ST. KILDA SOAY SHEEP PROJECT:
ANNUAL REPORT 2014

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POPULATION OVERVIEW ........................................................................................................... 2
REPORTS ON COMPONENT STUDIES ...................................................................................... 4
Vegetation .................................................................................................................................. 4
Vegetation and maternal care provisioning .................................................................................. 6
Vitamin D status predicts reproductive fitness in a wild sheep population ................................. 8
Markers of oxidative stress are uncorrelated in wild mammals ................................................ 9
Quantitative estimation of organ damage during a population crash in Soay sheep .................. 10
Immunology: T cells, differential white blood cells and antibodies .......................................... 12
Heterochrony in Soay sheep ........................................................................................................ 14
Heterogeneity of genetic architecture of body size traits in Soay sheep .................................... 15
Individual recombination rate is under genetic control in Soay sheep ...................................... 17
PUBLICATIONS ........................................................................................................................ 21
ACKNOWLEDGEMENTS ............................................................................................................. 22
APPENDIX A: PERSONNEL NEWS & SCHEDULE OF WORK ................................................. 22
Population Overview

The sheep population on Hirta entered 2014 at a moderate level and there was relatively high mortality over winter with 185 tagged animals being found dead within the study area. Lambing began on the 5th of April with 71% of lambs born surviving (Fig. 1).

Figure 1. The temporal distribution of lamb births during 2014.

In December 2014, 593 tagged sheep were believed to be alive on Hirta, of which 482 regularly used the study area, a decrease of 11.6% 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 2014.
Figure 3. The number of tagged sheep regularly using the study area since 1985.

One whole-island count yielded 1774 tagged and untagged sheep, with the details displayed in Table 1. The total population had increased by 0.02% since summer 2013 when it was estimated as 1742. This gives a delta (calculated as ln \((N_{t+1}/N_t))\) of +0.018. The whole island counts are also shown in Figure 3.

Table 1. Demographic and geographic distribution of sheep observed during the count of Hirta on August 10th 2014. Coat colours are DW = dark wild, DS = dark self, LW = light wild, and LS = light self.

<table>
<thead>
<tr>
<th>Location</th>
<th>Females</th>
<th>Males</th>
<th>Lambs</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DW</td>
<td>DS</td>
<td>LW</td>
<td>LS</td>
</tr>
<tr>
<td>Conachair/Oiseval</td>
<td>216</td>
<td>8</td>
<td>57</td>
<td>0</td>
</tr>
<tr>
<td>Mullach Bi / Cambir</td>
<td>241</td>
<td>7</td>
<td>74</td>
<td>2</td>
</tr>
<tr>
<td>Ruaival/Village</td>
<td>249</td>
<td>12</td>
<td>78</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>706</td>
<td>27</td>
<td>209</td>
<td>3</td>
</tr>
</tbody>
</table>
Vegetation.

Mick Crawley.

2014 was a year of superlatives as far as the plants were concerned. We recorded the highest numbers of flowering stems for many of the dominant grasses, the highest total shoot biomass since 2003, second highest tussock density and second lowest gap density since 1993. The most abundant grass of the inbye grasslands, *Holcus lanatus*, showed its highest ever biomass (Fig. 4), suggesting that a crash during winter 2014-15 is unlikely.

It is plausible that immediately post-crash (during the growing seasons of 2012 and 2013), the plants were investing in below-ground storage and reserve-replenishment following 8 years of continuously high grazing pressure. This, in turn, allowed a mass flowering in 2014 for grasses like *Holcus lanatus* and *Agrostis capillaris* and herbs like *Potentilla erecta*. In particular, *Cerastium fontanum* showed a huge increase in flower production compared with its long-term average, producing the highest ever mean value recorded from this species (Fig. 5). As usual, however, the grazing pressure was sufficiently high to prevent any flowering at all by the most palatable species like *Festuca rubra*, *Rumex acetosa* and *Achillea millefolium* except in places like sea cliffs and cleit roofs that are inaccessible to the sheep.

In parallel with the long-term increase in sheep numbers, there has been a long-term decline in the mass of dead organic matter (Fig. 6). This downward trend is mirrored by a long-term upward trend in the abundance of mosses and liverworts, especially in the winter months (data not shown). The steady long-term increase in heather biomass continues, measured both as green shoots or woody tissue (Fig. 7). Evidently, *Calluna* is not suffering as a result of prolonged exposure to the food-limited sheep population on Hirta, despite the increase in sheep numbers.

