

ST. KILDA SOAY SHEEP PROJECT: ANNUAL REPORT 2005

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POPULATION OVERVIEW

The sheep population on Hirta entered 2005 at a very high level and, as a result, there was substantial mortality in the first few months of the year. 429 sheep, of which 321 were tagged, were found dead within the study area between January and May of 2005. Lambing recruitment began on the 23rd of March with 58% of lambs born surviving (Fig.1).

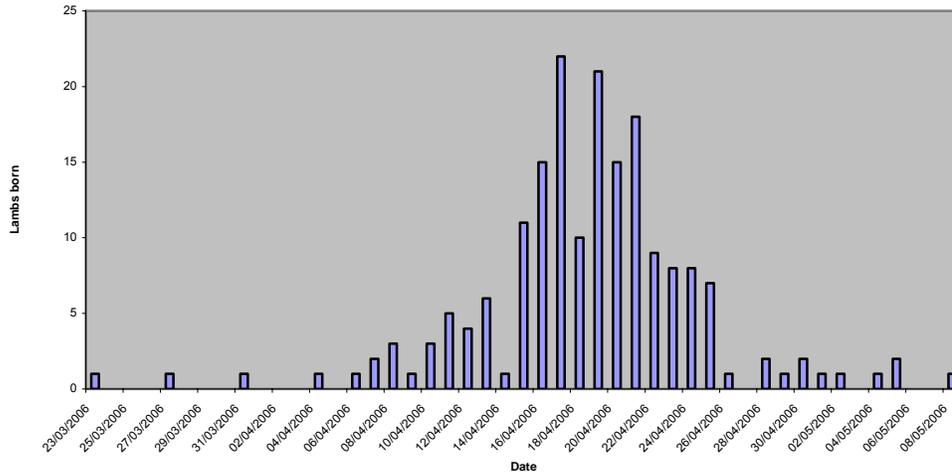


Figure 1. The temporal distribution of lamb births during 2005.

In December 2005, 547 tagged sheep were believed to be alive on Hirta, of which 405 regularly used the study area, a total decrease of 40% on 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.

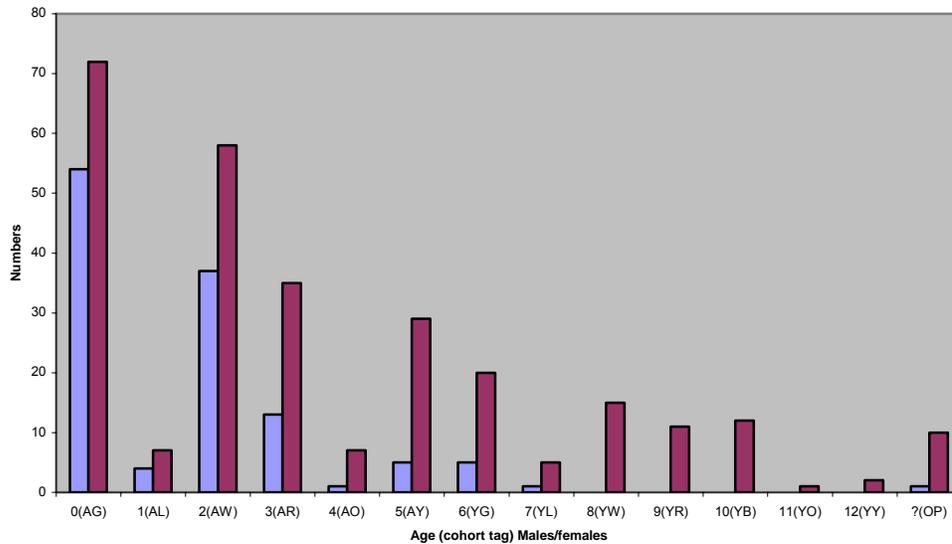


Figure 2. Age distribution of tagged Soay sheep presumed to be alive at the end of 2005.

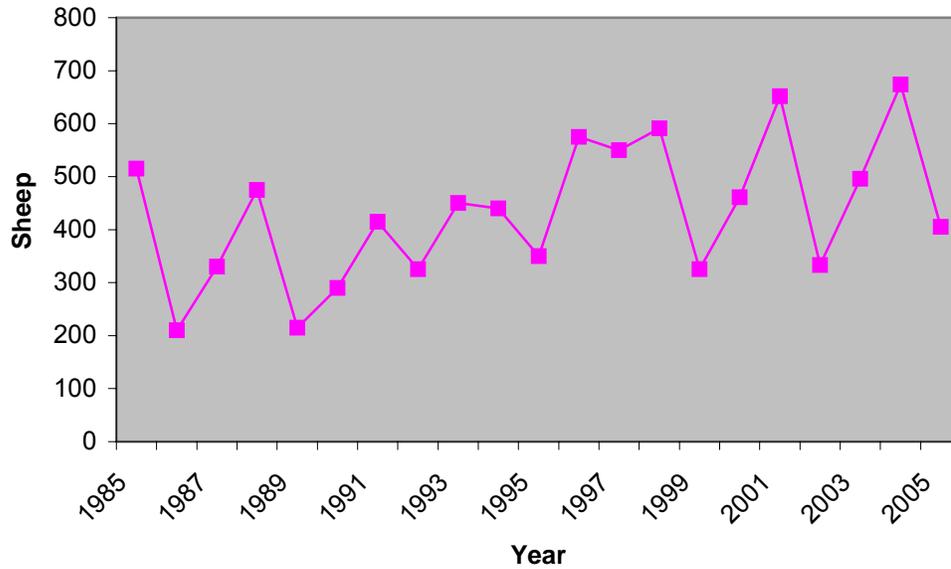


Figure 3. The number of tagged sheep regularly using the study area since 1985.

One whole-island count yielded 1362 tagged and untagged sheep, with the details displayed in Table 1. The total population had decreased by almost 32% since summer 2004, when it was at 1996. This gives a Δ (calculated as $\ln(N_{t+1}/N_t)$) of -0.38 .

Table 1. Demographic and geographic distribution of sheep observed during the count of *Hirta* on August 11th 2005. 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	197	9	81	3	43	1	8	0	151	493
Mullach Bi/Cambir	188	4	56	1	53	0	11	0	180	493
Ruaival/Village	175	2	39	3	47	4	9	1	96	376
Total	560	15	176	7	143	5	28	1	427	1362

REPORTS ON COMPONENT STUDIES

Vegetation.

Mick Crawley.

You will recall that in August 2004 we reported the highest ever whole island sheep count and our lowest inbye grass availability, leading to the prediction of a crash of $\Delta = -0.74$ and a predicted whole island count in August 2005 of just 952. As we now know, the mortality of winter 2004-05 was much less severe than this, and the whole island count in August 2005 was a whopping 1362, following a decline of just $\Delta = -0.38$.

It was interesting to see how the plants reacted to less-than-expected sheep mortality. In hindsight, the grass turned out to be highly prescient, with mean inbye sward height in August 2005 predicting a whole island count of more than 1500 animals. So at least the August sheep-grass relationship is consistent. Overall, the vegetation was definitely not in post-crash mode, and flowering was all over the place: it was high for *Cerastium*, intermediate for *Ranunculus* and low for *Anthoxanthum*.

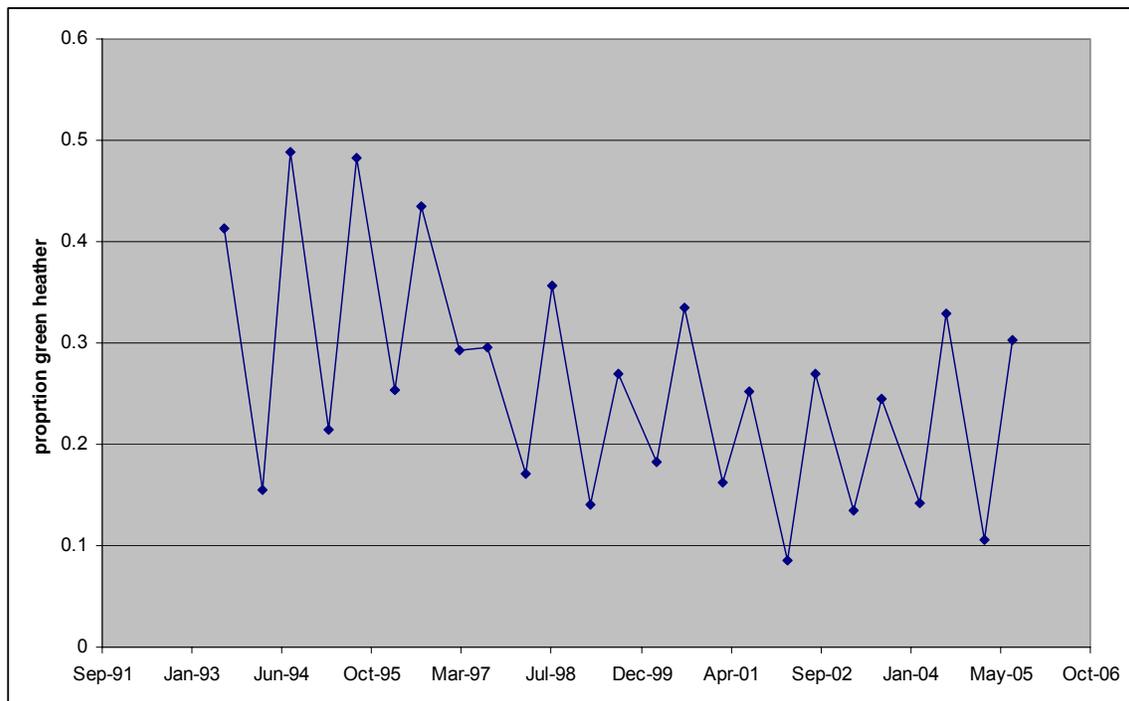


Figure 4. Within-year and between-year fluctuations in the proportion of destructively-sampled heather (*Calluna vulgaris*) biomass made up by green tissues. The data points are August and March values for each year.

