# ST. KILDA SOAY SHEEP PROJECT:

## 30TH ANNIVERSARY REPORT 2015

Photo: Anna Schroeer

**Editorial**

In 2015 the modern of era of Soay sheep research initiated by Tim Clutton-Brock, ably assisted by Steve Albon, reached 30 years. To mark this anniversary, in July 2015 we ran a celebration of the project at the Royal Society of Edinburgh, which was attended by many past project members and volunteers and other interested parties. Also, in December 2015 we ran a forward-looking session on Soay sheep research at the British Ecological Society annual conference, which was attended by a good sample of the 1,200 BES delegates. Various attendees at the RSE celebration, and some who could not attend, asked whether there would be a report of the event. In response, we decided to make this a 30th Anniversary Souvenir Issue of the Soay Sheep Project Annual Report, and we are sending it to all the email addresses we searched out for the RSE celebration. It starts with the usual review of events on the island in the 2015, but after that we present reports, loosely based on the talks at the celebration, of several of the major strands of the project's research over the past 30 years. In these reports, we have tried to pick out some of the major findings, interesting results and issues we are currently working on that we hope you might find interesting. Obviously, they are but a sample of the scientific output of the project, which has now reached over 170 refereed scientific papers as well as the 2004 book. To see the full list of papers, and keep informed about the study, please check the project website (http://soaysheep.biology.ed.ac.uk/) and if it is your thing, follow the project on Twitter (@SoaySheep).

We would like to take this opportunity to thank the very many people and organisations that have supported our research over the years. Chief of these is the National Trust for Scotland for allowing us to conduct the research on the island and its staff for on- and off-island support, plus Scottish Natural Heritage and Historic Environment Scotland for other relevant permissions. Our research has benefitted hugely from the existence of the base on St Kilda, and especially its supply helicopters, currently run by QinetiQ; many of the base staff have been very good to the project over the years. We also could not have conducted our research without the help of a succession of skippers and their boats to lift our teams there and back, currently Angus Campbell of Kilda Cruises running from Leverburgh, Harris who has brought a new level of comfort and reliability to the logistics as far as we are concerned. Core funding for the project has been through a succession of grants from the Natural Environment Research Council, to which we are hugely grateful for continuing support. Other organisations that have contributed include the Biotechnology and Biological Sciences Research Council, the European Research Council, the Wellcome Trust, the Leverhulme Trust, the Royal Society and the Natural Sciences and Engineering Research Council of Canada. Thanks to them all.

Finally we would like to highlight and thank two individuals who are critical to the success of the project but carefully avoid drawing attention to themselves. Jill Pilkington has now been the project field assistant since the early 1990s, leading all the core fieldwork on the island, seeing the data safely into the computer and arranging most of the project's logistics and catering. Anybody who runs a long term project will tell you that continuity is critical and Jill's presence over such a very long period has been completely central to the smooth running and systematic data collection of the project. Another person who keeps a low profile but is entirely central to the project is Ian Stevenson. Ian's success in weaning us off multiple Excel sheets and instead making us enter data with rigorous checking into a proper relational database, and write queries to generate our datasets, has been key to the accuracy and efficiency with which project members can extract the data set they want to interrogate. He also set up and maintains our Automatic Weather Stations on the island. Very many thanks to both.

**Josephine Pemberton & Dan Nussey**

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# POPULATION OVERVIEW 2015

The sheep population on Hirta entered 2015 at a moderate level and there was relatively high mortality over winter with 129 tagged animals being found dead with in the study area. Lambing began on the 2nd of April with 73.5% of lambs born surviving (Fig. 1).

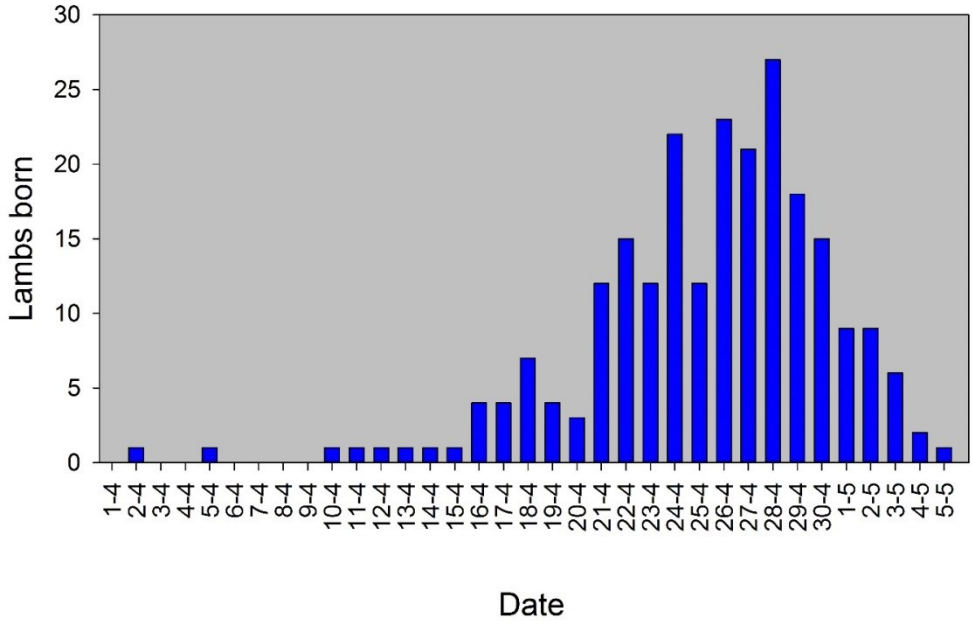


***Figure 1.*** *The temporal distribution of lamb births during 2015.*

In December 2015, 636 tagged sheep were believed to be alive on Hirta, of which 513 regularly used the study area, an increase of 6.43% 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.

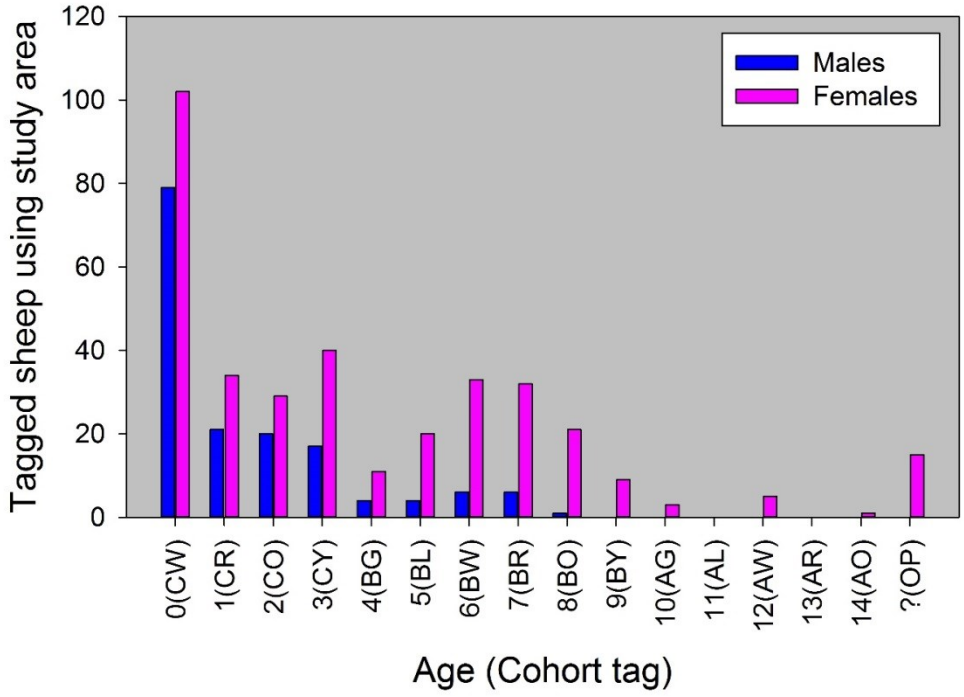


***Figure 2.*** *Age distribution of the 513 tagged Soay sheep using the study area in 2015.*

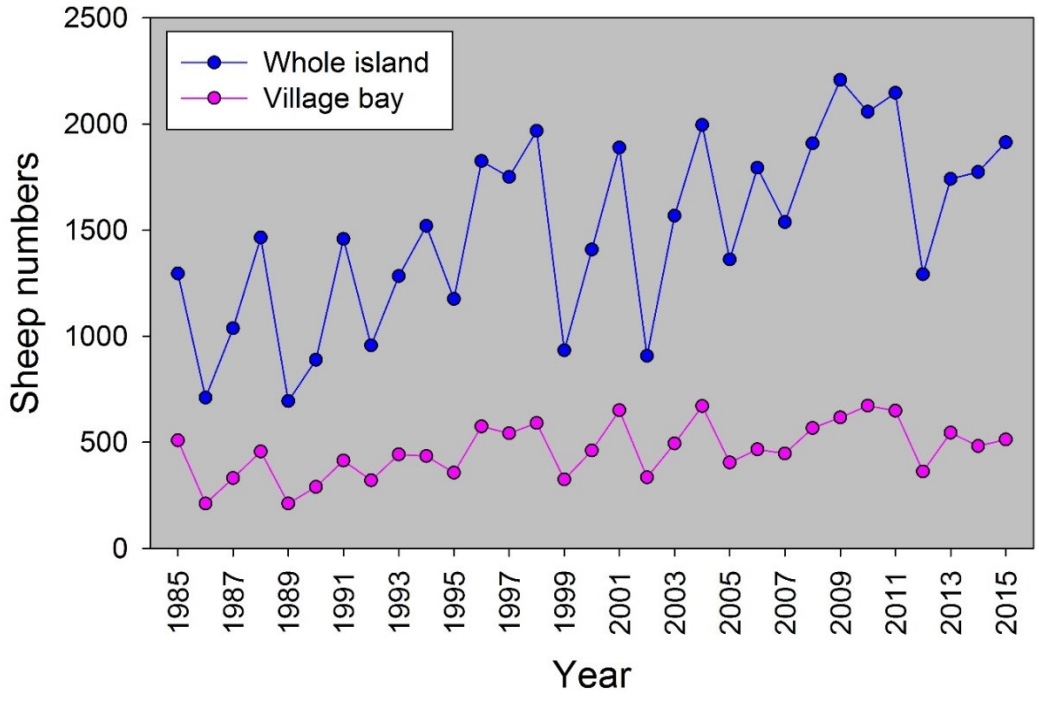


***Figure 3.*** *The number of tagged sheep regularly using the study area since 1985.*

One whole-island count yielded 1914 tagged and untagged sheep, with the details displayed in Table 1. The total population had increased by 7.89% since summer 2014 when it was estimated as 1774. This gives a delta (calculated as ln ($N_{t+1}/N_t$)) of +0.076. 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 16th 2015. 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** | 242 | 6 | 71 | 2 | 50 | 0 | 13 | 0 | 196 | **580** |
| **Mullach Bi / Cambir** | 281 | 11 | 75 | 11 | 45 | 2 | 11 | 1 | 263 | **700** |
| **Ruaival/Village** | 232 | 11 | 71 | 1 | 58 | 1 | 8 | 0 | 252 | **634** |
| **Total** | **755** | **28** | **217** | **14** | **153** | **3** | **32** | **1** | **711** | **1914** |

As can be seen from Figure 3, the number of tagged sheep using Village Bay and the whole island counts are very well correlated ($R^2 = 0.95$). Furthermore, both data series show a strong upward trend in sheep numbers over the 31 data points. Figure 4 shows the August Village Bay population size replotted on a more spread-out vertical axis and showing an increase of 7.4 sheep per year; the increase for the whole island amounts to some 30.9 sheep per year.

