Survival, Natural Selection and Foraging Efficiency in Soay Sheep on St. Kilda.

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Soay sheep grazing in the Village Bay study area on Hirta, St. Kilda, in March.

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Abstract

The feral Soay sheep of St. Kilda exhibit dramatic population fluctuations and recurrent crashes, the survivors of which are favoured by natural selection. In this thesis, I establish which factors influence over-winter survival. I investigate phenotypic selection of body size traits, and demonstrate their heritability, so establishing the occurrence of natural selection. Finally I explore the relationships between body size and survival in terms of foraging behaviour and diet selection.

Over-winter survival of lambs was influenced by both density and density-independent climatic fluctuations. Adults were less sensitive to both factors, especially females which showed no evidence of density-dependence. Generalised linear mixed modelling demonstrated that once between-year random variation was taken into consideration, body weight was the most significant determinant of survival in all age, sex classes.

Evidence was found of repeated directional selection of the three traits, body weight, hindleg length and incisor arcade breadth. Whilst selection differentials showed strong positive selection for all these traits in high mortality years, selection gradients demonstrated that body weight experienced direct selection whereas selection of other traits was indirect due to their correlation with body weight. No evidence of opposing selection was found. All the morphometric traits were significantly heritable. An evolutionary response would therefore be expected, but heritabilities were low, and because of environmental noise, no significant increase in body size was detectable over the 12 year period of data.

Observed grazing behaviour in relation to vegetation structure was not influenced by individual variation in body size during winter, although female body weight affected diet selectivity in summer. Seasonal patterns were very marked, with summer grazing behaviour influencing survival the following winter. Seasonal differences in faecal nitrogen content and a decline in faecal nitrogen with increasing body size were also apparent. These observations were interpreted using diet quality and body size arguments.

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CHAPTER 1.

General Introduction

General Introduction

Aims of the study

A number of studies have shown that during over-winter population crashes of the feral Soay sheep (*Ovis aries*) on the St. Kilda archipelago, Scotland (57°49' N, 08°34' W), differential mortality occurs (Clutton-Brock *et al.* 1992; Gulland *et al.* 1993; Bancroft *et al.* 1995a; Illius *et al.* 1995; Moorcroft *et al.* 1996; Clutton-Brock *et al.* 1997b). These crashes are therefore important selection events. Although phenotypic selection of some traits has been demonstrated in previous studies (Illius *et al.* 1995; Moorcroft *et al.* 1996), the inheritance component of natural selection (Endler 1986) has never been shown in this population. Furthermore, the longer-term patterns of sequential selection events and the evolutionary consequences of repeated selection have never been investigated. This study, focusing on three morphometric characters, traces the inter-relationships between body size and survival, natural selection and evolutionary response, from a foraging perspective.

The specific objectives were (i) to establish whether differential survival always favoured individuals of the same phenotype and consequently repeated selection events were always in the same direction, or whether opposing selection occurred under different environmental conditions. (ii) to determine whether the observed traits were heritable and therefore whether an evolutionary response could be expected. (iii) to investigate individual variation in foraging behaviour relative to body size in order to be able to establish a functional mechanism underlying the observed selection.

Survival

Survival is a major fitness component with important implications for life-histories. An individual's fitness is the contribution its genes make to the next generation and may be considered as the number of its progeny represented in the next generation (Falconer & Mackay 1996). But to make any genetic contribution to the next generation an individual must first survive to reproduce . Thereafter, the other major components of fitness are the individual's fertility, the quality of its offspring and its lifespan.

Age- and sex-specific survival has important consequences for the evolution of life histories (Cole 1954) and mammalian reproductive strategies (Partridge and Harvey 1988). Neonatal survival and first-winter survival are the periods often associated with the highest mortality rates, especially in mammals at high latitudes (Caughley 1966). Survivors of these first challenges will be at a greater selective advantage and in most cases, non-survivors will miss the opportunity of contributing genes to the next generation. By contrast, adult survival is generally much higher, at least until senescence is reached. However, senescence is often difficult to detect in wild populations (Gaillard *et al.* 1994; Slade 1995) as the majority of individuals die before physiological deterioration occurs (Rose 1991). Higher survival arises because fully grown adults, especially females, tend to be buffered against environmental and population fluctuations (Gaillard *et al.* 1998). When in poor condition they are usually able to respond by decreasing their reproductive output before survival is threatened.

An understanding of survival at the individual level is important when studying life-histories, the outcomes of natural selection and subsequent evolutionary responses. However, survival also plays an important role in population regulation (Sinclair 1989). Understanding what factors determine survival at the population level is essential if population dynamics are to be explained.

Density-dependent survival

In wild populations, density affects population dynamics in a number of different ways, both directly and indirectly, operating through its effects on survival, fecundity and emigration. As density rises survival tends to decline, resulting from loss of body condition due to starvation (Fowler 1987), disease (Leader-Williams 1982; Halls 1984), or the stress of overcrowding (Chitty 1957). Not all animals in the population will be equally affected (Begon 1984), leading to age-, sex- or phenotype-specific survival that may vary with population density.

There have been many studies in which evidence of density-dependent survival has been found. These include studies of *Drosphila* (Lewontin 1955; reviewed by Mueller 1997), other invertebrates (reviewed by Dempster 1983; Strong *et al.* 1984), fish (Ricker 1954; Jonsson *et al.* 1998), birds (Lack 1966), marine mammals (Fowler 1986), small mammals (Krebs & Myers 1974), ungulates (reviewed by Sæther 1997; Gaillard *et al.* 1998) and other large mammals (reviewed by Fowler 1987). Amongst large mammals, some of the most convincing examples come from ungulate populations (Fowler 1987) but it remains unclear whether the lack of examples from other well studied taxa, such as primates and carnivores, is due to a failure to detect density-dependence (Murdoch 1994) or its infrequent occurrence.

Many populations only exhibit density-dependence as they approach the carrying capacity of their environment (Fowler 1987). This non-linearity may also be exacerbated by a greater sensitivity of populations to temporal variability in the environment and to density-independent factors as they near the carrying capacity (Fowler 1987; Bowyer *et al.* in press ; Grenfell *et al.* 1998). At this point there tends to be a greater degree of variability in the regulatory factors, survival and possibly fecundity. Lack of food resources at high population densities is the principal factor cited as causing density-dependence within large mammal populations (Sinclair 1989). Intra-specific competition for food may only be limiting once the population density crosses a threshold at or around the carrying-capacity.

Energetics arguments, both at the individual and subsequently population level, can be used to explain mechanistically how density-dependence operates. Since energy intake affects body weight, fecundity and survival, individuals should feed as efficiently as possible on the available food resources to maximise reproductive output and hence, fitness (Brown *et al.* 1993). This may in turn require maximising body size (Sibly & Calow 1986), or achieving a threshold body weight (Jorgenson *et al.* 1993), which will also be dependent both on food availability and competition for it. It is therefore often assumed that natural selection acts to maximise digestible energy intake (Stephens & Krebs 1986; Karasov & Diamond 1988), a point that will be returned to later. Some individuals will be better suited to maximising intake rates under low population density conditions whilst others are better suited to high density conditions (Mueller *et al.* 1991) and foraging strategies and efficiencies will vary accordingly (Joshi & Mueller 1996). This provides opportunities for density-dependent selection to occur.

Density-independent survival

There are perhaps fewer demonstrations of density-independent factors affecting survival. This may result from fewer studies looking for density-independence than density-dependence. However, there are also cases where factors such as weather conditions have been shown to have no effect on survival rates. For example in bighorn sheep (*Ovis canadensis*) in Alberta, Canada, winter weather had no effect on survival (Jorgenson *et al.* 1997) despite neonatal survival and lamb over-winter survival being affected by temperature and precipitation the previous spring (Portier *et al.* 1998).

Evidence that climatic factors do influence survival in ungulate species includes the correlation between rainfall and survival in the greater kudu (*Tragelaphus strepsiceros*) in Kruger National Park, South Africa (Owen-Smith 1990), and numerous examples of the effects of harsh winters on survival. These may be direct effects, as observed in red deer (*Cervus elaphus*; Clutton-Brock & Albon 1982), roe deer (*Capreolus capreolus*; Gaillard *et al.* 1993) and Dall's sheep (*Ovis dalli*; Bowyer *et al.* in press). Alternatively they may be the indirect effects of bad weather on pregnant females resulting in poor quality offspring, born with low chances of survival as seen in reindeer (*Rangifer tarandus*; Preobrazhenskii 1961). Other examples are the positive relationship between offspring survival and spring temperatures in red deer (Albon *et al.* 1987) and a positive correlation between lamb survival and previous autumn precipitation in the desert mountain sheep, *Ovis canadensis nelsoni* (Douglas & Leslie 1986). In addition, climatic conditions may have a delayed effect on population dynamics. For example, Post & Stenseth (1998) found that rates of increase in populations of both moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), were influenced by global climatic fluctuations and winter severity, as measured by the North Atlantic oscillation index (Chapter 3), at 2- and 3-year lags.

Although it seems intuitively obvious that weather conditions have an important effect on survival, especially during the winter or dry season, the effect may only become apparent in combination with high population density. Recent studies of large herbivore populations have shown significant effects of stochastic environmental factors on population dynamics when combined with density-dependence (Sæther 1997; Gaillard *et al.* 1998). Conversely, at low densities, density-independent mortality caused by the abiotic environment is expected to have a greater influence on population regulation than density (Jonsson *et al.* 1998). Consequently, stochasticity in density-independent mortality results in greater changes in population size when the density-dependent mortality is weak than when it is strong (Sinclair 1989) leading to so-called density-vagueness (Strong 1986).

Natural Selection

Phenotypic selection

The differential survival of phenotypes provides opportunities for natural selection to occur. Darwin used the term natural selection to describe the principle by which every slight variation, if favourable, is preserved whilst if injurious, is rejected (Darwin 1859). This allows individuals with a slight advantage over others to have the best chance of surviving and procreating their kind. Fisher developed these ideas further with his fundamental theorem of natural selection (Fisher 1930). This states that "the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time". The 'character' that natural selection selects for is therefore 'fitness' (Falconer & Mackay 1996).

