ST. KILDA SOAY SHEEP PROJECT:
ANNUAL REPORT 2012

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The sheep population on Hirta entered 2012 at a very high level and, as a result, there was substantial mortality in the first few months of the year. 308 tagged and 75 untagged sheep were found dead within the study area between February and May of 2012. Lambing began on the 27th of March with 68% of lambs born surviving (Fig. 1).

Figure 1. The temporal distribution of lamb births during 2012.

In December 2012, 622 tagged sheep were believed to be alive on Hirta, of which 362 regularly used the study area, a decrease of 44.2% 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 2012.
Figure 3. The number of tagged sheep regularly using the study area since 1985.

One whole-island count yielded 1292 tagged and untagged sheep, with the details displayed in Table 1. The total population had decreased by 39.8% since summer 2011 when it was at 2147. This gives a delta (calculated as $\ln (N_{t+1}/N_t)$) of -0.51. 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 18th 2012. Coat colours are $DW =$ dark wild, $DS =$ dark self, $LW =$ light wild, and $LS =$ light self.

| Location               | Females | | | | Males | | | | | | Lambs | Total |
|------------------------|---------|---|---|---|-------|---|---|---|---|---|---|---|---|
| Conachair/Oiseval      | DW 168  | DS 7  | LW 44 | LS 0 | DW 24 | DS 0  | LW 1  | LS 0 | 138 | | 382 | |
| Mullach Bi/Cambir      | DW 202  | DS 5  | LW 56 | LS 2 | DW 17 | DS 0  | LW 6  | LS 0 | 180 | | 468 | |
| Ruaival/Village        | DW 180  | DS 9  | LW 58 | LS 1 | DW 38 | DS 1  | LW 4  | LS 0 | 151 | | 442 | |
| Total                  | DW 550  | DS 21 | LW 158| LS 3  | DW 79  | DS 1  | LW 11 | LS 0 | 469 | | 1292| |


Vegetation.
Mick Crawley.

If you are a regular reader of this column you will be familiar with our mantra: “More sheep, less grass”. This should have a flip side that might be expected to apply after crashes: “Less sheep, more grass”. But not this time. In 2012 we got less sheep, less grass, with a data point in a new part of the graph (Fig. 4). The cause of this was probably the protracted and unusually dry weather during the rapid growth phase.

![Figure 4](image.png)

**Figure 4.** August inbye grass biomass as a function of August whole-island sheep count. The data point for 2012 is the larger red symbol.

The productivity data from the pyramids (the movable temporary sheep enclosures) are now plentiful enough to have a look at. We had imagined that climate change associated with winter warming would mean that grass growth between August and March would increase, and that this would benefit the sheep by extending the amount of offtake available over the winter, during what farmers call the Hungry Gap. As you can see (Fig. 5) there is absolutely no hint of a trend in these data. On the other hand, and again completely contrary to what we had expected, there is a highly significant upward trend in summer grass growth over the same period since 2000 (Fig. 6).
The work to produce a fine-scale vegetation map of the study area is now complete. We have separate floras for each of the 100 x100 m squares with a species list for all the vascular plants along with percentage cover data to show the abundance of each. We can use these to calculate a food quality index for each hectare, and combining this with the home range data for individuals from the censuses, we can work out the quality and quantity of food to which each animal is exposed over its entire life span. Figs. 7 & 8 show two contrasting maps: high quality food as represented by *Holcus lanatus*, and low quality food as represented by *Calluna vulgaris*. The dots on the maps show hectares with more than median levels of the plant (in red) and hectares with less than median levels (in green). A spin off from this work is that we now know the identities of the commonest (*Anthoxanthum odoratum*) and rarest plant species (*Ophioglossum vulgatum*) in the study area.

*Figure 5.* Plant productivity as measured as the difference in green grass biomass inside and outside temporary sheep exclosures during the over-winter months August-March. There is no hint of any upward trend in over-winter grass growth in the period 2000-2012.

*Figure 6.* Plant productivity as measured as the difference in green grass biomass inside and outside temporary sheep exclosures during the growing season months March-August. There is a highly significant upward trend from the late 1990s to the present.
Figure 7. The hectare scale distribution of Holcus lanatus, showing the places where cover is greater than median (in red) and below median (green). The inbye grasslands within the Head Dyke show up clearly as do the coastal grasslands leading out to Ruaival.