![Figure 4](image-url)  
*Figure 4.* Holcus lanatus live biomass (mean g per 20x20cm quadrat) in August (upper points) and March (lower points) over the period from August 1993 to August 2014. The Holcus biomass was higher in August 2014 than in any previous year by more than 30%.
Figure 5. Flowering in Cerastium fontanum (Caryophyllaceae). Mean flower stem densities in August (averaged across \( n = 300 \) quadrats, each of 40x40cm) in the inbye grasslands over the period 1998-2014. The flower stem densities were higher in August 2014 than in any previous year by more than 15%.

Figure 6. The long-term increase in sheep numbers is associated with a long-term decline in dead organic matter in the sward of the inbye grasslands. Uneaten grass typically turns into dead organic matter before decomposing, and so tends to be higher in March than in August (the left-most point is August 1993 and the right-most is August 2014). Note, however, that relatively high grass growth and relatively low sheep numbers in 2013 and 2014 meant that we recorded relatively high dead organic matter by recent (post 2010) standards.
Figure 7. Increasing sheep numbers are associated with an increase in heather biomass (Calluna vulgaris, Ericaceae) in the out-by, measured as total biomass (green shoots plus wood; red points) or woody biomass (black points). The time series is made up of two points per year, one measured in March and one in August (the left-most point is from August 1993 and the right-most is from August 2014). The difference in elevation between the two lines represents the biomass of green shoots, potentially available as food to the sheep, and this is typically higher in August than in March.

Vegetation and maternal care provisioning.

Charlotte Regan, Mick Crawley, Per Smiseth and Josephine Pemberton.

Organisms are continually faced with choices over how to use the limited resources available to them, giving rise to trade-offs where a beneficial change in one trait results in a detrimental change in another. The idea of trade-offs is a key principle within life history theory, with the so-called cost of reproduction being perhaps the most prominent. Such an idea stems from the assumption that individuals are under selection to maximise the number of offspring they rear successfully over their lifetime. To do this, they must balance the benefits of investing in current offspring against those provided by future reproductive opportunities. The cost of reproduction consists of two major components, costs realised as reductions in survival and costs in terms of future reproduction. The cost of reproduction is inescapably linked with parental investment because parental investment increases the survival likelihood of offspring at a cost to the ability of a parent to invest in future offspring. Because of this, parental investment and consequently parental behaviour are at least partially determined by parental investment decisions in the past.
Though the study of life history theory and parental care goes back many decades there has been limited research surrounding the effect of environmental variation on life history trade-offs and parental care. The St. Kilda Soay sheep population provides a rare opportunity to do this due to the detailed information available on individual life history and the complex data available enabling us to investigate various sources of environmental variation including weather and vegetation quality/quantity.

Previous work has shown that differences in the availability of one grass species, *H. lanatus*, are associated with ewe lifetime reproductive success with this relationship driven at least partially by differences in lamb survival (see 2013 report). As a result, we wanted to understand if this difference in survival was driven by differences in maternal care provisioning. This was done by estimating home ranges for individual ewes using lifetime location data and using species composition data for each hectare of the study area, collected by MJC, to calculate mean percentage covers of *H. lanatus* for each individual female. Forty females were then selected to be the subject of behavioural watches, twenty of which had home ranges containing low *H. lanatus* covers (6-18%) whilst the other twenty had home ranges rich in *H. lanatus* (27-42%). These ewes and their lambs were watched for 1 hour, between 6 and 8 times within the first 1-15 weeks of the lamb’s life. During each watch data were collected on suckling frequency and duration, as well as the time each lamb spent grazing, playing and resting, in order to establish whether any difference in suckling behaviour impacted their investment into other behaviours.

We found a difference in care provisioning between ewes in the two groups. Lambs born to mothers whose home ranges were low in *H. lanatus* saw a greater proportion of their suckles rejected (Fig. 8). This occurred despite the fact that their total suckling frequency and duration were in line with lambs whose mothers had *H. lanatus*-rich home ranges. This suggests that despite suckling for the same amount of time, their nutritional needs were not being met and they were therefore attempting to suckle more frequently, though the ewe was unable to accommodate these extra attempts. It is not yet clear whether this difference in care provisioning translates into differences in other aspects of lamb behaviour. There was some evidence that lambs whose mothers inhabited areas low in *H. lanatus* ceased playing at an earlier age, but more data will be needed to fully establish this. A second year of behavioural data collection in 2015 will enable such questions to be more answered more conclusively.

