ST. KILDA SOAY SHEEP PROJECT: ANNUAL REPORT 2001

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POPULATION OVERVIEW

The sheep population on Hirta entered 2001 at a relatively high level and there was little mortality through the year. Only 16 sheep were found dead within the study area between January and May of 2001, 10 between May and September and 8 between September and December. Lambing recruitment began on the 1st of April with 89% of lambs born surviving (Fig. 1).
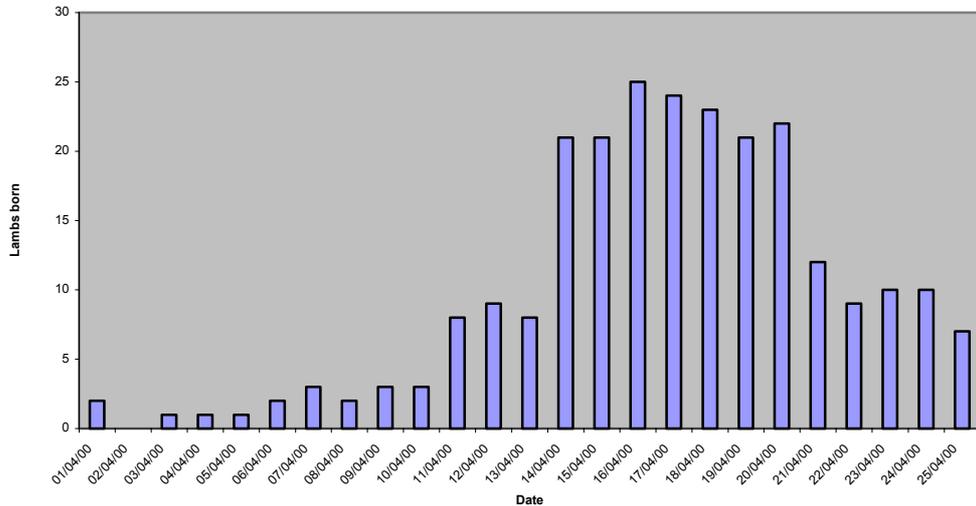
Figure 1. *The temporal distribution of lamb births during 2001.*

In December 2001, 747 tagged sheep were believed to be alive on Hirta, of which 552 regularly used the study area; in addition there were approximately 100 untagged lambs (untagged as a result of no tagging during the foot and mouth epidemic) also present, a total increase of nearly 41% 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.
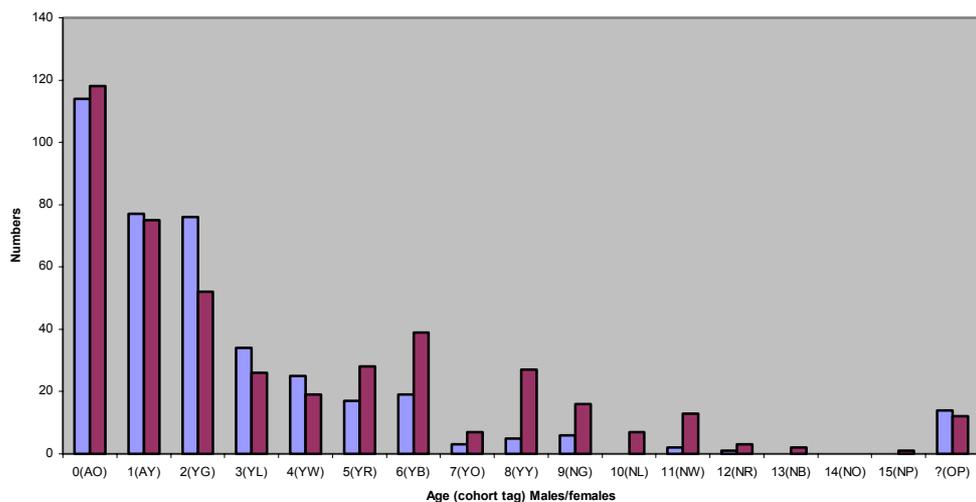
Figure 2. *Age distribution of tagged Soay sheep presumed to be alive at the end of 2001.*
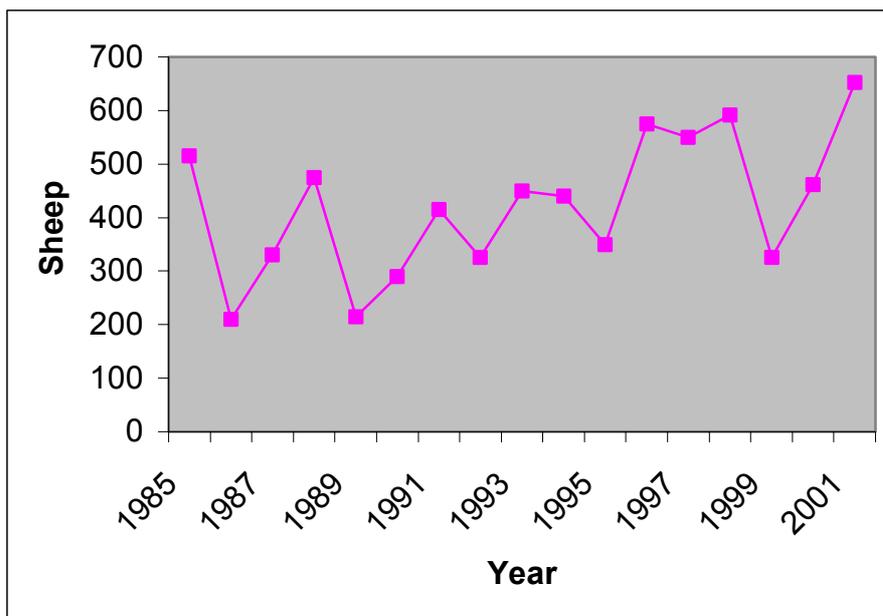
Figure 3. *The number of tagged sheep regularly using the study area since 1985.*

One whole-island count yielded an estimate of 1,889 tagged and untagged sheep on the whole island with the details displayed in Table 1. The total population had increased by 34% since summer 2000.

