Soay Sheep

Dynamics and Selection in an Island Population

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1.1 Sheep on St Kilda

Off the north-west coast of Scotland, beyond the protective chain of
the Outer Hebrides, lie the islands of St Kilda (Fig. 1.1). The fragmented
ring of a tertiary volcano, the four main islands are steep and craggy,
their low ground green with lush grass (Fig. 1.2). The steep sea-cliffs
of the islands are streaked with the droppings of seabirds for whom
the islands are a major breeding base. Over many centuries, the birds
have enriched the islands' soil and their eggs and young have attracted
humans for more than four thousand years. The earliest hunters left
few visible marks on the landscape, but the dry-stone walls built by
the farmers that followed still bisect the low ground and the ruins of
their cottages are scattered across the lower slopes of the hills.

Through these ruins, Soay sheep wander (Fig. 1.3a, b). Small, horned
and mostly brown or black, they are the survivors of the earliest do-
mestic sheep that spread through Europe in the Bronze Age, reaching
Britain's remotest islands between three and four thousand years ago.
In the course of time, they were replaced by larger, more productive
breeds, but a remnant population of original sheep was abandoned
on Soay, a 99-ha island where their existence was protected by the
difficulty of access (Fig. 1.4).

For many centuries, the human population of St Kilda ebbed and
flowed (Harman 1995) until, at the start of the twentieth century,
numbers fell to such a low level that continued occupation of the
islands was no longer feasible. In 1930, the last islanders left and Soay

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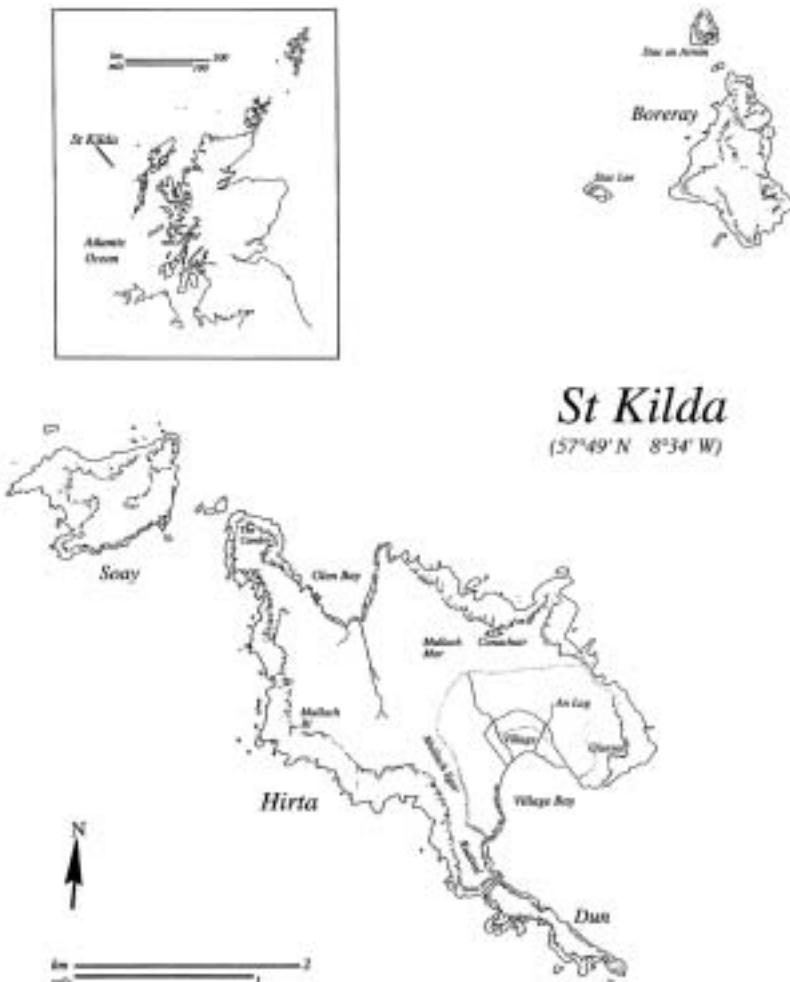
FIG. 1.1. St Kilda. The study area is enclosed by the interupted line. Inset shows the position of the islands off the north-west coast of Scotland.

sheep were returned to the largest island, Hirta, in 1932 to maintain the grazings. Their numbers were allowed to expand without human interference until they were limited by the supply of food.