This is however one of the first studies to demonstrate that environmental differences at the home range scale impact behaviour over the period of parental care in a naturally living mammal.
Figure 8. The proportion of failed suckles initiated by a lamb for ewes with home ranges low in H. lanatus (low group) and ewes with home ranges rich in H. lanatus (high group).

Vitamin D status predicts reproductive fitness in a wild sheep population.


Historically, vitamin D deficiency has been mainly linked to skeletal disorders such as rickets. However, over the past two decades vitamin D deficiency has been associated with a wide range of diseases and all-cause mortality in humans, and with poor reproductive performance in laboratory rodents. Circulating levels of vitamin D metabolites vary widely in healthy human populations. This variation has a heritable component, and it seems likely that this observed genetic variation has been shaped by natural selection in our evolutionary past. However, we currently have no idea how natural selection directly acts on variation in vitamin D metabolism due to a total lack of studies in wild animals. Soay sheep are a particularly attractive model system in which to probe the relationship between vitamin D and ecological fitness since we can dissect out the contribution that cutaneous production of vitamin D₃ and orally consumed vitamin D₂ make to overall vitamin D status.

We measured serum 25 hydroxyvitamin D (25(OH)D) concentrations, which is the most widely used marker of vitamin D status, from samples taken from 101 Soay ewes during the August catch in 2012. We found that total 25(OH)D was strongly influenced by age, and that light coloured sheep had higher 25(OH)D₃ (but not 25(OH)D₂) concentrations than dark sheep (Fig. 9). Since the coat colour polymorphism in Soay sheep is controlled by a single locus, this finding suggests that vitamin D status is heritable in this population. We also observed a very strong relationship between total 25(OH)D levels in summer and a ewe’s fecundity the following spring. This association resulted in a positive association between total 25(OH)D and the number of lambs produced that survived their first year of life, an important component of female reproductive fitness. Our study provides the first insight into
naturally-occurring variation in vitamin D metabolites, and offers the first evidence that vitamin D status is both heritable and under natural selection in the wild.

![Figure 9. Association between age, coat colour and serum vitamin D concentrations in female Soay sheep.](image)

### Markers of oxidative stress are uncorrelated in wild mammals.

Louise Christensen, Jane Reid, Colin Selman, Jon Blount and Dan Nussey.

Reactive oxygen species (ROS) are produced as part of normal metabolism, but can cause damage to lipids, proteins and DNA. To prevent this damage, organisms use a range of antioxidant molecules, which they obtain from their diet or synthesise within the body, that act to quench ROS molecules. The balance between ROS production and antioxidant defence is thought to be central to the maintenance of organismal function, and the accumulation of ROS-induced damage has been implicated as a cause of ageing. When the balance is tipped towards ROS production and ROS-induced damage, this is referred to as oxidative stress.

There is much current interest in oxidative stress within evolutionary ecology, and some suggestion that markers of oxidative stress are correlated with important life history traits like growth and reproduction. However, researchers have used a wide range of different markers of damage and antioxidant capacity in these studies. For findings about oxidative stress to prove general, we must assume that different markers of damage would be closely correlated and likewise, there would be strong associations between different antioxidant measures within study systems. However, this assumption is rarely tested.

Between 2010 and 2013, we measured two markers of ROS-induced damage and two markers of antioxidant defence in blood samples collected from Soay sheep each August.
Specifically, the markers we have used are: protein carbonyls (PC, an indicator of protein oxidative damage) and malondialdehyde (MDA, an indicator of oxidative damage to lipids), as well as superoxide dismutase (SOD) and total antioxidant capacity (TAC), two measures of antioxidant protection. We found no evidence of any consistent correlations amongst these four markers across or within years, age-groups or sex (Fig. 10). This suggests that different markers may be responding to oxidative stress or other factors in different ways, and does not support the contention that one can generalise findings across different markers of oxidative stress. Having established that these four measures need to be treated as independent biological markers, our next steps will be to investigate their relationships with life history traits at different life stages in the Soay sheep.