Table 1. *Demographic and geographic distribution of sheep observed during the count of Hirta on August 27th 2001. 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	128	4	37	1	51	0	19	0	148	**388**
Mullach Bi/Cambir	199	16	87	6	82	1	33	0	238	**662**
Ruaival/Village	260	10	125	8	93	5	36	1	301	**839**
Total	**587**	**30**	**249**	**15**	**226**	**6**	**88**	**1**	**687**	**1,889**

REPORTS ON COMPONENT STUDIES

Population dynamics of Soay sheep on Hirta

Panagiotis Besbeas, Giacomo Tavecchia, Byron Morgan, Ted Catchpole, Tim Coulson

Since 1955 the total number of sheep on the Island of Hirta have been counted each summer. More detailed studies of Village Bay occurred between 1959-1967 (by Peter Jewell *et al.*) and between 1985 and the present. The two detailed studies in Village Bay have shown that the population size shows periods of rapid increase to high density, followed by periodic "crashes" when up to 60% of the population can die in one winter. The whole island counts from 1955 to the present have periods when similar increases and declines occur (Fig. 4), but there are periods when the fluctuations in population size are surprisingly different. For example, between 1971 and 1978, the population showed a steady decline, which is difficult to reconcile with our current understanding of the way the population fluctuates. There has long been some uncertainty regarding the quality of the whole island counts in some years in the 1970s, so we decided to model the population dynamics in an attempt to reconstruct the dynamics between 1968 and 1984 using our current knowledge of the biology of the sheep.
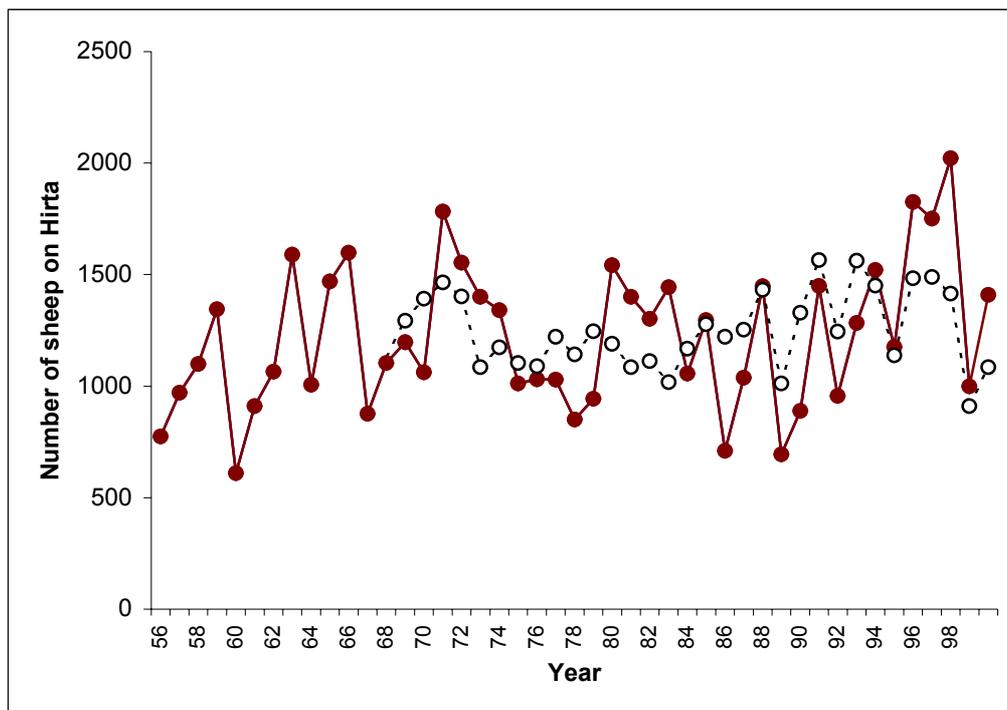
Figure 4. *Observed (solid circles and solid line) and predicted estimates from the Kalman filter (open circles and dashed line) of the total number of Soay sheep on Hirta. The observed data span 1956 to 2001; the predicted estimates span a shorter time frame (1968 to 2001) because the Kalman filter requires approximately time years to stabilise.*

By analyzing the detailed individual-based data collected between 1985 and the present we identified factors affecting survival and fecundity. Survival and fecundity were both strongly influenced by population size and winter weather. These relationships were combined into a

mathematical population model (e.g see Coulson *et al.* 2001). We took the population structure reported by Jewell *et al.* in 1967 and used our mathematical model to simulate the population dynamics. Next, we combined estimates from our simulation with the observed whole island count data using a powerful statistical method called the *Kalman filter*. The Kalman filter allowed us to simultaneously analyze the census data and the individual-based information.

By altering the relative importance of the population counts and the simulation model, we could reconstruct the population dynamics from 1968 to the present. The predicted population sizes from the Kalman filter captured the population dynamics between 1985 and the present remarkably well (see figure 1), especially considering our starting values for the simulation were from 1967. The Kalman filter also predicted population sizes between 1968 and 1984. Our results suggest that the population did not fluctuate as dramatically during the 1970s and early 1980s as the island count data suggest. They also suggest that the steady decline from 1973 to 1980 did not occur. One current concern about this model is that it underestimates fluctuations in population size between 1985 and the present. However, between 1985 and 2001 the sign (-/+) of the change in population size from one year to the next has been accurately captured by the Kalman filter. As more data are collected we hope to refine our estimates of population fluctuations during the 1970s and early 1980s.

Spatial genetic structure of the Village Bay population

Dave Coltman, Jill Pilkington and Josephine Pemberton

We have previously shown that the Village Bay population can be divided into three distinct subgroups or "hefts" (Coulson, Annual Report 1997). These "hefts", or groups of individuals that use the same area, are approximately located one in the east of the study area, one in the centre, and one in the southwest. Tim Coulson showed that there are differences between the hefts in vital demographic parameters such as survival, recruitment and dispersal. A question then arises as to whether individuals are more closely related within hefts than between them?