Like populations of many other animals, numbers of Soay sheep on Hirta are limited by the resources available in winter. In years when sheep numbers are high, over half of the sheep can starve in

(a)

(b)

FIG. 1.2. (a) Dun, Hirta and Soay from Boreray, with Stac Lee in the foreground. (Photograph by Ian Stevenson.) (b) Village Bay from the south-west showing the Head Dyke enclosing the village street, the meadows between the street and the sea, and the fields behind the street; Oiseval in the background. (Photograph by Ian Stevenson.)

(a)

(b)

FIG. 1.3. (a) Soay sheep grazing among cleits in the fields behind the street, Village Bay; Calum Mór's house in the foreground. (Photograph by Tim Clutton-Brock.) (b) A typical party of light wild and dark wild ewes with a range of horn types (left to right: scurred, polled, normal-horned, scurred). (Photograph by Sarah Lloyd.)

FIG. 1.4. Soay from Hirta. (Photograph by Ian Stevenson.)

late winter (Grubb 1974c). The occurrence of intermittent population crashes in the sheep makes it possible to investigate the causes and consequences of episodes of acute starvation. As Malthus (1798) and Darwin (1859) originally realised, starvation is one of the principal driving forces both of population regulation and of natural selection. As it is feasible to catch and mark large numbers of individual sheep on St Kilda and to monitor their growth, condition and breeding success throughout their lifespans, we can compare the effects of starvation on different categories of animals, allowing us to examine the interactions between population dynamics and selection. As a result, the Soay sheep population allows us to ask three questions of fundamental importance in understanding the dynamics and evolution of animal populations. First, what are the causes of fluctuations in population density and to what extent do different demographic processes contribute to changes in population size? Second, how do changes in population density affect the intensity and direction of natural and sexual selection? And, third, how does population density affect the costs and benefits of reproduction and the reproductive strategies that would be expected to evolve?

We are not the first biologists to recognise the opportunities offered by island populations. Studies on island populations of invertebrates, reptiles, passerine birds and rodents have all made crucial contributions to our understanding of population dynamics and evolution (Lack 1947, 1968, 1971; Carson 1959, 1982; Mayr 1963; Grant 1965, 1968, 1986; Schoener 1968; Clarke and Murray 1969; Berry *et al.* 1978). Nor are we the first to recognise the opportunities that island populations provide for studying ungulates. Resource-limited populations of ungulates occur on a substantial number of islands in both hemispheres, offering good visibility and easy access. They have been widely used in studies of population dynamics, reproduction and behaviour (Wilson and Orwin 1964; Woodgerd 1964; Clutton-Brock *et al.* 1982a; Orwin and Whitaker 1984; Leader-Williams 1988; van Vuren and Coblentz 1989). Studies of Soay sheep on Hirta were among the first detailed investigations of the population ecology of ungulates. Research on the ecology of sheep on Hirta was started by John Morton Boyd and Peter Jewell in 1955, intensifying between 1960 and 1968 when other scientists, including Peter Grubb, joined the project to investigate different aspects of growth, feeding ecology and reproductive behaviour. These studies led to a monograph on the Soay sheep population of Hirta (Jewell *et al.* 1974) which anticipated detailed studies of other large herbivores by several years, both in the questions that it investigated and in the quality of the answers that it provided. The work showed that sheep numbers on St Kilda were unstable and that the population suffered periodic crashes when large numbers of animals died (Fig. 1.5), though it did not provide an answer to why this occurred. Seventeen years later, we restarted the detailed monitoring of the sheep population initiated by Jewell and Boyd, using modern techniques of demographic and genetic analysis, to investigate the ecological causes and evolutionary consequences of this unusual instability.