**Figure 10.** The correlations (above right) and correlation coefficients (below left) between protein carbonyls (PC), malondialdehyde (MDA), total antioxidant capacity (TAC) and superoxide dismutase (SOD) from Soay sheep captured and sampled in 2011. N= 260.
Quantitative estimation of organ damage during a population crash in the Soay sheep.

Romain Garnier, Quentin Caudron, Bryan Grenfell and Andrea Graham.

Necropsies of individuals that die during population crashes can provide important information on causes of death, especially when samples are taken from specific organs and analyzed at a microscopic, or histopathological, level. However, classical techniques in histopathology have several limitations: e.g., the microscopy is very time consuming and somewhat sensitive to how precisely the samples have been preserved. Field conditions and the large number of individuals recovered on Hirta during crashes are thus far from ideal. Furthermore, classical histopathological results take the form of subjective semi-quantitative scores that are challenging to analyze at the rigorous level required in ecological studies. There is therefore increasing interest in quantitative, high-throughput methods for histopathological analyses.

We have now developed such methods. Because malnutrition contributes to mortality in the Soay sheep population of Hirta, we chose to first focus on the liver, an organ that plays a central role in protein metabolism. We quantified both structural and inflammatory liver damage in necropsy samples collected by the field team from over 140 sheep during the 2011-2012 winter. Samples were formalin-fixed and stained with Hematoxylin and Eosin, that respectively color the nuclei in blue/purple and the cytoplasms in red. We took high resolution micrographs at two different magnifications: a wide 4x view allows measurement of structural variations; a narrow 10x view allows quantification of cell nuclei in inflammatory foci. We used image-processing software to extract data from the images. We paired these analyses with a classical histopathology approach, to validate our measures.

Preliminary results show that the computer is able to detect the outlines of inflammatory foci as well as the human eye (Fig. 11, A and B). In addition, the image processing approach generates measures (notably of inflammation) that correlate with classical methods but can also provide new insights into the structure of the liver at the time of death. We are now studying these quantitative measurements along with plasma markers of malnutrition and immunity that are now available for the Soay sheep population. Ultimately, we aim to quantify the relative roles of nematodes and malnutrition in the death of Soay sheep during winter. Finally, our histopathological investigation has led to some surprising discoveries, including a potential role of bacterial infections at the time of death (Fig 11, C and D).
Figure 11: (A) Computer-aided determination of inflammatory foci in a 10x micrograph of Soay sheep liver. (B) Correlation between the size of the inflammatory foci determined by a human operator and by the image processing algorithm. (C and D) Examples of damage found in the liver of Soay sheep: focal granuloma with the presence of a high density of immune cells (C); and hepatic abscess with visible bacteria marked by an arrow (D).

Immunology: T cells, differential white blood cells and antibodies.

Rebecca Watson, Rose Zamoyska, Kathryn Watt, Jill Pilkington, Josephine Pemberton, Daniel Nussey and Tom McNeilly.

The immune system is hugely important in the defence against infectious diseases and pathogens, but this protection comes at a cost. Developing, maintaining and controlling such a complicated and diverse system requires resources which could otherwise be allocated to other systems, such as reproduction and growth. While there is a vast amount of research focusing on the immune system in both experimental and laboratory studies, we know little about how immunity impacts the ecology and life history of an individual. Studying immunology in a wild system such as the Soay sheep can allow us to better understand the relationships between immunity and other physiological systems.

We measured a wide range of immune markers, including T cell subtypes, differential white blood cell counts and various antibodies each August from 2011 to 2014. Analyses of the
2011 data suggest that there are no strong relationships between these markers, once age effects have been accounted for. This implies that there is no key marker which can adequately represent the immune system and strengthens the reasoning that it is crucial to measure a wide range of markers in ecological studies. There are clear age trends in most of the markers we have investigated (Fig. 12). There is a strong and significant decline in naïve CD4+, naïve C8+ and gamma-delta T cells. The decline in naïve cells is readily explained by the process of thymic involution, in which the thymus (the organ that produces naïve T cells) deteriorates rapidly from a relatively early age in mammals. We also know from veterinary literature that gamma delta+ T cells are important in young ruminants, but this is the first time that this strong decline has been shown in a wild system. We have also found increases in anti-strongyle nematode antibodies and eosinophil counts with age, which tallies with expectations as the sheep develop immunity to these parasitic worms through early life. 