We used three different statistical analyses of the genetic data to test whether there are consistent genetic differences between hefts from 1987 to 1999. First, we compared the allele frequencies of all microsatellite and protein markers that have been used in the study between each pair of hefts in each year. Allele frequencies were significantly different in 38 out of 42 of the year/heft comparisons. Secondly, we calculated Wright's fixation index (F_{st}), which is a statistic that indicates relatively how much of the genetic variation in the population is partitioned among the subgroups, for each year of the study. In all 14 years we found low but statistically significant values of F_{st}. Third, we estimated the level of relatedness, or pairwise genetic similarity, between all individuals within each heft and compared this to the relatedness between hefts. Individuals within hefts are more closely related to each other than are individuals between hefts in every year of the study. More detailed analyses of the data reveal that ewes from the same heft are significantly related at about the level of second cousins, on average (Fig. 5A). Ewes in different hefts, and rams either in the same or different hefts appear

not to be more related than any two randomly chosen individuals. It therefore seems that the genetic structure of the population is probably a consequence of the tendency of daughters to stay on the same range as their mothers, whereas sons roam more widely in the Village Bay.
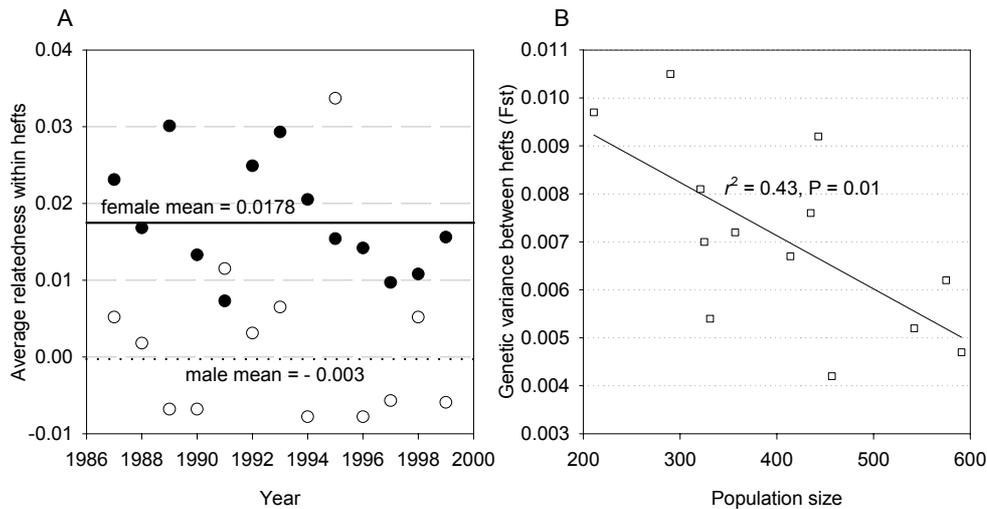
Figure 5. (A) Average relatedness within hefts of males and females from 1987 to 1999. An average relatedness of 0.0156 corresponds approximately to the level of second cousins, and a value of 0.0312 to the level of first cousins once removed. (B) Amount of total genetic variation that is partitioned between the hefts in relation to population size.

One implication of this finding is that we need to account for the correlation between genotype/matriline and home range use in future genetic analysis of phenotypic traits because there are differences in environmental conditions between the hefts. At least in females, the environment they experience throughout their lifetime is not independent of their pedigree. Also, the level of population genetic structure appears to vary with population size is systematic fashion (Fig. 5B). Increasing population size appears to be correlated with reduced population structure. This may be a consequence of demographic differences among matrilines, or a due to increased dispersal between hefts at high population density when animals may move more widely in search of good forage.

Genetic trade-offs between growth and resistance to scrapie

Loeske Kruuk

Variation at the *PrP* gene determines susceptibility to transmissible spongiform encephalopathies (TSEs) such as scrapie in sheep, new variant-CJD in humans and chronic wasting disease in deer. Surprisingly, however, selection has not resulted in the fixation of resistant alleles in populations exposed to TSEs. One plausible explanation for their maintenance is that susceptibility is associated with other traits such as growth rates that are under positive selection, either natural or artificial, creating a "cost" to resistance.

The St Kilda Soay population provide an ideal situation in which to test this explanation, as they have never been exposed to scrapie and so any associations with *PrP* genotype are independent of the effects of infection. In a pilot study, 42 randomly-chosen individuals were sequenced at the *PrP* genotype. Three out of the five known alleles were found to be segregating in the population: the ancestral type, ARQ, and two others, ARH and AHQ. Combining the genotypic data with the measurements of individual birth weight – available for 29 of the genotyped individuals – revealed highly significant differences between genotypes (Fig. 6). The birth weight of individuals carrying a copy of the ARH allele was 59% of that of the other genotypes.

Although patterns of susceptibility to scrapie vary with sheep breed and with strain of scrapie, the ARH allele is usually associated with resistance. The results in Fig. 6 suggest a possible cost to resistance in the national flock, but need to be confirmed with larger sample sizes. We also need to address the question of what is maintaining the polymorphism in the St Kilda population. I have applied for funding to sequence all sampled St. Kilda Soays at the *PrP* locus, and then relate genotype to a range of morphological and life history parameters.
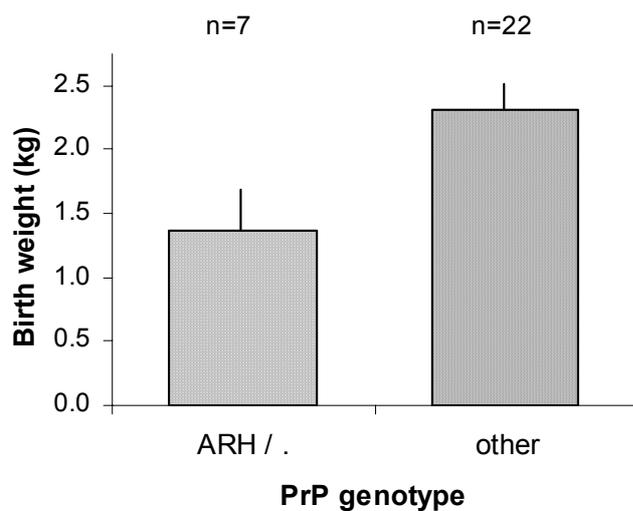
Figure 6. *Soay birth weight and PrP genotype.*

ARH / . represents ARH / ARQ and ARH / AHQ individuals (no ARH/ARH homozygotes were observed); other is all other genotypes. Birth weight was corrected for sex and litter size (singleton or twin). ARH / . individuals were significantly lighter than the other genotypes: difference = 0.951 ($\pm$ 0.341 s.e.) kg, t_{25}=2.79, p=0.010. Birth date and population density in year of birth were included in the initial model, but did not have a significant effect, nor did year of birth fitted as a factor. The significance of the *PrP* effect was not affected by the inclusion of these other terms in the model. There was no evidence of any sex-by-genotype interaction (t_{25}=0.11, p=0.915).