Figure 8. The hectare scale distribution of Calluna vulgaris, showing the places where cover is greater than median (in red) and below median (green). The upper slopes of Oiseval (right), Conachair (centre) and Mullagh Sgar (left) stand out clearly.
Parasitological & epidemiological research in Soay sheep.

Survey for viral and bacterial infections

To broaden our understanding of infections borne by the sheep, we have tested blood samples for evidence of exposure to viruses and bacteria that are common in sheep elsewhere in Scotland. Previous surveys (results of which were included in the 2001 Annual Report) revealed little or no evidence of such infections in the sheep but were limited in scope, in terms of the number of sheep tested, capture years sampled, and infectious agents targeted: 196 sheep were tested for Maedi-Visna in 1986 and 50 were tested for Enzootic Abortion of the Ewe (EAE), Border Disease, Mycoplasma ovipneumoniae and Johne’s disease in 2000. We’ve now undertaken a more comprehensive serological survey of 750 sheep sampled between 1997 and 2010 and also tested 2010 samples for a herpesvirus detectable by PCR of blood cells. Testing was contracted via Scottish Agricultural College Consulting Veterinary Services, the Animal Health and Veterinary Laboratories Agency, and Moredun Research Institute. Results are summarized in Table 2.

Table 2. Summary of results of infectious disease survey.

<table>
<thead>
<tr>
<th>Infectious agent</th>
<th>Present or absent, 1997-2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lentivirus (Maedi-Visna)</td>
<td>Absent; confirmation pending</td>
</tr>
<tr>
<td>Orfpox</td>
<td>Absent; confirmation pending</td>
</tr>
<tr>
<td>Ovine Herpesvirus (OHV-2)</td>
<td>Absent in 2010; confirmation pending</td>
</tr>
<tr>
<td>Parainfluenza</td>
<td>Absent</td>
</tr>
<tr>
<td>Pestivirus (Border Disease)</td>
<td>Absent</td>
</tr>
<tr>
<td>Chlamydophila spp. (EAE)</td>
<td>Absent; confirmation pending</td>
</tr>
<tr>
<td>Leptospira spp.</td>
<td>Present in up to 20% annually</td>
</tr>
<tr>
<td>Mycobacterium spp. (Johne’s)</td>
<td>Present in 1-6%; confirmation pending</td>
</tr>
</tbody>
</table>

Consistent with previous surveys, none of the viruses appear to infect the sheep (subject to testing of a few putative false positives, planned for spring 2013). However, the sheep are exposed to bacterial species, particularly Leptospira spp. Testing to confirm the absence of EAE and the presence of Johne’s is planned for spring 2013, as is testing to identify the circulating serovar(s) of leptospirosis.

Temporal dynamics of nematode transmission

The Soay sheep of St. Kilda present a rare opportunity to investigate temporal variation in the transmission of parasitic nematodes (worms), in relation to individual characteristics of the hosts (sheep). For example, host and parasite abundance are clearly coupled (Fig. 9), but how does this actually come about? We plan to use theory and the richly detailed information about individual sheep, including their ranging behaviour (which affects their exposure to infection) and their immunological
measures (see next report) to build mathematical models in order to understand the temporal dynamics better.

Figure 9. Temporal variations in host population size (black) and in strongyle faecal egg counts in lambs in August (grey). Annual host density & faecal egg counts are positively correlated ($r^2=0.41$). We are working to explain why, while testing canonical epidemiological theory about nematode transmission dynamics.

Immunological research in Soay sheep.
Dan Nussey, Rebecca Watson, Kathryn Watt, Josephine Pemberton, Andrea Graham, Jill Pilkington, Rose Zamoyska and Tom McNeilly.

The immune system plays a crucial role in defence against parasites and pathogens, but we still know surprisingly little about how variation in the immune response is associated with fitness-related traits such as survival and reproduction in wild animals. The Soay sheep are an ideal study system to put this right, and our collaboration of immunologists and evolutionary ecologists has been working over the last few years to find ways of characterising and measuring their immune response. Antibodies are a very important part of our immune arsenal against all kinds of parasites. A few years ago we measured ‘self’ antibodies, antibodies against molecules commonly found in our own cells (specifically we measured anti-nuclear antibodies or ANA) across a decade’s worth of Soay sheep blood samples. We found that adult female sheep with high ANA were more likely to survive subsequent crash winters. Recently to investigate the relationship between antibodies and survival further, we have measured a much larger suite of ten other types of antibodies in these same samples from females before three different crash winters. There were few associations between any of our antibody measures and a measure of the number of strongyle nematode parasite eggs in the faeces. However, there was a strong association between the levels of antibody that bind (and are therefore expected to be important in the immune response against) molecules found in the larvae of nematode parasites of the sheep and the individual’s subsequent survival. This association was independent of the previously documented association between survival and ANA, but was much stronger and more significant (Fig. 10). In general there appear to be complex associations between circulating antibody levels and measures of body mass.
and survival, but our results suggest that antibody-mediated immunity may be very important in adult over-winter survival of these sheep.