The proportion of heather biomass that was green (Fig. 4) does not seem to have been severely damaged by the great storm of 11 January 2005. The August 2004 and 2005 values counter what was beginning to look like a long-term decline in heather condition over the period since 1995. The within-year cycle in heather greenness (low in March high in August) is as pronounced as ever.

Ideal free distribution of Soay sheep?

Owen Jones, Jill Pilkington and Mick Crawley.

The spatial distribution of organisms is often regarded as being driven by a need to maximise fitness. Animals are, therefore, expected to aggregate within the most favourable habitat patches. The distribution of herbivores is often assumed to follow the ideal free distribution (IFD) model. This model assumes that organisms have an “ideal” (i.e. omniscient) knowledge of food quality within the area available to them and that they are “free” to move, with negligible cost, throughout their environment. Animals distributed according to the IFD model should track both seasonal and inter-year changes in foraging conditions. Thus, as seasonal changes occur in the relative quality of patches then the animals should alter their distribution accordingly because of differences in plant phenology. Inter-year changes in sheep density should also elicit a distributional response, with an increase in density causing animals to occupy poorer quality patches. The IFD assumes that, as density declines, the animals in poor patches migrate back to higher quality patches. Thus, we would expect that, at lowest population densities, all the animals would be found in the best habitat patches, with less desirable habitats being occupied step-wise as population density increases (Fig. 5).

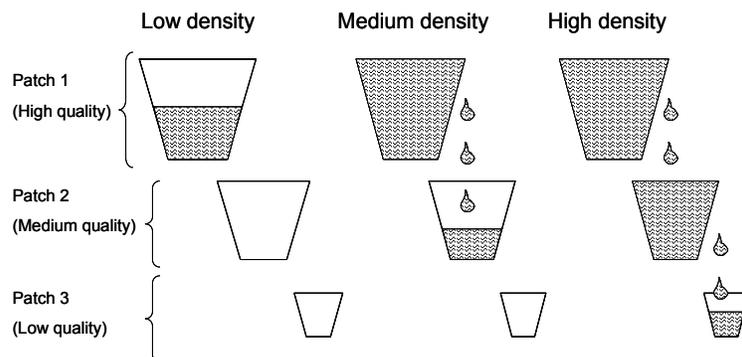


Figure 5. A schematic representation of the IFD occurring in a system with three patches of varying quality and at three population densities (low, medium and high). Patches are represented by buckets of different sizes (with size proportional to quality), while animals are represented by water. At low population densities all of the animals can occupy the best patch while at higher densities the best patch fills up and some animals ‘overflow’ to occupy the next best patch(es). It is assumed that as density decreases, the animals in the lower quality patches can move freely to higher quality patches as space becomes available.

We have used distributional data collected by census from St. Kilda’s Soay sheep population to examine sheep distribution in relation to plant community type and population density, and to test the IFD model. For each of several censuses conducted per year, three observers simultaneously traverse on different routes within the study area to locate individual ear tagged sheep to plant communities within 1ha blocks marked on a

grid-referenced map. Our dataset, restricted to spring and summer, included 84,453 observations.

Our analysis showed that the sheep were distributed in a highly non-random manner. For example, although the *Holcus-Agrostis* community makes up only 16% of the available grazing area within the study area it was regularly occupied by >70% of the sheep (Fig. 6). Overall, selection was greatest for *Holcus-Agrostis* dominated grassland on the previously cultivated ground within the Head Dyke. The four least-favoured swards were consistently wet heath, *Calluna* heath, dry heath and the *Molinia* dominated grassland – all of which occur mainly outside the Head Dyke. The maritime *Festuca-Plantago* swards have very low biomass yet are favoured by the sheep: despite the very low sward height, sheep are consistently over-represented in these areas, given the area available (Fig. 6). *Festuca rubra*, the commonest *Festuca* species on St. Kilda, is nutritious and highly palatable to the sheep and, it seems, even a very small biomass return is worth the investment in grazing time. These broad patterns are consistent with earlier qualitative work on Soay sheep published in the 1974 book, “Island Survivors”, and are broadly similar to observations of domesticated sheep in Scotland.

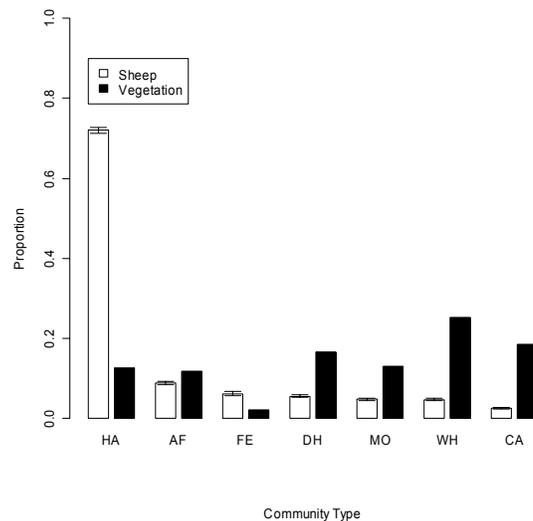


Figure 6. Comparison of the proportion of sheep occupying particular vegetation community types, with the proportion of the study area covered by that vegetation type. Error bars represent $\pm 1\text{SEM}$. Communities were; *Agrostis-Festuca* grassland (AF), *Calluna* heath (CA), dry heath (DH), *Festuca* grassland (FE), *Holcus-Agrostis* (HA), *Molinia* grassland (MO) and wet heath (WH).

Our multinomial logistic model for the probability of a sheep occupying a particular plant community showed that population density and season were both important determinants of occupancy ($p < 0.0001$; Fig. 7). In both spring and summer the preference (i.e. probability of occupancy corrected for available area) of the sheep for *Calluna* heath and *Agrostis-Festuca* decreased with increasing population density. The preference for *Holcus-Agrostis* increased with density in the spring yet remained fairly constant in the summer at a probability of occupancy ~ 0.55 . The preference for *Festuca*, *Molinia* and

wet heath increased with density in both seasons. Preference for dry heath remained constant in both seasons with a probability of occupancy of ~ 0.03 .

The decrease in occupancy of the *Calluna* heath, and the increase in occupancy of the *Holcus-Agrostis* and *Festuca* swards with increasing sheep density are contrary to the predictions of the IFD model. Therefore, although the IFD model *does* predict density-dependence in proportional distribution amongst patches, the IFD model is clearly not applicable in this case, because the direction of the changes in distribution are mainly the opposite of the IFD's predictions. We believe that this is because the IFD model fails to take into account the dynamic nature of the resource. The swards are not composed of discrete items; rather they are a growing resource that is continually replenished. The gross rate of replenishment depends on the productivity of the constituent species within the sward while the net rate of replenishment depends upon the rate of consumption by herbivores which is, in turn, closely associated with population density. Thus, each of the swards has a different response to increasing grazing pressure, with high-productivity swards such as the *Holcus-Agrostis* within the Head Dyke being more resilient to grazing pressure than low-productivity swards such as the heathland outside the Head Dyke. Consequently, as population density changes, the relative quality of the different plant communities is altered which, in turn influences foraging choice and distribution.

We therefore argue that although the IFD model has proved useful in investigations of animal distribution, it may be inappropriate, without modification, for investigating the distribution of foraging ungulates across a heterogeneous and dynamic food resource.

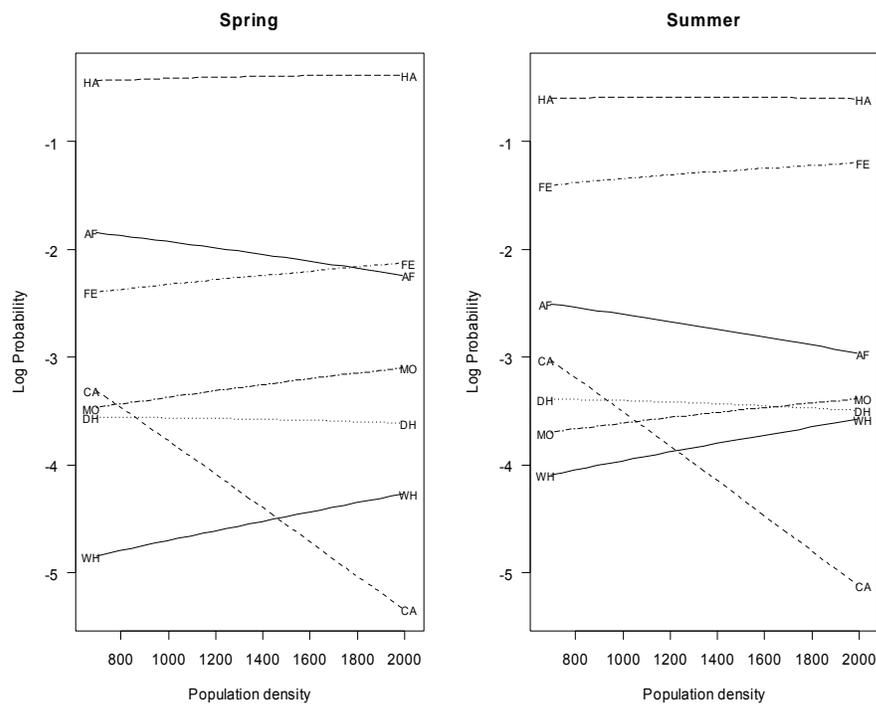


Figure 7. The relationship between the log probability of a sheep occupying each the seven plant community types (*Agrostis-Festuca* grassland (AF), *Calluna* heath (CA), dry heath (DH), *Festuca* grassland (FE), *Holcus-Agrostis* (HA), *Molinia* grassland (MO) and wet heath (WH)) and population density in spring and summer. The lines are predictions from a multinomial model.