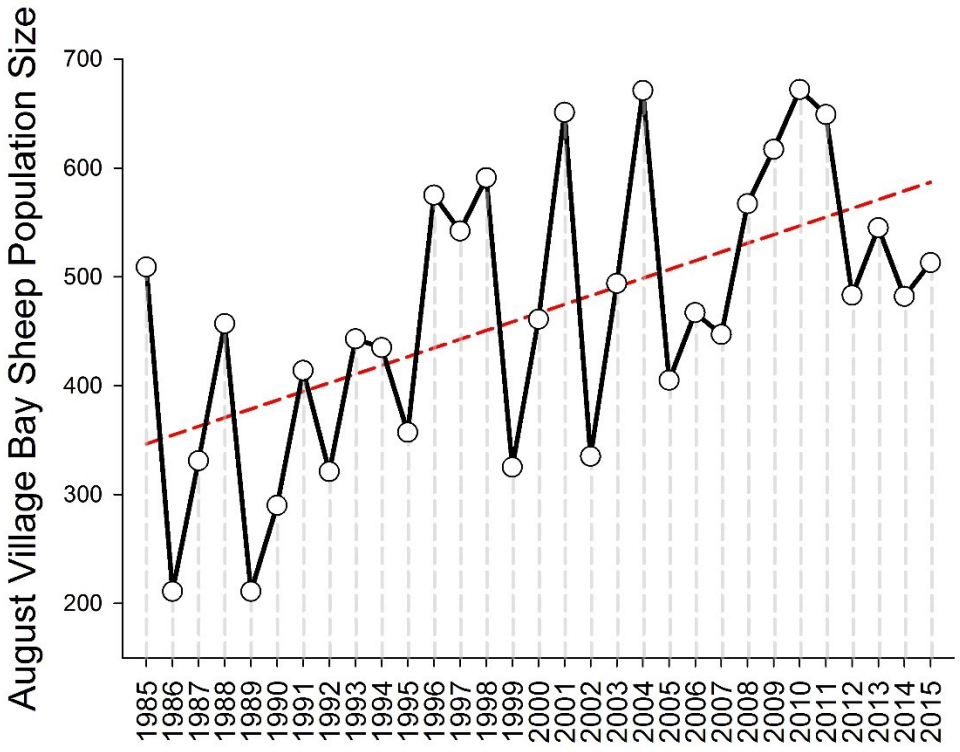


***Figure 4.*** *August Village Bay sheep population size showing upward trend in sheep numbers over the 30 years of the project. The fitted red line indicates a slope of 7.4 more sheep per year.*

# PUBLICATIONS 2015-16


Fairlie, J., Holland, R., Pilkington, J.G., Pemberton, J.M., Harrington, L. & Nussey, D.H. (2016) Life-long leukocyte telomere dynamics and survival in a free-living mammal. *Aging Cell*, 15: 140-148. DOI: 10.1111/acel.12417.

Graham, A.L., Nussey, D.H., Lloyd-Smith, J.O., Longbottom, D., Maley, M., Pemberton, J.M., Pilkington, J.G., Prager, K.C., Smith, L., Watt, K.A., Wilson, K., McNeilly, T.N. & Brulisauer, F. (2016) Exposure to viral and bacterial pathogens among Soay sheep (*Ovis aries*) of the St Kilda Archipelago. *Epidemiology and Infection*. DOI: 10.1017/S0950268816000017.

Handel, I., Watt, K.A., Pilkington, J.G., Pemberton, J.M., Macrae, A., Scott, P., McNeilly, T.N., Berry, J.L., Clements, D.N., Nussey, D.H. & Mellanby, R.J. 2016. Vitamin D status predicts reproductive fitness in a wild sheep population. *Scientific Reports*, 6: 18986. DOI: 10.1038/srep18986.

Watt, K.A., Nussey, D.H., Maclellan, R., Pilkington, J.G. & McNeilly, T.N. 2015. Fecal antibody levels as a noninvasive method for measuring immunity to gastrointestinal nematodes in ecological studies. *Ecology and Evolution*, 6: 56-67. DOI: 10.1002/ece3.1858.

Christensen, L.L., Selman, C., Blount, J.D., Pilkington, J.G., Watt, K.A., Pemberton, J.M., Reid, J.M. & Nussey, D.H. 2015. Plasma markers of oxidative stress are uncorrelated in a wild mammal. *Ecology and Evolution*, 5: 5096–5108. DOI: 10.1002/ece3.1771.

Regan, C.E., Pilkington, J.G., Pemberton, J.M. & Crawley, M.J. 2015. Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*). *Ecology Letters*, 19: 171–179. DOI: 10.1111/ele.12550.

Hayward, A.D., Moorad, J., Regan, C.E., Berenos, C., Pilkington, J.G., Pemberton, J.M. & Nussey, D.H. 2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. *Experimental Gerontology*, 71: 56–68. DOI: 10.1016/j.exger.2015.08.003.

Bérénos, C., Ellis, P.A., Pilkington, J.G., Lee, S.H., Gratten, J. & Pemberton, J.M. (2015) Heterogeneity of genetic architecture of body size traits in a free-living population. *Molecular Ecology,* 24: 1810-1830. DOI: 10.1111/mec.13146.

Worthington, H., King, R., Buckland, S.T. (2015) Analysing Mark-Recapture-Recovery Data in the Presence of Missing Covariate data via Multiple Imputation. *Journal of Agricultural, Biological, and Environmental Statistics*, 20:28-46. DOI: 10.1007/s13253-014-0184-z

Arthur, C., Watt, K., Nussey, D.H., Pemberton, J.M., Pilkington, J.G., Herman, J.S., Timmons, Z.L., Clements, D.N. & Scott, P.R. 2015. Osteoarthritis of the temporo-mandibular joint in free-living Soay sheep on St Kilda. *Veterinary Journal*, 203:120-125. DOI: 10.1016/j.tvjl.2014.10.014.

# PERSONNEL NEWS & SCHEDULE OF WORK IN 2015

***Personnel News***

Adam Hayward has taken up an 'Impact Research Fellowship' at the University of Stirling to conduct further work on host-parasite relationships in Soay sheep. Bilal Ashraf joined Jon Slate's group in Sheffield to work on genomic prediction in Soay sheep, funded by NERC. Rona Sinclair, Rachael Adams and Hannah Froy all joined Dan Nussey's research group in Edinburgh to work on immunity, telomere dynamics and ageing in Soay sheep, funded by BBSRC. Alex Sparks joined the project doing a MRC-funded PhD with Dan Nussey on "*Helmith-specific immunity and fitness in a wild mammal population*". Sadly, Becky Holland left the project in October 2015 to pursue her art; we wish her all the best.

***Schedule of work on St Kilda***

***Winter - Spring***

From March 10th until May 8th, Jill Pilkington, Xavier Bal, Alex Chambers and Darren Hunter carried out ten population censuses and tagged and sampled lambs, with assistance during the peak of lambing from Michael Morrissey and Louise Christensen. 234 lambs were born to 218 ewes; these figures include 16 sets of twins (10 ewes held both lambs, 3 ewes held one lamb and lost one and 3 ewes lost both lambs). 172 lambs (76 male and 96 female) were caught and tagged, a 100% tagging rate for the first time in 30 years; a further 62 lambs died before any tagging attempt. Mick Crawley and two assistants collected vegetation data. Charlotte Regan, Kara Dicks and Rachel Steenson collected suckling data.

***Summer***

Jill Pilkington, Conor Bolas and Rona Sinclair returned to Hirta on July 10th to carry out ten population censuses, conduct mortality searches (yielding 4 tagged dead animals), and prepare for the main catch-up of study area sheep. Charlotte Regan conducted further suckling watches assisted by Rachel Steenson. Alex Chambers carried out faecal collections prior to the catch up. The catch-up took place from August 5th – 19th and was conducted by a team of 12 additional project members and volunteers. 242 sheep were caught and processed, of which 104 were lambs (45 males and 59 females), 22 were yearlings (7 males and 15 females), 14 were adult males, and 102 were adult females. All animals were weighed and measured to monitor growth, and sampled for parasite and genetic analyses. 18 Sheep were retagged because of damaged or missing tags. 12 previously untagged lambs and 4 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 19th to December 8th Jill Pilkington, Alex Chambers and Louise Milne carried out ten population censuses, monitored the mating period, capturing and processing 17 incoming tups, 3 resident tups and 11 resident ewes. 29 previously darted, non-resident tups were seen in the study area during this rut. No dead sheep were found.

# ACKNOWLEDGEMENTS FOR FIELDWORK 2015

As ever, we are very 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 Elior 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, Kevin Grant the Archaeologist on the island and Gina Prior the Seabird and Marine Ranger.

We are also grateful for the help of volunteers without whom the fieldwork for 2015 would not have been possible: James Ashton, Xavier Bal, Ana Bento, Conor Bolas, Sam Collins, Emma Goodyer, Helen Hipperson, Andrew Mathews, Louise Milne, Rona Sinclair and Rachel Steenson. Thank you.

Our current research is supported by grants, fellowships and studentships from the Natural Environment Research Council, the Biotechnology and Biological Sciences Research Council, the European Research Council, the Leverhulme Trust and the Royal Society.

# REPORTS ON COMPONENT STUDIES 1985-2015

## The sheep and their food supply

**Mick Crawley, Department of Biological Sciences, Imperial College.**

The Soay Sheep on St Kilda represent an ideal model system for studying plant-herbivore interactions. The sheep have no competitors (there are no rabbits, deer or goats), they have no predators (there are no foxes), and the plant communities on which they graze are unusually simple. There is no immigration or emigration from the island, so the population dynamics are unusually straightforward, driven solely by births and deaths. This means that the sheep population is food-limited, and we can attribute grazing impacts on the vegetation unequivocally to the sheep.

What would the vegetation of Hirta look like without the Soay sheep? We know the answer to this question from the plant communities found on sheep-free islands like Dun, and from ungrazed places like the roofs of steep-sided cleits. There is a fundamental trade-off between palatability and growth rate which means that plants that grow most rapidly are expected to be the least well defended (because they invest in green-leaf accumulation rather than in defence). This means that the species that dominate in the absence of grazing are likely to be the most palatable to the sheep (e.g. grasses like *Festuca rubra* and herbs like *Rumex acetosa*) and this is exactly what we see.

The relationship between the dynamics of the plants and their herbivores on St Kilda will depend on changes in the biomass of vegetation, and sheep numbers over time. In the absence of grazing by sheep, plant biomass would rise to a limit imposed by competition for light, water and nutrients. The basic idea is very simple:

Change in plant biomass = plant growth – herbivore offtake
Change in sheep numbers = sheep births – sheep deaths

The important questions concern the forms of the relationships governing plant growth, herbivore offtake, sheep births and sheep deaths. In particular we need to understand the extent to which these terms are density dependent and the degree to which they act immediately or after a time lag. The simplest plausible model for the interaction makes several key predictions. First, the higher the death rate of the sheep and the lower the birth rate of the sheep, the taller the grass at equilibrium. More surprisingly, though, in these models plant growth parameters have absolutely no impact on plant biomass. If the plants grow quicker, we get more sheep, but the grass stays exactly the same length. If this model is correct, it makes a very strong and testable prediction: plant biomass will not be a function of mean sheep numbers. Let's see what the data say from the last 22 years of vegetation work on Hirta (Figure 5):