![Graph showing antibody levels against larval stage T. circumcincta and survival](image)

**Figure 10.** The levels of antibodies against larval stage T. circumcincta, a major gut parasite of Soay sheep (labelled “IgG-T.circ” on graph) in August strongly predicts over-winter survival (zero for died, one for survived) in adult females measured before three crash winters. The line is the predicted relationship from a generalised linear model of survival (with dashed lines reflecting the standard error around the prediction).

**Investigations into osteoarthritis and bone pathology in Soay sheep.**
John Ryan, Dylan Clements, Dan Nussey and Kathryn Watt.

Osteoarthritis and other forms of bone pathology are the focus of considerable attention in veterinary and human medicine. Very little is currently known about the prevalence and importance of bone pathology in wild animals, although a few recent studies have suggested they may be important in wild ruminants. In 1990, Juliet Clutton-Brock published a survey of Soay sheep bones and identified pathology bearing a striking resemblance to elbow osteoarthritis (OA) in a large proportion (22%) of the animals. However, the significance of OA on the health and fitness of the Soay population was not addressed. We assessed the left hip and elbow joints of 46 sheep which died in the 2012 winter population crash for the presence of gross and microscopic elbow osteoarthritis. Mild cartilage damage was identified in 46% of hip joints and 24% of elbow joints, and the age of sheep with OA was significantly greater than those with normal (healthy) joints. It should be noted that the severity of the disease identified was relatively mild (in comparison with that previously reported in the osteological survey), and on the basis of our knowledge of OA in other species was not suspected to be of importance to the health and wellbeing of individual Soay sheep.
We are also investigating the prevalence of dental pathology and temporomandibular joint (TMJ) osteoarthritis in Soay skull and mandible specimens in the archive of skeletal samples held at the National Museum of Scotland’s site at Grantham, Edinburgh. A number of cases of suspected cases of dental abscessation and TMJ OA have already been identified, of severity which would have been expected to have resulted in significant morbidity to the affected individuals. Two honours students are now in the process of evaluating a large number of samples from the archive to ascertain the true prevalence rates of these diseases in the Soay population. Concurrently we are also evaluating the skeletal mineralisation of bone samples in the archive, using quantitative computed tomography, to assess whether bone mineral content is a marker of poor health and fitness and/or senescence. The results of these ongoing investigations will shed new light on the role and importance of bone and dental health in natural populations.

**Oxidative stress, life history and ageing in Soay sheep.** 
Louise Christensen, Jon Blount, Dan Nussey and Colin Selman.

Reactive oxygen species (ROS) are produced primarily as by-products of normal metabolism, and have been shown to be important elements in many aspects of cell signalling and in the immune response. However, ROS also appear to be capable of damaging various cellular components (e.g. proteins, lipids and DNA). While individuals have a suite of antioxidant defence mechanisms in place to counteract the negative effects of ROS, it would appear that not all ROS are neutralised completely by these antioxidants, and consequently cellular damage can build up over time. According to the oxidative stress theory of ageing, this oxidative damage is the primary causative mechanism of ageing and of age-related disease. Theory suggests that at times when individuals need to invest energy in costly activities such as growth and reproduction, a resource trade-off occurs that reduces investment in bodily maintenance, which may include a reduction in antioxidant protection mechanisms leading to an increase in ROS induced-damage accumulation. The current project will use specially collected and stored blood samples (since August 2010) to investigate whether there are any correlations between various life-history parameters and markers of oxidative stress (antioxidant protection and ROS-induced damage) in the Soay sheep on St Kilda.