Peri-parturient rise in parasite burden in Soay ewes.

Louisa Tempest and Ken Wilson.

During the spring there is a characteristic rise in parasite burden, that coincides with lambing (April to June), which is termed the Peri-Parturient Rise (PPR). PPR is usually measured in nematode strongyle egg counts in faecal samples, known as faecal egg counts (FEC). The PPR appears to occur as a cost of reproduction; in domestic sheep it has been shown that it does not occur in ewes that fail to breed or have lost their lamb. More specifically, the PPR appears to occur as a cost of lactation, possibly mediated by the hormone prolactin. It is thought that ewes become immuno-compromised at lambing, which allows parasitism to increase in several possible ways. These include (a) an increase in establishment of newly acquired larvae; (b) the maturation of arrested larvae acquired some months previously; (c) a decrease in the expulsion of developing and adult worms; and (d) an increase in the fecundity of existing adult worms.

Soay sheep that successfully rear a lamb also suffer from this increase in parasitism, whereas non-lambing adult ewes do not. In contrast, non-lambing *yearling* ewes do suffer from an increase in parasite burden at this time, despite incurring only minimal costs of reproduction, probably as a consequence of poor body condition and a lack of acquired immunity to parasites. Male Soays can also suffer an increase in parasitism during the spring, even though they do not incur reproductive costs at this time, suggesting that the spring rise in parasitism is partly associated with poor body condition.

We report here some of the results obtained from part of a larger experiment designed to determine the effects of parasite burden on ewe reproductive success. Specifically, how their over-winter body condition (experimentally controlled by manipulating parasite burden) affects the expression of the peri-parturient rise in adult Soay ewes.

During the annual August catch-up of 2003, 51 female Soay sheep aged four to seven years old, were caught and processed in the usual way, and randomly assigned to either the Bolus (treated) or Control (not treated) group. The ewes in the Bolus group were administered with an anthelmintic bolus (*Captec* slow-release bolus; active ingredient Albendazole) which temporarily removes the parasite burden. The manufacturers' state that the bolus is effective at preventing establishment of parasites for approximately 100 days in domestic sheep, after which time, parasites may become re-established.

Pivotal to this experiment, administration of the anthelmintic bolus successfully removed the parasite burden from the treated ewes, as the low FEC measured in the days following treatment clearly demonstrated (Fig. 8a). We can therefore be confident that the treated ewes had reduced costs of fighting parasite infection going into, and probably throughout much of the winter, since densities of infective larvae on the pasture are very low during the winter months. However, seven months later, just before lambing (late March / early April) and prior to the onset of the characteristic spring rise in parasite burden (PPR), there were no detectable differences between the parasite burdens of treated and control sheep (Fig. 8b). Measurement of body condition (using an index of their size and weight) in August 2004 clearly showed that bolussed ewes had significantly reduced loss in condition compared to control ewes (Fig. 9). This supports the notion that the bolussed ewes had superior body condition throughout the winter.

As all the ewes in this experiment were adults (4 - 7 years old) with well developed acquired immunity, and nearly all ewes (apart from 2 out of 43) reared a lamb successfully, much of the age- and fecundity-related variation that affects spring parasite burden was avoided. This allowed assessment of the effect of ewe body condition during the preceding winter on the spring peri-parturient rise.

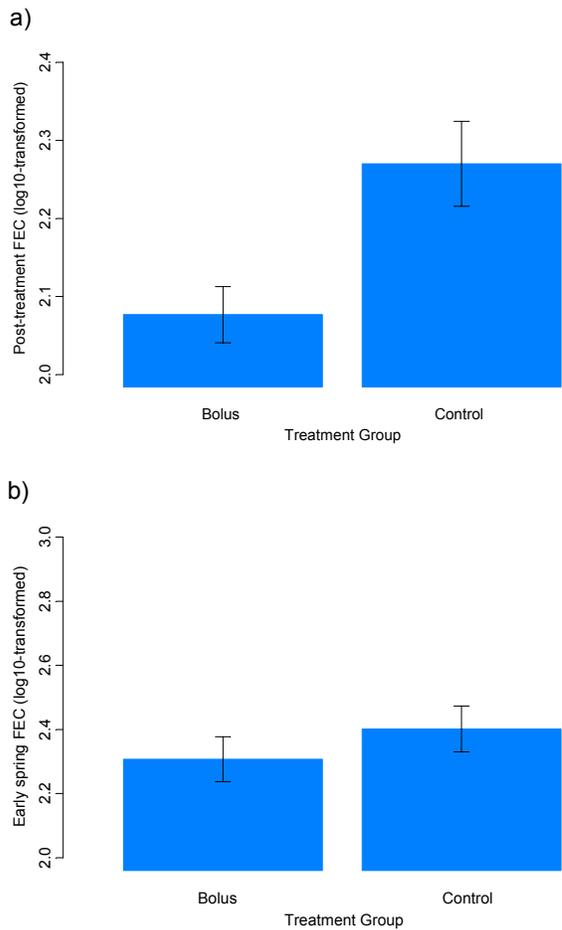


Figure 8. Faecal egg counts (FEC) in experimental ewes (bolus and control sheep) **a)** post-treatment (August 2003), and **b)** prior to lambing in 2004 (end of March/early April). FEC data are log10-transformed for graphs. Error bars are standard errors. Analysis on non-transformed data (GLM with Poisson errors): **a)** post treatment, $F_{1,38} = 8.45$, $p=0.006$, **b)** prior to lambing, $F_{1,50} = 0.64$, $p=0.43$.

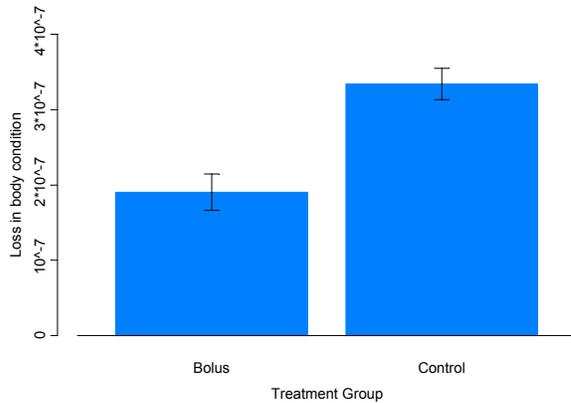


Figure 9. Effect of treatment group (Bolus or Control) on loss of body condition from August 2003 to August 2004 ($F_{1,20} = 4.69$, $p=0.043$). Error bars are standard errors.

Multiple faecal samples were collected from each ewe during the lambing period (spring 2004), and faecal egg counts were measured. Analyses of these data clearly showed that all ewes incurred a peri-parturient rise in FEC; however, ewes treated with anthelmintic bolus the previous summer had a smaller PPR than the untreated control ewes (Fig. 10). The peri-parturient rise occurs as the ewes become immuno-compromised, due to the costs of gestation, parturition, and particularly lactation. Although the direct effect of the treatment had worn off by the start of spring, (no detectable difference in FEC between bolus and control ewes in early spring) the putative benefits of having reduced costs of fighting parasitic infection during the winter, appear to allow treated ewes to enter the spring in a better condition and to deal with these reproductive costs more successfully. This was manifested, at least partly, in a reduced peri-parturient rise in parasite burden.

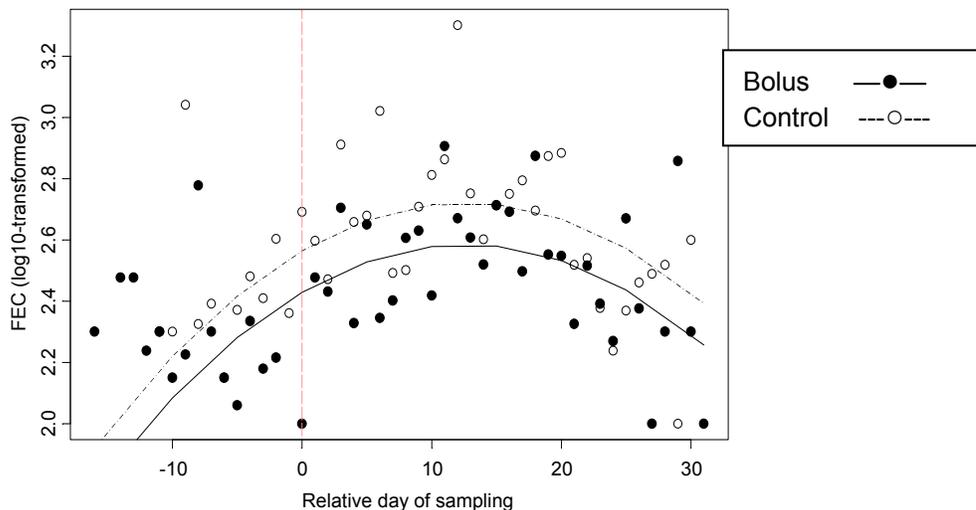


Figure 10. Faecal egg counts (FEC) relative to the day of parturition, and treatment group. FEC is the log10-transformed density of strongyle eggs per gram of faeces, and the vertical dashed line indicates day 0 (the day of lambing). The peri-parturient rise in FEC is shown for ewes in the Bolus and Control groups. Data points are daily grouped means. Fitted lines are drawn from model predictions.

Estimating Individual Contributions to Population Growth: evolutionary fitness in ecological time.

Tim Coulson.

Population biology is concerned with describing and predicting change that is measured at the level of the population. For example, population ecologists are interested in explaining how population size fluctuates, while evolutionary ecologists work towards understanding how and why allele or trait distributions change over time. These changes are caused by the birth, death and dispersal of individuals within the population. Although this has long been appreciated, measures of individual performance that are widely used typically cannot easily be combined across individuals to give population performance. I developed a new method, called de-lifing, which calculates an individual's contribution to statistics that describe the overall population. For example, de-lifing allows population growth rate to be decomposed into contributions from individuals within the population. Furthermore, these contributions can be decomposed further into contributions from survival and recruitment. The method is remarkably easy to apply.