The coccidian parasites of St Kilda Soay Sheep

Barbara Craig

Co-existing with helminth parasites in the intestines of the Soay sheep are a diverse fauna of parasitic protozoa. Collectively known as coccidia, these unicellular organisms shed the final stage of their life-cycle, the oocyst, in the faeces alongside the eggs of helminths. Coccidian oocysts can be two to twenty times smaller than the average helminth egg, yet when sporulated (made to become infective) and considerably magnified, it is possible to assign them to species level on the basis of their morphology. Initial morphological analysis of the oocysts occurring in the August 2001 catch faecal samples, has revealed there to be eleven species of *Eimeria* and *Cryptosporidium parvum*.

The eleven *Eimeria* spp. are highly host specific and represent the full set already described from domesticated sheep, namely: *E. ahsata*, *E. bakuensis*, *E. crandallis*, *E. faurei*, *E. granulosa*, *E. intricata*, *E. marsica*, *E. ovinoidalis*, *E. pallida*, *E. parva* and *E. weybridgensis*. Mixed infections are usual and depending on various factors, including the predominant species involved, can cause a clinical disease called coccidiosis. This cannot, however, be diagnosed by finding oocysts in the faeces alone. Healthy animals can shed many thousands of oocysts without symptoms and others may die before any are shed.

Figure 7. Relative sizes of some of the parasites found in the sheep faeces. (Modified from MAFF. (1986). Manual of Veterinary Parasitological Laboratory Techniques. London:HMSO.)

Cryptosporidium parvum is notoriously ubiquitous throughout the animal kingdom and is consequently a significant zoonosis. Already sporulated when shed, unlike *Eimeria* spp., *C. parvum* oocysts are instantly infective and highly resistant in the environment, even surviving water chlorination. Cryptosporidiosis is the clinical condition caused by the parasite and young lambs are particularly susceptible, as are immuno-compromised individuals. In healthy animals, however, the infection is self limiting and a level of aquired immunity is achieved to subsequent challenge.

C. parvum oocysts are very small (see Fig. 7) and a special staining technique, called Ziehl-Nielsen, was necessary for their detection. In positive faecal smears oocysts stain red against a blue background. Age-specific prevalence in August 2001 is shown in Table 2.

Table 2. Prevalence of Cryptosporidium parvum among age classes of Soay sheep caught in August 2001. In a preliminary logistic regression analysis of the presence/absence of Cryptosporidium, none of the main effects of age, sex or weight were significant, but there was a significant interaction between age and weight ($X^2 = 6.16$, 1 d.f., $P = 0.013$). In young animals the presence of Cryptosporidium was not associated with weight, but among older age classes Cryptosporidium was associated with higher weights.

Age class	Year born	Total number	Number positive	% positive
Lambs	2001	83	29	34.9%
Yearlings	2000	54	15	27.8%
Adults	1999 and earlier	105	21	20.00%

A survey of bacterial and viral pathogens of Soay sheep on St. Kilda.

K. Wilson & J.M. Pemberton.

Although we know a quite a lot about the prevalence and impact of the macroparasites (nematodes, tapeworms, etc) of Soay sheep on St. Kilda, we know very little about their microparasites (i.e. their bacteria, protozoa and viruses). This is a glaring gap in our knowledge because many of the most important diseases of livestock and humans belong to this class of parasite. This omission is particularly important because we have recently found that Soay resistance to gastrointestinal nematodes is strongly associated with variation within the interferon gamma gene – a gene involved in switching immune responses between

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macroparasite and microparasite defences. It is possible that variation at this locus is being maintained by genetic trade-offs between resistance to macroparasites versus resistance to microparasites.

The Scottish Agricultural College (SAC) Veterinary Science Division routinely screens domestic sheep for a range of agriculturally-important pathogens. Of these, the following appear most likely to be present on the St. Kilda: Johnes disease, Border disease, EAE and *Mycoplasma ovipneumoniae.*

Johnes disease (paratuberculosis) is a chronic gut disease of cattle, sheep, goats and deer resulting in diarrhoea, weight loss and eventually death. It is caused by infection with a very slow growing bacterium, *Mycobacterium paratuberculosis* (referred to as *Map*). It survives for long periods of time in the environment and animals are usually infected with *Map* in the first few weeks after birth, but do not develop clinical disease until they are 18 months or older.

Border disease is a congenital disease of sheep that was first reported in the border counties of England and Wales. Border disease is cased by a pestivirus closely related to bovine viral diarrhea virus (BVDV) and swine fever virus (hog cholera). Transmission of the virus occurs via oral and/or intranasal routes in sheep, and can be spread from BVDV positive cattle to sheep. Intrauterine infections of ewes can result in abortion or stillbirths. In lambs, infection is associated with death within the first few days of life and increased susceptibility to other parasites and bacteria. In rams, it is associated with poor quality semen.

Chlamydial abortion of sheep, also known as ***enzootic abortion of ewe*** (***EAE***), is caused by *Chlamydia psittaci*. This bacterium invades the placenta (afterbirth) of the sheep and the damage caused can lead to the death of the foetus. The placenta is a danger to uninfected ewes and to lambs.

Mycoplasma ovipneumoniae causes clinical pneumonia in sheep, characterised by fever, nasal discharge, pneumonitis and pleuritis.

We contracted SAC to test plasma samples from 50 sheep (36 ewes; 14 rams) collected in August 2000. All animals were at least two years old when sampled, to maximise the chance that they had been exposed to any pathogens on the island. The youngest sheep tested belonged to the 'YL' cohort, born in 1998; the oldest were born in 1990, the 'NW' cohort.

All samples were negative for antibody to *Mycobacterium paratuberculosis*, Border Disease Virus and *Mycoplasma ovipneumoniae*. One animal (NW513) had a low positive titre (2/32) to *Chlamydia psittaci*, all others were negative. Back in 1986, a MAFF survey also failed to detect Maedi-Visna virus in the population (J.M. Pemberton unpublished).

These results indicate that the major pathogens of domestic sheep on the mainland are generally absent or at very low prevalence on St. Kilda. It is unclear at present whether the single positive result for *Mycoplasma ovipneumoniae* indicates its presence on the island or whether this could be a false positive result. Further tests will be required. Overall, perhaps the host population is too small and isolated to allow many microparasite infections to persist over time.

Male mate choice influences female promiscuity in Soay sheep.