We are currently undertaking further analyses to test whether and how our panel of immune markers from August 2011 predict August weight, strongyle faecal egg count and over-winter survival of the 2011/2012 population crash.

**Figure 12.** Variation with age in our panel of 11 immune markers, measured in August 2011, with individuals categorised in the lambs, yearlings, adults (2-6 years old) and geriatrics (7 or more years old).
**Heterochrony in Soay Sheep.**

Elis Damasceno and Chris Klingenberg.

It is known that the average body size for the Soay sheep population in St. Kilda has decreased, and a possible reason may be climate change. Because the winters are becoming shorter and less severe, slow growing, smaller animals manage to survive winter, causing both an increase in population size and a decrease in average body size. In this study, we wanted to test if this change in body size is reflected in changes in skull shape. Many studies have already shown that size and shape are intimately correlated, and this correlation is called Allometry. Our results show a strong correlation between size and skull shape (Fig. 13), and therefore, a gradual change in the average skull shape along with size. Shape changes associated with altered growth rates (in this case, slower growth) is a well-studied phenomenon known as heterochrony. Our results show that at least a portion of the sheep are undergoing heterochronic processes, since their skull shape is altered by retarded development. Several different species in several animal families have been found to have undergone heterochronic processes, including salamanders, frogs, rodents, elks, several dog breeds, and even us humans. Studying and discovering cases of heterochrony in the wild is fundamental to the understanding of its causes and consequences as well as its importance as regards to evolutionary processes. The possibility that climate change might be associated with this phenomenon in the Soay sheep sheds new light on the possible consequences of global warming, in a way that hasn't been explored before.

*Figure 13. Scatterplot showing the strong correlation between a measure of a Soay sheep's skull shape and skull size.*
Heterogeneity of genetic architecture of body size traits in Soay sheep.

Camillo Bérénos, Philip Ellis, Jill Pilkington, S. Hong Lee, Jake Gratten and Josephine Pemberton.

Body size in Soay sheep is positively associated with fitness components such as juvenile overwinter survival and fitness predictors such as parasite resistance. Despite this, body size has declined since the start of the project in 1985. Recent studies have shown that the association between size and fitness is non-genetic and that the reduction in body size is likely due to increased over-winter survival of smaller individuals as a result of changing environmental conditions.

To date, most of our knowledge of the genetic architecture of Soay sheep body size has been obtained using pedigree-derived, and more recently, genome-wide SNP marker-derived estimates of relatedness in a quantitative genetic framework. The quantitative genetics of body size is well understood in this system. For example, we know that genes explain a sizeable proportion of phenotypic variance in Soay sheep body size (heritability), heritability of body size increases with age, and genetic correlations among five proxies for body size are fairly large, suggesting that there is overlap in the set of genes which explain phenotypic variation in the different body size traits.

However, in order to better understand how body size evolves, we would like an answer to the following question. Is variation body size traits largely a result of a few genes with large effect, or of many genes each with a small effect? And do certain regions in the genome explain variation in more than one trait? Previous analyses using linkage mapping revealed one significant QTL and several suggestive QTL underlying various body size traits, but it is expected that the current genomic tools will have less bias and far superior power and precision to unravel the genetic architecture of traits in Soay sheep.

We have used genetic information at ~37,000 variable genetic markers (Single Nucleotide Polymorphisms, SNP) in combination with body size data for ~1000 adult Soay sheep to dissect the genetic architecture of five body size traits. We have used three traits which are measured during the annual summer expedition in August (foreleg, hindleg, weight), and two traits which are measured in skeletal remains from individuals found dead (metacarpal length, which is a part of the foreleg bone, and jaw length).

We first partitioned genetic variance for each of the five traits between the 26 sheep autosomes. We found that for all traits, many chromosomes were contributing significantly to phenotypic variation, indicating that genes underlying these traits are widely distributed throughout the genome (Fig. 14). We were then interested whether the physical length of a chromosome predicted the proportion of phenotypic variance it explained. This would be suggestive evidence for the trait being determined by many genes with small effect. The rationale behind this is that those genes are randomly distributed throughout the genome, therefore larger chromosomes harbour more functional loci than smaller chromosomes, consequently giving rise to a positive correlation between chromosome length and phenotypic variance explained. And indeed, for weight and jaw length we observed such a correlation, indicating that these traits are likely influenced by many small effect genes. Interestingly, this correlation was not observed for the three leg length traits (foreleg, hindleg and metacarpal length).
Figure 14: A) The proportion of phenotypic variance for the body size traits explained by each of the 26 autosomes. B) Scatterplot showing the correlation between the physical length of a chromosome and the phenotypic variance it explains. Solid lines are shown for linear regressions which were significant.