Having developed the method I applied it to the Soay sheep data as an example of how the approach can be used. I demonstrated how it can be used to measure selection, and to work out how different age classes contribute to population growth. In the figure overleaf I demonstrate how different ages contribute to population growth on average (Fig. 11a). Lambs, which are numerous, but which have lower survival and lower fecundity rates, are the age-class that contributes most to population growth. However, because they perform less well than adults their contribution has a negative value. Most adult ages contribute positively to population growth, with three year olds performing best. These contributions vary with time (Fig. 11b). This demonstrates how different ages contribute to different extents to population growth in different years – a result that supports our previous work on the contribution of age-structure fluctuations to the population dynamics. Finally in (Fig.11c) I show how different cohorts contribute to population growth to different extents. This shows that cohorts born in crash years (i.e. immediately prior to a population crash) tend to contribute negatively to population growth. In contrast, those cohorts born in non-crash years typically make large, positive contributions.

Ongoing work is currently using the de-lifing approach to examine selection in unprecedented detail in the Soay sheep population, and next year I hope to be able report evidence, or not, of balancing selection across a range of phenotypic traits.

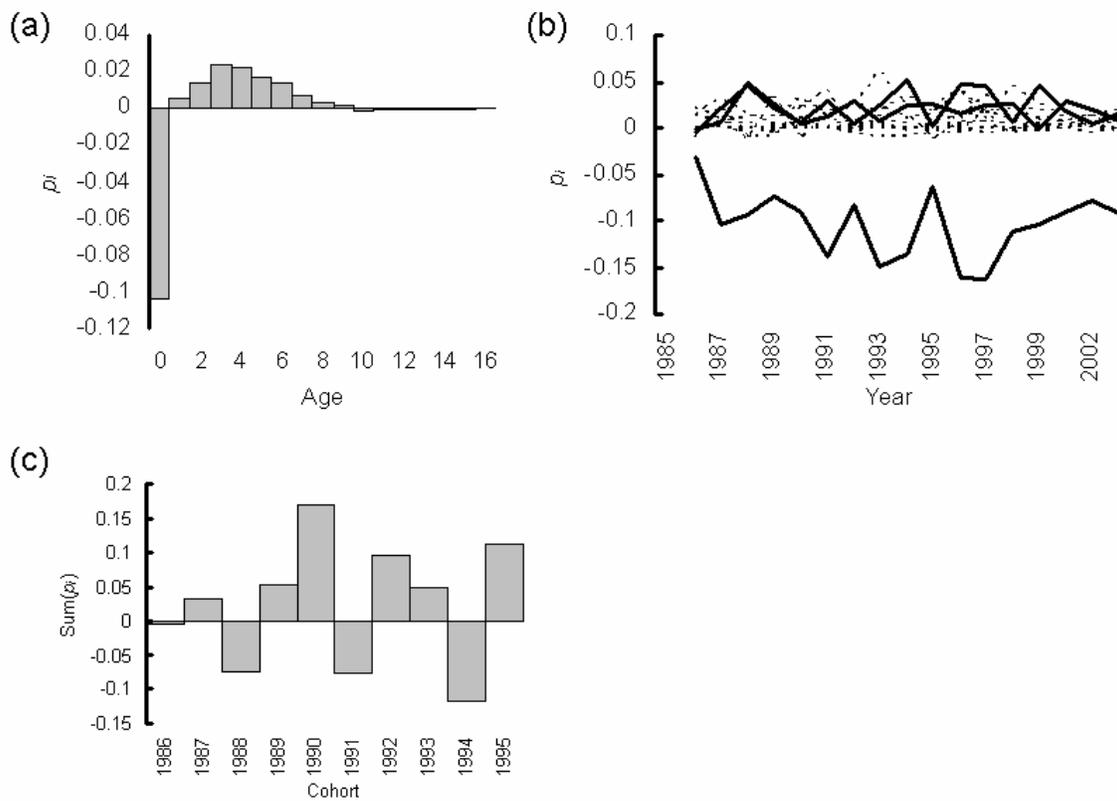


Figure 11. Individual contributions to population growth (p_i) summed across individuals in the same phenotypic states for the Soay sheep. (a) age-specific values of p_i for the Soay sheep averaged across years 1986-2003, (b) time series of age-specific contributions to population growth. The solid lines represent lambs (negative values of p_i , and four and five year olds (positive values). There is substantial inter-annual variation in the contribution of different age-classes to population growth and (c) the contribution of different cohorts to population growth. Note that the foot and mouth outbreak means data are not available for this year.

Testes size, testosterone production, and reproductive drive in Soay rams.

Brian Preston, Ian Stevenson, Gerald Lincoln, Louisa Tempest, Steven Monfort, Jill Pilkington, and Ken Wilson.

Reproductive hormones, such as testosterone (T), are known to have a profound influence on the reproductive behaviour and physical attributes of many animal species. However, relatively little is known about how T production is regulated under natural circumstances, and why some individuals are, for example, more sexually motivated or aggressive than others. We've routinely measured testosterone levels in the bloodstream of rutting Soay rams since 1997 (using radioimmunoassay techniques), allowing us to examine how different seasonal and environmental factors influence its secretion, as well as identifying the physical characteristics of males that determine their own specific testosterone profile.

As with other species where males physically compete for access to mates, Soay ram's T levels peaked around the time that the first oestrous females were observed within the study area, and thereafter declined over the remainder of the rutting season (Fig. 12a); this temporal effect is known to be triggered by shorter day-length on the approach to the rutting season. On top of seasonal changes in T production, we found a weak, but nonetheless detectable influence of the number of oestrous females within the study area, which appeared to stimulate males to produce additional T.

Of a number of different male characteristics that we investigated (including their horn size, body size, and condition), we found that the age of rams appeared to have an important influence on their T profile, as rams' T levels increased from birth until they reached full sexual maturity at 4 to 6 years of age, and declined thereafter (Fig. 12b). These patterns match age-specific patterns of siring success that have previously been shown to occur through the lifetime of Soay rams. Importantly, we also found that size of rams' testes exerted a strong effect on their circulating T levels, with larger testes apparently being able to produce greater quantities of testosterone (Fig. 12c).

Although it has long been known that mammalian testes are the site of production for 95% of the body's T, the cells responsible for secreting T comprise only a tiny fraction of the total mass of testes, and so a strong association between testes size and T production was not expected. The intimate structural integration of T and sperm producing cells (which account for the majority of testicular tissue), alongside the dependence of sperm production on high local levels of T, seem likely to account for this finding, and suggests that selection for higher rates of sperm production results in a concomitant increase in T production. Recent analysis of rams' behaviour during the rut illustrates one of the numerous potential consequences of this association, as testes size is a key predictor of both their levels of aggression, and their libido (Fig. 13a and b), presumably because of their greater T production.

This association between sperm and T production appears likely to have important evolutionary consequences, as conditions that drive the evolution of larger testes because of their higher sperm production rates, need not favour concurrent changes in other T dependent reproductive traits, such as aggression. Future research on Soay sheep, which have evolved testes that are some 4 times larger than would be expected for their body size, will assess the wider impact of this relationship.