1.2 Individuals and populations

So what is the point – as visitors to St Kilda commonly ask – of expending so much effort counting sheep over so many years? Can we – as the more sceptical visitors enquire – really hope to discover anything
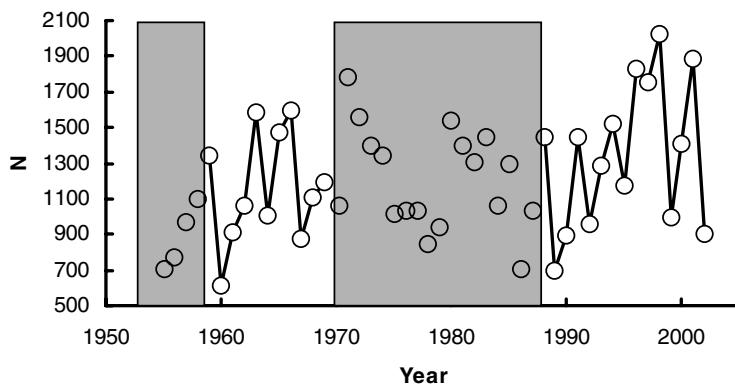
FIG. 1.5. Total numbers of sheep counted on Hirta 1955–2000. Between 1959 and 1969 annual counts were carried out systematically by Boyd, Jewell and Grubb (see Grubb 1974c) while between 1985 and 2001 a similar system was used by members of the current research team. During the other periods of the time series (shown shaded in the figure) counts were carried out less systematically by a single observer and several values are surprising given numbers in the preceding or succeeding year. We consequently believe that analyses of changes in population size are best confined to the periods 1959–69 and 1985–2001.

new? And, if we do, is it likely that it will shed light on the regulation of other animal populations?

Let us start on firm ground. The successful conservation, management and control of animals needs to be based on an understanding of the impact of environmental factors on survival and breeding success and their relative contributions to changes in population size (Riney 1982; Caughley and Sinclair 1994). Without this knowledge, too much effort can easily be spent attempting to modify aspects of the environment or components of the life-history that have little impact on population size. But is further research really necessary to achieve this? Are there really still important gaps in our understanding? Such questions reflect a fundamental misconception of the current state of ecological knowledge. In fact, our knowledge of the ecological processes underlying changes in population size in wild animals is very limited (Murdoch 1994; Turchin 1995). Only in a small number of studies of vertebrates has it been possible to measure the effects of

population density and climatic variation on average survival, breeding success and recruitment (Fowler 1987; Saether 1997; Gaillard *et al.* 1998; Newton 1998). Only in a small minority of these studies has it been feasible to monitor the life-histories of individuals though, without records at this level of resolution, many important processes remain invisible. In particular, it is usually impossible to distinguish changes in fecundity from changes in juvenile mortality, to measure rates of emigration and immigration, to assess the costs of reproduction, or to estimate the effects of variation in early development on reproductive performance and survival in adulthood.

Most vertebrate studies that have investigated population dynamics using populations of marked individuals have involved monogamous birds (Newton 1998). The list of classic studies includes research on blue and great tits (Kluijver 1951; Lack 1966; Perrins 1979); Galapagos finches (Grant and Grant 1989); collared flycatchers (Gustafsson 1988); song sparrows (Smith 1988); house martins (Bryant 1979); Seychelles warblers (Komdeur 1996); red grouse (Watson *et al.* 1994); sparrowhawks (Newton 1985); oystercatchers (Ens *et al.* 1992); kittiwakes and fulmar petrels (Coulson and Wooller 1976; Ollason and Dunnet 1988; Thomas and Coulson 1988), barnacle geese (Owen 1984) and flamingoes (Johnson *et al.* 1999). However, research on the population dynamics of monagamous birds cannot be reliably generalised to mammals where most species are polygynous and substantial sex differences in body size, growth, dispersal, survival and age-related breeding success are common (Clutton-Brock 1988b). Fewer studies of mammals have been able to investigate demographic changes using individual-based data: exceptions include some rodents (Cockburn 1988; Wolff 1992), a few carnivores (Schaller 1972; Packer *et al.* 1988; Caro 1995; Creel and Creel in press), one or two primates (Crockett and Rudran 1987a, b; Altmann *et al.* 1988; Pope 2000), and several ungulates, including roe deer (Gaillard *et al.* 1993; Langvatn and Loison 1999), black-tailed deer (McCullough 1979), red deer (Clutton-Brock *et al.* 1985b), kudu (Owen-Smith 1990) and bighorn sheep (Festa-Bianchet *et al.* 1998).

The relative stability of many populations of longer-lived vertebrates means that exceptions are of particular interest since they may offer important insights into the factors generating stability and instability. Over the last twenty years, an increasing number of studies of large mammals have documented substantial changes in population size (Sinclair and Norton-Griffiths 1979; Prins and Weyhauser 1987; Leader-Williams 1988; Milner-Gulland 1994; Sinclair and Arcese 1995). Several of the cases where numbers fluctuate persistently involve resource-limited populations of ungulates living on islands – including feral goats on the Isle of Rum (Boyd 1981), mouflon in the sub-Antarctic Kerguelen Islands (Boussès *et al*. 1991) and reindeer on Antarctic and Arctic islands (Leader-Williams 1988).