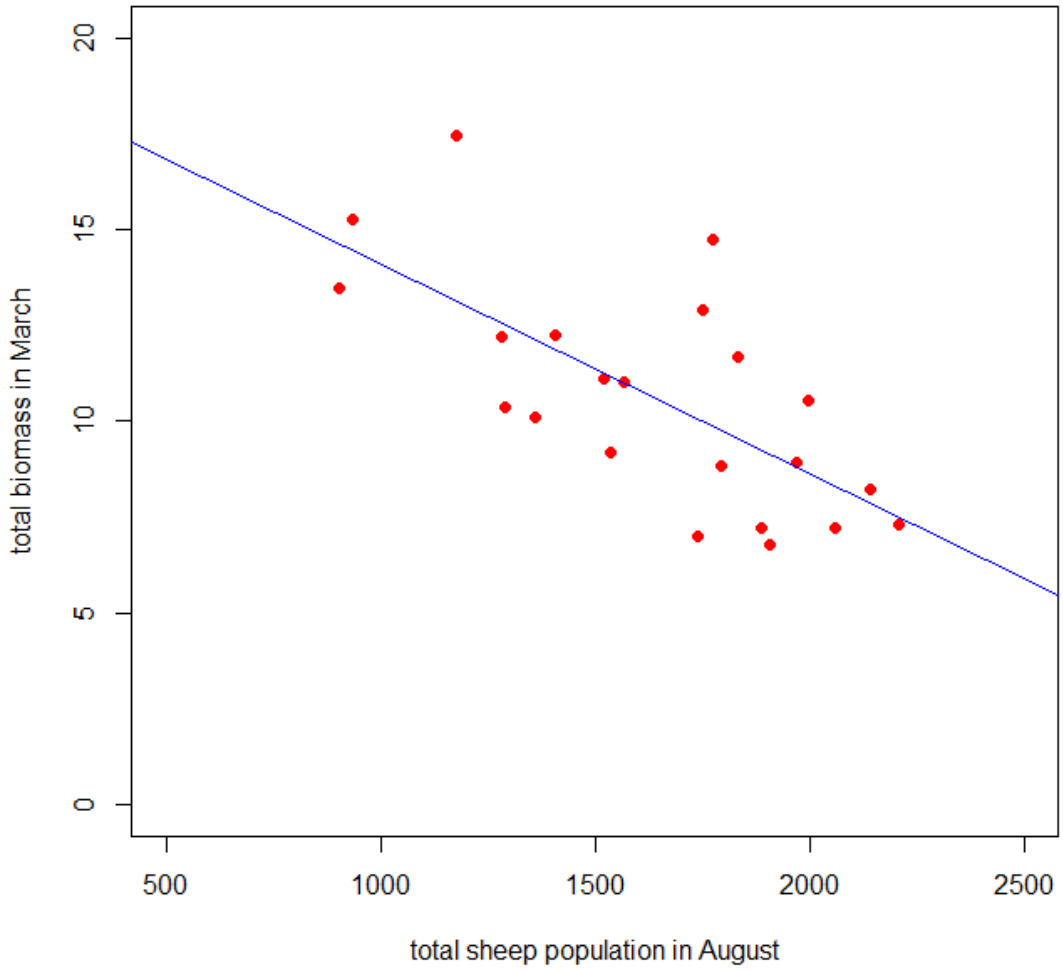


***Figure 5.*** *Relationship between total plant biomass in March and the whole island sheep count the previous August.*

It could not be clearer: more sheep means less grass. The model is clearly wrong.

The key to understanding what is going on lies in knowing about plant productivity (the rate at which new green biomass is produced) rather than just plant abundance (the amount of green biomass per unit area at any given time). In all of science, amounts are easy, but rates are hard. On St Kilda, we estimate productivity by temporarily excluding the sheep using movable pyramids (Figure 6). The pyramids are relocated twice per year: once in March when things are as hard for the sheep as they get, and once in August when things are as easy for the sheep as they get. Most of the year's grass growth occurs between March and August, but most of the issues for the sheep occur between August and March (this is when large numbers of animals starve to death in the occasional 'crash years').

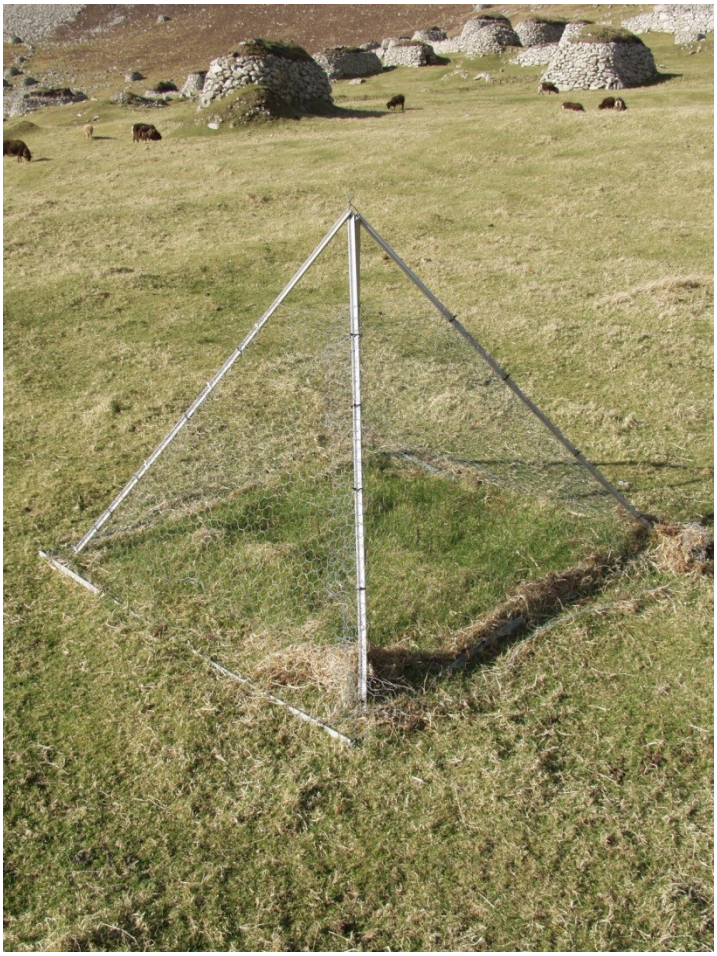

***Figure 6.*** *A pyramid in March in a year when sheep numbers are high (the grass outside the pyramid is very closely grazed, and there are very few tussocks of dead organic matter) but over-winter grass growth was low (there is rather little green leaf inside the pyramid). The difference in biomass inside versus outside the pyramid is our best estimate of grass productivity, and this is largely determined by weather conditions.*

As the sheep population has increased over the 30-year study period from about 1000 animals to about 2000, it has remained food limited, so the question immediately arises as to how this can be so? One plausible suggestion is that grass productivity has increased over this same period, and this has allowed sheep numbers to almost double. If we plot plant productivity (the extra green mass inside the pyramids compared to outside) against years (since we started measuring productivity in 2002) then we see two clear patterns, shown in Figure 7. First, autumn-winter productivity shows no trend at all (the red symbols) and, second, spring-summer productivity has increased significantly (the black symbols).

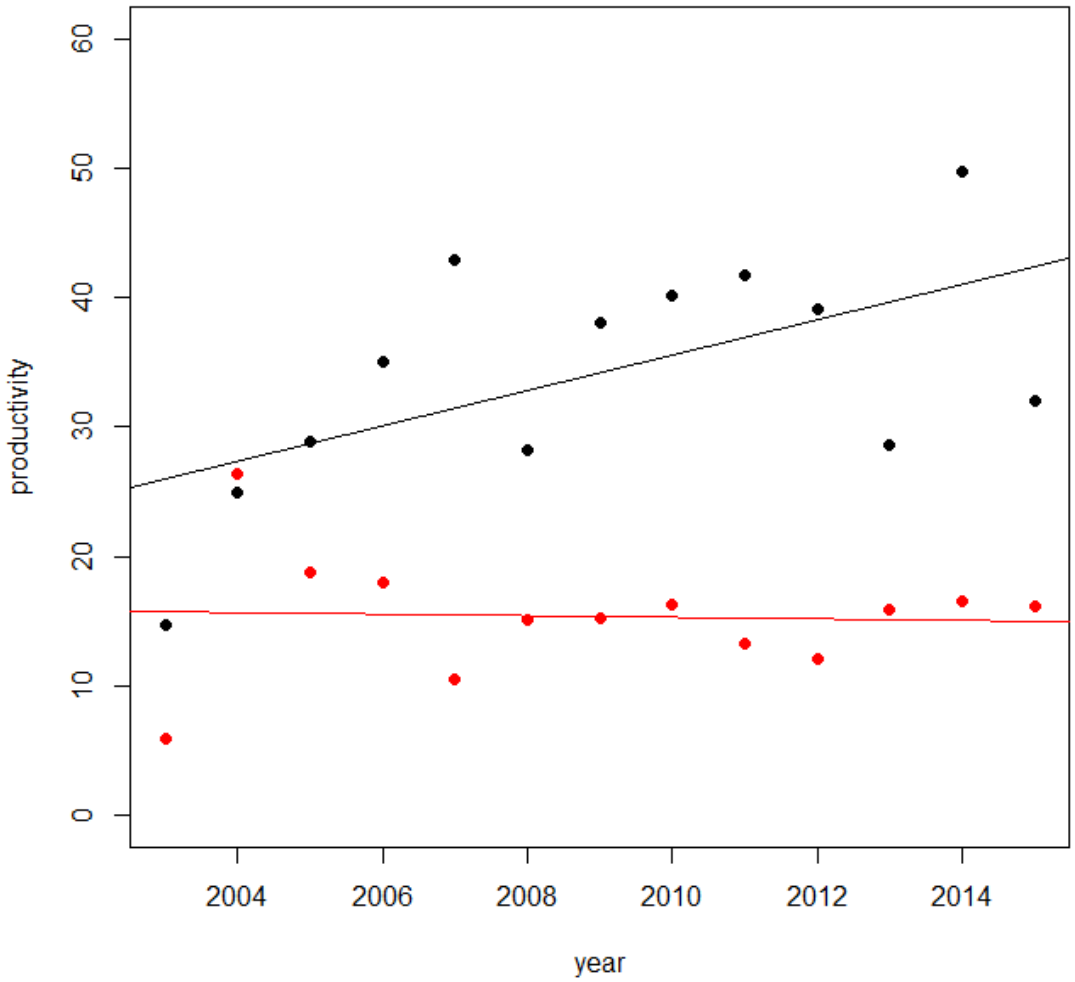


***Figure 7.*** *Plant productivity (measured as the difference (g dry matter in 20x20 cm quadrats) inside versus outside the pyramid) over time in Village Bay. Red points and line: productivity over autumn and winter (August to March); Black points and line: productivity over spring and summer (March to August).*

It turns out that weather after March is the principal driver of this grass productivity, and our present understanding is that accumulated day-degrees above a threshold temperature of 5C from the beginning of March onwards are the main driver of grass growth. It looks as if this has the effect of improving the body condition of the sheep going into the next winter, resulting in improved sheep survival and hence higher sheep numbers. The most obvious hypothesis, that starvation in winter would be reduced by greater winter food supply, appears not to be the case.

What remains for us to do now is to build a model for sheep-plant interactions that makes the right predictions for the right reasons.

# Population dynamics in an island population.

**Dylan Childs, Department of Animal and Plant Sciences, University of Sheffield.**

The study of population dynamics is one of the oldest sub-disciplines of ecology. Scientists working in this area aim to understand the factors that drive variation in the density (the number of individuals in a given area) and distribution (where they occur) of organisms. This endeavor requires us to unpick the roles of *intrinsic* and *extrinsic* processes. Intrinsic processes are those that involve interactions between individuals—such as competition for food or access to mates—that limit the growth of populations. Extrinsic drivers of change include factors such as climate that induce variation in population growth. Once these processes are understood, ecologists are able to use data gathered from a population to predict future changes in abundance or guide its management.

The Soay study is undoubtedly one of the best systems in the world for studying the causes and consequences of population dynamics in the wild. The numbers of Soay sheep on Hirta fluctuate widely as a result of variation in winter mortality, ranging from about 200-700 individuals in the Village Bay population over the last 30 years (see Figure 3). Although winter conditions are a key driver of these fluctuations, there remains obvious structure to these dynamics that cannot be solely explained by environmental variation. Historically, years of very high mortality ("crash" years) have tended to be interspersed by two years of population increase, although in the last decade this apparent regularity has broken down somewhat. These patterns raise a number of interesting questions. What ultimately limits population growth? What drives the growth/crash dynamics? What role, if any, does variation in population structure play? Why is the population increasing? The rich, long-term data provided by the Soay study—coupled with the relative simplicity of an island system (see previous report)—has provided a unique opportunity to address these fundamental questions.