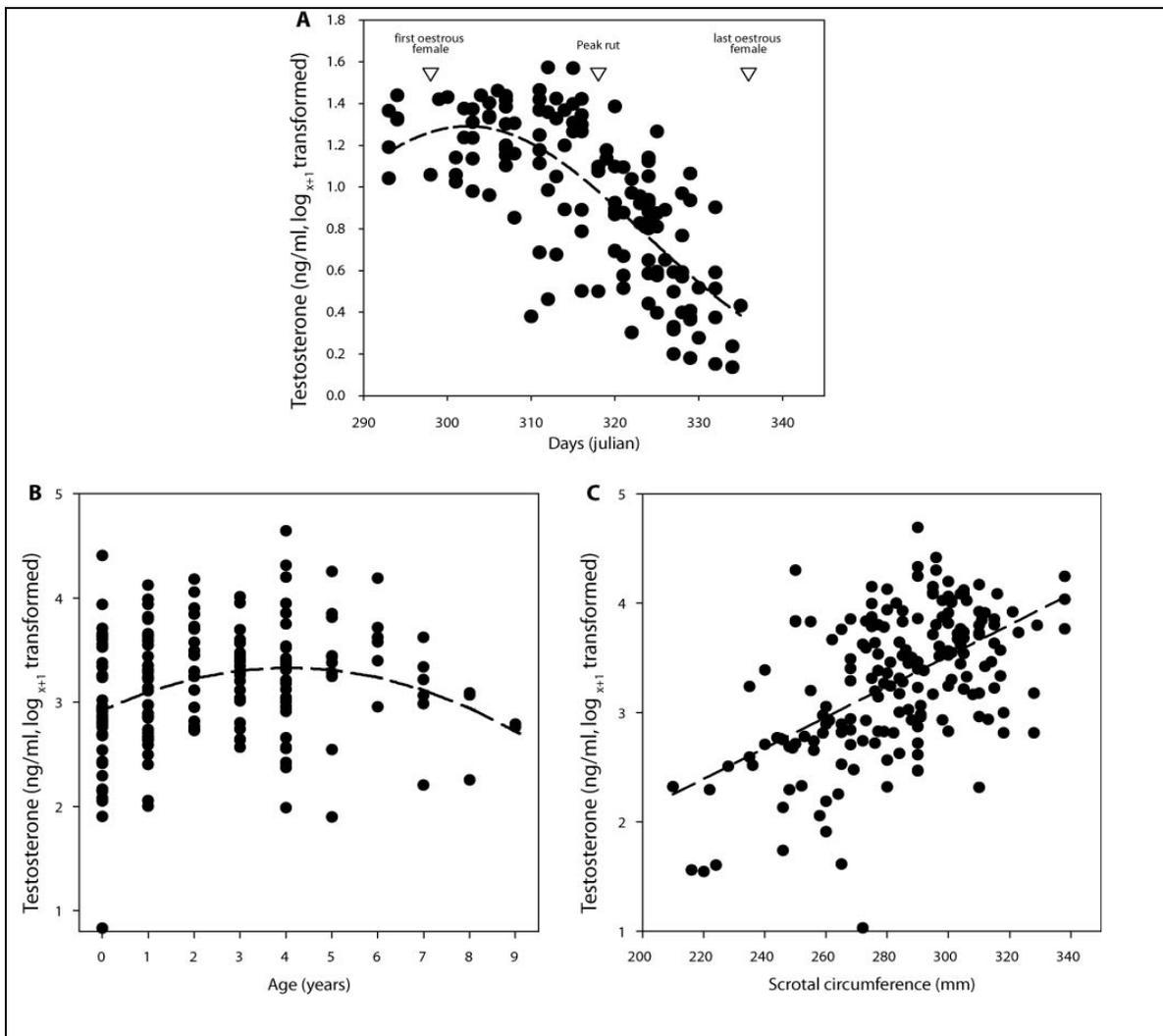


Figure 12. Testosterone profiles in Soay rams. (A) Testosterone levels peak during the early stages of the rut, before declining as the rut progresses. (B) Testosterone increases in rams until they are 4 to 6 years of age, and declines thereafter. (C) The size of ram's testes (as measured by their scrotal circumference) accurately predicts their testosterone levels. These plots are derived from a GLMM analysis which investigated the factors that influenced ram's testosterone levels, and control for other significant factors.

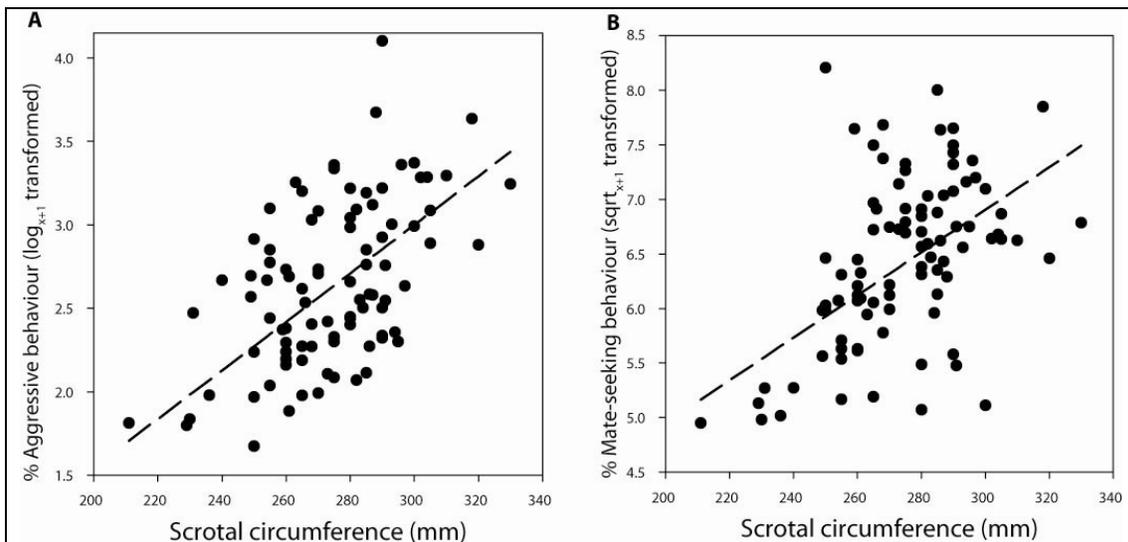


Figure 13. Testes size predicts Soay rams ‘reproductive drive’ (A) The time (during hour long focal watches) that males spent engaged in aggressive activity increased in relation to their scrotal circumference. (B) Males with larger testes spent more time searching for prospective mates. Plots are derived from separate GLMM analyses that investigated the determinants of male reproductive drive, and control for other significant factors. To preclude any confounding influence of mate guarding behaviour on our analyses, response variables were restricted to periods in which males were not guarding oestrous females. For illustrative purposes, data are grouped by individual within years.

Live fast, die young: A balance of natural, sexual and antagonistic selection maintains the weaponry polymorphism in male and female Soay sheep.

Matt Robinson, Josephine Pemberton & Loeske Kruuk.

Males are predicted to compete for reproductive opportunities, with sexual selection driving the evolution of large body size and weaponry through the advantage they confer for access to females. However, abundant variation is still found in the size and form of weaponry in natural populations, which could influence breeding success (sexual selection) and survival (natural selection) in both sexes. Soay sheep display a phenotypic polymorphism for horn type with normal-horned and reduced horned (scurred) males and normal-horned, scurred and polled (absence of horns) females, and further variation in size exists within horn morphs.

Variation may be maintained in numerous ways, but little testing has been conducted, particularly in wild populations. Firstly there may be trade-offs between different components of fitness, meaning that reproduction and survival may be balanced, with different phenotypes faring better in different situations. Previous work on Soay sheep, has found that scurred males gain a lower number of paternities per year compared to normal-horned males, but have better over winter survival. Secondly, selection may act in a contrasting manner in males and females. In Soay sheep, this sexual antagonism may act to maintain the scurred phenotype, with previous work suggesting that scurred

females have higher conception, weaning rates and over winter survival. The function of horns in females is currently unknown. Finally, selection may vary and interact with the environment and thus certain phenotypes may be favoured in different conditions depending upon their abundance, or selection may be stronger at certain times. Previous work has shown that density of sheep on Hirta affects how strong selection acts upon horn type in females, and the year in which an animal is born has a great impact upon its life.

Methods

We explored the balance between sexual and natural selection acting upon the form and size of weaponry in both males and females, through a series of analyses. We considered the effects of selection on horn type and then horn size in both sexes acting via lifetime breeding success, and its two components, annual breeding success and longevity. First, associations between horn type and breeding success in a given year for males and females was determined, whilst also taking into account selection on body size and population size in the year of the rut. The model was then repeated with horn size nested within horn type to assess the association of horn size within normal-horned and scurred males and females. Models were then conducted to test the associations of horn type and then horn size nested within horn type, on longevity and lifetime breeding success, whilst also taking into account selection on body size (measures of hindleg length recoded at death which were age adjusted), birth weight, birth status (twin or singleton) and population at year of birth. Here, specific model results are not shown, but residual values are plotted against horn type and then horn size to show the relationships which were found.

Trade-offs

Annual breeding success was greatest in normal-horned prime-aged males between three and six years of age (Fig. 14a). When compared, non prime-aged normal-horned males and scurred males did not differ in their annual breeding success (Fig. 14a). Greater horn length in normal-horned males gave greater annual breeding success, a result not found in scurred males (Fig. 15a and b). Results from the analysis of longevity appeared to support the hypothesis of a trade-off in Soay males. Being normal-horned in males appeared to be associated with reduced longevity compared to that of scurred (Fig. 16a). There was also a negative association between increased horn length and longevity in normal-horned males (Fig. 17a). Therefore there appeared to be no difference in lifetime breeding success between normal-horned and scurred males (Fig. 16c) as it appeared that the negative associations in longevity were sufficient to overcome any beneficial associations in annual breeding success.

Antagonism

The percentage of females conceiving each year increased with age, until the age of eight, with no significant difference in annual breeding success across different horn types (Fig. 14b). No significant associations between horn size and annual breeding success were found in females (Fig. 14b). No antagonistic effects were found between horn types in males and females. Being polled in females was associated with reduced longevity (Fig. 16b) and reduced lifetime breeding success (Fig. 16d) but no differences in longevity or

lifetime breeding success were found between scurred and normal-horned females (Fig. 16b, d). There were, however, negative associations between horn size and both longevity and lifetime breeding success of normal-horned females (Fig. 17b and 17d). These associations may balance the positive association between horn size and annual breeding success in normal-horned males if an underlying genetic correlation can be found.

Summary

In summary, we found evidence for selection acting upon horn type and size within both male and female Soay sheep, independent of body size. Estimates of phenotypic selection were dependent upon the specific component of fitness measured, with a balance between short-term annual selection, through annual breeding success, balanced by longevity to give lifetime breeding success. Analysis of lifetime breeding success showed no difference between scurred and normal-horned males stemming from a trade-off between annual breeding success and longevity. Displaying a polled phenotype was disadvantageous in females, with no difference in lifetime fitness between scurred and normal-horned males. Selection through longevity for horn size favoured reduced horn growth in both sexes, balanced in males by a positive association with annual breeding success. Clear examples of a balance of natural selection countering sexual selection are rare; and in this case exemplified by the existence of different horn morphs in both males and females. Our results therefore illustrate the contrasting conclusions that may be drawn when different components of fitness are used in selection analyses, and underline the need to use as comprehensive an estimate of fitness as possible for a full representation of evolutionary processes.