We then wanted to know which parts of the genome harboured genes which contributed to body size. We divided the genome into regions of 150 adjacent SNP, which had a mean length of 10Mb, and 1) asked how much of the total phenotypic variance was explained by each 150 SNP region and 2) tested whether or not these regions explained significant amounts of phenotypic variance. We found that for each trait, many regions contributed to phenotypic variance. In addition, more often than not, regions significantly explained variance in multiple traits, highlighting that many of the body size traits have a shared genetic basis. The contribution of regions to trait values was highly correlated between leg length traits, more modestly correlated between hindleg and weight, and weakly correlated between the remaining traits, reflecting that the genetic basis is shared more between some traits than between others.

The previous analyses could not discriminate between a scenario where a chromosome or region contained one (or a few) genes with a large effects, or one where it harboured many linked genes with small effect. We therefore used a method called genome-wide association (GWAS), which tests whether individual SNP loci are associated with trait values and is thus indicative of the presence of a locus with a major effect. No individual SNP was associated with either weight or jaw length, which confirms our suspicions based on the chromosome partitioning analyses (Fig. 14) that these traits are likely only influenced by small effect genes. For the three leg length traits a different pattern was observed, as SNPs on chromosome 16 and 19 were significantly associated (Fig. 15). Both loci had a large effect on leg length, with a reduction in leg length of 10% for individuals homozygous for the rare allele compared to individuals homozygous for the common allele. When we tested how much of the phenotypic variance each of these SNPs explained, they both explained more than 10% of the additive genetic variance for leg length, and explaining virtually all of the genetic variance attributed to the chromosomes or regions they were found on.
Figure 15. Genome-wide association (GWAS) of metacarpal length in Soay sheep. All points above the solid line are genome-wide significant after Bonferroni correction for multiple testing.

In summary, we demonstrate 1) that all five proxies for body size are influenced by many loci distributed across the genome, 2) that there is a substantial overlap in genetic basis underlying the various traits, and 3) that leg length is additionally influenced by two SNPs with a relatively large effect.

Individual recombination rate is under genetic control in Soay sheep.

Susan Johnston, Jon Slate and Josephine Pemberton.

Recombination is a molecular process that takes place during the early stages of gamete production (meiosis), and involves the exchange of large segments of DNA between maternal and paternally inherited chromosomes. This "crossing-over" process breaks down linkage between adjacent loci, and is an important factor in preventing the accumulation of deleterious genetic mutations. The number of cross-overs that occur on a given chromosome will vary; for example, longer chromosomes tend to have more cross-over events, whereas the shortest chromosomes tend to have a higher number of cross-overs in relation to their length.

The importance of recombination in evolution has been the subject of a vast theoretical body of literature, but empirical studies have been limited by a lack of genetic resources. In recent years, improvements in genomic technologies have shown that variation in the frequency of crossing-over can be heritable and can be associated with variation in reproductive success. However, in-depth studies have been limited to model species, such as humans and mice, or animals under strong selection regimes, such as cattle. Therefore, we aimed to use genetic data in the Soay sheep to answer three questions about how and why recombination rate can vary in a wild population:
1. How does recombination rate vary across the genome?
2. Is individual recombination rate associated with phenotypes, life-history or fitness?
3. Is recombination rate heritable, and is it driven by particular gene variants?

We used data from the Ovine SNP50 BeadChip to characterise variation at ~40,000 single nucleotide polymorphisms (SNPs) in ~5,600 Soay sheep. This allowed us to estimate the frequency and approximate positions of cross-over events across the genome in 1860 gametes (that had originated from 614 different individuals), incorporating genetic information from focal individuals (i.e. the individual in which the gamete was formed), their parents and their offspring. We summarised information on cross-overs to create “linkage” maps of chromosomes, where chromosome length is measured in centiMorgans (cM, where 1 cM is equivalent to 1 crossover event per 100 meiosis events). Within focal individuals, “global” recombination rates were defined as the total number of cross-overs detected within a gamete.