B. T. Preston, I. R. Stevenson, J. M. Pemberton & K. Wilson.

In most animal species females make a greater investment in offspring than do males. As a result, the number of offspring they have the potential to produce is lower. An important consequence of this asymmetrical investment is that males are able to breed more often, and so will compete with each other to mate with receptive females and increase their reproductive success.

Females may also increase their reproductive success if they can produce high quality progeny, which have enhanced prospects of reproduction or survival. One way of achieving this is by choosing to mate with males that will provide the best possible environment or genes for their offspring. Thus, as a 'rule of thumb', the *number* of offspring is the important determinant of reproductive success for males, and the *quality* of offspring is of importance for females. However, this general rule may not apply where male mating opportunities are limited, or female quality is highly variable. Under these conditions males are also predicted to be choosy about mates. Such conditions exist in the promiscuous mating system of Soay sheep.

Rams on St. Kilda compete fiercely for mates, and it has previously been shown that males of larger body size, with longer horns, are at an advantage in these competitions (see annual report for 1999). However, a highly synchronised mating season, intense sperm competition (which occurs where females mate promiscuously within a single oestrus), and constraints on sperm production (see annual reports for 1998 & 2000) appear to limit the number of offspring that males are able to sire. Furthermore, Soay ewes vary substantially in their ability to produce successful offspring. Consistent with the theory outlined above, we find that competitive rams appear to preferentially guard and mate with heavier females (Fig. 8), who are more likely to rear successful offspring. This discrimination between potential mates by males is reflected in assortative patterns of paternity, as competitive rams also sire the offspring of heavier females (Fig. 9). Soay sheep thus provide a rare demonstration of a species in which the sex that experiences greatest competition for reproductive opportunities, also chooses between prospective mates.

Examining the duration of mate guarding episodes within females' oestruses reveals a further consequence of assortative mating. Because lighter females are defended by less competitive rams, which are less able to maintain stable consorts, rival males are able to disrupt or take-over the consort from the defending ram. Lighter ewes therefore experience a series of

relatively short consorts throughout their oestrus, and so are mated by a greater number of rams. Male mate choice thus appears to influence the degree of female 'promiscuity' in Soay sheep (Fig. 10).
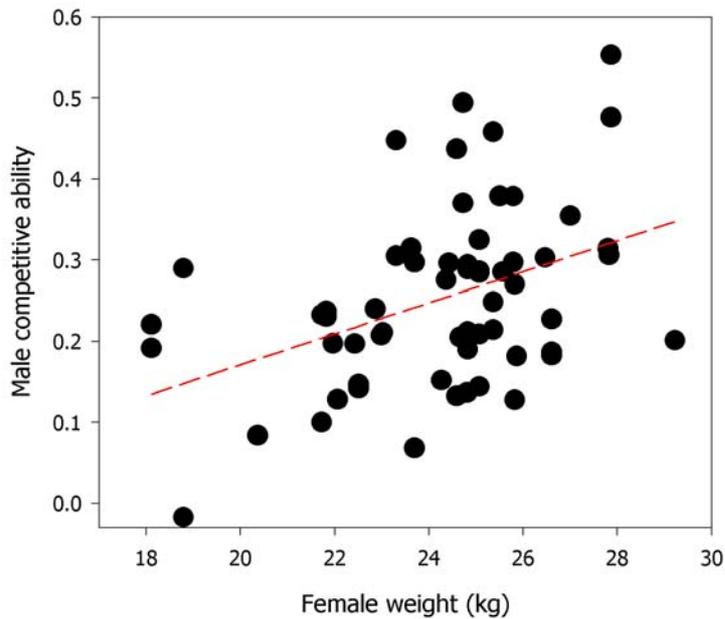
Figure 8. *Male preferences for heavier females. 'Competitive ability' of the guarding male is shown plotted against the weight of female held in consort (P=0.002). Competitive ability is predicted from the results of a statistical analysis (using GLMM) that described rams' behavioural success in gaining copulations with females, and is calculated from the horn length and body size of the individual (see annual report 1999).*
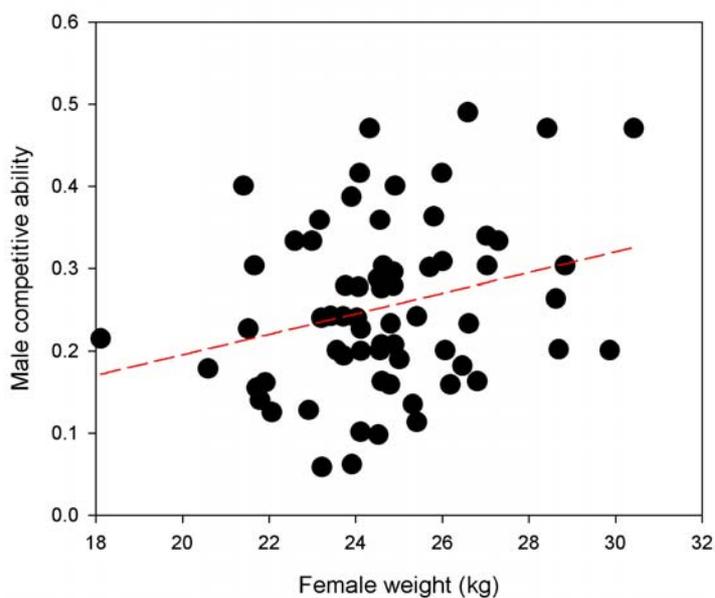
Figure 9. Female weight as a predictor of the siring ram's competitive ability. The figure shows the association between the siring ram's competitive ability (see Fig. 8 legend) and ewe's weight (P=0.03). Only paternities assigned at the 95% confidence level are included here.
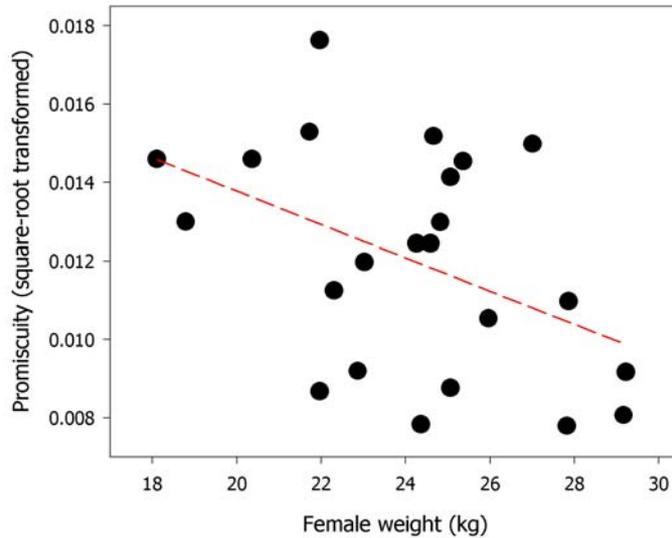

Figure 10. Female weight as a predictor of promiscuity. The figure shows consort change rate per hour (square-root transformed) over two days of oestrus, as a function of female weight (P=0.035).