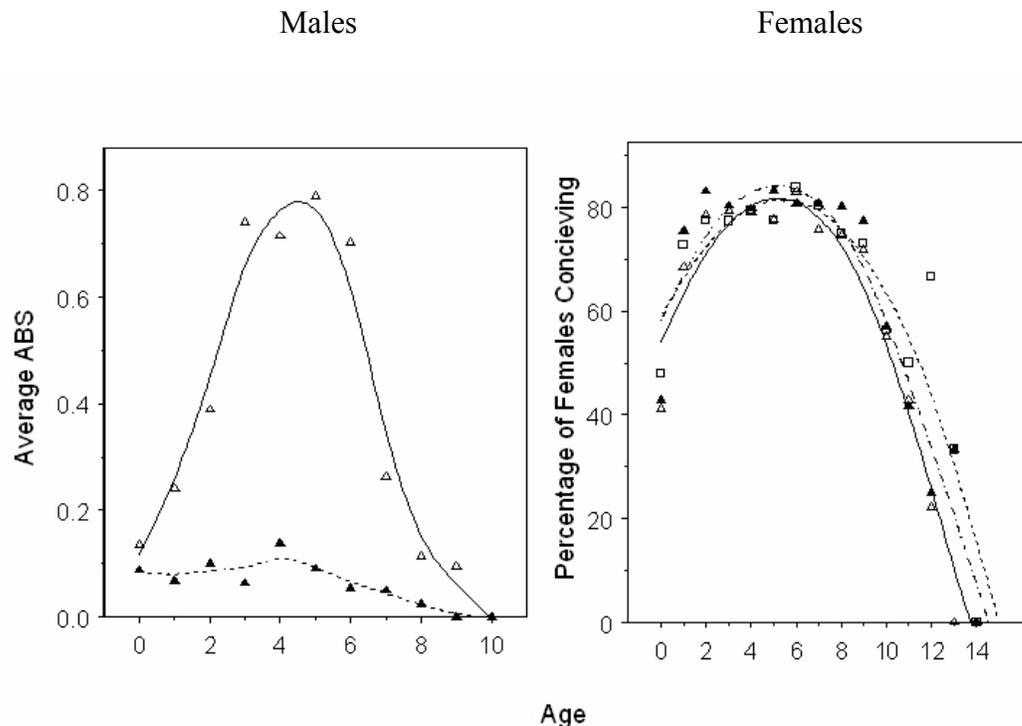


Figure 14. Changes in annual breeding success (ABS) in males (A) and the percentage of females conceiving each year (B) with age. Normal-horned individuals are depicted by open triangles and solid lines; scurred individuals: solid triangles and dash-dot line; polled individuals: open squares and dashed line.

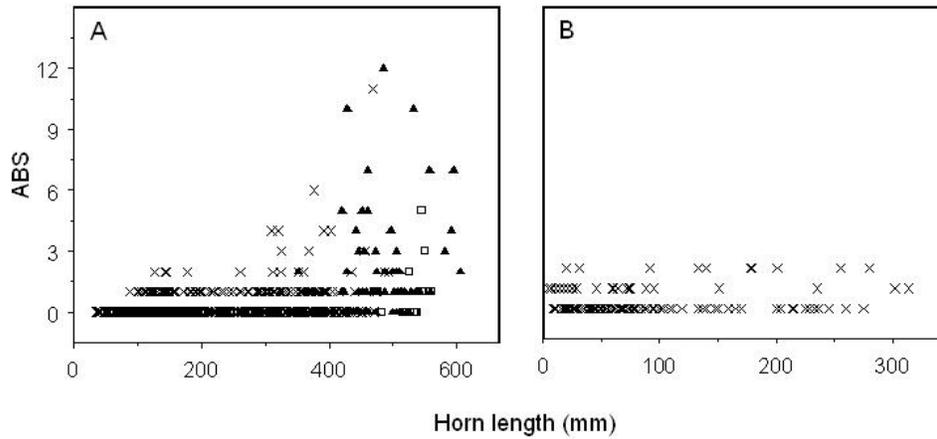


Figure 15. Changes in annual breeding success (ABS) with horn length in normal-horned (A) and scurred (B) males. Normal-horned males are divided into three age categories; crosses: age one to three years; triangles: three to seven years; open squares: seven years and above.

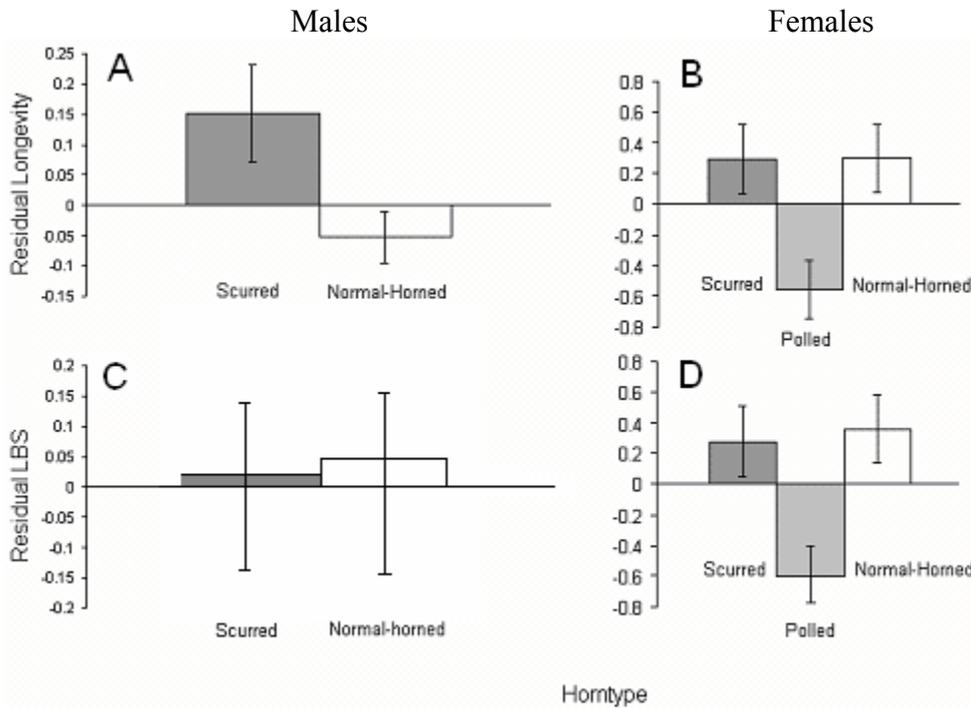


Figure 16. Bar charts (with SE) showing average residual longevity and LBS for males (A,C) and females (B,D) within each horn type. Residuals were obtained from models of longevity and LBS containing birth weight, density in year of birth, twin, and age-adjusted hindleg.

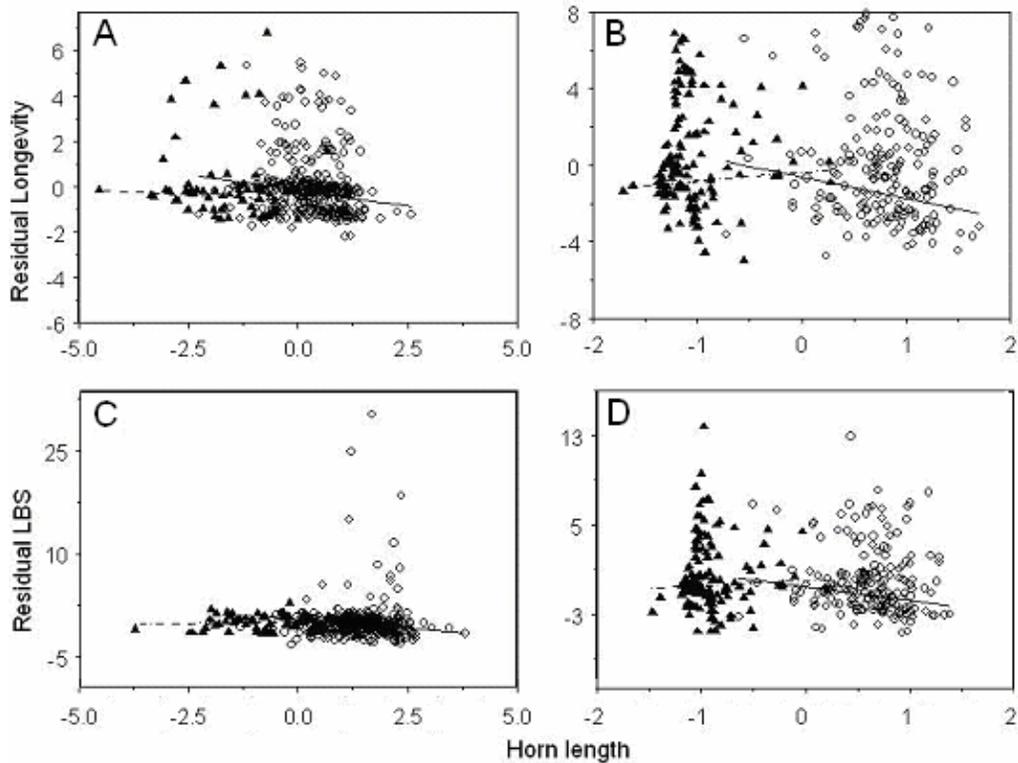


Figure 17. Changes in residual longevity and lifetime breeding success (LBS) with mean horn size in (A & C) males and (B & D) females. Residuals were obtained from models of longevity and lifetime breeding success containing hind leg (age adjusted), density in year of birth, twin, and horn type. Horn size is age-standardized for age at death (see Methods). Scurred individuals (Sc): solid triangles and dot-dash line; Normal-horned individuals (NH): open diamonds and solid line. Lines show linear regression between two variables (A: NH $F=5.299$, $r^2=0.014$, $p=0.022$, Sc $F=0.385$, $r^2=0.006$, $p=0.537$; B: NH $F=6.504$, $r^2=0.013$, $p=0.012$, Sc $F=0.038$, $r^2<0.001$, $p=0.845$; C: NH $F=0.012$, $r^2<0.001$, $p=0.911$, Sc $F=0.739$, $r^2=0.001$, $p=0.393$; D: NH $F=5.589$, $r^2=0.010$, $p=0.021$, Sc $F=0.029$, $r^2<0.001$, $p=0.866$).

Environmental variation and the evolution of birth weight in Soay sheep.

Alastair Wilson.

Evolution proceeds when natural selection acts on a trait with a heritable genetic basis, changing the expression of that trait in future generations. Simple quantitative genetic models allow this evolutionary change to be predicted from the strength of selection and the amount of genetic variance (usually expressed as the heritability). However, these simple models usually assume a constant environment, while natural populations normally live in highly variable environments. This is important because environmental variation in nature may cause variation in the parameters that determine evolution. For example, the strength of selection on a trait might vary considerably from year to year,

and it is increasingly recognised that environmental conditions also influence the heritability.

