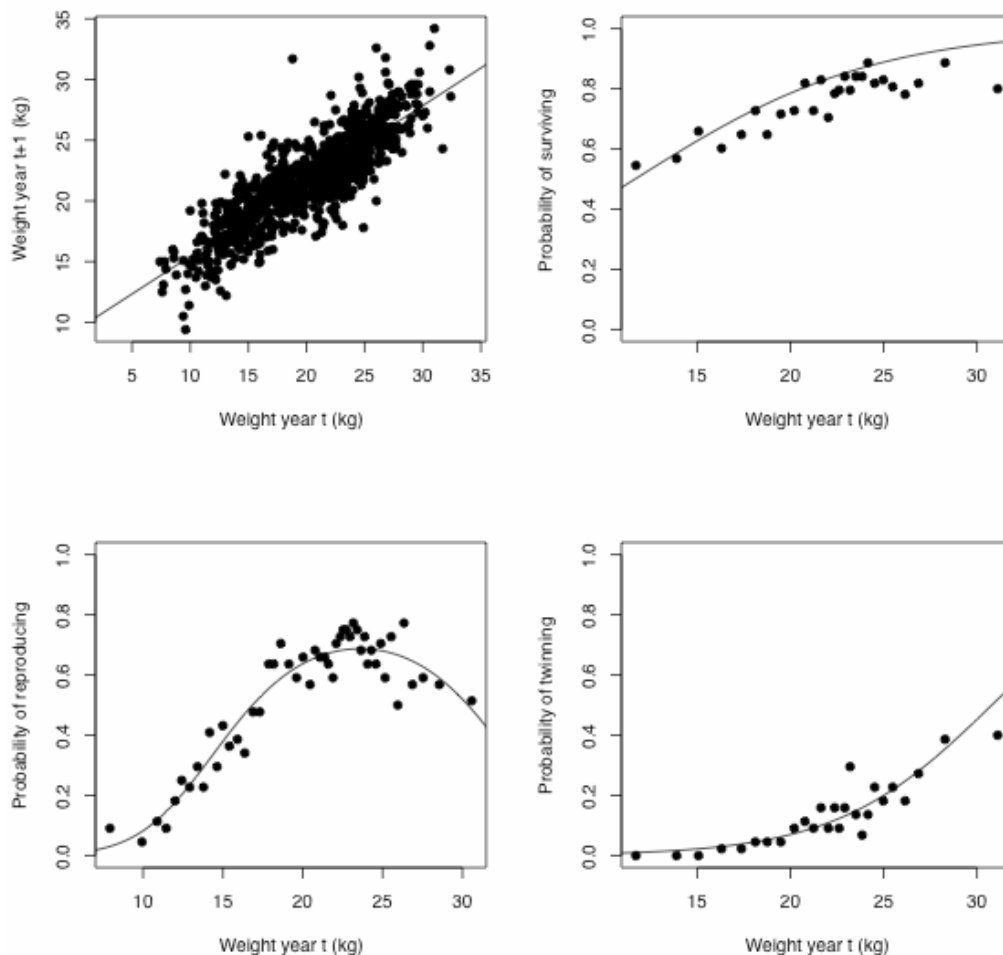


Figure 16. Component functions describing adult Soay sheep demography in a constant environment. A further two functions describe the within season survival and growth of lambs (not shown). Together, these can be used to construct an integral projection model of the Soay sheep population.