For natural selection of a trait to occur there must be variation in that trait within the population, there must be differential fitness associated with the variants and the variation must be heritable, that is, able to be passed from one generation to the next (Fisher 1930; Endler 1986). Quantitative geneticists divide the natural selection of metric traits into phenotypic selection and genetic response, the latter reflecting heritability (Endler 1986). The term phenotypic selection has subsequently been used for the association between fitness and the phenotypic value of a trait (Alatalo *et al.* 1990). Arnold (1983), a proponent of the idea that inheritance and selection can be treated as separate issues that together describe evolutionary change, breaks the selection aspect down further to a two stage process in which the first stage shows the functional relationship between the trait and its task, and the second demonstrates a fitness advantage of possessing the trait (Arnold 1983; Grant & Grant 1989).

A classical demonstration of the means by which natural selection operates comes from Hermon Bumpus' data on the differential survival of house sparrows (*Passer* *domesticus*) after a severe storm in 1898 (Johnston *et al.* 1972; O'Donald 1973; Lande & Arnold 1983; Manly 1985). By making measurements of a number of size variables, Bumpus showed that survivors were large males and intermediate sized females so these individuals were at a selective advantage. This suggested that in males directional selection and in females stabilising selection (see below) were in operation (Johnston *et al.* 1972). All the characters measured were highly correlated so selection was for a suite of advantageous size characters rather than an individual one. This example is, however, purely of phenotypic selection rather than natural selection *per se*, since no conclusions about inheritance can be drawn.

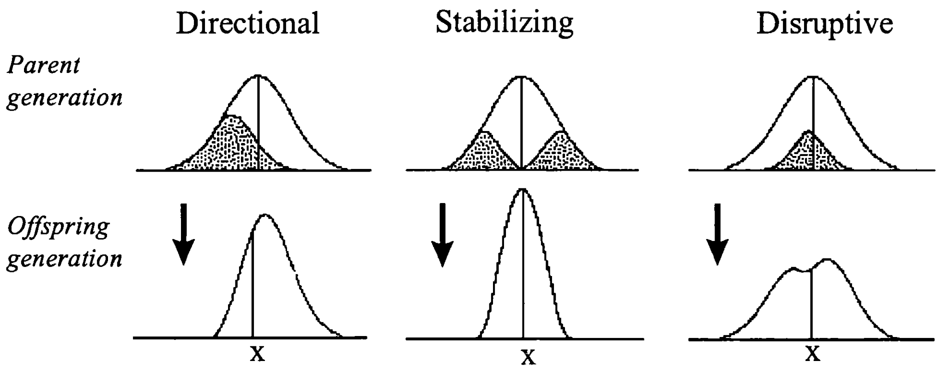
The phenotypic value of a quantitative trait consists of genetic and environmental components (Falconer & Mackay 1996) and even when a heritable morphological character shows directional phenotypic selection there still may not be any evolutionary consequences (natural selection), if selection is acting on the nonheritable environmental deviation alone (Alatalo *et al.* 1990).

Modes of selection

As alluded to above, the process of natural selection may have a variety of outcomes depending on its effect on the frequency distribution of the trait (Endler 1986). This can be illustrated for continuously varying, quantitative traits, such as the body size traits examined in this thesis, by Figure 1.1.

Directional selection occurs when individuals from one end of the frequency distribution are favoured by natural selection, as in the male house sparrow example given above, and in Darwin's medium ground finch, *Geospiza fortis* (Price *et al.* 1984). This leads to a shift in the trait mean and the variance may also decrease (Endler 1986; Price & Boag 1987). By contrast, stabilising selection occurs when intermediate phenotypes are favoured such as in Bumpus's female house sparrows and also body size of both sexes of the song sparrow, *Melospiza melodia* (Schluter & Smith 1986). As a result the trait mean remains constant but the variance decreases. The third type is disruptive selection which occurs when more than one phenotype within a population is favoured (Smith 1990). Although this results in the mean remaining constant, two optima may develop and the variance will increase. An example is the selection of bill width in the polymorphic African finch, *Pyrenestes ostrinus* (Smith 1990). In this case

Figure 1.1 Modes of selection for quantitative traits. The vertical axis represents the proportion of individuals and the area under the curve is the total number of individuals. The population mean of the trait is marked x and is shown before (upper row) and after (lower row) selection. Individuals from the shaded area are selected against (adapted from Endler 1986).



selection is related to food quality but in other cases disruptive selection may be brought about by density-dependent or frequency-dependent selection (Endler 1986).

The mode of selection may depend on either, or both, the size and phenotypic composition of the population. This is the case in both frequency-dependent and density-dependent selection (Endler 1986). The latter is particularly pertinent to the case of the Soay sheep which exhibit density-dependent survival (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992). The concept of density-dependent selection and the idea that individual fitness values may be dependent on allelic frequencies and population composition were developed as far back as the 1940s (Salisbury 1942; Wright 1948). Since then, a number of theoretical of models density-dependent selection have been proposed (MacArthur 1962; Anderson 1971; Charlesworth 1971; Roughgarden 1971; Clarke 1972; Clarke & Beaumont 1992; Ebenman *et al.* 1996).

Despite such interest, there are few studies in which density-dependent selection has been demonstrated empirically (Endler 1986). Those that have tend to come from laboratory populations of bacteria or invertebrates such as *Drosophila* (Joshi & Mueller 1996; Mueller 1997; Sokolowski *et al.* 1997). One of the few exceptions from a wild, mammalian population comes from the Soay sheep of St. Kilda. Moorcroft *et al.* (1996) showed that the magnitude of selection of two conspicuous inherited polymorphic traits, coat colour and horn type, varied with changes in population density. However, the functional mechanisms involved in selection of these two traits remain unclear and it may be that coat colour and horn type are in fact linked to other less obvious genetic characters on which selection is acting.

As with density-dependent survival, the relationship between density and selection is not necessarily linear. In this thesis I show that density-dependent selection of body size traits is repeated over a number of consecutive mortality events, but the strength of selection appears to depend on crash severity. As well as being a function of population density, crash severity depends on a number of extrinsic factors such as weather conditions and vegetation productivity.

If directional selection is persistent over a number of sequential selection events, it may lead to long-term changes in trait means. This has been documented in the Darwin's medium ground finch, *Geospiza fortis*, in which large beak and body size were favoured in recurrent periods of food shortage (Price *et al.* 1984). However, in situations in which the direction of selection changes between consecutive selection events, oscillating selection occurs. This has also been demonstrated in Darwin's finches, this time in the large cactus finch *G. conirostris*, under the contrasting environmental conditions of an El Niño event (see below; Gibbs & Grant 1987; Grant & Grant 1989). Alternatively persistent directional selection may occur without there being any evolutionary response if countervailing selection is occurring in the opposite direction, at some other point in the life history (Pemberton *et al.* 1991).

Heritability

A genetic response to selection is required for an evolutionary response to occur. Inheritance, a consistent trait relationship between parents and their offspring, is therefore Endler's (1986) third condition necessary for the process of natural selection. The degree of resemblance between relatives is determined by the heritability (h^2) in the narrow sense, that is, the ratio of the additive genetic variance to the total phenotypic variance (V_A / V_T) (Falconer & Mackay 1996). This should not be confused with heritability in the broad sense (also known as the degree of genetic determination) which expresses the extent to which an individual's phenotype is determined by its genotype (Falconer & Mackay 1996). Broad sense heritability is the ratio of genotypic variance (of which the additive genetic variance is one component ($V_G = V_A + V_D + V_I$ where V_D is dominance variance and V_I is the interaction variance)) to the total phenotypic variance (V_G / V_T). However, since the genotypic variance can not be estimated directly, heritability in the broad sense is of little practical use. Consequently all further references to heritability refer specifically to heritability in the narrow sense.

Body size, survival and foraging

Body size and diet selection

The relationship between an animal's body size and its feeding behaviour, through the spatial distribution of its food items in the environment, was commented upon by Bell (1970, 1971) and Jarman (1974). They recognised that large herbivores with relatively low metabolic requirements per unit body weight can generally tolerate lower quality food than smaller species. This is explained by the greater gut capacity of large animals (Demment & van Soest 1985) allowing longer retention of digesta and so increasing digestive efficiency (Illius & Gordon 1991). Since low quality food items tend to be abundant and evenly distributed in the environment, lower levels of selectivity are required by bulk-feeding large herbivores with higher absolute energy requirements. Smaller species, together with a few large specialists such as moose (*Alces alces*) and greater kudu (*Tragelaphus strepsiceros*), browse on discrete, highly nutritious, plant parts that are dispersed in the environment. These species are described by Hofmann (1989) as 'concentrate selectors'. An ability to feed selectively is critical to their foraging efficiency because they tend to have low rates of cellulose digestion, regardless of body size (Prins *et al.* 1984).

The differing feeding habits are reflected by anatomical adaptations, both of the digestive systems (Demment & van Soest 1985; Hofmann 1989) and mouthparts (Arnold 1983; Grant & Grant 1989; Smith 1990), that have evolved to maximise foraging efficiency. Within ungulates, browsers tend to have narrow muzzles enabling a high degree of selectivity whilst grazers have broad muzzles enabling high intake rates (Owen-Smith 1982; Janis & Ehrhardt 1988). Similarly, the incisor arcade breadth of ungulates differs in relation to body size with feeding habit (Illius & Gordon 1987), grazing species having wide incisor arcades relative to browsers. Differential allometric scaling of metabolic requirements and incisor arcade breadth relative to body weight

(Clutton-Brock & Harvey 1983) has been proposed as a mechanism allowing the differing feeding ecology of males and females in the sexually dimorphic red deer (Clutton-Brock *et al.* 1982; Clutton-Brock *et al.* 1987a; Illius & Gordon 1987).

In the continuum of herbivores from highly selective browsers to unselective grazers, sheep fall at the selective end of the grazers and, compared with other livestock such as cattle, can be considered highly selective (Nicholson *et al.* 1970; Grant *et al.* 1985). In general, the proportion of green grass leaf in the diet of sheep is considerably greater than that in the grazed horizons of the sward, indicating a strong selective preference for green grass leaf over other, poor quality, sward components such as dead reproductive stems and pseudostems (L'Huillier *et al.* 1986).