Arguably the first question we should ask in any study of population dynamics is: How is the population regulated? That is, we need to understand how differences in competition associated with variation in the number of organisms affect population growth. This simple question is typically tackled by considering the relationship between the annual growth rate of a population and its density. In high-density years we expect a population to decline, while in low-density years it should increase. The shape of this relationship is important though, as it determines the likelihood of population crashes or even cycles. In the first such analysis of the Soays it was noticed that population growth and density are unrelated at low densities, but that at high densities the population is strongly influenced by density (Grenfell et al., 1998; Figure 8). Subsequent work extended this analysis to consider the role of a key climate phenomenon (the North Atlantic Oscillation, NAO). It found that the strength of the relationship exhibited at high densities is modulated by climate conditions (Coulson et al., 2001, Stenseth et al., 2004). Taken together, this work provided the first key insights into the nature of the growth/crash dynamics in Soays. Population growth is essentially unconstrained at low densities, but once a threshold is crossed it becomes sensitive to both climate and density, leading to a crash when density is high and winter weather is severe. Nonetheless, although important first steps, these analyses were only able to explain about 20% of the observed

variation in population growth rate. Accounting for the unexplained variation required a more subtle analysis.

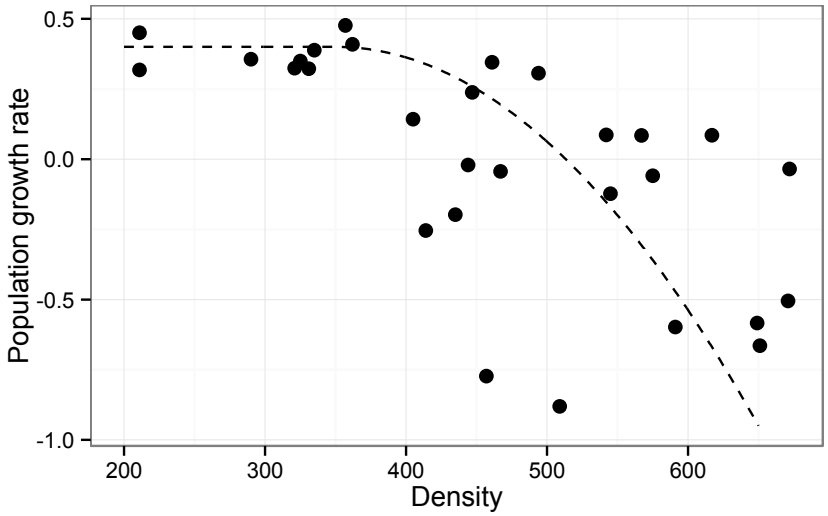


***Figure 8.*** *Population growth rate as a function of population density in the Village Bay Soay sheep population. Dashed line summarises the average relationship derived from a statistical model.*

Classical approaches for the study of population dynamics assume that the individuals which constitute a population are identical (or at least nearly identical). That is, we assume they respond to the environment and contribute to competitive effects in much the same way. This isn't because population ecologists really believe this to be true—it is just a convenient assumption that allows us to work with simple models. Because we know so much about the population, the Soay system has provided ecologists with the opportunity to carefully evaluate population-level consequences of individual differences. It is clear that different classes of individuals respond to their environment in very different ways. For example, the density of adult rams is far more variable than that of adult ewes, as is that of lambs relative to adults (see Figure 9). These kinds of effects lead to a decoupling of fluctuations in population density and the age and sex structure of the population. Studies of these patterns showed that they occur because Soays of different age and sex respond differently to density and weather (Coulson et al., 2001). For example, adult rams are much more sensitive to winter conditions than females, presumably because they expend so much energy in the autumn rut seeking opportunities to mate. Consequently, identical environmental conditions can result in different dynamics in populations of similar size. Further work showed that by considering this kind of "demographic" information, the predictive performance of population models is much improved (Coulson et al., 2008). This work provides a clear warning to ecologists against over-reliance on simple methods.

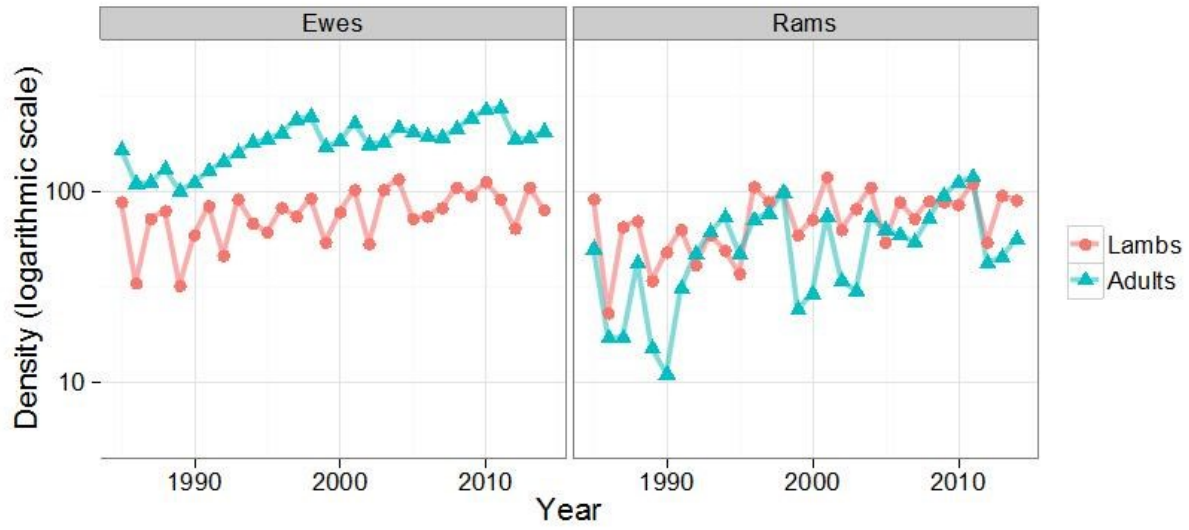


***Figure 9.*** *Abundance of the Village Bay Soay sheep population from 1985 to 2014, separated into sex and age (lambs vs. adults) classes.*

Early work on the Soays focussed on how density, demography and the environment influence their population dynamics. More recently, there has been a shift away from research investigating the *causes* of variation in population density toward efforts to understand the *consequences* of demographic variation and population dynamics. A recent study investigated the cause of a long-term decline in the average size of Soays (Ozgul et al., 2009). The study found that because winter conditions are becoming less challenging, slower-growing, smaller sheep are more likely to survive the winters than they once were. This, together with the so-called "young mum effect", whereby young ewes produce smaller offspring, explains why the average size of sheep is decreasing. It is thought that these changes are being driven by trends in the climate and vegetation on Hirta, though much more work will be needed to firmly establish this link (see more on this topic in later report on quantitative genetics). Another recent study constructed a mathematical model of the Soays that accounts for population structure (age and size differences) and density to explore how natural selection shapes the optimal frequency of twinning in the Soays (Childs et al., 2011). Using ideas from game theory, the authors found that such a model could accurately predict the optimal twinning strategy, and that this strategy depends on the nature of density dependence, and the size-dependence of growth, survival and reproduction in ewes.

## Parasite infection and immune responses of Soay sheep.

**Adam Hayward, Department of Biological and Environmental Sciences University of Stirling.**
**Andrea Graham, Department of Ecology and Evolutionary Biology, Princeton University, USA.**
**Ken Wilson, Department of Biological Sciences, Lancaster University.**

Soay sheep on Hirta harbour many different parasite species, which are broadly similar to those that infect domestic sheep. This fact means that the biology of these parasites is relatively well-understood

compared with many other wildlife populations and consequently the Soay sheep are something of a model population for studying wildlife-parasite interactions.

Parasites documented in the Soay sheep include ectoparasites living on the skin such as lice and keds, and endoparasites living in the gut, including protozoa, tapeworms and nematode worms (Craig et al., 2007, Craig et al., 2006, Wilson et al., 2004); bacterial and viral infections are rarer (Graham et al., 2016). The major parasites of Soay sheep are the strongyle nematode worms, a group of several species which live in the small intestine and abomasum ('true stomach'). Adult worms in the gut produce eggs (Figure 10), which are shed onto the pasture in sheep faeces, and eggs hatch into larvae which then develop to become infectious and are swallowed by grazing sheep.

Post-mortem examination of Soay sheep dying during winter has revealed intestinal pathology caused by strongyle worms, which prevents efficient protein uptake (Gulland, 1992). The contribution of strongyle worms to mortality has been demonstrated by experiments showing that treatment with anthelminthic drugs reduces the number and species diversity of infecting worms (Craig et al., 2009) and increases survival into the winter (Gulland, 1992).

***Figure 10.*** *Eggs of worm species infecting Soay sheep on Hirta, observed in sheep faecal samples. (A) the whipworm* Trichuris ovis*; (B) the nematode* Capillaria longipes*; (C) the tapeworm* Monieizia expansa*; (D) the nematode* Nematodirus*; (E) a strongyle nematode egg.*

A count of the eggs shed in faecal samples is used to estimate the number of strongyles a sheep is harbouring, and how resistant they are to infection: a sheep with few eggs in its faeces is likely to harbour few worms and be more resistant (Wilson et al. 2004. Thus, 'faecal egg count' (FEC) is a measure of worm burden and resistance. Individuals with higher FEC tend to have lower body weight (e.g., Wilson et al 2004; Hayward et al., 2014b) and, especially among lambs, lower survival of the winter (Hayward et al., 2011).

Research conducted over the past 25 years has revealed the major causes of variation in FEC. Extrinsic factors are important: in years where the sheep population size is higher (Figure 11) and the weather is warm and wet, transmission of infection is greater (Wilson et al 2004; Hayward et al., 2014a). FEC also tends to be higher in spring, when reproducing females and sheep in poor condition following winter shed large numbers of eggs (Wilson et al 2004).

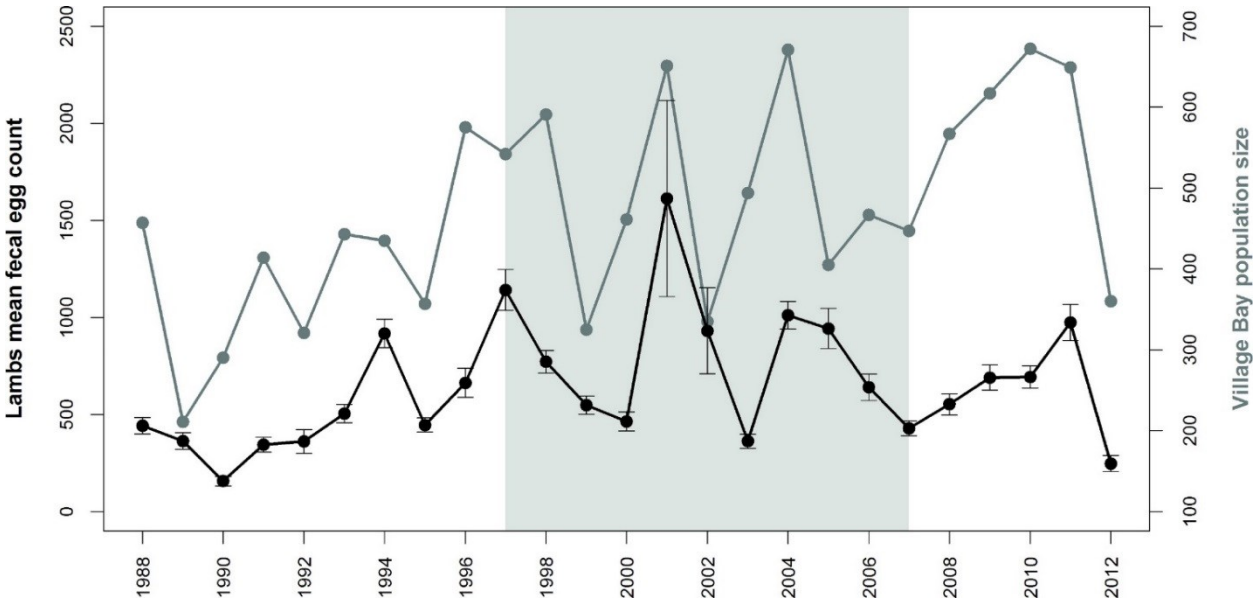


***Figure 11.*** *Time series of Village Bay population of Soay sheep in the Augusts 1988-2012. There is a significant correlation between the number of sheep in Village Bay (right axis, grey points and line) and the strongyle worm faecal egg counts of lambs (black points and line). This suggests that at higher sheep numbers, transmission of infection is greater and worm infections are larger.*

Important intrinsic factors driving variation in FEC include age, sex and genetics. Young lambs experience very high worm burdens, but then FEC declines in mature adults (Craig et al. 2006), before increasing again in the oldest adults (Hayward et al., 2009). In common with many wildlife parasitology studies, males suffer from higher FEC than females (Gulland and Fox, 1992; Craig et al 2006). A significant proportion of the variation in FEC can be explained by genetic differences between individuals. For example, the lower weights of sheep with higher FEC is underpinned by a genetic correlation between weight and FEC (Coltman et al., 2001a), suggesting that genes linked to high FEC are also linked to low weight. Meanwhile, certain regions of the genome have been shown to be linked to lower FEC (e.g. Beraldi et al., 2007, Coltman et al., 2001b, Paterson et al., 1998).