We are in the process of analysing our data from plasma samples collected in the 2010, 2011 and 2012 August catches. Currently we have determined ROS-induced damage to proteins (protein carbonyls) and to lipids (malondealdehyde). In addition, we have measured plasma levels of the antioxidant enzyme superoxide dismutase and determined total antioxidant capacity in plasma from the same individuals. Preliminary data suggests that the levels of protein damage in plasma from animals sampled in 2012 are very high when compared with samples from 2010 and 2011 (Fig. 11). In addition, data from 2010 revealed a significant negative correlation between lamb antioxidant levels and parasite load; we aim to see whether this is observed across all years.
Figure 11. Average (with standard error bars) of plasma protein carbonyl levels (a marker of oxidative damage to proteins) from Soay sheep in captured and sampled in Augusts of 2010, 2011 and 2012.

Telomeres are the specialized structures that cap the ends of all mammalian chromosomes. Their purpose is to protect the integrity of coding DNA, in doing so they get progressively shorter with each cell division as an individual ages. This process is considered to be part of natural ageing. It has been suggested that the rate at which telomeres shorten is sensitive to the health and biological fitness of a mammal. Numerous studies looking at telomere length (TL) in human white blood cells (WBC) have demonstrated a link between lifestyle stress and increased telomere attrition and therefore subsequent associated survival and health. TL has also recently been a focus of interest in ecological and evolutionary studies with the suggestion that measuring TL can be indicative of individual fitness and longevity.

We plan to investigate the relationship between white blood cell telomere length, ageing and health in the Soay sheep. To do this we will use the immense amount of stored WBC fractions, which have been collected over decades by the Soay sheep project team. These samples once processed could potentially provide us with unparalleled data on variation of telomere length and maintenance in a wild mammal population.

We have successfully optimised measuring Soay sheep telomeres using the Telomere Restriction Fragment (TRF) technique and quantitative real time PCR (qPCR). Our
first step has been to validate the qPCR methodology against the TRF method, which is often referred to as the ‘gold standard’ measurement of TL but requires far more DNA and is so time consuming it would be impossible to use for a large scale, longitudinal study. We found a close correlation between measures of TL on Soay sheep using the two methods (Fig. 12). This suggests our automated high throughput qPCR method can be used with confidence and this will facilitate very rapid and consistent sample processing. Our plan over the coming year is to use this approach to measure TL across the lifetimes of females born in four years that differed markedly in environmental conditions and juvenile mortality patterns. We hope to assess how genetic and environmental variation generates among- and within-individual variation in telomere length, and test whether telomere lengths predict subsequent fitness of sheep independent of their age.

Figure 12. The association between TRF and qPCR telomere length measurement techniques from white blood cell samples from 32 Soay sheep taken in August 2010.

Predictions of phenotypic evolution of adult morphometric traits in Soay sheep.
Michael Morrissey.

Understanding and predicting generation-to-generation evolutionary change in natural populations is a major challenge. Across many populations and species, evidence exists that the two main ingredients for evolutionary change are present: many kinds of traits often seem to be subjected to natural selection, and such traits are generally heritable. The Soay sheep of St Kilda present an ideal study system in which to study the generation-to-generation mechanics of natural selection, genetics, and evolution, since we can go beyond standard practices for assaying natural selection and genetic variation.
We compared two predictive equations for evolutionary change of adult morphometric traits in Soay sheep. First we applied two versions of the standard breeder's equation, which predicts evolution by combining separate inferences about the genetics and selection of a series of traits. Second, we applied the much less-widely applied secondary theorem of selection, which predicts evolutionary change directly by assessing the genetic basis of the joint relationships between traits and fitness. We found that the two methods generate different predictions for body size traits (Fig. 13), but generally concordant results for two other traits, male horn size and scrotal circumference. The breeder's equation predicts evolution of increased body size as a result of substantial segregating genetic variation for size, and strong relationships between body size and fitness. However, the secondary theorem of selection predicts little, or even negative (i.e., smaller sizes), evolutionary change of body size. These findings suggest that the interpretation of the phenotype-fitness covariance of body size with fitness is not indicative of selection, and that some factor or factors, perhaps a feature of the environment, causes the apparent covariance, which should not be taken to be indicative of natural selection.