Using data on the fitness-related trait of birth weight from the Village Bay population of Soay sheep, I found, dramatic variation between years in the strength of selection (standardised selection gradients ranged from 0.04 to 0.53 using neonatal survival as the measure of fitness). Although selection was always positive (i.e., favouring heavier born lambs), the strength of selection is negatively correlated with the quality of the environment (E , defined as s the average neonatal mortality in each year). Thus selection is significantly stronger in years of poor environmental quality (Fig. 18).

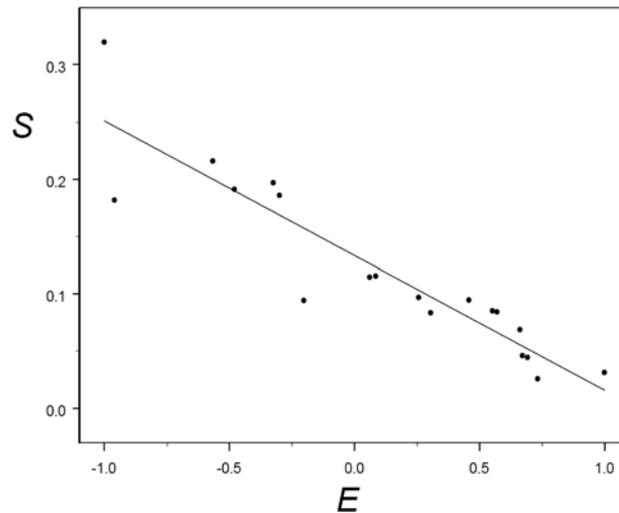


Figure 18. Selection differential on birth weight (S) against environmental quality (E). Each point represents the values measured in one year and the solid line shows the least-squares linear regression of S on E .

Subsequently, by employing a new analytical method, namely “random regression”, in which genetic effects are modelled as functions of E , I showed that total heritability also varies with environment (h^2_T ranging from 0.14 to 0.24). Furthermore, total heritability of birth weight also shows an increasing trend as environment quality improves. Note that the total heritability includes contributions from maternal genetic as well as additive effects, and the observed trend results from higher levels of maternal genetic variance in years of better environmental quality (Fig. 19).

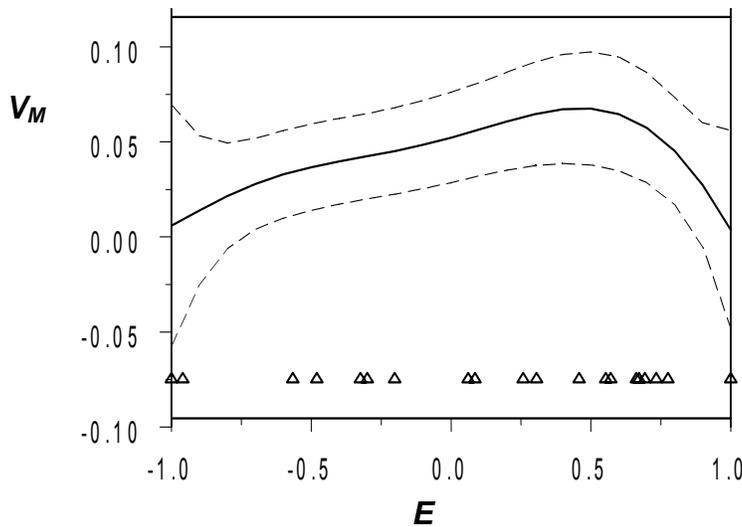


Figure 19. Maternal genetic variance (V_M) across environments (E). Dotted lines indicate approximate 95% confidence limits and triangles indicate actual distribution of E across years.

The shared dependence on environment quality results in a negative relationship between the strength of selection and the magnitude of heritable genetic variation for birth weight in different years (Fig. 20). Harsh environmental conditions were associated with strong selection for increased birth weight but low genetic variance, and *vice versa*.

Consequently the potential for increased birth weight to evolve in this population will be constrained by either a lack of heritable variation (in poor environments) or by a reduced strength of selection (in good environments).

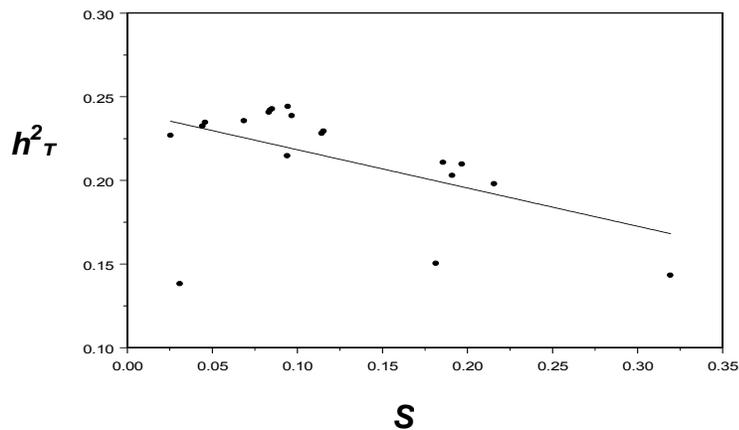


Figure 20. Selection differential on birth weight (S) against estimated total heritability (h^2_T). Each point represents the values measured in one year. The solid line shows the least-squares linear regression of h^2_T and S . The strength and direction of this relationship is unchanged by removal of outliers in the lower portion of the graph.

Using Soay sheep for genetic mapping of discrete and quantitative traits.

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

A key question for evolutionary biologists is the paradoxical maintenance of genetic variation: natural selection should wipe out disadvantageous genetic variants, yet adverse genes persist in wild and domesticated populations. A way to address this dilemma is to identify (i.e. to map) chromosomal regions harbouring genes under selection, in order to track the action of evolution in the wild at the DNA level. The principle of genetic mapping relies on finding a statistical association between a character value and a genetic region among related individuals who share part of their genome. The trait values are recorded from field work whereas the genetic regions can be identified by means of DNA markers which are variable regions in the genome whose position is known.

The Soay sheep is amenable to this kind of study as different traits showing variation and selection (e.g. the coat colour or body weight) have been recorded on many related individuals, an accurate pedigree has been compiled, and many DNA markers have been already detected in domestic sheep. For this project we selected from the larger Soay sheep database a pedigree of 882 animals and we genotyped 588 of them at 251 marker loci in order to cover ~90% of the sheep genome.

Here we report the mapping of the genes responsible for coat colour (dark or light coat), coat pattern (uniform colour of the body or contrast between belly and coat) and horn type (normal, polled or scurred horns). These traits are coded by one or a few genes and show discrete variation which normally is not influenced by the environment. In contrast, quantitative traits like weight and parasite resistance are probably coded by a number of genes interacting with the environment. We analysed a variety of quantitative traits and we identified regions suspected to carry genes affecting birth weight, adult body weight, adult hind leg length, and lamb parasite resistance.

Summary linkage mapping results are reported in Table 2. The coat colour gene was mapped to chromosome 2, and further analyses have characterized at the DNA level the responsible gene (see Gratten *et al.* in this issue) and its surrounding region (see Slate *et al.* in this issue). The coat pattern gene was localized on chromosome 13 where a strong candidate gene (*Agouti*) lies, and thus it should be feasible to identify the molecular basis of colour pattern variation. Finally, in agreement with previous findings in domestic sheep, chromosome 10 carries at least one gene determining the three types of horns observed in Soay sheep. With respect to the quantitative analysis, we found suggestive evidence of a region affecting birth weight on chromosome 8 (LOD= 2.53, the LOD is a measure of statistical evidence); adult body weight shows suggestive linkage on chromosome 6 (LOD= 2.05); hind leg length seems to be affected by a region on chromosome 15 (LOD= 2.75). Finally, parasite resistance in lambs is possibly due to genes on chromosome 16 (LOD= 2.18). The region identified for parasite resistance does not correspond with those previously reported (see Beraldi *et al.* Annual Report 2004); this inconsistency is probably due a more refined definition of parasite resistance and a more complete analysis of the data here.

This information can now be integrated into ecological studies to relate the genetic make up of an individual, or population, to its environment in order to understand the pressure of selection and the trend of evolution on target genetic regions.

Table 2. – Summary of the linkage mapping

Trait	Heritability (%) ^a	Chromosome (Position cM) ^b	LOD ^c
Coat colour	100	2 (96.8)	29.5
Colour pattern	100	13 (74.6)	3.89
Horn type	100	10 (21.1)	6.12
Birth weight	16	8 (130)	2.53
Body weight	19	6 (6)	2.05
Hind leg length	46	15 (113)	2.75
Parasite resistance	17	16 (52)	2.18

^a, the heritability is the proportion of variation due to the effect of (non-interacting) genes; ^b, distance from one chromosomal end, cM (centimorgan) is a measure of genetic distance; ^c, the LOD score is the significance for the presence of a genetic effect in a tested region. LOD>3.3 means highly significant, LOD>1.86 means suggestive significance.

The genetic basis of coat colour variation in Soay sheep.

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

Soay sheep on Hirta, St Kilda are either dark brown or light tan, depending on inheritance of a single gene with two alleles, where dark is dominant to light. Using a candidate gene approach, we have previously shown that this gene is likely to be tyrosinase-related protein 1 (*TYRPI*), a melanocyte specific protein involved in the production of dark pigments, which are known as eumelanins (Gratten *et al.* 2004 Annual Report). In this report we combine an analysis of the *TYRPI* coding region with whole genome linkage mapping to demonstrate that coat colour variation in Soay sheep is determined by a single mutation in *TYRPI*.