1. **Recombination rate across the genome.** Individuals had an average of 30.5 cross-over events per gamete. There was a strong correlation between physical chromosome length and the linkage map length (linear regression, Adjusted $R^2 = 0.95$; Fig. 16A). The recombination rate on individual chromosomes was highest in the shortest chromosomes, and decayed as the physical length increased (Fig. 16B).

2. **Association between recombination rate and phenotype.** We examined the association between recombination rate and a number of phenotypes (sex, weight, gut parasite loads), fitness measures (annual and lifetime survival, annual and lifetime reproductive success) and common environmental variables (birth year, offspring birth year, population density). We found that recombination rate was not associated with any of these factors, with the exception of sex, where males had an average of 7 more crossover events per gamete ($P < 0.001$; Fig. 17).

3. **Heritability of recombination rate.** We used an animal model approach using a genomic relatedness measures to determine how much variation in recombination rate is due to genetic effects. Around 12% of variation in recombination rate is heritable ($h^2 = 0.127$), whereas the rest is likely due to chance processes. We adapted this model to look at the effect of specific regions of the genome on recombination rate (regional heritability analysis), and found that a region on chromosome 3 explains around 27% of heritable variation (Fig. 18). Future work aims to identify candidate genes which may occur in this significant region.
Figure 16. Comparisons of recombination rate by chromosome. **A:** Comparison of physical chromosome length in megabases (MB) and linkage map length in centiMorgans (cM); **B:** Comparison of physical chromosome length and chromosome-wide recombination rate (MB per cM). Numbered points indicate the chromosome number (1 to 26) or the X chromosome.

Figure 17. Recombination rate in female (930 observations in 416 individuals) and male Soay sheep (930 observations in 198 individuals).
**Figure 18.** Regional heritability analysis of recombination rate. Each point represents a 150 SNP interval in which models with and without a particular genomic region were compared. The horizontal line indicates the significance thresholds for genome-wide significance; any point above this line indicates a region of the genome with a significant effect on recombination rate across the rest of the genome.
PUBLICATIONS


IN PRESS

ACKNOWLEDGEMENTS

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APPENDIX A: PERSONNEL NEWS & SCHEDULE OF WORK

Personnel News

Maria Joao Janeiro and Darren Hunter started PhD studentships at St Andrews with Michael Morrissey, studying aspects of natural selection on Soay sheep and in other study populations. Alex Chambers started a PhD in parasitology at the Royal (Dick) Vet school, Edinburgh.

Schedule of work on St Kilda

Winter - Spring

From March 11th until May 13th, Jill Pilkington, Kara Dicks and Conor Bolas carried out ten population censuses and tagged and sampled lambs, with assistance during the peak of lambing from Michael Morrissey and Will Fincham. 238 lambs were born to 214 ewes; these figures include 24 sets of twins (16 ewes held both lambs, 6 ewes held one lamb and lost one and 2 ewes lost both lambs). 161 lambs (86 male and 75 female) were caught and tagged; a further 69 lambs died before any tagging attempt. Mick Crawley and two assistants collected vegetation data. Charlotte Regan, Elis Damasceno and Phoebe Hopper collected suckling data.

Summer

Jill Pilkington, Becky Holland and Conor Bolas returned to Hirta on July 11th 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. Charlotte Regan conducted further suckling watches assisted by Will Fincham. The catch-up took place from August 6th – 20th and was conducted by a team of 12 additional project members and volunteers. 314 sheep were caught and processed, of which 125 were lambs (68 males and 57 females), 28 were yearlings (8 males and 20 females), 25 were adult males, and 136 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic
analyses. 16 Sheep were retagged because of damaged or missing tags. 12 previously untagged lambs, 3 yearlings and 6 adults were caught and processed. Mick Crawley and two assistants collected vegetation data. Jill Pilkington and two volunteers remained on Hirta until 2nd September to complete parasite counts and pasture larvae counts.

**Autumn**

From October 23rd to December 9th Jill Pilkington, Michael Morrissey and Xavier Bal carried out ten population censuses, monitored the mating period, capturing and processing 40 incoming tups, 28 resident tups and 3 resident ewes. 23 previously darted, non-resident tups were seen in the study area during this rut. Nine dead sheep were found.