Herbage intake of grazers is influenced by factors attributable both to characteristics of the pasture such as sward height and density, and to factors associated with the grazer such as age, and body size (Allden & Whittaker 1970). The relationship between energy intake and body weight is consequently a function of both bite dimensions and the nutrient density of the food source (Illius & Gordon 1987). Many studies have investigated herbage intake and diet selectivity in sheep (reviewed by van Dyne *et al.* 1980; Hodgson 1985). A general finding is that when provided with a choice of sward, sheep preferentially select the sward that maximises herbage intake rate (Black & Kenney 1984). This agrees with the expectation that natural selection will act to maximise energy intake (Stephens & Krebs 1986). Intake can be considered as the product of the time spent grazing, the bite rate during grazing and the size or weight of the bite. In many studies, a derived value for bite size is used, calculated from herbage intake rates and bite rates (Allden & Whittaker 1970) or from bite mass and herbage density (Black & Kenney 1984). By measuring incisor arcade breadth (Illius & Gordon 1987) a more empirical estimate of bite dimensions can be made, for a given sward height.

As mouth size, incisor arcade breadth and consequently bite size, increase so does food intake rate (Allden & Whittaker 1970; Gordon *et al.* 1996), but if by increasing bite size, the amount of poor quality material that is ingested also increases, a large incisor breadth may not be an advantage. Furthermore, under sparse vegetation conditions the advantage of a large mouth would be lost, and small mouthed individuals could even be at a competitive advantage if they were able to prehend the available forage more easily (Allden & Whittaker 1970).

Foraging efficiency has a functional significance in determining survival through its influence on nutrient and energy intake. The requirements of an individual will be dependent on a number of factors such as its phenotype, age, sex, body size and reproductive status. How these requirements are then met will be a function of the food environment and a trade-off between the quality and quantity of food intake, whilst minimising costs such as locomotion, heat loss and predation risk (Stephens & Krebs 1986).

Body size and fasting endurance

In strongly seasonal environments, abundance and quality of food may be insufficient to meet maintenance requirements regardless of how efficiently an individual is able to forage. Adaptive responses to the resulting negative energy balance are energy storage (Millar & Hickling 1990) and a shift in the metabolism to reliance on lipid catabolism. Fat deposition is the most common form of energy storage amongst mammals, but these reserves are limited by the ability of the animal to maintain and carry them (Pond 1978). Energy reserves become a greater fraction of body mass as size increases among mammals (Lindstedt & Boyce 1985; Millar & Hickling 1990) and larger individuals are able to metabolise somatic stores at a lower weight-specific rate. Consequently, when populations encounter periods of food shortage that will lead to starvation, it is the smallest individuals that will deplete their reserves first (Lindsey 1966). The effect is exacerbated by the relatively greater energy expenditure of smaller mammals to stay warm at low ambient temperatures (Peters 1983; Lindstedt & Boyce 1985). This forms the basis of the fasting endurance hypothesis for the evolution of body size in seasonal environments (Lindstedt & Boyce 1985; Millar & Hickling 1990).

If large body size is important in enhancing survival of terrestrial vertebrates during periods of resource shortage (Zeveloff & Boyce 1988), directional selection for larger size should occur in seasonal areas (Millar & Hickling 1990). Survivors will then enjoy low competition and abundant resources during the growing season (Ashmole 1963), so will attain large size and have a high fitness advantage, further promoting large body weight. Furthermore, in fluctuating resource environments if there is strong selection pressure for endurance on poor quality diets, large body mass will also be favoured (Gordon & Illius 1996).

The advantages of large body size, such as an ability to feed on poor quality forage, are however, countered by disadvantages where food quantity is limited (Lomolino 1985). This suggests that the upper limit to ungulate body size is determined by the ability to extract nutrients from feeding niches at the lowest point of the seasonal cycle of resource quality and abundance (Illius & Gordon 1992). Losses incurred during fasting must be recouped whilst meeting high maintenance requirements, so frequent periods of food shortage would not favour large size (Millar & Hickling 1990). But, whilst there is evidence from birds that smaller individuals may survive better when food is in chronically short supply but is predictable (Price & Grant 1984), there are no similar data for mammals (Millar & Hickling 1990).

One would expect that interspecific survival patterns would also hold within species, since within a species, body fat is the most variable component of body mass (Pond 1978) and differences in weight between large and small adult individuals are mainly due to differences in the mass of fat. In fact, since evolutionary changes in body size require selection among individuals (rather than among species), intraspecific patterns of metabolism and fat deposition should be more pronounced than interspecific patterns (Lindstedt & Boyce 1985). Belovsky (1987) showed that foraging models using intraspecific allometric functions can be used to predict differences in diet between individuals of different body size. This provides the rationale for exploring some of the body size / foraging hypotheses at the intraspecific level within the Soay sheep population.

If natural selection acts to maximise energy acquisition, high foraging efficiency is required whatever the body size, especially under conditions of constrained resources. Under high population density conditions this may also mean being a good intraspecific competitor. Selection for foraging efficiency is therefore likely to be strong.

Survival, selection and foraging efficiency

Although there are many studies, in which fitness advantages of specific traits are demonstrated (Endler 1986), few also show a functional relationship between the trait and its task (Arnold 1983). Arnold (1983) illustrates his approach with a hypothetical example of selection of morphological characters involved in foraging efficiency in terms of ingesting and swallowing prey in snakes. Lemon (1991) has demonstrated the fitness consequences of a behavioural trait, foraging patch choice, in which the functional relationship is implied. But the most notable examples of selection of traits with functional relationships with survival comes from the studies of beak morphology in Darwin's finches in the Galápagos (Grant *et al.* 1976; Grant 1985; Gibbs & Grant 1987).

Functional and ecological aspects of trait variation were used to show an interpretable fitness advantage in foraging and hence survival, conferred on finches with certain beak shapes (Grant & Grant 1989). For example, selection for beak size in *Geospiza conirostris*, the large cactus finch, was found to oscillate under the contrasting environmental extremes caused by an El Niño event (Grant 1985; Gibbs & Grant 1987; Grant & Grant 1989). During a year of abnormally high rainfall the usual food supply of *Opuntia* cactus flowers and fruits (Grant & Grant 1981) became scarce and individuals with the long, deep beak required for cracking hard *Opuntia* seeds were at a selective disadvantage and bill length declined. This was followed by two years of drought during which the principal food supply was arthropods within the rotting cactus pads. Those finches able to tear open the pads were the ones that survived to breed and they had significantly deeper beaks, leading to positive selection for beak depth. The initially strong selection for a decrease in beak length was therefore counteracted by the indirect effects of subsequent selection acting in the opposite direction on the positively correlated trait of bill depth (Grant & Grant 1989).

A similar, but shorter term study of song sparrows, *Melospiza melodia*, revealed that the morphological features that selection was most often associated with were beak length and tarsus length (Schluter & Smith 1986). The functional significance of beak length is through its relationship with food resources, whilst tarsus length is significant in determining habitat use (important for species differentiation), acting through foraging mode.

There are few comparable examples of selection of foraging traits in mammals, despite the obvious connection between foraging efficiency and survival. Belovsky (1987), approaching the problem from the other side, has examined the relationship between foraging efficiency and selection of body size in moose (*Alces alces*), snow shoe hares (*Lepus americanus*) and the Kung! San hunter-gathering people of the Kalahari. However, one example of two independent foraging traits that affected over-winter survival comes from the Soay sheep on St. Kilda, during the winter of 1991/92 (Illius *et al.* 1995). These traits were incisor arcade breadth, which influences foraging efficiency directly, and parasite burden, which affects nutrient assimilation. Although it has subsequently been shown that incisor arcade breadth is generally less important in determining Soay sheep survival than body weight (Chapter 4), incisor breadth was nonetheless the only morphometric character to be related to survival of adult males in any winter. Furthermore, the functional significance of incisor arcade breadth for survival is supported by experimental evidence that bite dimensions and food intake rate are closely related to incisor arcade breadth in sheep and goats (Gordon *et al.* 1996). Therefore, the relationship between body size, incisor arcade breadth and foraging behaviour is explored further in this thesis.

Thesis outline

In Chapter 2, I introduce the study area on St. Kilda and give a brief over-view of some of the previous research that has been carried out on the population dynamics of the Soay sheep. General methods are given for the long-term population monitoring and for the measurement of the three morphometric traits on which this study focuses.

Chapter 3 concerns the factors affecting over-winter survival of the Soay sheep. I set out to determine the relative importance of density-dependence and density-independent climatic factors on survival in different age-sex classes. I also investigate the influence of individually varying parameters such as body size traits and parasite burden in each age-sex class. In all cases, body weight proves to be the most important factor determining survival.

I then go on to explore the consequences of differential survival for natural selection in Chapter 4. In particular I look at the patterns of selection over the period 1990-1996 to determine whether there were consistent trends over consecutive winters or whether the direction of selection depended on population density. In addition, I disentangle the effects of direct selection from indirect selection caused by correlation between traits.

In Chapter 5, the heritabilities of the morphometric traits are determined for each sex. This allowed the scale of expected evolutionary response to selection to be predicted, which in turn has implications for the evolution of body size. Genetic variation in particular traits is related to their importance for fitness, expressed in terms of the amount of selection they experience.

Chapter 6 is based on observational foraging data from which I attempt to determine the influence of morphometric traits on individual variation in diet selectivity during summer and late winter. This is supported by faecal nitrogen data, from which arguments about the relationship between diet quality and body size are drawn, particularly with respect to selection of foraging efficiency.

Finally, I draw together my findings in Chapter 7 and discuss their implications for the evolution of body size and foraging efficiency. I also consider the prospects for future research .

CHAPTER 2.

The Soay Sheep on St. Kilda

The Soay Sheep on St. Kilda

The Study Site

The study island, Hirta (638 ha), is the largest of the four islands in the St. Kilda archipelago (57°49'N 08°34'W), which is situated 72 km west of the Outer Hebrides (Figure 2.1). The islands, of volcanic origin, lie in the Atlantic storm belt and experience a harsh, maritime climate of high winds and fierce seas (Boyd 1974). Hirta is cliff-bound on all sides except for the south-east facing storm beach of Village Bay whilst the smaller island of Soay (99 ha) is completely surrounded by cliffs making it virtually inaccessible. Village Bay on Hirta lies at the foot of a horseshoe of steep hills, Oiseval, Conachair, Mullach Mor and Mullach Sgar which comprise the boundaries of the main study area (174 ha, approximately one third of the whole island) (Figure 2.2 & 2.3). Within this area there are fields that were cultivated by the St. Kildans, and above the head dyke that separated the in-bye from the out-bye, there is open hill covered with heather moorland. The more fertile soils of the meadows, dominated by *Holcus/Agrostis* pasture, are now the preferred grazing area of the Soay sheep.