![Figure 13](image)

**Figure 13.** Predictions of phenotypic evolution of adult morphometric traits in Soay sheep on St. Kilda using the univariate breeder's equation (UVBE), the multivariate breeder's equation (MVBE), and the empirical application of the secondary theorem of natural selection. Error bars show standard errors.
This finding is important beyond the Soay sheep system because it may indicate that positive selection of organismal size, which appears common based on simple relationships between aspects of size and fitness, should be interpreted with more caution. The extensive individual-based trait and pedigree data in the Soay sheep makes these inferences possible in ways that are not generally possible elsewhere. Quite generally, these findings point the way for future studies of the natural selection of heritable traits in the wild, both in the Soay sheep system and more generally. Meaningful inference of natural selection will require greater attention to the environmental variation experienced by different individuals.

**Testing for inbreeding depression in Soay sheep using a high-density genetic marker panel.**
Camillo Berenos, Phil Ellis and Josephine Pemberton.

Inbreeding, the mating of related individuals, can have detrimental effects on offspring traits related to fitness, such as growth rate and survival. This phenomenon, called inbreeding depression, has been observed in a wide variety of organisms, and is believed to be the result of increased homozygosity in inbred individuals. There are several reasons to believe that the Soay sheep on St. Kilda might suffer from inbreeding depression. First, in a small island population, which has likely been isolated for many generations, there are ample opportunities for matings between close relatives. Second, skewed mating success in rams leads to some large paternal sibship sizes, further increasing the potential for mating between close relatives. Despite this background, there is only weak evidence for inbreeding depression in Soay sheep to date. A possible explanation is that the current pedigree underestimates the true level of inbreeding of an individual. This postulated underestimate could be due to a combination of factors, such as missing parentage data resulting in short and incomplete pedigrees and the assumption that the founders of and immigrants to the Village Bay pedigree are unrelated. Furthermore, the inbreeding coefficient calculated from a pedigree is an expected mean value and it has recently been shown that high density genetic marker panels can detect variation around the mean expectation using the so-called realised or genomic inbreeding coefficient. Using of a panel of 38,000 variable DNA markers, which has recently become available for the Soays, we expect to have more precise estimates of inbreeding coefficients, and in turn more power to detect inbreeding depression.

We first set out to investigate how much inbreeding we could detect. The mean genomic inbreeding coefficient was -1.82x10^{-4} with a variance of 8.91x10^{-4} (Fig. 14, Left panel), which shows that while the mean is lower than pedigree inbreeding coefficients (Mean: 1.09 x 10^{-3}), the variance was much higher than found for pedigree inbreeding coefficients (1.44 x 10^{-4}). Of the 4,413 sheep genotyped at high density markers 1,906 had positive inbreeding coefficients (Table 3). While the majority of these had quite low inbreeding coefficients, 109 sheep had inbreeding coefficients exceeding the expected inbreeding coefficient of half-sib or grandparent-grandchild matings.
Table 3. Summary table of positive genomic inbreeding coefficients.

<table>
<thead>
<tr>
<th>Inbreeding coefficient bin</th>
<th>Number of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-0.03125</td>
<td>1549</td>
</tr>
<tr>
<td>0.03125-0.0625</td>
<td>248</td>
</tr>
<tr>
<td>0.0625-0.125</td>
<td>77</td>
</tr>
<tr>
<td>0.0125-0.25</td>
<td>23</td>
</tr>
<tr>
<td>0.25-0.5</td>
<td>9</td>
</tr>
</tbody>
</table>

We next wanted to establish how well pedigree inbreeding coefficients predict genomic inbreeding coefficients in the study population. We found that while the two measures are correlated, the pedigree inbreeding coefficients only explain 8% of the variance in genomic relatedness (Fig. 14, Right panel). In particular, there are many individuals where genomic inbreeding coefficient is relatively high, but pedigree inbreeding coefficient is zero, probably due to incomplete pedigree information.

![Figure 14](image.png)

**Figure 14.** (Left panel) Histogram of realised inbreeding coefficients calculated using 38,000 genetic markers in 4,413 sheep. (Right panel) Genomic inbreeding coefficient as a function of pedigree inbreeding coefficient.

We next wanted to examine whether the higher variance in realised inbreeding coefficients allowed us to detect inbreeding depression in birth weight, where a previous study relying on the pedigree to calculate inbreeding coefficients was unable to detect any adverse effects of inbreeding. We found that inbreeding did depress birth weight, but this effect was only observed through inbreeding in the mother (Fig. 15), as inbreeding coefficient in the lambs did not correlate significantly with birth weight.
Figure 15. Lamb birth weight as a function of the inbreeding coefficient of the mother. The numbers above the points denote the number of observations within the respective bin.