FEC is therefore linked to survival, weight and genetics. It is, however, a complicated measurement, dependent upon how many worm larvae are encountered by the sheep ('exposure'), how many worms develop into adults and how many eggs the worms produce (Grenfell et al., 1995). Although exposure is likely to be generally high, research shows that sheep can avoid patches of larvae-contaminated pasture and thus reduce their exposure (Hutchings et al., 2002). Meanwhile, worm development and egg production is likely to depend upon both genetic variation in the worm and variation in host immune responses. Research since 2010 has therefore focused on measuring sheep immune responses to infection and identifying the factors driving variation in immunity.

Veterinary studies have shown that immunity to strongyle worms is provided by antibodies, which can readily be measured in blood samples and which slow worm growth and reproduction (e.g. Stear et al., 1995). Antibody concentrations have a genetic basis in the Soay sheep (Coltman et al 2001b; Graham et al., 2010; Hayward et al 2014a), which raises a conundrum: if resisting worms is good for sheep, why do all sheep not show high resistance? Recent work has shown that while high antibody concentrations promote sheep survival, they may also limit reproduction (Graham et al 2010; Hayward et al 2014a). Thus, sheep can either (1) produce lots of antibodies and survive but reproduce less, or (2) produce few antibodies and reproduce lots but have a lower chance of surviving. This trade-off can explain the observed variation in immune responses. Further work examining a greater diversity of antibody responses has presented a more complex picture, with certain types of antibodies more closely linked to survival than others (Nussey et al., 2014).

In addition to resistance (reducing worm size and fecundity), sheep can also control the effects of infection by showing tolerance (limiting the damage caused by heavy infections). Recent work showed how tolerance varies between individuals, with some sheep losing lots of body weight when heavily infected and others losing very little weight (Hayward et al 2014b). Those sheep which lose less weight and which are more tolerant have higher breeding success (Hayward et al 2014b), although individual tolerance is not related to resistance (Hayward et al 2014a).

As the St Kilda Soay sheep project passes its 30-year anniversary, there are many outstanding questions relating to host-parasite biology which the project will be at the forefront of tackling. Increasingly sophisticated immunological techniques are now being applied, including assaying a greater range of immune markers (Nussey et al., 2012) and techniques for collecting antibody data from faecal samples (Watt et al., 2016). Ongoing and developing research projects will show how ageing affects the immune system; investigate the role of the host microbiota (gut bacteria) in sheep-nematode interactions; provide insight into maternal provisioning of immunity to lambs through milk. These questions are important and interesting for the fields of ecology, evolutionary biology, immunology, epidemiology and veterinary science, continuing the broad appeal of the first 30 years of host-parasite research on Soay sheep into the future.

# Senescence

**Dan Nussey, Institute of Evolutionary Biology, University of Edinburgh**

Senescence is the deterioration of physiological function with age. Understanding the reasons why individuals differ in when and how they senesce is an increasingly important challenge in modern biology. Soay sheep, just like many other wild populations of birds and mammals, show clear evidence of declines in function and fitness during later adulthood. Several studies have now demonstrated that from around six years of age the sheep show a progressive decline in their prospects of surviving the winter (Catchpole et al., 2000; Figure 12A). Reproductive performance also declines from six years onwards in ewes (Figure 12B). The combination of exceptional longitudinal records, tracking individuals all the way from birth to death, and the availability of a detailed population pedigree (see next section) has allowed the Soay sheep project to provide some of the first evidence that senescence in the wild has a genetic basis. A study of survival and reproductive data showed that ewes varied in their rate of senescence and that this variation had a heritable basis (Wilson et al., 2007a).

More recently, we have been investigating physiological measures and markers which might tell us more about how and why individuals vary in their rate of senescence. We have found, using the long-term data on sheep body weight collected each August, that elderly females lose around a kilogram across the two summers before they die – but exactly how old the animal is has no bearing on this weight loss (Nussey et al., 2011). This suggests that there is considerable variation in exactly when an individual sheep starts to show serious physiological decline. One possible reason for the observed weight loss is a deterioration in immune function against the many parasites that infect the sheep (see previous report on parasites). As they grow old, female Soays suffer increasing levels of infection by parasitic worms, measured as faecal egg counts, and their lambs likewise have higher worm burdens than offspring born to younger mothers (Hayward et al., 2010, Hayward et al., 2009). The rate of increase in parasite egg counts with age was exacerbated if females had experienced poorer environmental conditions earlier in their lives. Recent studies suggest that antibody measures associated with immunity to these worms predict subsequent survival in adult ewes (Nussey et al., 2014), and ongoing work aims to identify whether there is evidence of declining anti-worm immunity in late life and whether this contributes to senescence in survival and reproductive performance.

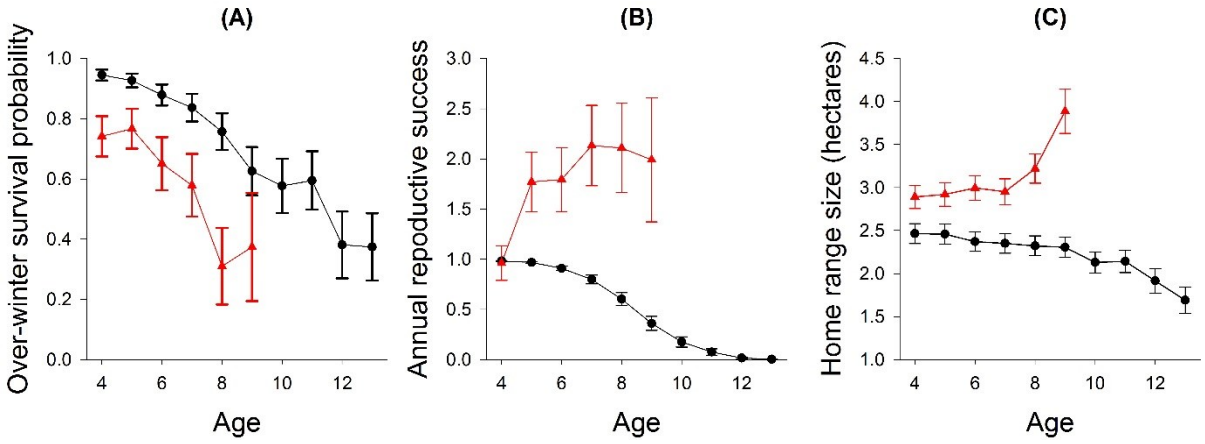


***Figure 12.*** *Age-related changes for females (black circles) and males (red triangles) in (A) overwinter survival, (B) annual reproductive success (probability of breeding for females, since probability of twinning does not vary with age in later life, and total number of lambs sired in males), and (C) annual home range size.*

Another interesting biological marker associated with ageing which we are investigating is telomere length. Telomeres consist of repetitive DNA sequences at the ends of our chromosomes which help preserve chromosome function and integrity, but shorten progressively as cells divide and do so more rapidly under stress. Research in humans has found that an individual's average blood cell telomere length is shorter in people who have experienced high stress or trauma, and short telomeres may be associated with increased chances of developing some late-onset diseases (e.g. diabetes, heart disease). We measured blood cell telomere length repeatedly across the lifetimes of around two hundred Soay ewes and found that short telomeres were associated with higher risk of death over winter in early life but not in later life (Fairlie et al., 2016). Over the next few years, we aim to measure telomere length in many more of the available samples collected on St Kilda and determine what this marker can tell us about variation in senescence and fitness under natural conditions. The exceptional quality of data and availability of archived frozen blood samples mean that the Soay sheep population on St Kilda has incredible potential to unlock the reasons for variation in lifespan and senescence patterns in mammals experiencing complex environmental conditions. Yet we still have a long way to go in our understanding of how and why different measurements, different individuals and the two sexes vary in their patterns of senescence in Soay sheep. A recent study revealed just how complex the processes involved might be. We investigated ageing patterns across more than 20 available measured traits from the long-term study on St Kilda (Hayward et al., 2015). This research showed evidence of surprising sex differences as well as the first evidence that behavioural changes occur in later life. Although the rate of senescence in survival is similar in males and females, males show little evidence of decline in their reproductive performance in later life (Figure 12B). And whilst home range size and quality (measured as percent high quality vegetation) decline with age in females they seem to increase in males (Figure 12C). We hope to soon address why such patterns are observed and how they impact individual fitness and population dynamics.

# The Soay sheep pedigree

**Josephine Pemberton, Institute of Evolutionary Biology, University of Edinburgh**

Evolutionary studies of wild animals are greatly enhanced if the individuals studied are related to each other via a pedigree or family tree. Pedigrees can be built when we know the father and mother of each individual. A female mammal suckling an offspring, or a female bird provisioning chicks in a nest is often a good guide to who the mother is. However, identifying fathers is much more challenging, especially in promiscuous species like sheep. On the Soay sheep project we have used a series of increasingly powerful DNA profiling methods to confirm maternity and work out paternity for each lamb.

Knowing exact family relationships allows us to measure and study many phenomena of central importance in evolutionary biology and genetics. First, it allows us to see how many offspring, grand-offspring, or more generally descendants, an individual has. For example Figure 13 (overleaf) illustrates the descendants of a single ram (NR049) in each cohort of lambs. Second, it allows us to understand how striking variation like that for coat colour, coat pattern and horn type is inherited (see the next report). Third, it allows us to estimate the relatedness between individuals, which is critical to understanding the extent of genetic control of traits like body size (see later report 'Quantitative Genetics') and also to estimate how inbred individuals are.

Developing the pedigree has been a task to which many people have contributed: Camillo Berenos, Kate Byrne, Dave Coltman, Tristan Marshall, Anna Montazam, Sheena Morrissey, Michael Morrissey, Andy Overall, Matt Robinson, Jon Slate and Judith Smith. Thanks to them all.