The vegetation and soils of Hirta have been mapped and described (Gwynne *et al.* 1974; Figure 2.3). Thin podzols and peaty soils predominate with scree and bare rock being significant on the steep upper slopes (Gwynne *et al.* 1974). The cool, wet climate causes intense leaching, resulting in acidic soils but this is to some extent compensated for by the heavy deposition of minerals from sea spray and the fertilising effect of the large sea bird colonies and sheep (Campbell 1974). The distribution of vegetation communities follows the pattern of soil fertility and wetness, such that the western and northern slopes are dominated by species-rich dry *Calluna* heath, and in patches of poor drainage by *Molina*, whilst eastern slopes are characterised by a wetter, species-poor *Calluna* heath with *Eriophorum* and *Trichophorum*. Below the heaths there is a band of *Agrostis/Festuca* dominated grass along the outside of the head dyke. Within the head dyke, the tussocky growth form of *Agrostis capillaris*, and the dominance of the preferred graze species *Holcus lanatus* between the tussocks has led to a heterogeneous mix of less grazed tussocks and heavily grazed gaps. *Festuca, Anthoxanthum* and *Poa*

Figure 2.1 Map of St. Kilda showing its location and the study area in the south-east of Hirta. Reproduced with permission from I.R.Stevenson.

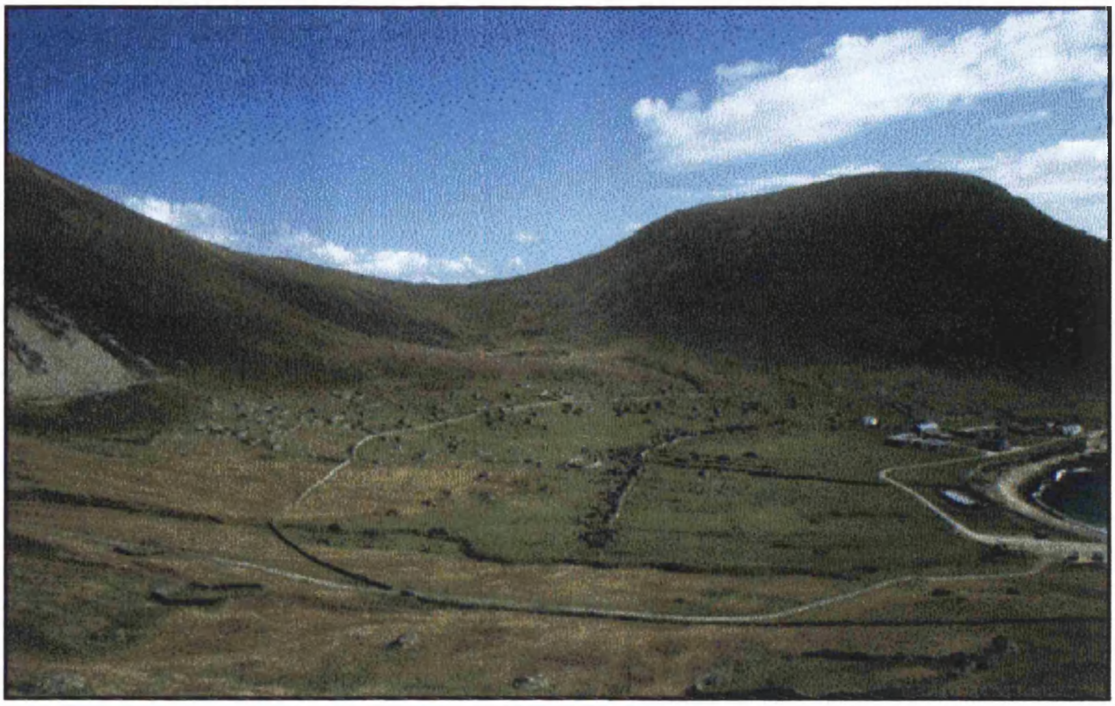


Figure 2.2 Village Bay, Hirta, St. Kilda from Mullach Sgar, showing the study area boundaries, the hills, Oiseval (right) and Conachair (left). The prefered grazing areas are the *Holcus/Agrostis* community on the more fertile soils, within the circular head dyke.

are also abundant in this community (Gwynne *et al.* 1974). The other notable grass community is the very short, *Festuca* sward occurring in areas subject to considerable sea spray. This is distinguished by the presence of three species of *Plantago* (*P. coronopus*, *P. lanceolata* and *P. maritima*) and an unusually high proportion of the favoured graze species, *Festuca rubra*. Consequently this community is heavily grazed and never achieves a high standing biomass.

The Study Population

Soay Sheep

Soay sheep (*Ovis aries*) are the most primitive breed of sheep in western Europe, still resembling the original wild species (Campbell 1974; Clutton-Brock, J. 1981). The origins of sheep on St. Kilda are a matter of speculation. They could result from introductions by the Vikings in the 9th or 10th centuries A.D. or may date back to prehistoric times (Campbell 1974). Historically, they have been restricted to the

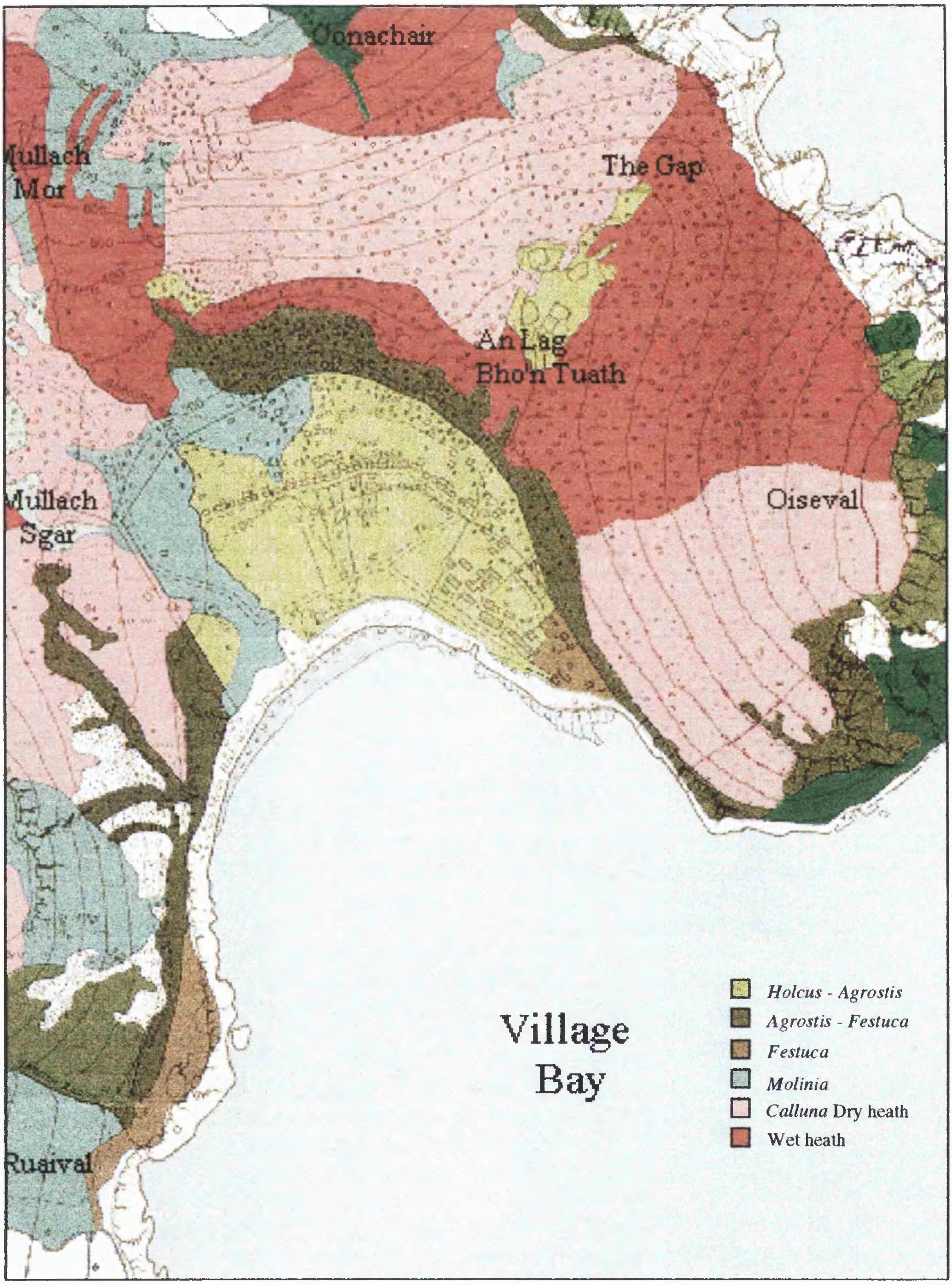


Figure 2.3 Map of the study area showing the principal vegetation communities. (Adapted from Gwynne *et al.* 1974).

uninhabited and inaccessible island of Soay and consequently have remained largely unchanged. The current population of Soay sheep on Hirta stem from 107 individuals that were introduced from Soay in 1932, two years after the evacuation of the St. Kildan people and their domestic Blackface flocks.

Soay sheep are considerably smaller and leaner than domesticated breeds and tend to have relatively longer legs. They are similar in proportions and build to mouflon and other wild sheep (Doney *et al.* 1974). There are two distinctive colour morphs; dark, chocolate brown and light buff. Both these colourations occur in two forms, the 'wild type' which have an almost white belly and rump, and 'selfs' which are uniformly coloured. Over 2/3 of the sheep are 'dark wild' and about a quarter are 'light wild'. 'Dark self' sheep are entirely black and account for about 3% of the population. 'Light selfs' are extremely rare, particularly in males. Distinct horn types occur too, such that both sexes may have normal horns, which spiral in males, scurs which are deformed, or they may be hornless (polled). Nearly all males are normal horned whereas only about a third of females are (Doney *et al.* 1974; Stevenson 1994).