We sequenced the entire coding region of *TYRPI* (1614 base pairs) in six dark and six light Soay sheep, identifying six polymorphic sites (Table 3). Two of these mutations were interesting because they would change the protein sequence (non-synonymous mutations), whereas the other four mutations would make no difference to the protein sequence (synonymous mutations). One of the non-synonymous substitutions was rare (position 1339), but the G→T substitution at nucleotide position 869 in exon IV (hereafter *TYRPI* 869^{G→T}) was perfectly associated with coat colour; all light sheep had two copies of T at this position, whereas dark sheep had either one or two copies of G (Fisher's exact test, $p=0.002$). This fits the most likely model of inheritance in which dark (G allele) is dominant to light (T allele). We then genotyped *TYRPI* 869^{G→T} in a pedigree of 585 Soay sheep and demonstrated an almost perfect association with coat colour (X^2

test, $p=3.21 \times 10^{-11}$, LOD=110.20). The only exceptions were three individuals; one dark individual with a ‘light’ genotype (TT) and two light individuals with ‘dark’ genotypes (both GT; see below).

Table 3. Sequence polymorphisms in the *TYRP1* coding region in dark and light Soay sheep. Dots indicate identity to the sequence in the top row. Non-synonymous polymorphisms are shown in bold font.

Sheep ID #	Phenotype	TYRP1 Nucleotide position					
		90	869	1107	1339	1422	1470
6048	Dark	C/C	G/G	C/C	A/A	T/T	A/A
6034	Dark	C/T	.	C/T	A/G	.	A/C
6047	Dark	T/T	G/T	.	.	C/T	A/C
6037	Dark	C/T
5551	Dark	C/T	G/T	.	.	C/T	A/C
5591	Dark	C/T	G/T	.	.	C/T	A/C
5919	Light	T/T	T/T	.	.	C/C	C/C
5467	Light	T/T	T/T	.	.	C/C	C/C
4308	Light	T/T	T/T	.	.	C/C	C/C
5822	Light	T/T	T/T	.	.	C/C	C/C
5632	Light	T/T	T/T	.	.	C/C	C/C
5927	Light	T/T	T/T	.	.	C/C	C/C

The *TYRP1* 869^{G→T} polymorphism is predicted to cause the replacement of a polar amino acid (cysteine) with a non-polar amino acid (phenylalanine) at codon 290 (C290F); this is significant because changes in the polarity of amino acids can influence the three dimensional structure and activity of enzymes. An amino acid alignment for *TYRP1* indicated that the cysteine residue at codon 290 is conserved within vertebrates (data not shown), suggesting that nucleotide position 869 is under strong functional constraint. Together these observations suggest that the *TYRP1* 869^{G→T} mutation may cause changes in the conformation and activity of alternate *TYRP1* proteins, such that the quantity (or quality) of eumelanin produced in individuals with two copies of the recessive T allele is reduced, resulting in light coat colour. In domestic sheep tan coat colour is known to result from a decrease in the ratio of eumelanin to pheomelanin (light pigment), relative to black sheep. The *TYRP1* 869^{G→T} polymorphism segregating in Soay sheep is novel, but single base mutations in *TYRP1* are known to be associated with coat colour variation in other domestic mammals and with albinism in humans.

To confirm the results of the candidate gene analysis we added *TYRP1* 869^{G→T} to a Soay sheep genetic linkage map of ~250 microsatellite markers (see Beraldi *et al.*, this report) and performed a whole genome scan for the coat colour locus. *TYRP1* mapped to chromosome 2, in the vicinity of marker BMS678, and the genome scan revealed extremely tight linkage between coat colour and *TYRP1* (LOD=29.50, recombination fraction=0cM; Figure 1). No other genomic region was linked to coat colour. The strong consensus between the candidate gene and linkage mapping analyses is convincing enough to suggest that the three cases where *TYRP1* 869^{G→T} did not co-segregate with coat colour were due to errors in the pipeline from field to final genotype.

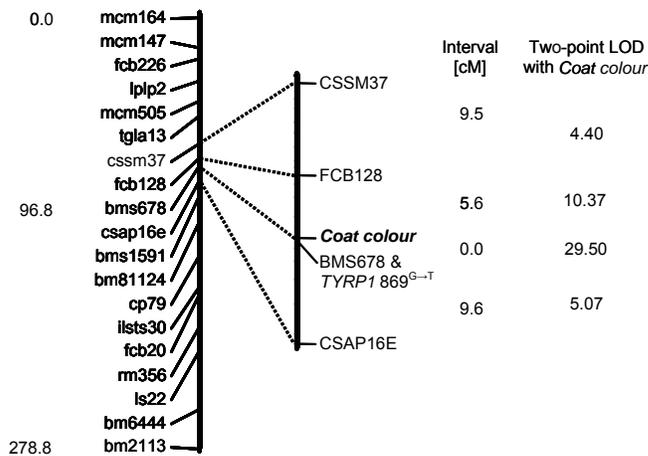


Figure 21. Detailed linkage map of Soay sheep chromosome 2, showing the location of *TYRP1* 869^{G→T} and coat colour. Intervals are sex-averaged and reported in Kosambi centiMorgans.

We have identified the causal mutation underlying coat colour variation in Hirta Soay sheep. Our next aim is to genotype the *TYRP1* 869^{G→T} mutation in all individuals that have been sampled in the history of the project. We will also examine DNA sequence variation within and adjacent to *TYRP1*. These data will allow us to examine alternate hypotheses for the maintenance of genetic variation for coat colour in the study population, including balancing selection and admixture (see Slate *et al.*, this report).

Are Soay sheep an admixed breed?

Jon Slate, Jake Gratten, Dario Beraldi, Bethan Lowder and Josephine Pemberton.

Elsewhere in this report we describe how coat colour in Soay sheep appears to be determined by DNA variation in the coding region of the *TYRP1* gene (See Gratten *et al.*, previous item). Analysis of sequence variation in and around this gene can reveal how selection and demographic factors have operated in the past. Interestingly, the allele that causes the light coat colour (known as the *T* allele) is perfectly associated with an allele at BMS678, the (physically) closest microsatellite DNA marker to *TYRP1*. All sheep with two copies of the *T* allele have two copies of an allele at BMS678 called 124. All sheep that lack the *T* allele have zero copies of the 124 allele at BMS678. This type of statistical association, known as linkage disequilibrium, can reveal much about a population's history. Extrapolating from the sequenced cattle genome, the gene and the marker are at least 20,000 basepairs apart from each other, on chromosome 2. To see an association as pronounced as this, over this distance, requires either (a) selection to be acting on the gene or (b) some sort of admixture between Soay sheep and another population of sheep which introduced the light colour variant to the population. If the former is true, we would not expect to see similar patterns elsewhere in the genome, but admixture should cause similar patterns elsewhere. We have now examined genetic variation and linkage disequilibrium at three other regions of the genome (on chromosome 3 and two different regions of chromosome 13), and we see similarly pronounced levels of linkage disequilibrium elsewhere. This suggests that reasonably recent (within the last few hundred years) admixture has occurred.

Before the St. Kildans left Hirta in 1930 they farmed more modern breeds such as Cheviot sheep. These animals were taken with the St Kildans during the evacuation and all stragglers were reputedly shot before Soay sheep were introduced in 1932. However, it is possible that some animals survived and subsequently bred with Soay sheep on Hirta. If this scenario were true, then Hirta Soay sheep are not purebreeds but Soay sheep on Soay could be. We regard this explanation as unlikely, because both the light and dark coat colours occur on Soay. If admixture is responsible for the coat colour polymorphism we see today, then admixture must have occurred on Soay itself. A feasible hypothesis is that the St Kildans occasionally put Cheviot, Blackface or Boreray sheep onto Soay so admixture occurred *prior* to the establishment of the Hirta population in 1932. It has been suggested that when the St Kildans were taxed one sheep in seven, the Factor may have stored these sheep on Soay. More data are required to test the various hypotheses, which at present must be regarded as speculative. Analysis of the *TYRPI* gene in Cheviots, Blackface and Boreray sheep may help shed light on this mystery.

Our findings do not lessen the interest or uniqueness of Soay sheep, since even with the signature of another breed within them, they appear uniquely separated from all other European sheep breeds in wider genetic analyses.

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APPENDIX A: PERSONNEL CHANGES & SCHEDULE OF WORK

Personnel Change

This year Barbara Craig and Louisa Tempest completed their PhD studies.

Schedule of work on St Kilda

Winter - Spring

Jill Pilkington, Josephine Pemberton and two volunteers monitored mortality from February 4th until May 13th. During this period, detailed data and skeletal material were collected on individual sheep found dead, and samples were taken for parasitological study from a random selection of 12 lambs, yearlings and adults, 6 males and 6 females in each age class.

From mid March until May 13th, Jill Pilkington, and four volunteers carried out ten population censuses and tagged and sampled lambs for ongoing genetic studies. 207 lambs were born to 193 ewes; these figures include 14 sets of twins (7 ewes held both lambs, 3 lost one twin and 4 lost both lambs). 119 lambs (49 male and 70 female) were caught and tagged; a further 88 lambs died before any tagging attempt.

Summer

Jill Pilkington and two volunteers returned to Hirta on July 19th to carry out ten population censuses, conduct mortality searches (yielding 2 tagged dead animals), and prepare for the main catch-up of study area sheep. The catch-up took place from August 9th – 21st, was led by Josephine Pemberton, and conducted by a team of 11 additional project members and volunteers. 149 sheep were caught and processed, of which 56 were lambs (23 males and 33 females), 3 were yearlings (all male), 14 were adult males, and 76 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic analyses. 21 Sheep were retagged because of damaged or missing tags. 6 previously untagged lambs were caught and processed. Gina Prior, a long term volunteer, remained on Hirta until 30th August to complete parasite counts and vegetation monitoring.

Autumn

From October 18th to December 2th Jill Pilkington and two volunteers monitored the mating period, capturing and processing 17 incoming tups, 11 resident tups and carrying out ten population censuses. Three dead sheep were found.

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