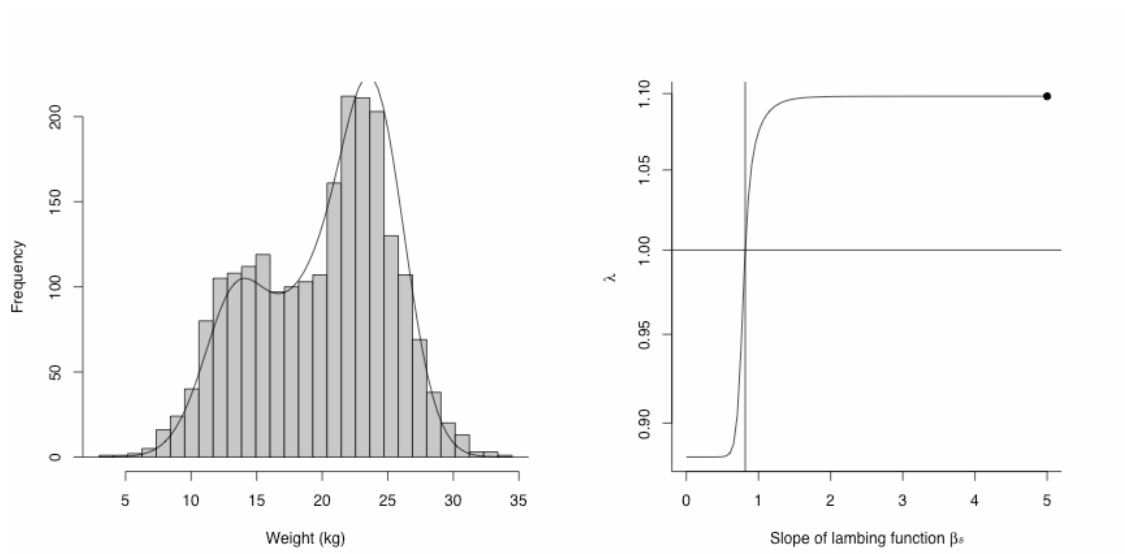


Figure 17. Stable size distribution (left panel) observed in the population (histogram) and predicted by the model (continuous line). Fitness landscape (right panel) for the twinning function, as predicted by a constant environment model of the population. The constant environment model predicts runaway selection on twinning, i.e. females should twin every year.

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In press:

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ACKNOWLEDGEMENTS

We are grateful to the National Trust for Scotland and to Scottish Natural Heritage for permission to work on St Kilda, and for their assistance in many aspects of the work. The project would not be possible without the generous assistance and support of MOD, QinetiQ and E.S.S. staff stationed on St Kilda and Benbecula and servicing the island. We are particularly grateful to Neil Mitchell and John Easton the NTS wardens for St. Kilda, especially for counting the number of sheep on the different islands of the St. Kilda group, to Sarah Money, the NTS Seabird and Marine warden and to Samantha Dennis the Archaeologist on the island.

We are also grateful for the help of volunteers without whom the fieldwork for 2005 would not have been possible: Elli Birtles, Hannah Buswell, Ali Donald, Charlotte Frearson, Mike Garratt, Martina Koch, Kenny Kombat, Sean Morris, Vicky Parker, Michael Perring and Anne Roels. Thank you.

Our research is supported by grants and studentships from the Natural Environment Research Council, the Biotechnology and Biological Sciences Research Council, the Wellcome Trust, the Leverhulme Trust, the Royal Society and the Natural Sciences and Engineering Research Council (Canada).

APPENDIX A: PERSONNEL CHANGES & SCHEDULE OF WORK

Personnel Change

This year Dario Beraldi completed his PhD thesis. Fanie Pelletier joined the project on a Natural Sciences and Engineering Research Council (Canada) fellowship, working with Tim Coulson at Imperial College, London. Dylan Childs and Mark Rees, based at Sheffield University started analysis of life-history evolution using Soay sheep data. Susan Johnston started a PhD mapping the gene underlying the horn polymorphism at Sheffield University.

Schedule of work on St Kilda

Spring

From March 14th until May 12th, Jill Pilkington, Matthew Robinson and three volunteers carried out ten population censuses and tagged and sampled lambs for ongoing genetic studies. 200 lambs were born to 184 ewes; these figures include 16 sets of twins (13 ewes held both lambs, 3 lost one twin). 151 lambs (76 male and 75 female) were caught and tagged; a further 39 lambs died before any tagging attempt.

Summer

Jill Pilkington and two volunteers returned to Hirta on July 14th to carry out ten population censuses, conduct mortality searches (yielding 7 tagged dead animals), and prepare for the main catch-up of study area sheep. The catch-up took place from August 6th – 18th, was led by Josephine Pemberton, and conducted by a team of 11 additional project members and volunteers. 174 sheep were caught and processed, of which 68 were lambs (42 males and 26 females), 22 were yearlings (6 males and 16 females), 17 were adult males, and 67 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic analyses. 26 Sheep were retagged because of damaged or missing tags. 10 previously untagged lambs, 1 yearling and 1 adult were caught and processed. Jill Pilkington and two volunteers remained on Hirta until 1st September to complete parasite counts and vegetation monitoring.

Autumn

From October 17th to December 8th Jill Pilkington and two volunteers carried out ten population censuses, monitored the mating period, capturing and processing 23 incoming tups and 15 resident tups. 35 previously darted, none resident tups were seen in the study area during this rut. One dead sheep was found.

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