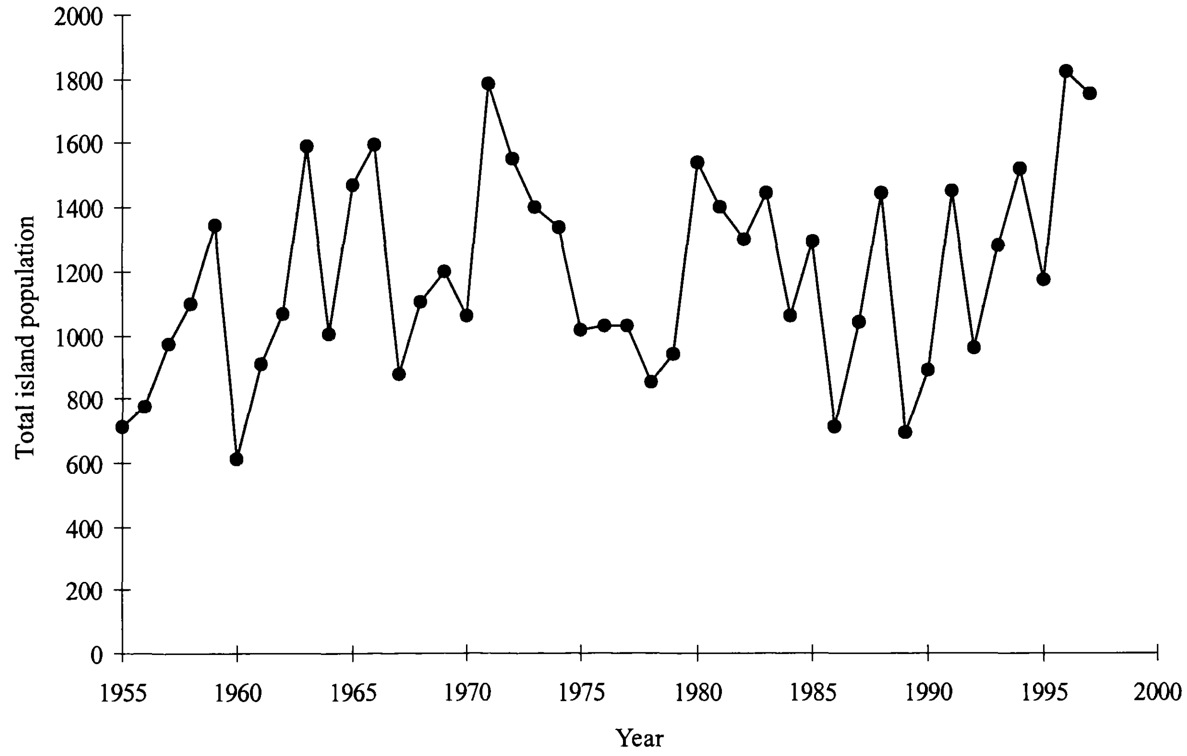
Population Dynamics

Interest in the Soay sheep population of Hirta began in the 1950s when a group from the Nature Conservancy began visiting the island on an annual basis and the first organised censuses were carried out (Jewell *et al.* 1974). Intensive monitoring of the population was undertaken between 1960 and 1968. By then it was apparent that the population was under-going recurrent crashes with a periodicity of approximately three to four years (Boyd 1974). The project was taken up again by a team from Cambridge University in 1985 and continues to date. Throughout both studies and during the intervening period, an annual total island population census has been conducted using the protocol of Boyd *et al.* (1964). The population has continued to fluctuate between 600 and 2000 individuals (Figure 2.4a) throughout the entire period (Clutton-Brock *et al.* 1991; Clutton-Brock *et al.* 1992; unpublished data).

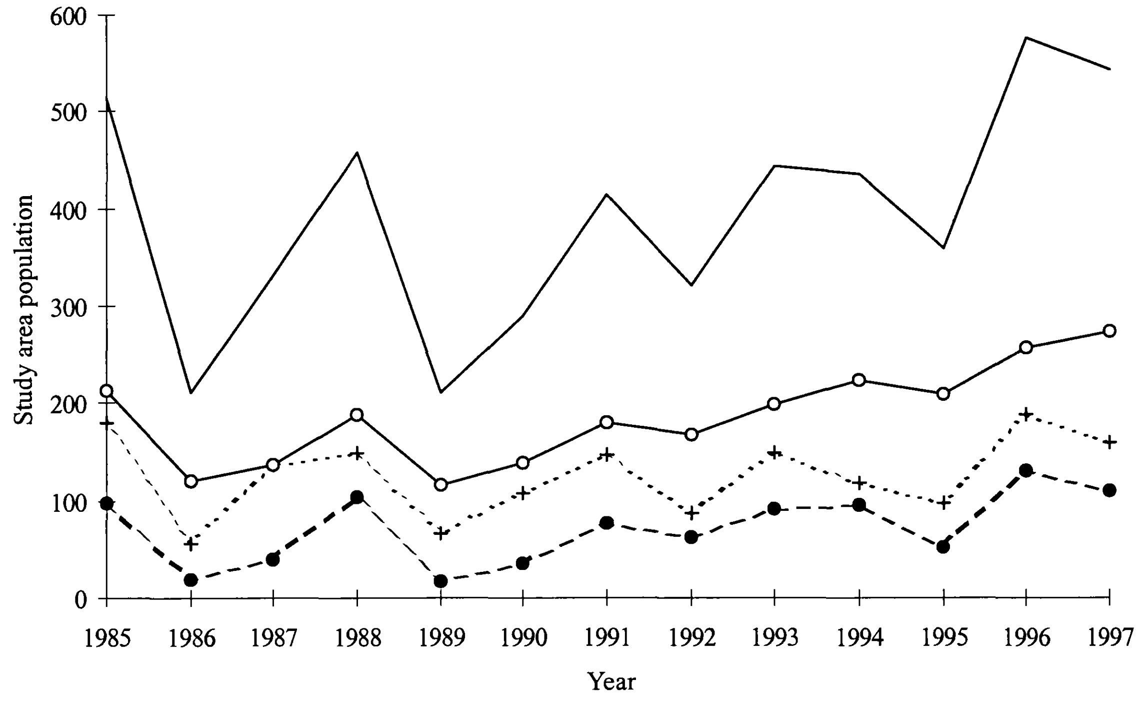
Over-winter survival is strongly density-dependent (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992) and in years of high summer population up to 50-70% of sheep may die of starvation during the subsequent winter when the standing crop of vegetation has been depleted (Grubb 1974b; Clutton-Brock *et al.* 1991). Starvation is exacerbated by high

Figure 2.4 Fluctuations in (a) total population size of Soay sheep on Hirta since 1955 and (b) population size within the Village Bay study area since 1985.

(a)



(b) Total number of sheep (——) and numbers broken down by age and sex class: lambs (---+---), adult females (—O—), adult males (--●--).



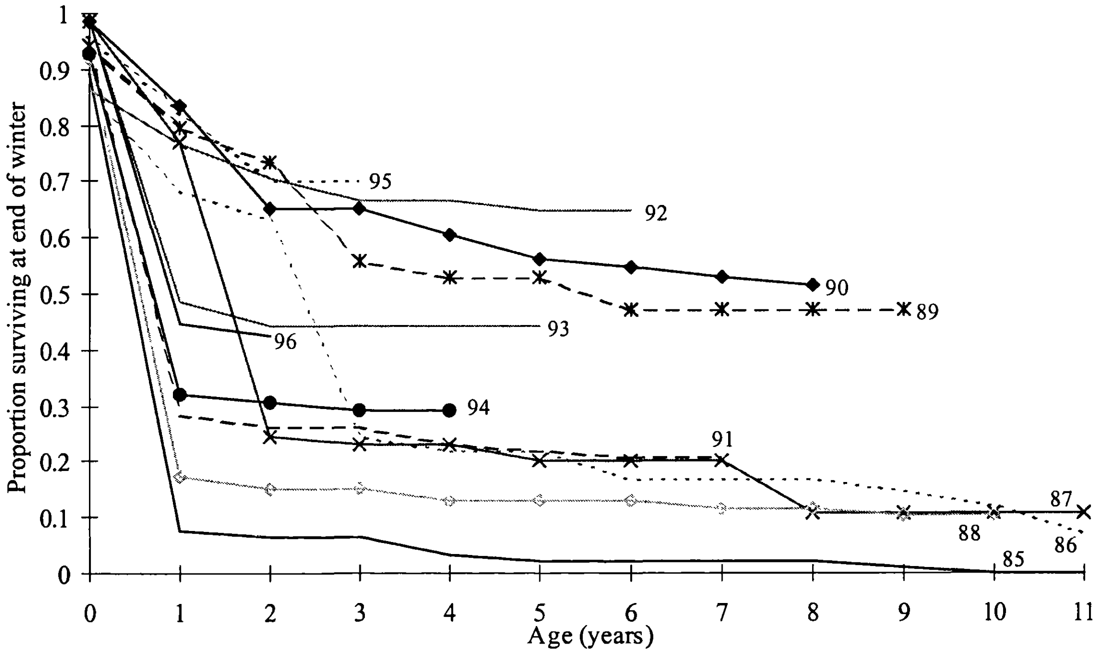
gastrointestinal parasite burdens (Gulland 1992; Gulland *et al.* 1993). However, in recent high population years, anticipated crashes have not occurred, especially amongst the adult component of the population. It has become apparent that at high population sizes the system is particularly sensitive to a combination of density-dependent and independent factors (Grenfell *et al.* 1998).

Differential mortality occurs which is strongly biased towards lambs and young males (Clutton-Brock *et al.* 1991) resulting in an unbalanced sex ratio (the actual ratio varies depending on the stage of the population cycle). In some years entire male cohorts have died (Stevenson 1994). Consequently there are strong year and cohort effects which are manifest in many aspects of the sheeps' life histories. This point is illustrated very clearly in survival profiles of each cohort (Figure 2.5). From these it can be seen that animals are most affected by year effects in their first year and males are affected more strongly than females. There is also considerable variance in age-specific survival probabilities depending on year of birth. For this reason, year is fitted as a random effect in the survival models in Chapter 3, and year and cohort are both controlled for in the morphometric trait models in Chapter 5. Similarly, strong cohort effects on life-histories have been observed in the red deer on Rum (Albon *et al.* 1987; Rose *et al.* 1998) and, in the mountain sheep of North America (Geist 1971), life expectancies vary depending on whether the population is stable, declining or expanding.