The existence of persistent fluctuations in these island populations raises questions about their causes and also provides an opportunity to investigate their consequences. Why do numbers not stabilise? To what extent are changes in population size caused by changes in survival versus reproductive success? What effects do changing numbers have on growth and reproductive performance? To what extent does climatic variation interact with the effects of population density? And do neighbouring populations show synchronous fluctuations? Answers to these questions are relevant to more general issues. Is the magnitude or frequency of fluctuations in population size related to the potential growth rate of the population? Are fluctuations in population size likely to be larger and more persistent in isolated populations than in larger ones from which dispersal is possible? And are populations that lack predators particularly likely to fluctuate in size? Since many populations of large herbivores are now contained within circumscribed ranges and are no longer subject to natural predators, answers to these questions are of relevance to the management and conservation of many populations of large mammals.

The first part of the book focuses on the causes of changes in population size in the St Kilda sheep and the consequences of these changes for growth, breeding success and survival. Chapter 2 describes the historical background of the St Kilda sheep population and the factors affecting reproduction and survival. Chapter 3 outlines the

dynamics of the population, reviews our attempts to predict population size and examines the effects of variation in population size on development. Chapter 4 investigates the effects of changes in sheep numbers on the production and diversity of the island's vegetation while Chapter 5 examines relationships between sheep numbers and parasite densities and impact. Finally, Chapter 6 describes the distribution of reproductive success in males and examines the extent to which this changes with population density.

1.3 Population density and selection

Stimulated by the demographic analyses of Malthus (1798), Darwin's description of natural selection in the *Origin of Species* (Darwin 1859) focuses on the evolutionary consequences of differences in survival between phenotypically different individuals in populations close to carrying capacity. However, as Haldane and his successors pointed out, selection operates through differences in breeding success and survival or longevity is only one of several components of fitness (Haldane 1956; Futuyma 1986).

For practical reasons, few studies of selection in natural populations have been able to measure individual differences in breeding success, or to compare changes in the relative contributions of survival and fecundity during periods of population increase, stasis and decline or between stages of the life-history (see Endler 1986; Clutton-Brock 1988a). As a result, we know relatively little about the frequency with which selection changes in intensity or direction. A number of examples are known where the intensity or direction of selection in natural populations changes either between stages of the life-history or between periods of population growth (Hall and Purser 1979; Grant 1986; Pemberton *et al*. 1991). In addition, there is more extensive evidence of variation in the direction of selection between stages of the life history in laboratory populations of *Drosophila* (Simmons *et al*. 1980; Rose and Charlesworth 1981; Rose 1984; Luckinbill *et al*. 1984). These results have fuelled a debate as to whether selection in natural populations is typically 'hard' (strong and consistent across environmental conditions) or 'soft' (intermittent or inconsistent in strength or direction as environmental conditions change) (Wallace

1975; Kreitman *et al.* 1992). This debate is directly relevant to understanding the maintenance of genetic diversity, which is likely to erode more rapidly if selection pressures are 'hard' than if they are 'soft'.

Studies of large, long-lived animals provide unusual opportunities for comparing selection pressures on different components of fitness and investigating their stability. Though selection through mortality can be easily identified in small organisms with rapid life-histories, it is usually difficult to measure individual differences in breeding success in natural populations. (See above). Moreover, survival is often strongly affected by short-term changes in climate in smaller animals, so that the effects of phenotype or genotype on breeding success or survival of individuals are often obscured by stochastic environmental variation. Studies of selection in iteroparous vertebrates have the advantage that it is possible to measure the reproductive success of the same individual in several breeding seasons, increasing the chances of recognising and controlling for stochastic effects and detecting the consequences of variation in phenotype or genotype (Clutton-Brock *et al.* 1988b).

We have investigated three groups of questions about selection in the Soay sheep population. First, how do changes in population density and climate affect the total opportunity for selection, the extent to which different components of fitness contribute to this, and their relationships between fitness components? Second, how do density and climate affect the intensity of selection on particular phenotypic and genetic traits? And, third, to what extent are genetic differences responsible for differences in breeding success and survival? Chapter 7 describes selection pressures on different phenotypic traits while Chapter 8 examines selection pressures on genetic characteristics.