The analyses presented here demonstrate that a high-density panel of molecular markers make it possible to, first of all, estimate inbreeding coefficients with superior precision and second of all, detect inbreeding depression with improved power compared to the existing pedigree. The analyses presented here have been conducted on a preliminary dataset. Now that we have access to an even larger genotype dataset, we will further extend the analyses to a wider range of traits associated with fitness.
Publications on the shelf in 2012


In press:

ACKNOWLEDGEMENTS

We are grateful to the National Trust for Scotland and to Scottish Natural Heritage for permission to work on St Kilda, and for their assistance in many aspects of the work. The project would not be possible without the generous assistance and support of MOD, QinetiQ and E.S.S. staff stationed on St Kilda and Benbecula and servicing the island. We are particularly grateful to Susan Bain, the Western Isles Manager for the NTS, Paul Sharman the NTS Ranger for St. Kilda, to Andy Walsh the Archaeologist on the island, and to Gina Prior the Seabird and Marine Ranger.

We are also grateful for the help of volunteers without whom the fieldwork for 2012 would not have been possible: Gebre Asefa, Katie Hatton, Helen Hipperson, Rebecca Holland, Adrian Leach and Clare Pemberton. Thank you.

Our research is supported by grants and studentships from the Natural Environment Research Council, the Biotechnology and Biological Sciences Research Council and the European Research Council.

APPENDIX A: PERSONNEL NEWS & SCHEDULE OF WORK

Personnel News

Emily Brown obtained her PhD ‘Detection and selection of parasite resistance genes in a free-living mammal population’ from the University of Sheffield.

Three new PhD students joined the project in autumn 2012: Rebecca Watson began her PhD on immune ageing in a wild mammal population at IEB, University of Edinburgh, Louise Christensen began her PhD on oxidative damage, life history and ageing in a wild mammal population at the University of Aberdeen and Elis Marina Damasceno Silva began her PhD on analysis of cranial features of Soay sheep at the University of Manchester.

Romain Garnier began a postdoc on ‘Heterogeneities in host resistance and tolerance as drivers of the transmission dynamics of strongyle nematodes’ at Princeton University in autumn 2012.

Katie Hatton volunteered with the Project for almost two years and has now moved on to work with the Tsaobis Baboon Project in Namibia.
Schedule of work on St Kilda

Winter - Spring

Jill Pilkington monitored mortality from February till May with help from Kathryn Watt and volunteers. During this period, detailed data were collected on individual sheep found dead, and bones, joints and tissues samples were taken for genetic, parasitological and ageing studies.

From March 20\textsuperscript{th} until May 11\textsuperscript{th}, Jill Pilkington, Katie Hatton and Rebecca Holland carried out ten population censuses and tagged and sampled lambs, with assistance during the peak of lambing from Michael Morrissey and Rebecca Watson. 155 lambs were born to 152 ewes; these figures include 3 sets of twins (2 ewes held both lambs and 1 ewe lost both lambs). 105 lambs (47 male and 58 female) were caught and tagged; a further 50 lambs died before any tagging attempt. Mick Crawley and two assistants collected vegetation data.

Summer

Jill Pilkington, Katie Hatton and Rebecca Holland again returned to Hirta on July 17\textsuperscript{th} to carry out ten population censuses, conduct mortality searches (yielding 5 tagged dead animals), and prepare for the main catch-up of study area sheep. The catch-up took place from August 10\textsuperscript{th} – 24\textsuperscript{th} and was conducted by a team of 12 additional project members and volunteers. 161 sheep were caught and processed, of which 55 were lambs (23 males and 32 females), 9 were yearlings (2 males and 7 females), 17 were adult males, and 80 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic analyses. 24 Sheep were retagged because of damaged or missing tags. 6 previously untagged lambs and 3 yearlings were caught and processed. Mick Crawley and two assistants collected vegetation data. Jill Pilkington and two volunteers remained on Hirta until 7\textsuperscript{th} September to complete parasite counts and pasture larvae counts.

Autumn

From October 23rd to December 4\textsuperscript{th} Jill Pilkington and Katie Hatton carried out ten population censuses, monitored the mating period, capturing and processing 25 incoming tups and 3 resident tups. 11 previously darted, non-resident tups were seen in the study area during this rut. No dead sheep were found.
Circulation List - (Please advise J. Pilkington of any changes or additions)

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