Vegetation Dynamics

M.J. Crawley

In the first few months of 2002, there has been a sheep population crash, and now we are starting to get a much clearer picture of the relationship between the sheep and their food supply. The relationship between sheep numbers in August and total standing crop biomass in the following March is reasonably well defined ($r^2 = 0.70$):
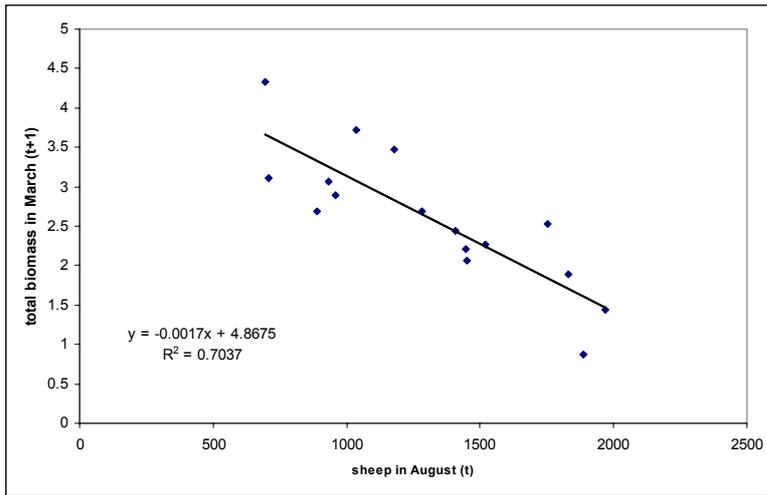
Figure 11. The relationship between the whole island sheep population in summer and plant biomass the following winter.

Likewise, the relationship between March biomass and year-to-year variation in population size (delta = $\log(N_{t+1}/N_t)$) is strongly positive but asymptotic (there is a maximum rate at which the sheep population can recover from low densities; $r_{max} \approx 0.45$).
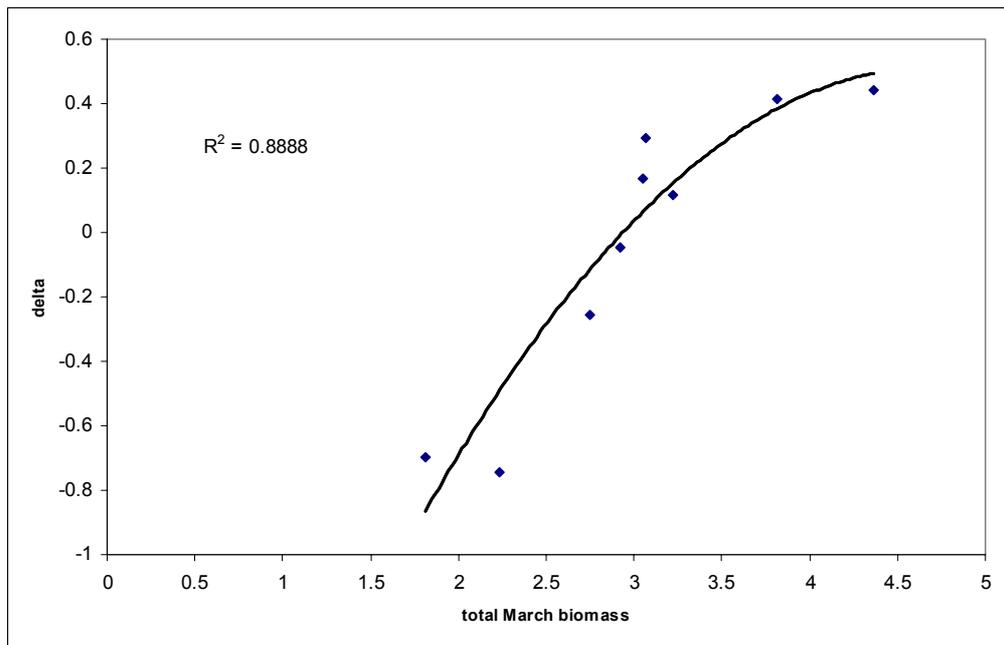

Figure 12. The relationship between the whole island sheep population in summer and change in sheep population size in the following year (see text for details of the measure delta).

All of the increasing populations were associated with total biomass in March of more than 3 t ha^{-1}. In the years of steepest population decline (1999 and 2002) the standing crop in March was much lower than this (2.23 and 1.80 t ha^{-1} respectively). In those high density years when the population did not crash (e.g. 1996 and 1997) the total biomass in March was not

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depressed below 2.8 t ha^{-1}. In a multiple regression model, March biomass is a much better predictor of delta (deletion test, $p = 0.036$) than is population size ($p = 0.347$), presumably because it incorporates annual variation in plant productivity (especially, over-winter plant growth) as well as the number of mouths.