1.4 Adaptation in a changing environment

Just as an understanding of selection needs to be set in the context of population dynamics so, too, does an understanding of adaptation. Over the last thirty years, research has led to a rapid development in our understanding of the costs and benefits of different reproductive strategies in natural populations (Wilson 1974; Stearns 1992; Krebs and Davies 1993). Several recent studies show that many (if not all)

of the costs and benefits of particular strategies change with environ-
mental conditions and vary between different categories of animals
(Albon *et al*. 1987; Clutton-Brock *et al*. 1987a; McNamara and Houston
1992; Festa-Bianchet *et al*. 1998). For example, in red deer, the costs of
breeding increase in years when autumn rainfall is heavy or popula-
tion density is high (Albon *et al*. 1987; Gomendio *et al*. 1990) and vary
with individual differences in age (Clutton-Brock *et al*. 1983, 1987a, b;
Albon *et al*. 1987). These results emphasise the dangers of measuring
the costs or benefits of different reproductive strategies in a single sea-
son or in a particular category of animal: if the season is favourable
or the sample of individuals selected is in good condition, average
costs are likely to be underestimated while costs measured under ad-
verse circumstances or in animals with few reserves are likely to be
overestimates. Variation in the costs of breeding in female and male
sheep is described in Chapters 2 and 9 respectively while Chapter 9
uses these estimates to investigate whether the unusually low breed-
ing age and high reproductive rate of Soay sheep on St Kilda is likely
to be maintained by selection.

Where breeding costs fluctuate, individuals may be able to increase
their fitness by adjusting their investment in reproduction in rela-
tion to changing conditions or to individual differences in reproduc-
tive costs (McNamara and Houston 1992). Several recent studies of in-
vertebrates provide convincing evidence that individuals adapt their
breeding strategies to the circumstances they encounter. For exam-
ple, some parasitoid wasps are more likely to lay eggs in sub-optimal
hosts under environmental conditions likely to cause high mortality
among adults (Roitberg *et al*. 1993; Fletcher *et al*. 1994). Similarly, in
dung flies, the duration of copulation is adjusted to variation in body
size (Parker and Simmons 1994). Though density-dependent changes
in fecundity or maternal investment are usually regarded as inevitable
consequences of food shortage, evidence of adaptive adjustments of
this kind raises the possibility that some density-dependent changes
in vertebrate life-histories may also represent adaptive responses to
changing optima (Clutton-Brock *et al*. 1996). In the second part of
Chapter 9, we use estimates of the costs and benefits of breeding dur-
ing alternating periods of high and low population density to examine

whether the sheep adjust their reproductive strategies to variation in the likely costs of breeding.

1.5 Soay sheep as a model system

Our study uses the St Kilda sheep population as a model system where it is possible to investigate questions of relevance to the population dynamics, selection and adaptation of other species. The final chapter of the book synthesises our understanding of population dynamics, selection and adaptation in the Soay sheep and examines the implications of our results for our understanding of the same processes in other mammals. The unusual aspects of the St Kilda population (including the constraints on movement imposed by the size of the island and the lack of effective predators) mean that the relative importance of particular demographic parameters in the sheep will not necessarily reflect their importance in other ungulate populations. Nevertheless, periodic starvation is a feature of many animal populations and the processes that we study are likely to be widespread in other populations where it is not feasible to investigate their effects.

1.6 Methods of research

Since 1985, members of the project have monitored the breeding success, growth, habitat use and survival of virtually all the Soay sheep living in the Village Bay area of Hirta. For this whole period, over 95% of sheep using the area have been marked with colour-coded ear tags, so that they are recognisable as individuals. We organise three main expeditions to the islands each year. In late February or early March, three or four members of the project visit Hirta for the first time that year, usually staying until early May. Ten censuses of the whole study population are carried out and data are logged directly into hand-held computers (Psion II). Each sheep seen is identified from its ear tag number and its location, activity, the plant community it is on and the other members of its group are recorded. These censuses provide estimates of the distribution of different individuals, the extent to which they associate with each other, and their use of different plant communities. In addition, we search the whole study area for carcasses and ear tags, especially the dry-stone shelters (cleits) which the

sheep often use for shelter in bad weather. To allow us to investigate selection of anatomical characters, skulls are removed and allowed to rot, before being cleaned and removed for storage, complete with their horns. Jaws (complete with teeth) and one foreleg are cut off, boiled, dried and stored. As further animals die, their dates of death are recorded. In total, we find the bodies of at least 85% of all animals tagged as lambs in the Village Bay study area and also collect a substantial number of sheep from other parts of the island that have died in Village Bay during the winter (Clutton-Brock *et al*. 1992).