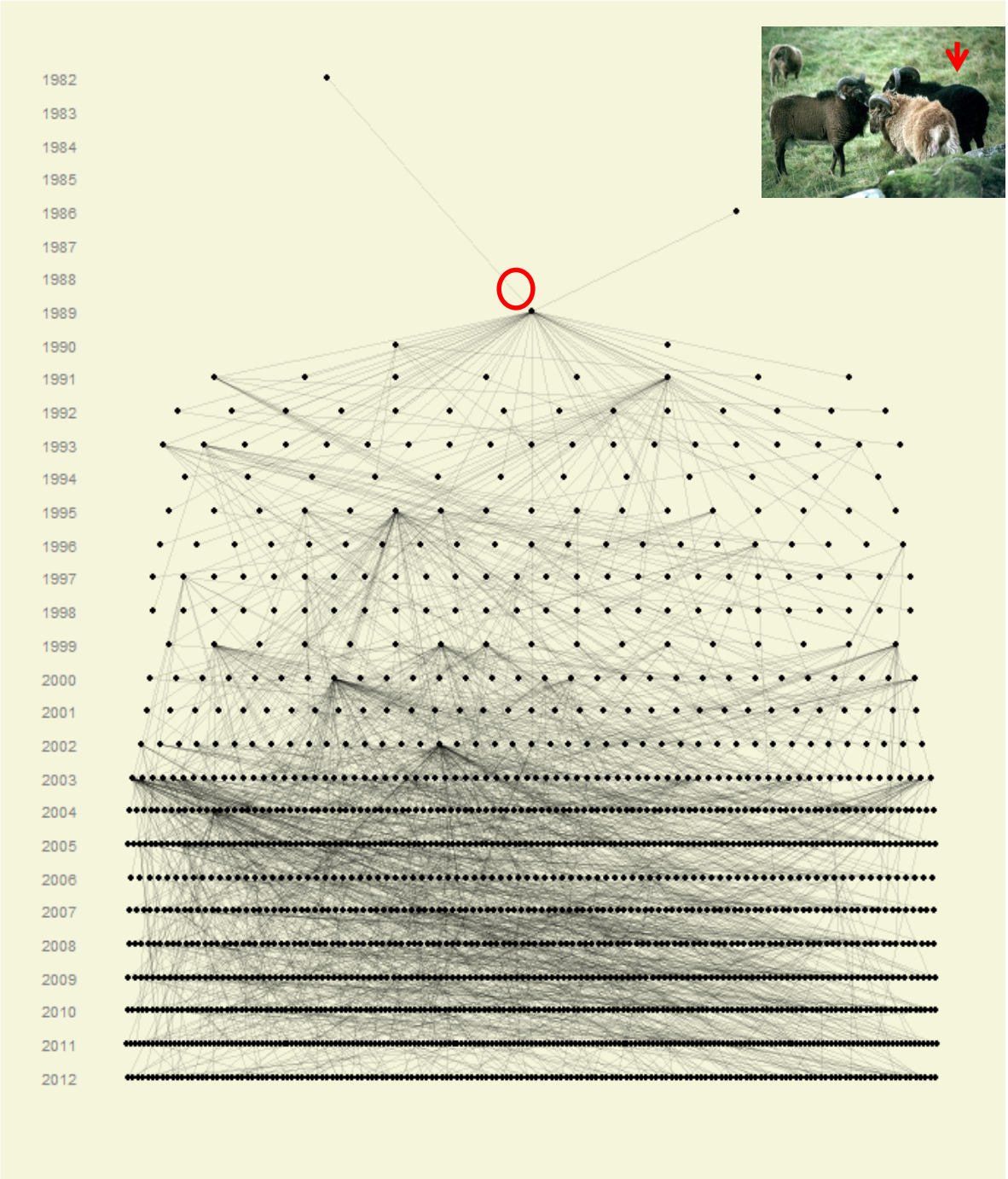


***Figure 13.*** *Parents and descendants of NR049. NR049 (circled in red) was a dark self ram (arrowed in photo) which was born in 1989 and died in 1995; his parents were OW001 born in 1982 and OP137 born in 1986. NR049 fathered a lot of lambs - at least 50 born between 1990 and 1995 and as can be seen, some of them were also very successful in their own right. By now NR049 has a very large number of descendants – but the process of chromosome segregation and crossing-over in each generation means that many of them contain only small very small fragments of NR049's genome. (Photo by Andrew MacColl and pedigree by Susan Johnston).*

# Mendelian traits – the evolution of coat colour and horn size.

**Susan E. Johnston, Institute of Evolutionary Biology, University of Edinburgh.**
**Jake Gratten, Queensland institute for Medical Research, Brisbane, Australia.**
**Josephine Pemberton, Institute of Evolutionary Biology, University of Edinburgh.**
**Jon Slate, Department of Animal and Plant Sciences, University of Sheffield.**

Soay sheep show a remarkable diversity in their colouration and in the types and sizes of their horns (Figure 14). Dark sheep are heavier and have more offspring than light sheep; wild-type sheep survive better than self-coloured sheep; males with larger horns are more likely to win access to females during the rut. Therefore, we would expect that sheep with these traits are more likely to pass on their genes to the next generation, meaning that light and self-coloured sheep and males with smaller should die out. However, instead of disappearing, light and self-coloured sheep have been very slowly increasing in number over the past decades. Similarly, a number of males continue to develop very small or deformed horns (scurs, Figure 14C), compromising their ability to mate successfully during the rut. Inheritance patterns have shown that all three traits have a simple genetic basis, which begs the question – why do genes for light coats, self-colouration and small horns persist on St Kilda?

These observations present a common puzzle in evolutionary biology, which cannot be solved by examining the trait alone. Therefore, a key aim of the Soay sheep project has been to identify the genes controlling such traits, so that we can examine their relationship with individual fitness (that is, their ability to survive and reproduce). Examining variation at the genetic level helps us explain why such apparently counter-evolutionary trends occur in nature.

The inheritance pattern in the pedigree told us that coat colour in Soay sheep is controlled by a single gene, with the dark (D) dominant to light (L). The search for the specific gene responsible ended when we sequenced several candidate genes known to be involved in mammal colouration and related variation at these genes to coat colour in the Soay sheep. We discovered that variation in one of these genes, Tyrosinase-related protein 1 gene (*TYRP1),* was perfectly associated with coat colour, meaning that DNA samples from all sheep could now be tested to determine which copies of the gene they carried (Gratten et al., 2007). We went on to examine the relationship between DD, DL and LL sheep, their body weight and their fitness (Figure 15). As expected, both DD and DL (i.e. dark coloured) sheep were heavier (Figure 15A), but sheep carrying only dark or light copies (DD and LL) had lower fitness, whereas sheep carrying one copy of each (DL) had the highest fitness (Figure 15B; Gratten et al., 2008). Not only are DL sheep the most successful, but they also pass the light copy on to 50% of their offspring, increasing the chances that some offspring will be light. This has caused the light copy to gradually increase in the population, though we predict it should stabilize at a level at which there are still plenty of classic dark Soay sheep!

***Figure 14.*** *Conspicuous traits in St Kilda Soay sheep. A. Dark (front) and light (back) coat colours; B. Self (left) and wildtype (right) lambs. C. Scurred (left) and normal-horned (right) males; Photographs by Aimeric Blaud, Arpat Ozgul and Jill Pilkington*

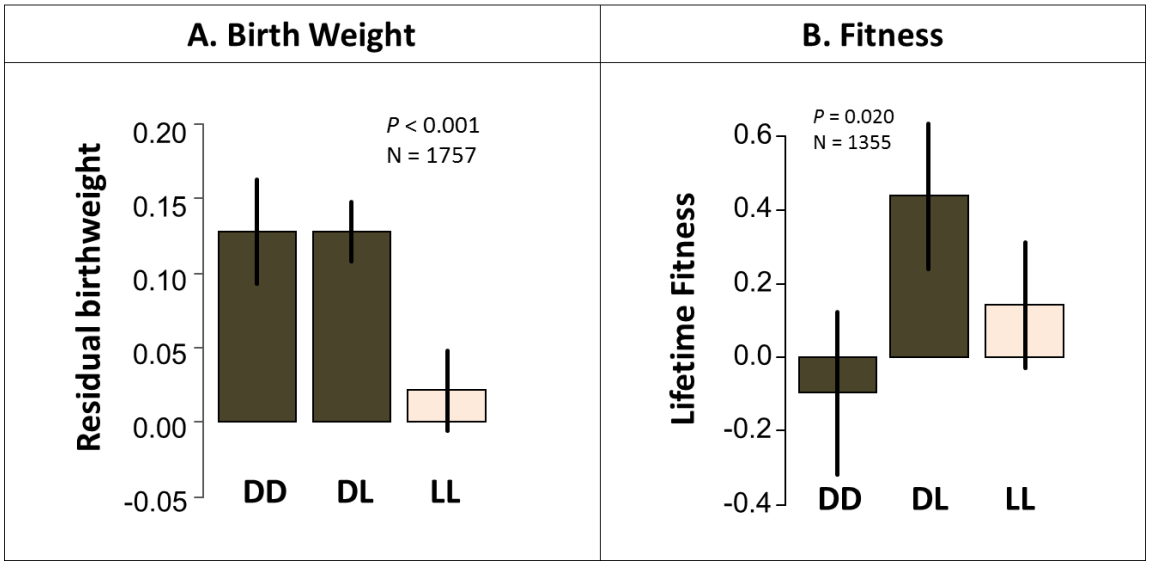


***Figure 15.*** *The relationship between coat colour genotype and (A) birthweight and (B) lifetime fitness.*

We have also tracked down the gene responsible for coat pattern, at which wildtype is dominant to self. The variation is due to mutations in the Agouti signalling pattern (*ASIP*) gene (Gratten et al., 2010). A study of selection on coat type and *ASIP* genotypes revealed that while self-coloured lambs are less likely to survive and recruit to the adult population, if they do recruit they actually have higher reproductive success than wild-type sheep (Gratten et al., 2012). These effects are such that not only is the self-coloured gene retained in the population, it is actually slowly increasing, though self-coloured sheep are still strikingly rare in the population.

Turning to the horn polymorphism, the Soay sheep rut features strong competition between males for access to oestrous females. Studies have shown that males with larger horns sire more offspring (Preston et al., 2003), yet variation in horn size and type (i.e. normal vs. scurred) persists (Figure 16). It was known from inspecting the Soay sheep pedigree that horn type shows fairly simple inheritance, however unlike coat colour there were no clear candidate genes for us to target with DNA sequencing to identify the genes responsible. We used a different approach using an 'Ovine SNP50 BeadChip': a tool developed by animal breeders that examines 50,000 mutations dispersed throughout the sheep genome. We studied the relationship between each mutation and variation in horn type, and identified a single region of the genome associated with both horn size and type, which included a gene called RXFP2, which is associated with osteoporosis and male sexual development in humans and mice. This discovery allowed us to develop a genetic test to identify "normal" (+) and "polled" (P) copies of the gene and distinguish between individuals carrying ++, +P or PP. We found that having more copies of + resulted in the larger horns (Figure 16a), whereas having more copies of P resulted in smaller horns or scurs (Figure 16c, d); males with one of each copy (+P) developed intermediate-sized horns (Figure 14b; Johnston et al., 2011).

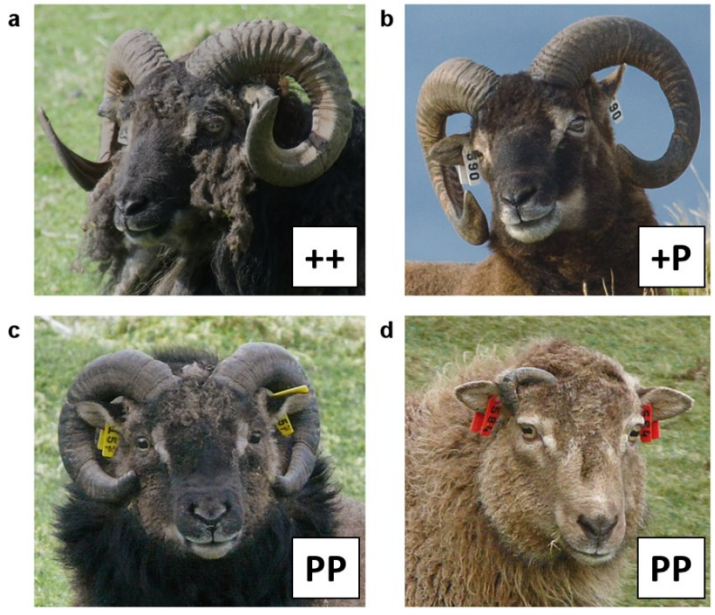


***Figure 16.*** *Horn types in Soay sheep males in (a) a four-year old, large-horned male; (b) a 5 year old medium-horned male; (c) a five year old small-horned male; and (d) a five year old scurred male. The boxes indicate which combinations of the + and P copies are carried by each male. Photos by Arpat Ozgul and Susan Johnston.*

We examined the relationship between individual fitness and *RXFP2* genotype, and found a trade-off between reproductive success and survival. ++ males had more offspring but decreased survival whereas PP males had fewer offspring but increased survival (Figure 17 a, b). However, males carrying one of each copy (+P) had as high reproductive success as ++ males, and as good survival as PP males, meaning that they had the highest fitness (Figure 17c). As with coat colour, this means that +P males will continue to pass the P copy onto 50% of their offspring, so small-horned and scurred males will continue to appear within the population (Johnston et al., 2013). We think that these associations between genotype and fitness are being driven by differences in mating strategies during the rut among males with different sized horns. The largest horned males enter fights at a younger age, with the most dominant rams spending less than 5% of their time feeding and suffering increased mortality during and after the rut. Conversely, smaller-horned and scurred males instead spent 50% of their time feeding, and searching the island for unguarded females (Preston et al. 2003). Males with +P may achieve some balance between these strategies; but also, because they live longer, their horn size may eventually match that of younger ++ males.