It has been suggested that the observed patterns of recurrent crashes and density-dependent mortality could be caused by overcompensation (Grenfell *et al.* 1992). An important aspect of this is the high net reproductive rate of Soays expressed both by a high twinning rate in two year and older ewes, and a high proportion of ewes giving birth in their first year (Clutton-Brock *et al.* 1992). Recovery from crashes may consequently be very rapid.

An alternative explanation arises from analysis of synchronous population fluctuations between Hirta and the neighbouring island of Boreray where there is a population of Scottish Blackface sheep of unrelated stock. A high degree of environmental correlation, part of which can be explained by large-scale weather variations, between the populations is required to achieve the observed level of synchrony (Grenfell *et al.* 1998). This indicates the importance of extrinsic influences on population dynamics

(a) Females



(b) Males

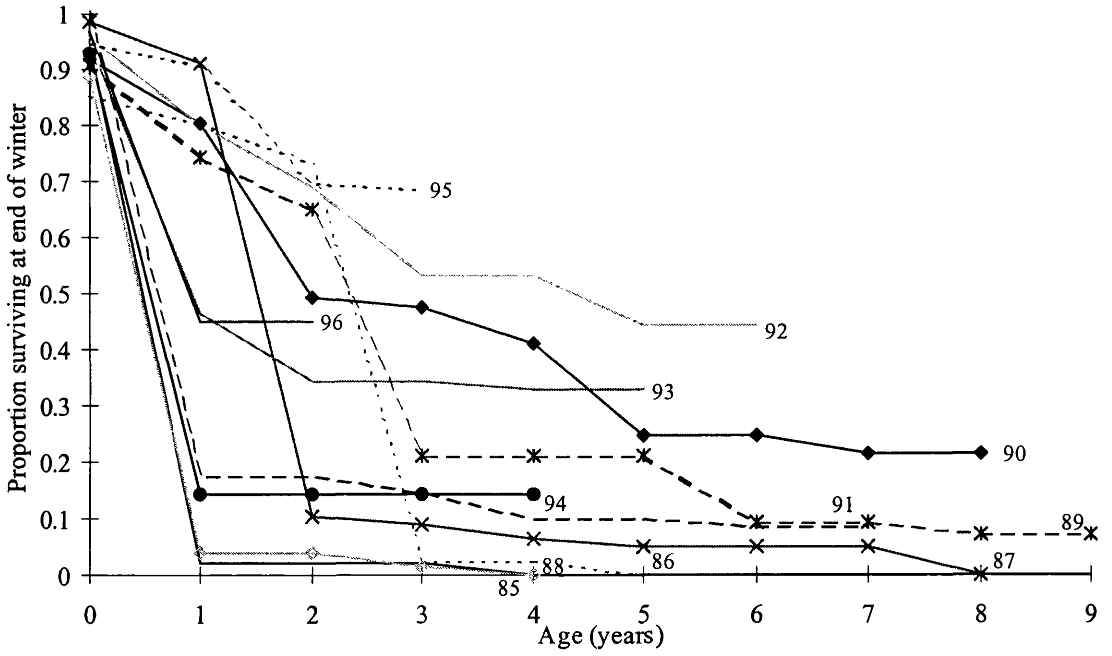


Figure 2.5 Survival profiles for cohorts of (a) female and (b) male Soay sheep on St. Kilda. The year of birth is marked for each cohort since 1985. Neonatal mortality accounts for the proportion surviving at age 0 being less than 1 in most cases.

which will be explored further in Chapter 3. I focus in particular on the North Atlantic oscillation (Wilby *et al.* 1997) caused by fluctuations in the atmospheric circulation over the North Atlantic, during the winter months. This index provides a single integrative measure of winter severity, encapsulating temperature, wind speed and direction, and precipitation.

The Soay sheep of St. Kilda are ideal for investigating natural selection in the wild since they are a remote island population, free-living in the absence of either competing herbivores or predators. In addition, a detailed long-term data set of individually-known animals is available from which complete life-histories and genealogical relationships can be determined. The fact that the population is also exposed to extreme crashes which represent major selection events means the system provides a very rare opportunity to for addressing evolutionary questions.

Data collection

Population data

In most years since 1985, about 95% of lambs born in the study area have been caught and tagged within a few days of birth. The mothers' identity is recorded and blood samples and ear punches are taken for genetic paternity analysis. The entire life-histories of individuals can therefore be monitored. Regular censusing in March, July and November yield data on activity patterns, habitat utilisation, social behaviour and survival. This is complemented by daily winter mortality searches from February to April providing information on the dates and locations of mortality (Clutton-Brock *et al.* 1991). Approximately 85% of animals tagged as lambs are followed throughout their lives until eventually they die and their bodies are recovered.

The Village Bay population size is taken as the number of sheep using the study area at the start of winter and is estimated from census data (Figure 2.4b). This number is well correlated with the total island sheep population, representing approximately one third of it (Clutton-Brock *et al.* 1991).

Morphometric traits

In most years, over half of the study area population is caught in August or September (median proportion 0.56, range 0.18 - 0.70; Table 4.2), allowing body measurements, blood and faecal samples to be taken. Detailed information is therefore available on individual growth patterns, condition, parasite burdens and genotypes for most of the study population. The three measurements that I focus on in this thesis are :

1) Body weight - the live mass, measured to the nearest 0.1kg. This is a composite measure of body size and condition. Gutfill and wetness of fleece are factors influencing weight that cannot be controlled for and therefore contribute to the error in this measure (Illius *et al.* 1995). The period of catching during late summer was a time of considerable daily weight gain (0.12 kg day^{-1} in lambs, 0.08 kg day^{-1} in adult females and 0.20 kg day^{-1} in adult males). Catch date was variable during the 1980s, particularly in 1985 and 1988, whilst throughout the 1990s was restricted to a much shorter period. The effect of catch date on body weight therefore had to be taken into consideration in analyses including data from the 1980s.

2) Hindleg length - the distance from the tubercalcis of the fibular tarsal bone to the distal end of the metatarsus, measured to the nearest mm. This has been recorded from 1988 onwards.

3) Incisor arcade breadth - the distance between the outer left and right edges of the fourth incisor (incisiform canine) on the lower jaw (Figure. 2.6), measured from dental impressions of the incisor arcade made using Tenacetin dental modelling wax (Associated Dental Products, Swindon, UK). Incisor breadth has been measured since 1990. The measurements used throughout the analysis were made by one person to avoid inconsistencies between measurers. Despite this, incisor breadth remained a measure with poor repeatability (Chapter 5). Incisor arcade breadth is a size measure with functional significance for survival through its relationship with bite size and food intake rate (Gordon *et al.* 1996).

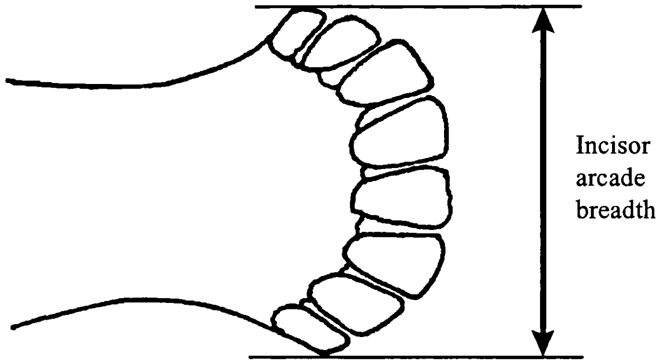


Figure 2.6. Schematic diagram of the lower jaw and anterior dentition of a sheep, indicating where the measurement of the incisor arcade breadth is made.

Parasitism has an effect on both body weight (Coop *et al.* 1982), survival (Gulland 1992) and foraging behaviour (Gregory *et al.* 1985; Fox *et al.* 1989) so had to be taken into account in most of the analyses in this thesis. Faecal egg counts were used as an index of parasite burden. The number of strongyle eggs per gram of faeces (Gulland & Fox 1992) from samples collected during the August catch, were counted and transformed as follows :

$$\log \mathit{faecal\ egg\ count} = \log\left(\frac{\mathit{strongyles} / g}{100} + 1\right)$$

In the years 1988-1991 and 1995, some of the individuals caught in August were dosed with anthelminthic treatments to combat intestinal parasites. Subsequent records for these sheep have been excluded from all analyses as their survival was influenced by the treatment (Gulland *et al.* 1993).

Genetic and Foraging data

Details of all methods used in the determination of genetic relationships for the heritability analysis are given in Chapter 5. A full description of the methods used for the foraging observations and faecal sampling is given in Chapter 6.

Analyses

Details of all statistical analyses are given in the relevant chapters. Genstat 5, release 3.2 (Genstat 5 Committee 1993) was used throughout, except for determining the heritabilities. Custom-designed software packages (PEST and VCE; Groeneveld, Kovac & Wang, University of Illinois, 1993) were used for this, details of which are given in Chapter 5.

In all tables of results, the following symbols are used to indicate the statistical significance of terms: † $P<0.10$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

CHAPTER 3.

Factors affecting over-winter survival and its interannual variation.*

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* J.M. Milner, D.A. Elston & S.D. Albon (accepted subject to minor revision) Contributions of population density and climatic fluctuations to interannual variation in survival. *Journal of Animal Ecology.*

Factors affecting over-winter survival and its interannual variation.

Summary

The relative importance of density-dependent and -independent factors on interannual variation in over-winter survival was investigated in the fluctuating population of Soay sheep on St. Kilda, Scotland, over the period 1985-1996.

Population density had a negative effect on survival in lambs and adult males whilst adult female survival showed no evidence of density-dependence. Climatic fluctuations associated with the winter North Atlantic oscillation index (NAO) also affected survival, which decreased in winters that were relatively warm, wet and windy. The effect was most pronounced in lambs.