Biomass composition in March also varies with the size of the sheep population (see fig. 13).
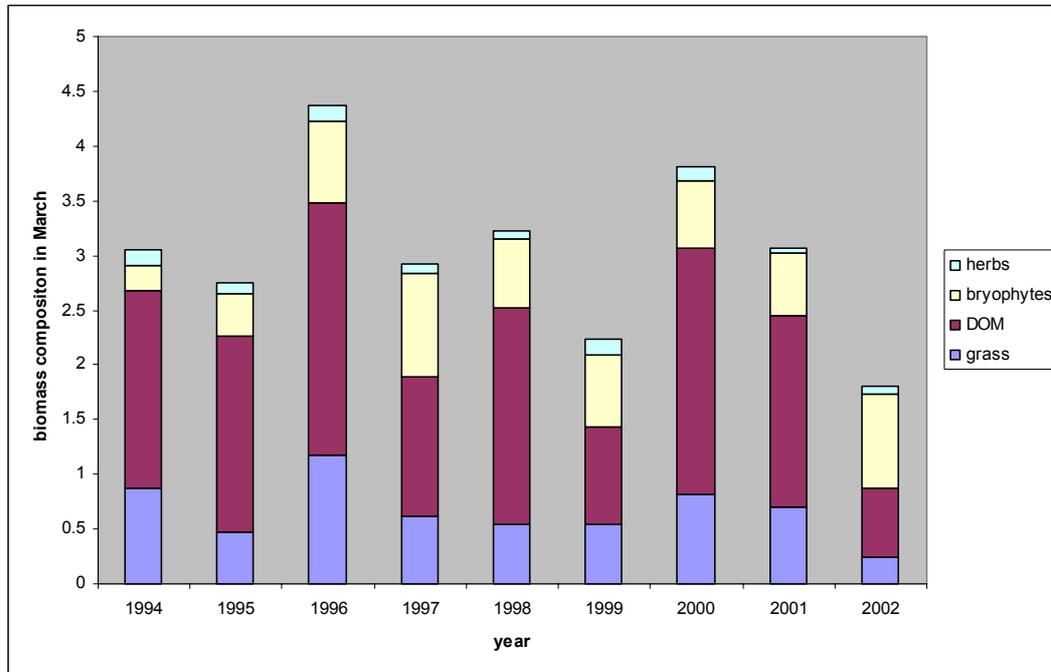
Figure 13. *Plant biomass composition in March in each year since 1994. Biomass is measured in t ha^{-1}.*

The most notable feature of the composition dynamics is the fluctuation in the standing crop of dead organic matter (DOM); lowest in the crash years of 1999 and 2002, and highest in the years when sheep numbers were low. Total green grass biomass was at its lowest ever level in the crash of 2002, but was as low in the non-crash years of 1995, 1997 and 1998 as in the crash year of 1999. The DOM biomass in March is a crude correlate of body condition for the sheep. This is because the transfer of grass to DOM in late summer and autumn is greater in low density years when the rate of consumption of grass by sheep is lowest. High values of DOM are therefore symptomatic of low grazing pressure. Although high values of DOM in the sward are usually regarded as indicating low food quality, these high values are actually the result of low grazing pressures, and hence are likely to be correlated with high body condition in the sheep.

The two recent crash years were associated with the lowest-ever values of the 'green heather index' (total green heather biomass / total non-green heather biomass measured outside the Head Dyke), with values of 0.086 in March 2002 and 0.141 in 1999 (the March average for non-crash years is 0.204). The biomass of bryophytes was high in the crash year of 2002 but not in the crash of 1999.

All of these March-based measures are *descriptors* of the crash, rather than explainers of anything profound ("more sheep, less grass"). Are we in any better a position to *predict* the timing of the next crash ? To the extent that the crash depends on the weather in late winter, then obviously not. But the important ecological parameters are becoming clearer (i.e. the necessary conditions for a crash). For the last 10 years, crashes can be predicted purely on the basis of the August sheep count. There have been 2 crashes, and both involved whole island counts that were greater than 1880 animals. Recent crashes are also well predicted by an August food availability index, calculated from the whole-island sheep count, and an estimate

of grass biomass from the area inside the Head Dyke (mean g dry weight per 0.04 m^2):

$$\text{'grass per sheep' index} \;=\; 100 \times \frac{\text{grass weight in August}}{\text{sheep numbers in August}}$$

Both recent crashes had index values < 0.5, while years of rapid population increase (1995-6 and 1999-2000) were associated with index values > 1. For the 5 years with intermediate values (0.5 < index < 1.0) there was no correlation between delta and the index.

A persistent puzzle has been the apparent upward trend in the size of the density threshold necessary to cause a crash. It is possible that the trend is due to improving counting technique, but it could equally well be the result of climate change. Since 1956, the 8 crashes (defined as years with delta < -0.4) have occurred from densities ranging between 1296 and 1968 (mean = 1573):

Table 3. *Summary of measures associated with population crashes on Hirta.*

Year	Population	Crash size (delta)
1959-60	1344	-0.78995
2001-2	1889	-0.75 (estimate)
1998-9	1968	-0.74637
1988-9	1447	-0.73478
1985-6	1296	-0.60177
1966-7	1598	-0.60114
1963-4	1590	-0.45775
1991-2	1449	-0.41483

Only once has a population greater than 1573 *increased* in size (1997-8). But there have been 4 cases in the last 10 years when 'crashable' populations (i.e. more than 1296 animals) failed to produce crashes (in 1994-5, 1996-7, 1997-8 and 2000-1). It would be well worth investigating the winter weather during these years in more detail, in order to see if winter grass growth might have been unusually good, rescuing the sheep from what would otherwise have been a crash. Equally, it would be interesting to see if the weather for grass growth was unusually poor during the winters when crashes occurred from relatively low populations (1959-60, 1985-6, 1988-9, 1991-2), when the sheep might have been expected to have been in relatively good condition going into the winter.

If it turns out that an index based on August grass biomass and sheep counts really is a reliable predictor of population crashes, then we shall have to re-think the importance of late winter weather in causing crashes. Alternatively, the weather might change, so that we revert to finding low density crashes (i.e. from populations lower than 1573) in years with unusually severe winter weather. These crashes would not be predicted from the August food-availability index.

Maternal and environmental effects on lamb birth weight and early survival.

Owen Jones & Mick Crawley

Juvenile survival is often a critical mechanism in the regulation of wild animal populations. It is influenced by characteristics inherited from the parents, by environmental factors such as weather severity and forage availability, and by the amount of maternal provisioning. Maternal resource provisioning occurs during gestation and during the six week long suckling period. Environmental factors operate through forage availability and via weather severity, which influences thermoregulation and the time available for foraging.

In this study we used 11 years of life-history and vegetation data collected on St. Kilda between 1989 and 2000 to investigate the relationship between maternal condition and forage availability on birth weight and early survival. We used the North Atlantic Oscillation Index (NAO) as a measure of weather severity. NAO is a measure of the pressure gradient between Portugal and Iceland and provides an encapsulation of a number of variables including temperature, wind-speed and direction and precipitation. This gradient is important because it signifies the arrival of low- or high-pressure systems to Europe, which have highly significant implications for weather patterns.

We found that birth weight was positively influenced by both maternal condition and forage availability. For every 25g/m^2 increase in "green" forage availability there was a 0.11kg increase in birth weight.