In late March or early April, the first lambs are born. Mothers usually move away from the grazing groups and stay close to their lambs. Approximately 95% of all lambs born in the Village Bay area are caught each year. We try to avoid catching lambs within twenty-four hours of birth to avoid desertions but catch as many as possible during the next twenty-four hours. Lambs run when approached closely but, until they can run up-slope (at around ten days), they can usually be caught. When lambs are caught, we record their mother's identity, their sex, coat colour and weight. They are tagged with Dalton's Jumbo 'Rototags', colour-coded for their year of birth and carrying a unique number, which is entered into our records. We collect small skin samples from the tag hole in their ears for genetic analysis (see Chapters 6 and 8). In 1988 and 1989, samples of individually identifiable lambs were stalked when asleep, caught and reweighed at intervals of two to thirty-six days, providing direct measures of increase in body mass throughout the first six weeks of life (Robertson *et al*. 1992). We subsequently use growth rates calculated from these data to estimate birth weight, reducing the observed weight by 108 g for every twenty-four-hour period since lambs were born.

A second visit occurs in July and August. Initially, a small team carries out ten censuses of the study population, while a larger team of fifteen people subsequently attempts to catch, weigh and, where necessary, re-tag as many of the sheep in the Village Bay area as possible. In the early years of the project, we relied on catching sheep in cleits or darting them using an immobilising gun to provide estimates of the weight of adults. Subsequently, with the help of an experienced team from the Mammal Conservation Trust, we developed methods

of catching large numbers of sheep by enclosing them in temporary corrals. By this method, we have caught over 50% of the animals in the Village Bay sub-population each year since 1989. After sheep have been caught, they are weighed, re-tagged if their tags are broken or worn, and checked for reproductive status and milk. Horn and leg length are measured, samples of wool, blood and faeces are collected, ectoparasites are counted and the sheep are subsequently released. In addition, a count of the sheep on the entire island is carried out, with three groups of observers counting different sectors (see Fig. 1.5). While these counts give an estimate of the relative size of the population, some sheep can easily be missed and they are likely to be less accurate than our estimates of the Village Bay population, which are based on identifiable individuals.

Finally, between October and December, a third team visits the island to collect data on rutting activities. In the early years of the study, a small team carried out repeated censuses each day, recording the location and activity of individual males. More recently, a larger team carries out ten censuses of the whole population, checks for oestrus in all females each day, and collects samples of focal watches on particular males (see Chapter 9). Untagged rams, which immigrate into the area for the rut, are immobilised, tagged, measured and sampled for genetic analysis. After this, the sheep are left alone until the next spring, when we return to count and identify which individuals are still alive.

Long-term field studies have a reputation for collecting large amounts of data that are jealously guarded by their originators and are never fully analysed. We have tried to avoid this pitfall in the St Kilda sheep study. Research on the sheep was restarted in 1985 by members of the Departments of Zoology and Physiology at Cambridge (T. H. Clutton-Brock, S. D. Albon and P. A. Jewell), but the project rapidly came to involve several other groups. Over the last fifteen years, the project has involved members of the Institute of Cell, Animal and Population Biology at Edinburgh, the Institute of Biological Sciences at Stirling, the Institute of Zoology, Department of Biological Sciences at Imperial College (London), the Centre for Ecology and Hydrology (Banchory) and the Macaulay

Institute (Aberdeen) in addition to staff from Cambridge. Though the work initially focussed on population demography and dynamics, specialists in related disciplines have extended the study to involve the genetics of the sheep, their impact on the plant populations they live on and the effects of parasite populations on their survival and breeding success. More recently, our data have helped demographic theoreticians from the University of Kent (UK) and from the Macquarie University (Australia) to test and extend new methods of analysing demographic change (Catchpole *et al.* 2000) and to test methods of estimating population viability (Chapman *et al.* 2001). Each additional specialist that has joined the Soay sheep study has contributed new insights into the pattern and distribution of changes in survival and reproduction. Each has, in turn, benefitted from access to a population of recognisable individuals of known age, genotype and reproductive history – a situation which would otherwise require many years of preliminary work.