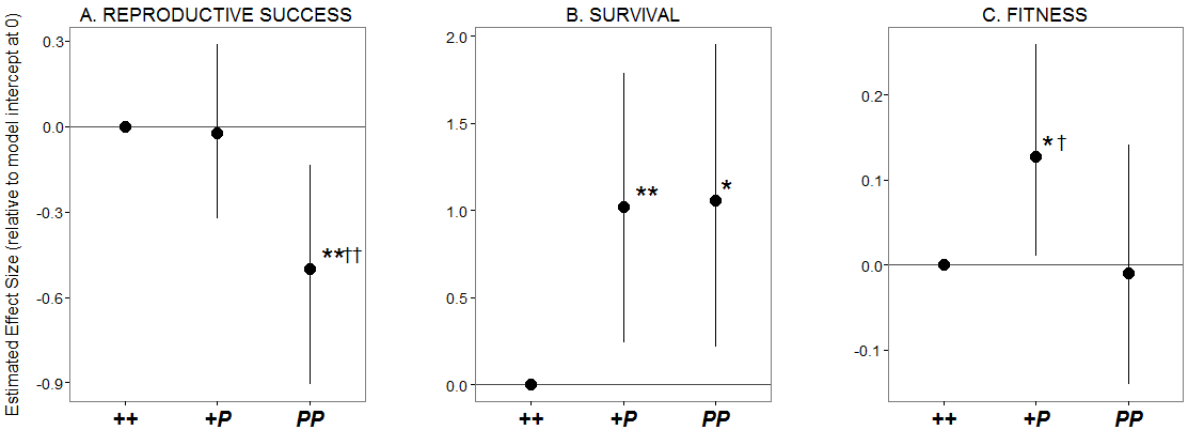


***Figure 17.*** *The relationship between copies of RXFP2 and (A) Number of offspring, (B) Survival and (C) Fitness. * and † indicate significant differences compared to ++ and +P, respectively.*

Females have smaller horns than males, and also show variation in their horn type. They can be either normal-horned (++), scurred (+P), or lack horns completely (polled, PP). We conducted the same analysis in females, but found no relationship between their RXFP2 genotype and fitness. Thus, variation in horn type in the population is driven by its effects on fitness in males.

Overall, our studies of coat colour, coat pattern and horn type on St Kilda have shown how finding genes responsible for traits helps us explain apparently counter-evolutionary trends. Critically, the appearance of the animal does not give us full information on the underlying genetics; indeed, it is the genotypes that are more informative for evolutionary studies. All three studies described here have been key findings for understanding why we see variation in natural populations. They are also unusual for the fact they reveal examples of "heterozygote advantage", where it is more advantageous to carry two different copies of a gene than two of the same copy, for which there are relative few good case studies in natural populations.

# The genetic history of Soay sheep

**Jon Slate, Department of Animal and Plant Sciences, University of Sheffield.**
**Philine Feulner, Swiss Federal Institute of Aquatic Science and Technology, Switzerland.**
**Jake Gratten, Queensland institute for Medical Research, Brisbane, Australia.**
**Josephine Pemberton, Institute of Evolutionary Biology, University of Edinburgh.**

The history of sheep breeds on the St Kilda group of islands is fairly complicated, and includes several breeds that are no longer on the islands (Clutton-Brock et al., 2004). However, the current study population on Hirta has only been on the island since 1932, and the history of sheep on the island before then is closely tied up with the farming practices of the human inhabitants. Written records suggest that the St Kildans used to keep ancestors of what are today known as Hebridean (or sometimes St Kilda) sheep, and also the now extinct Dunface sheep or Old Scottish Shortwool. Soay sheep would only have been on the island of Soay during this period. In the mid-late 1800s, the Scottish blackface sheep become the dominant breed throughout the Highlands and Islands, and was introduced to Hirta during this period. Eventually, the Blackface replaced the earlier breeds (Dunface and Hebridean), but not before the Boreray breed was created by crossing the Dunface with the Blackface (Morton Boyd, 1981). This breed is still found as a free-living population on Boreray today. Importantly, this means that Boreray sheep can be thought of as a sort of 'living museum' in which Dunface genes have been preserved. When the people of St Kilda left the island in 1930 they took all of their sheep with them. Two years later, 107 Soay sheep were moved from Soay to Hirta (Clutton-Brock et al., 2004).

The fact that different sheep breeds have spent overlapping periods on the islands of course means that there has been potential for hybridisation between different types of sheep. In fact, there is a written record of just such an event happening. The botanist and natural historian Henry John Elwes established from Donald Ferguson, the groundmaster of St Kilda in the late 1800s, that the breed which 'preceded the introduction of Black-faced rams were once introduced into Soay but they did no good' (Elwes, 1912). Elwes interpreted this to mean that Dunface sheep were deliberately introduced into the population of Soay sheep on Soay. If this is true, then it means that all contemporary populations of Soay sheep may have a genetic contribution from Dunface sheep that took place around 150 years ago.

We first became aware of the possibility that admixture between Soay sheep and another breed could have happened when we were working on the coat colour and coat pattern polymorphisms described in the previous section. When we found the genes for light coat colour and the self coat pattern, we made a surprising observation. Soay sheep with light coloured or self patterned coats didn't just differ from the classic dark wild sheep at the genetic nucleotide (a nucleotide is simply a 'letter' of the genetic code) causing the change in coat, but also at a number of other nearby positions on the same chromosome. If light coats or self patterns were caused by mutations that had appeared in Soay sheep in their past, we would only expect to see differences at the actual causative mutation. The pattern that we actually observe is usually caused by introgression – the spread of genes from one population into another.

Therefore, we set out to test whether Soay sheep had interbred with another sheep breed in the past, and whether light coats and self patterns had been caused by this interbreeding.

We used genetic information collected by the International Sheep Genomics Consortium (ISGC), which developed the Ovine SNP50 BeadChip which probes 50,000 positions in the sheep genome and used the chip to examine genetic variation across a range of breeds including Soay, Boreray, Scottish Blackface and, to check the method, a distantly related breed of sheep called the red Maasai (Kijas et al., 2012). Dunface sheep are extinct, and we are unaware of any museum specimens that we could have used. However, the profiles from Boreray sheep are useful because this living museum breed will carry Dunface genes. When we analysed available genetic data from Soay, Boreray and Scottish Blackface sheep, we found a pattern that was remarkably consistent with the story described by Elwes: that Dunface sheep exchanged genes with Soay sheep in the 1800s (Feulner et al., 2013). Figure 18 shows that the Soays contain genetic material shared with Boreray sheep, which themselves share material with the now extinct Dunface breed, but not with Scottish Blackface sheep. We cannot rule out other scenarios, but what seems clear is that Soay sheep have received genes from another breed in the last few hundred years, and that the 'donor' breed does not appear to have been Scottish Blackface sheep. This last point is relevant, because it has long been speculated that when the St Kildans departed from Hirta in 1930, they may have inadvertently left a few sheep on Hirta, which could have subsequently bred with the Soays that were introduced in 1932. We can probably rule out that scenario, given that the donor breed do not appear to be Blackface sheep.

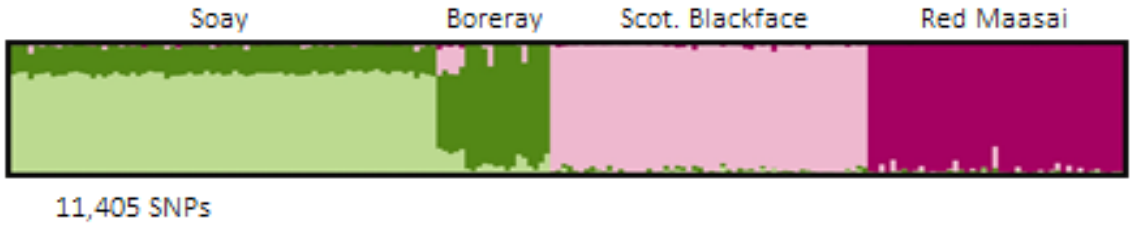


***Figure 18.*** *The results of an analysis testing the degree to which different breeds share genetic material. Samples from Soay sheep are made up of more than one colour: the light green is unique to Soay sheep and represents the original Soay sheep genes, while the dark green is found in Boreray sheep and is not found in Scottish Blackface sheep. Therefore, it represents the Dunface-derived part of the Boreray sheep genome. This is consistent with Soay sheep having undergone admixture with Dunface sheep, the scenario described by Elwes.*

Having established that admixture probably occurred, we next set out to test whether the polymorphisms in coat colour and coat pattern that we observed today could have arisen due to the introgression of new genetic variants (Feulner et al., 2013). We were able to do this by comparing the segments of chromosomes (termed haplotypes) around the coat colour and coat pattern genes between Soay sheep and all of the other sheep breeds profiled by the International Sheep Genomics Consortium. The idea behind these analyses is that if a gene has a recent ancestry in two breeds, then the haplotypes are very similar between the breeds, whereas if the gene does not have a recent co-ancestry, haplotypes will be less similar between the two breeds. Haplotype sharing diminishes over time if two populations are kept

apart, because the process of genetic recombination affects the two populations differently. At the TYRP1 gene (see previous report) we compared dark coated and light coated Soay haplotypes with haplotypes in all of the other breeds. The dark coated haplotypes in Soay sheep do not have a very high similarity to haplotypes in other breeds, reflecting the long period of isolation of Soay sheep on St Kilda. However, the light coat haplotype has a high degree of sharing with similar haplotypes found in Boreray sheep. This is consistent with the light coat colour gene being introduced to Soay sheep by admixture with the ancestors of Boreray sheep (i.e. Dunface sheep). We did a similar analysis at ASIP, the gene that determines whether Soay sheep have the wild type or self type coat pattern (see previous report). Again, the wild type haplotype shows weak sharing with all other breeds, consistent with Soay sheep being isolated for a long time, while the self type haplotype is also seen in Boreray sheep, reflecting a recent co-ancestry of this gene in the two breeds. Therefore, it seems likely that prior to admixture, Soay sheep had the 'classical' dark wild phenotype, similar to that seen in mouflon sheep, the ancestor of all modern sheep. The light coat colour and the self coat pattern are probably a result of the admixture with Dunface. There is no evidence that the horn polymorphism in the population was introduced in a similar way (Johnston et al., 2013).

It seems likely that Soay sheep hybridised with another sheep breed sometime before they were introduced to Hirta, meaning that all contemporary populations of Soay sheep carry the legacy of that event (summarised in Figure 19). The result was that new genetic variants were introduced, some of which are likely to have been favoured by natural selection. Biologists are increasingly coming to appreciate how these kinds of events can provide the material for adaptive evolution, and indeed it now seems clear that interbreeding between humans and Neanderthals introduced favoured genetic variants into our own species. Soay sheep can be regarded as providing an excellent example of what is now known as adaptive introgression.