Furthermore, birth weight was also the most influential variable in determining the chances of survival to weaning. The odds increased by 5.62 for every kilogram increase in birth weight (Fig. 14a). It was followed in importance by the amount of available vegetation, which increased the odds of survival by 10.68 for every kg/m^2 increase in biomass (Fig. 14b).

Maternal condition the previous August was also an important factor and interacted with the

sex of the lamb. Although an increase in maternal weight improved the chances of survival of both sexes, below a threshold of about 22kg, females had a higher probability of survival than males. Above this weight the survival probabilities were not significantly different (Fig. 14c).

It is likely that these differences are driven by the difference in the growth rates of the two sexes. Males grow faster than females and by late-August are about 20% heavier. Obviously the male "fast-growth" strategy is costly if mother is in poor condition. However, when the ewes are in good condition it allows the male offspring to attain a greater weight, which is an advantage during the rut when they compete for mates.

It was perhaps surprising that we found no significant effects of weather severity upon early survival. This could mean that its importance is outweighed by the importance of food availability. On the other hand, it could mean that the NAO measure is inadequate for this study and that further analyses using the individual weather covariates such as rainfall, temperature etc. are required. This avenue is currently being explored
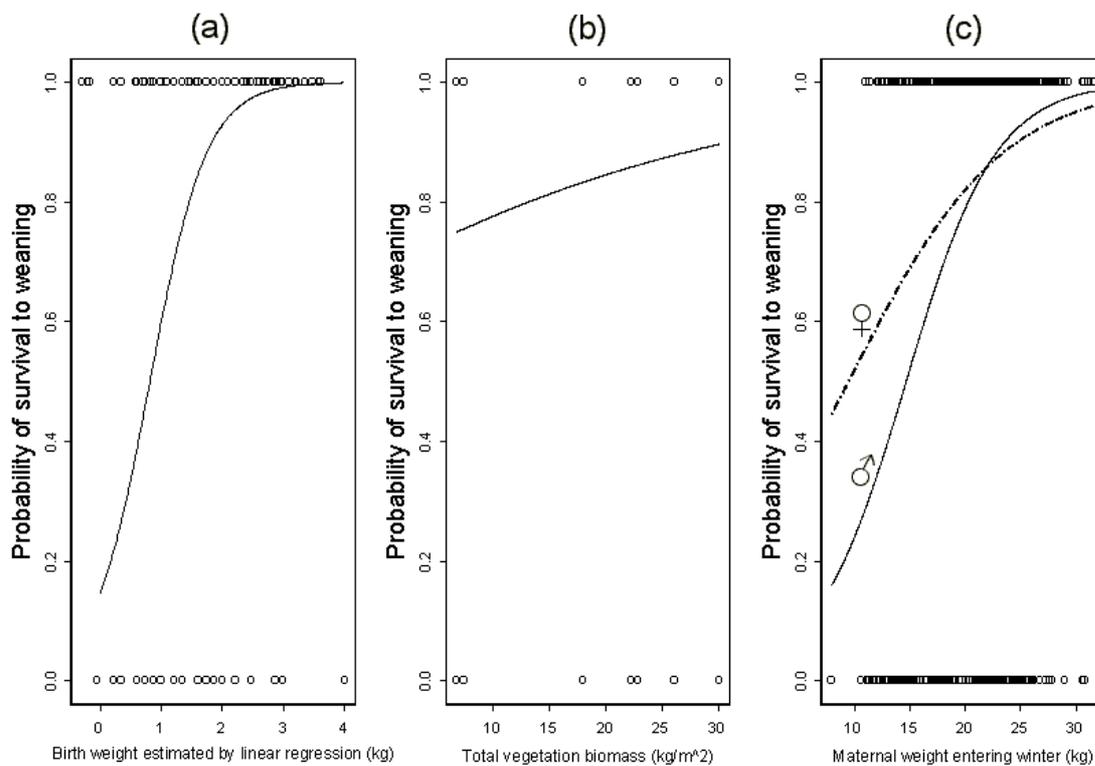
Figure 14. The effect of (a) birth weight, (b) available biomass of vegetation, and (c) the interacting effects of sex and maternal weight, on the probability survival to weaning. In (c) the unbroken line shows the prediction for males while the broken line shows the prediction for females.

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APPENDIX A: PERSONNEL CHANGES & SCHEDULE OF WORK

Personnel Changes

In May and August 2001 respectively, Andy Overall and Kate Byrne started postdocs at ICAPB, University of Edinburgh, on inbreeding depression in Soay sheep and red deer. In August Barbara Craig started a PhD at ICAPB, on parasite diversity in Soay sheep and in September Louisa Tempest started a PhD at IBS, University of Stirling, on the interaction between parasites and the costs of reproduction.

Schedule of work on St Kilda

Winter - Spring

Due to the Foot and Mouth outbreak on the mainland, our usual schedule of work was not carried out in spring 2001. On February the 8th Ian Stevenson, Owen Jones and one volunteer returned to St Kilda to carry out double labelled water analysis but they stopped handling the sheep in mid March. No further members of the project were permitted to arrive until May so the three people on island stayed on to perform ten study area censuses, and Owen Jones stayed on a further month to monitor the lambing period by observation only. No lambs were caught or tagged during this period. Owen finally left the island on the 26th of April. Jill Pilkington returned on the 16th of May for two weeks to complete the lambing monitoring.

Summer

Jill Pilkington, Owen Jones and one volunteer returned to Hirta on July 17th to carry out ten population censuses, conduct mortality searches (yielding 5 tagged and 5 untagged dead animals), catch and tag any lambs feasible (25!) and prepare for the main catch-up of study area sheep. The catch-up took place from August 4th-16th, was led by Josephine Pemberton, and conducted by a team of 11 other project members and volunteers. 305 sheep were caught and processed, of which 107 were lambs (49 males and 58 females), 66 were yearlings (31 male and 35 females), 31 were adult males, and 101 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic analyses. 42 sheep were retagged because of damaged or missing tags. 111 previously untagged sheep (107 lambs and 4 yearlings) were caught and processed. Jill Pilkington, Owen Jones, Barbara Craig and one volunteer remained on Hirta until 4th September to complete parasite counts.

Autumn

From October 12th to December 7th Jill Pilkington, Ian Stevenson, Owen Jones, Louisa Tempest and eight volunteers monitored the mating period, carrying out focal watches, capturing and processing 63 incoming tups and carrying out nine population censuses. Eight dead sheep was found. Faecal samples were also collected for hormonal analysis.

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