Survival was modelled using generalised linear mixed modelling (GLMM). This allowed year to be fitted as a random effect, incorporating stochastic year to year variation in survival. Results were compared with those of logistic regression analysis of the same data. Parameter estimates were similar using both methods but the standard errors of the year-dependent covariates, population size and NAO, were under-estimated using logistic regression. Consequently, incorrect inferences about the relative significance of terms would be made from the logistic regression analysis.

Using both modelling approaches, density-dependence was found to have a greater influence on survival than the effect of NAO in lambs and adult males, whereas in adult females NAO was the more important. Once random between-year effects were taken into account, the individually-varying terms such as body weight and faecal egg count were the most significant factors explaining differences in survival.

Introduction

There has been a recent increase in interest in the influence of density-independent factors and environmental stochasticity on survival and population dynamics (Sæther 1997; Leirs *et al.* 1997; Gaillard *et al.* 1998; Grenfell *et al.* 1998). A growing body of evidence shows that ecological processes are affected by climatic fluctuations (Grant & Grant 1989; Post & Stenseth 1998; Forchhammer *et al.* 1998a). This has implications for the debate concerning the relative importance of intrinsic (density-dependent) and extrinsic (density-independent) factors on population changes. Sæther (1997) suggested that, in the absence of predation, the population dynamics of ungulates were determined by a combination of both density-dependent and stochastic environmental effects, operating through changes in survival and fecundity rates. An example is the density-independent cohort effects of spring temperatures on birth weight of red deer (*Cervus elaphus*) which were found to significantly influence over-winter survival rates (Albon *et al.* 1987; Rose *et al.* 1998), whilst the effects of birth weight on survival were intensified at high densities (Clutton-Brock *et al.* 1987b). Post & Stenseth (1998) have shown that growth in the moose (*Alces alces*) population on Isle Royale, USA, and increases in white-tailed deer (*Odocoileus virginianus*) abundance in Superior National Forest, USA, were both influenced by delayed density-dependent feedback, as well as global climatic fluctuations and predation by wolves (*Canis lupus*).

Measures of age- or sex-specific survival rates have, until recently, been based on transversal life-table methods, with little knowledge of their reliability (Gaillard *et al.* 1993). However, several long-term studies of ungulate populations with individually known animals (reviewed by Sæther 1997; Gaillard *et al.* 1998) have enabled accurate estimates of vital rates to be made, partly due to advances in the modelling of capture-mark-recapture data (Lebreton *et al.* 1993). Jorgenson *et al.* (1997) remarked that the degree to which survival rates varied between years remained largely unknown. Gaillard *et al.* (1998) have subsequently demonstrated that across 16 species of large herbivore, the coefficients of variation in survival between-years varied little in prime-aged females (from 2-15 %) but were very variable in juveniles (from 12-88 %). Furthermore, it has been shown that juvenile survival is more sensitive to both density-dependence and, in particular, to seasonal food availability and therefore stochastic variation, than adult survival (Sinclair 1977; Gaillard *et al.* 1998). Analyses of the Soay sheep were therefore conducted separately on lambs, adult females and adult males to investigate the different susceptibilities of these components of the population.

It has previously been demonstrated that over-winter survival of the Soay sheep (*Ovis aries*) on St. Kilda was strongly density-dependent (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992) but in recent high population years, anticipated crashes have not occurred, especially within the adult population. It has become apparent that, at high population sizes, the system is particularly sensitive to a combination of density-dependent and independent factors. Consequently populations above a certain threshold can increase, decrease or remain constant in size depending on the extrinsic environmental conditions (Grenfell *et al.* 1998). It would generally be expected that the effects of weather on population dynamics should become more evident as a system approaches the ecological carrying capacity (Fowler 1987; Sinclair 1989). In support of this, it has been shown that population growth rates or survival were more variable at high density, when density-independent effects were stronger, in populations of red deer on Rum (Benton *et al.* 1995), bighorn sheep (*Ovis canadensis*) in the Canadian Rocky mountains (Portier *et al.* 1998) and in Dall's sheep (*Ovis dalli*) in Alaska (Bowyer *et al.* in press).

Grenfell *et al.* (1998) found that the effects of March gales and April temperatures had a greater influence on Soay sheep survival above a threshold density, than at low density. Here, I have investigated the influence of a stochastic environmental variable, climatic fluctuation, on over-winter survival. In northern Europe, fluctuations in winter climate are strongly correlated with interannual variations in the atmospheric circulation over the North Atlantic (Wilby *et al.* 1997). An annual index of this North Atlantic oscillation (NAO) can be measured by the difference in normalised sea level pressures between Lisbon, Portugal, and Stykkisholmur, Iceland, between December and March (Hurrell 1995). In the British Isles, high positive values are associated with warm, wet winters with strong westerly winds, whereas low negative values indicate cold, dry winters (Wilby *et al.* 1997). Variations in the abundance of zooplankton species have already been linked with fluctuations in NAO, with the implication that the NAO may play a comparable role to the El Niño southern oscillation in pelagic ecosystems (Fromentin & Planque 1996). In terrestrial systems, breeding phenologies of a number of species of birds and amphibians have been shown to be well correlated with fluctuations in NAO (Forchhammer *et al.* 1998a). Furthermore, direct and delayed effects of the NAO on population dynamics of red deer have been found in Norwegian populations (Post *et al.* 1997; Forchhammer *et al.* 1998b), and in moose and white-tailed deer populations in the United States (Post & Stenseth 1998).

Most of the previous analyses of survival of Soay sheep on St. Kilda have used logistic regression analysis (Clutton-Brock *et al.* 1992; Bancroft *et al.* 1995a; Illius *et al.* 1995; Moorcroft *et al.*1996; Clutton-Brock *et al.* 1996). This has advantages over other techniques, such as the analysis of one-way contingency tables, in that several factors can be controlled for simultaneously. However, logistic regression, as applied through generalised linear modelling, does not allow a distinction to be drawn between fixed and random effects and cannot take account of more than one source of variation in the data. Here I investigate the effects of density-dependent and stochastic year to year variation in the survival of the Soay sheep, using the more statistically sophisticated, generalised linear mixed modelling (GLMM), which allows random year effects to be fitted. The appropriateness of logistic regression for analysing survival data across years was assessed by comparing results with those obtained using GLMM.

Materials and Methods

MODEL PARAMETERS

Survival

Survival data were obtained from censuses and winter mortality searches. An individual was considered to have survived a winter if it was known to be alive on 15th May the following year. Years ran from spring to spring such that the winter of 1985 covered the period from autumn 1985 until spring 1986.

Population size

The pre-winter Village Bay population size estimated from census data was used (Figure 2.4b).

Environmental variables

Climatic conditions, in particular the severity of March gales, April temperatures (Grenfell *et al.* 1998) and March rainfall (E.A.Catchpole *et al.* unpublished manuscript),

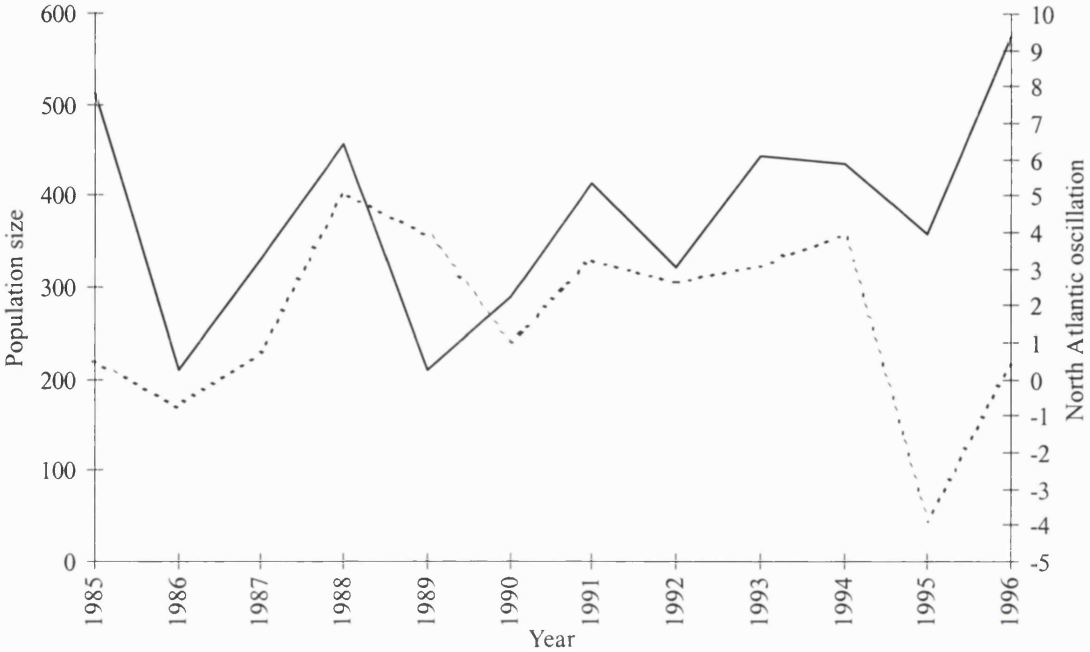

Figure 3.1 The size of the Village Bay Soay sheep population (——) entering each winter, between 1985 and 1996, and the winter North Atlantic oscillation indices (------) over the same period. NAO indices covered the period December to March and are plotted against the calendar year in December, at the start of the winter.

and variations in plant productivity (Forchhammer *et al.* 1998b; M.J.Crawley unpublished data) were important extrinsic factors that could influence the scale of over-winter survival. The North Atlantic oscillation index (Climate Analysis Section, http://www.cgd.ucar.edu:80/cas/climind/) provided a single variable to encapsulate between-year differences in a number of weather variables such as temperature, wind speed and direction, and precipitation, at the time of year when most mortality occurred. Winter NAO indices covered the period from December to March so were used with data collected during the preceding summer and the pre-winter population size. For example, the NAO index for 1985/86 was matched with the sheep population size and individual variables from 1985. Other weather data came from the Meteorological Office's station on the island of Benbecula (Outer Hebrides) but unfortunately this station was closed at the end of 1995 so subsequent data were unavailable. Correlations between these variables are shown in Table 3.1. Once NAO was fitted in the models, the effects of March gale days and rainfall were not significant. Despite a visual impression of association between population size and NAO (Figure 3.1), these two variables were

Table 3.1 Correlations between weather variables and population size on St. Kilda. Population and NAO data were available over the period 1985/86 - 1996/97, but correlations involving the other weather variables were restricted to the period 1985/86 - 1994/95. Population size was the number of sheep in the Village Bay area entering the winter and NAO indices covered the same winter period. The weather variables were collected during the period of winter mortality and were correlated with the pre-winter population size i.e. in the previous calendar year.