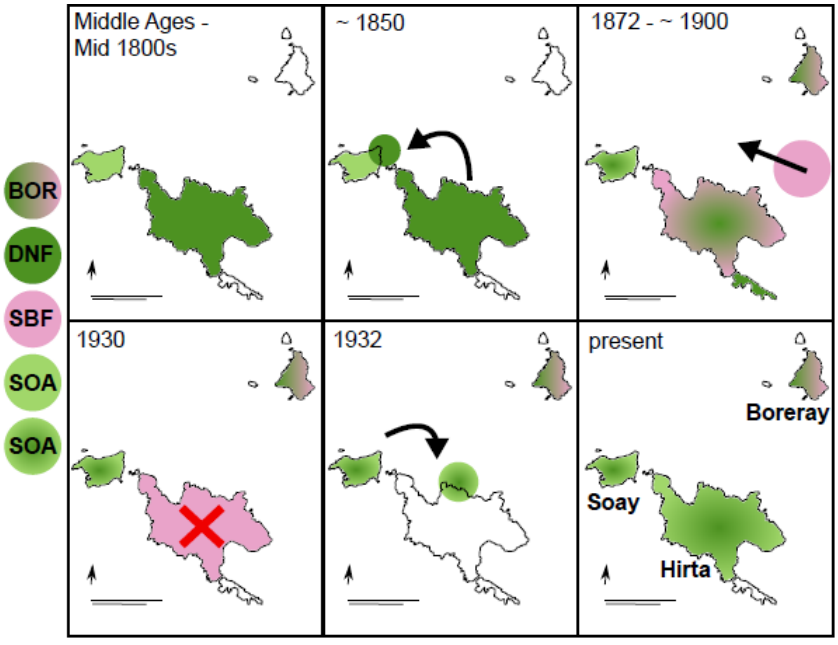


***Figure 19.*** *Possible history of sheep on St Kilda. Codes: BOR – Boreray, DNF – Dunface, SBF – Scottish Blackface, SOA – Soay. The light green Soay symbol represents the pre-admixture population and the variable shading of green represents the post-admixture Soay population. The proposed admixture event between Dunface sheep and Soays is shown in panel 2. The present populations comprise of post-admixture Soay populations on Soay and Hirta, and Boreray sheep (created by crossing Dunface with Scottish Blackface sheep) on Boreray.*

# Quantitative traits – selection and heritability, but a surprising response.

**Josephine Pemberton, Institute of Evolutionary Biology, University of Edinburgh.**
**Alastair Wilson, Centre for Ecology and Conservation, University of Exeter.**

Quantitative traits are those characteristics of organisms that vary in a small way from one individual to the next. Human height is a classic quantitative trait but so too, on St Kilda, is Soay sheep body weight (Figure 20). Variation in such traits is expected to be controlled by both genetics and the environment. Specifically, many genes situated across many different chromosomes are thought to affect such quantitative traits; each alone is likely to have only a modest effect on the trait, but all together they may be an important source of variation between individuals. Meanwhile the environment, in the shape of the weather or how much food there is, will also affect quantitative traits and so represents the other main source of variation among individuals. The study of how quantitative traits evolve (or not) in natural populations has attracted much interest in recent years because new methods in genetics and statistics have enabled new analyses of the topic.

***Figure 20.*** *Measuring quantitative traits on St Kilda. (a) Louise Christensen weighs a day-old lamb before tagging. (b) Alastair Wilson weighs a tagged lamb in August.*

One of the first questions that was asked by Soay sheep project researchers was whether quantitative traits such as size were under natural selection, i.e. whether there was any evidence that smaller, larger or even middle-sized sheep had higher fitness in that they were more likely to survive or breed. We found that lambs that weighed more in August were more likely to survive the following winter, especially if it

was a crash winter (Figure 21; Milner et al., 1999). This result has been repeated in many ways over the years: among Soay sheep, in order to survive, it is better to be bigger.

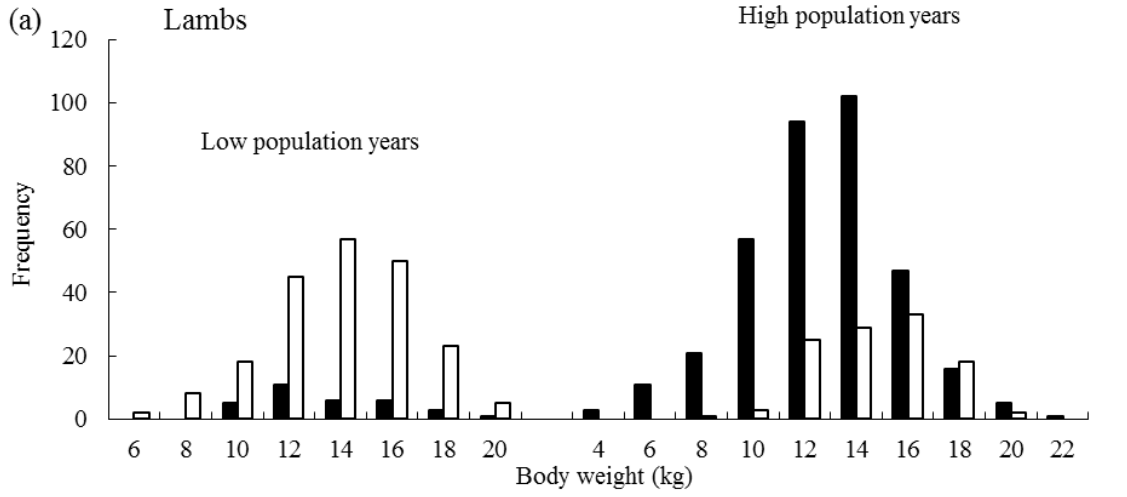


***Figure 21.*** *Selection on August weight (in kg) in Soay lambs. The bars show the number of individuals that died (black bars) or survived (white bars) after years of low or high population density. In both cases, but especially after a high density year, it is clear that small sheep are less likely to survive their first year.*

For selection like this on a quantitative trait to generate evolution (i.e. genetic change across generations), at least some of the variation must be due to genetic rather than environmental effects. The extent of genetic determination is described by a parameter called the heritability, which is measured by assessing how similar relatives are for the trait. If relatives – who share genes – are much more similar than non-relatives, then genes must be important in determining the traits. Calculating heritability therefore depends on knowing who is related to whom, which is provided by the pedigree (see section on the Soay sheep pedigree).

The heritability of August body weight was duly estimated to lie between 5% and 40% depending on the age at which it was measured (being higher in older animals; Coltman et al., 2001a, Wilson et al., 2007b) and these values have been refined as the dataset and pedigree has accumulated (Bérénos et al., 2014). This means that whereas genetics plays a rather small role in determining body weight at birth, it plays a large role in adult weight, explaining up to 40% of the variation present. Using this approach, we have also estimated the heritability of a large number of other traits in the study population, e.g. birth date, twinning rate, faecal egg count and antibody levels. These results show that despite the extreme variability in the environmental conditions that the Soay sheep on St Kilda face, for example in terms of weather and density, individuals' genes also still play a role in determining differences between individuals even in these continuously-varying traits. The same kind of data set also allows us to work out whether different traits are controlled by the same underlying genes. This is measured by a genetic correlation. For example the genetic correlation between August weight and August hind leg length in adult Soay sheep is about 40%, meaning that just under half the genetic variation in weight and hindleg length is controlled by the same genes (Bérénos et al., 2014).

If a trait is under selection and heritable, then the history of domesticated plants and animals, experience in the lab, and the theory of Darwinian evolution by natural selection tells us that the population should evolve in the selected direction. In the example of Soay sheep body mass, we would clearly expect genes for heavier sheep to becoming more common over generations. Imagine our surprise, then, when it first became clear that Soay sheep were not getting bigger. They were not even staying the same, they were getting lighter on average over time (Figure 22; Wilson et al., 2007b). This is true across all sexes and ages and multiple measures of body size. Soay sheep aren't changing in the predicted direction, and in this respect they are in good company: across other long-term projects studying individuals, there are several examples in which predicted changes are not taking place, or - as on St Kilda - traits are changing in the opposite direction to that we predict. What is going on? An explanation is called for!

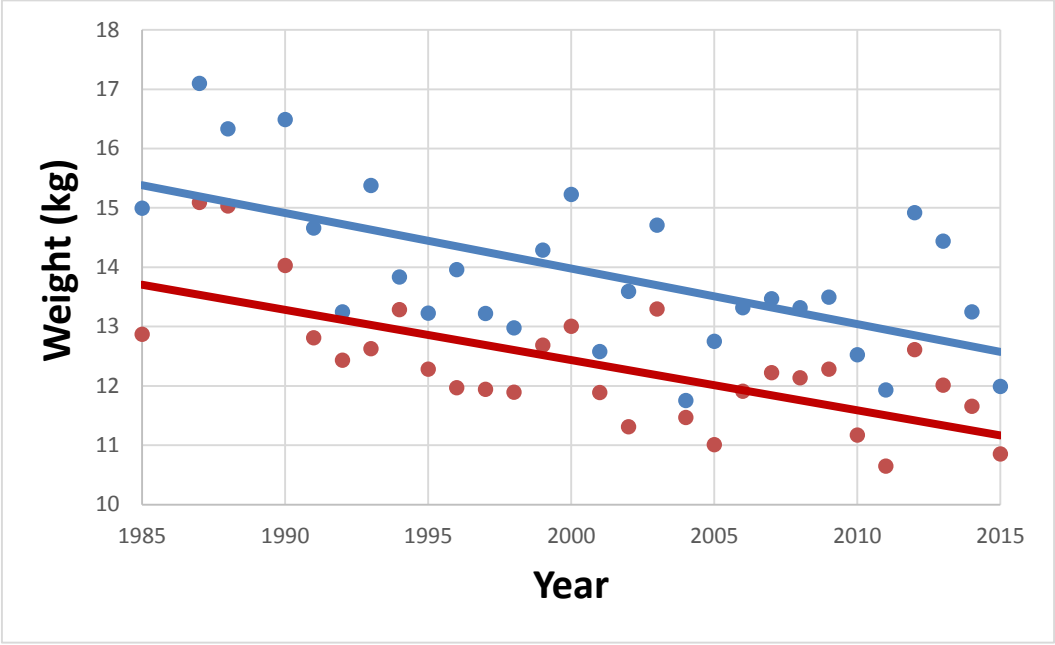


***Figure 22.*** *Mean weight of lambs weighed each August since 1985. Males are shown in blue and females in red. We find this decline in body weight in both sexes at all ages for which we have large samples, and in hind leg length.*

A key difference between natural populations and the farm or lab is that in the wild the environment is perpetually changing in an uncontrolled way, and each individual has a different life experience in terms of the environment, which will affect the phenotype it shows for a particular trait. In contrast, on farms and in labs the environment is tightly controlled to be identical over time and across individuals. Thus while the animal breeder can easily pick out the genetically superior animal, natural selection cannot. In support of this, we have shown that, while Soay sheep are getting lighter on average over time, the genes underlying body mass are not showing any appreciable change over time (Hadfield et al., 2010). Similarly, we could find no evidence for any genetic correlation between body mass and fitness (Morrissey et al., 2012). This shows that while heavier sheep are fitter on average, this relationship is due to environmental rather than genetic variation and so natural selection is not expected induce any evolutionary change in

this trait. If Soay sheep are not changing size genetically, then what is causing them to get smaller over time? Current analyses suggest that the change is being brought about by two processes relating to other long trends in the data. First, perhaps because of the rising average density of sheep over time, and hence more competition for food, lambs are growing more slowly than they used to. Second, as winters have been getting milder in recent years, more poorly-grown lambs have managed to survive – i.e. there has been some relaxation of overwinter selection on body size (which has, of course, contributed to the population size trend; Ozgul et al., 2009).

A key message from this tale is that when researchers find changes over time in quantitative traits, for example changes in the timing of breeding seasons that have been linked to climate change, these changes are not necessarily due to evolutionary (i.e. genetic) changes in the population. They can also occur via direct effects of a changing environment on individuals (a phenomenon known as phenotypic plasticity), a relaxation of selection or changes in the age and sex structure of the population. More generally, this is but one of several sets of results from the investigation of quantitative traits in the Soay sheep that has driven forward our knowledge of how ecology and evolution interact in free-living populations in real time, and provides an intriguing puzzle for us to solve in future.

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