	Population size	NAO	March gale days	March rainfall
NAO	0.106	1.00		
March gale days	0.352	0.461	1.00	
March rainfall	0.154	0.457	0.711*	1.00
April temperature	-0.753*	-0.283	-0.495	-0.497

not significantly correlated (r=0.106, P>0.6), allowing the estimates of their effects on survival to be nearly independent. Population size and NAO were common to all sheep but varied from year to year. Together with catch date which varied more between years than within years, these variables will be considered as year-dependent covariates. For all other variables, the main source of variation was considered to be between individuals, within years.

Morphometric measurements

From survival models in which all three morphometric traits, body weight, hindleg length and incisor breadth, were fitted simultaneously, it was apparent that body weight was the size measure with the best explanatory power (Table 3.2). Consequently it was the trait used in the analysis presented in this chapter. Since the date of capture and measurement influenced body weight because of daily weight gain throughout the summer (Chapter 2), catch date was included as an explanatory variable to control for this to some extent.

Parasite burden

Strongyle egg counts, used as an index of gastrointestinal parasite burden (Gulland & Fox 1992; Chapter 2), have only been recorded since 1988. Models for lamb and adult female survival which included faecal egg count, were therefore restricted to the period 1988-1996 whereas adult male models without faecal egg count, ran from 1985-1996 to maximise the use of available data.

Table 3.2 Analysis of deviance tables for logistic regression models of over-winter survival in (a) Soay lambs, (b) adult females and (c) adult males, between 1990 and 1996 inclusive, to examine the relative influence of the three morphometric characters and include the effect of parasite burden. Deviance values show the effect of removing that term from the simple model and are distributed as χ^2.

(a) Lamb over-winter survival

Term	coefficient	se	df	deviance	*P*
Constant	65.2	14.70			
Catch date	-0.143	0.046	1	13.6	<0.001
Population size	-0.121	0.094	1	46.8	<0.001
Faecal egg count	-0.802	0.157	1	28.4	<0.001
Body weight	-14.21	4.09	1	26.3	<0.001
Sex (M)	3.01	1.39	1	8.4	<0.01
Incisor breadth	-7.72	3.17	1	4.2	<0.05
Population . Weight	0.044	0.010	1	24.3	<0.001
Population . Sex (M)	-0.009	0.003	1	8.0	<0.01
Residual			430	434.7	
Total			438	607.4	
Excluded terms :					
Population . Incisor breadth			1	0.9	ns
Hindleg length + Pop . Leg length			2	0.0	ns

(b) Analysis of deviance for the model of adult female survival. Age was added as a two level factor of prime (1-6 years) and old (≥7 years) individuals.

Term	coefficient	se	df	deviance	*P*
Constant	-13.43	3.23			
Catch date	-0.140	0.061	1	5.3	<0.05
Body weight	5.68	1.09	1	29.9	<0.001
Ageclass (Old)	-2.296	0.413	1	31.4	<0.001
Faecal egg count	-0.694	0.229	1	9.2	<0.01
Residual			592	271.0	
Total			596	338.9	
Excluded terms :					
Population size + Pop . Weight			2	1.7	ns
Pop + Hindleg length + Pop . Leg length			3	1.8	ns
Pop + Incisor breadth + Pop . Incisor breadth			3	0.5	ns

(c) Analysis of deviance of adult male survival

Term	coefficient	se	df	deviance	*P*
Constant	3.271	0.870			
Population size	-0.005	0.002	1	6.6	<0.05
Residual			187	200.9	
Total			188	207.5	
Excluded terms :					
Body weight + Pop . Body weight			2	3.5	ns
Incisor breadth + Pop . Incisor breadth			2	1.0	ns
Hindleg length + Pop . Leg length			2	1.8	ns
Catch date			1	2.8	ns
Faecal egg count			1	0.3	ns

Age

Survival of lambs (individuals less than one year old) over their first winter was analysed separately from that of yearlings (individuals aged 12 - 23 months) and adults (over two years old) because of the particular susceptibility to mortality of juvenile animals (Clutton-Brock *et al.* 1992). Differences in survival between yearlings and adults were less marked and it was found that the use of two age classes in adult females, 'prime' (yearlings and 2-6 year-olds) and 'old' (7 years and over) individuals, was the most parsimonious way of explaining variation due to age. Adult males rarely lived to 7 years so insufficient data were available to test for a decline in survivorship with old age. Although survival of yearlings was lower than that of adults over 2 years old, differences were not significant. Consequently all adult and yearling males were grouped in a single age category. Data from adult males and females were analysed separately because of the differential survival of the sexes, brought about by male rutting activity (Stevenson & Bancroft 1995). There were a number of marked animals of unknown birth year, and hence age, in the study population. These individuals have been excluded from the analysis.

Analysis

Generalised linear mixed models

Over-winter survival data were analysed by fitting generalised linear mixed models (GLMM; Welham 1995) to ascertain the relationship between survival, density, climatic fluctuations and individual attributes. GLMMs are generalised linear models with additional random effects to enable the analysis of stratified data with more than one error term. GLMMs can be fitted in several statistical packages by combining algorithms that fit generalised linear models (GLMs) with algorithms for fitting linear mixed models (Schall 1991). The GLMM, an extension of the logistic regression model, fitted a probability curve through the binomially distributed survival data (0 died, 1 survived) using the logit link function.

$$P(y_{ij} = 1) = \frac{\exp(a + b_1 x_{1ij} + \ldots . + b_m x_{ijm} + c_{1i} + c_{2j})}{1 + \exp(a + b_1 x_{1ij} + \ldots . + b_m x_{ijm} + c_{1i} + c_{2j})}$$

$y_{ij}=1$) was the probability that individual i would survive winter j, a was a constant, $b_1 \ldots b_m$
coefficients
endent
as $x_1 \ldots x_m$

where c_{1i} and c_{2j} were random effects for individual and year which were assumed to be uncorrelated with each other and drawn from normal distributions with zero means and variances.

Model fitting with GLMM proved to be slow and there were some problems with convergence. Consequently significant variables from the best fitting logistic regression models (see below) were used as the fixed effects in GLMMs and random terms were then added. The significance of terms in GLMMs were assessed by the Wald statistic at the final iteration of the algorithm, for each term when fitted last in the model. Wald statistics were distributed as χ^2, except for year-dependent covariates for which Wald statistics were tested against $F_{1,r}$ where r was the residual degrees of freedom of years.

In all GLMMs, year was fitted as a random effect to account for stochastic between-year variation in survival. When modelling adult survival, there were multiple appearances in the data set of a proportion of individuals that had survived more than one winter and consequently had repeated records. The influence of repeated records was also investigated by fitting the identity of the individual as a second random effect in adult survival models. However, no significant individual effect was found in either sex, so this was discarded. Whether this arose due to particular features of the data set or was a general result was not clear and will be discussed later.

Logistic regression models

Logistic regression analysis (Cox 1970) was used to select the best-fitting fixed effects models. A comparison was also drawn between parameter estimates, and their corresponding standard errors, made using the two modelling approaches. All continuous variables were centred about the mean values. The logistic probability curve had the form:

$$P(y_{ij}=1)=\frac{\exp(a+b_1x_{1ij}+\ldots..+b_mx_{mij})}{1+\exp(a+b_1x_{1ij}+\ldots..+b_mx_{mij})}$$

where $P(y_{ij}=1)$ was the probability that an individual i would survive winter j, a was a constant and $b_1 \ldots b_m$ were coefficients of the independent variables $x_1 \ldots x_m$,.

Model parameters were estimated by maximum likelihood (McCullagh & Nelder 1989) and significance was measured by the change in deviance that occurred when a term was dropped from the maximal model. Terms were dropped sequentially and re-fitted if significant, until the model included only significant terms. Change in deviance was assumed to follow a χ^2 distribution, with degrees of freedom equal to the change in the residual degrees of freedom .

To avoid the potential problems of non-independence due to repeated records, previous logistic regression analyses of the Soay sheep survival data have been restricted to animals that have never experienced a crash (Bancroft 1993), conducted age- or crash-specific analyses (Clutton-Brock *et al.* 1992; Stevenson 1994; Illius *et al.* 1995) or excluded multiple data records (Stevenson 1994). In the analysis conducted here all repeated records were used since no significant individual effect had been found using GLMM.

Random between-year variation

When assessing the significance of year-dependent covariates, logistic regression analysis was unable to make a direct allowance for stochastic variation in survival between years because no random effects could be included. A correction for this was therefore made by multiplying the standard error of the regression coefficients for these covariates (population size, NAO and catch date) by the square root of the mean deviance due to the year effect (McCullagh & Nelder 1989).

The relative significance of the year-dependent covariates was investigated by comparing the variation in survival that they explained with that due to the residual between-year variation. The comparison was made using *F*-ratios of the mean deviance due to the year-dependent covariate when fitted second-last with the mean deviance due to the year effect when fitted last.

Results

FACTORS AFFECTING SURVIVAL

Lambs

Over-winter survival probability declined sharply with increasing population size and index of the North Atlantic oscillation (Table 3.3a). The NAO effect indicated that survival was reduced in warm, wet winters with strong westerly winds. The relationship between predicted survival and population size fitted the observed points for each year well (Figure 3.2a). The relationship between survival and NAO fitted the observed points less well, particularly in 1989 when the observed survival was very high and much greater than would have been predicted from the NAO index in that year (Figure 3.2b). However, that year followed the crash of 1988/89 and the population density was sufficiently low that a high survival rate was possible regardless of NAO.

In addition, the probability of survival in lambs increased with body weight whilst parasite burden had a significant negative effect. Female lambs had higher survival rates than males (Table 3.3a). These terms had the most significant effect on lamb over-winter survival when random between-year variation was taken into consideration.

There were no significant interactions between NAO and any of the individual variables. However, there was a significant positive interaction between population size and body weight resulting in an increased probability of survival of heavy individuals at high population density and a decline in survival of heavy lambs relative to light ones at low densities. This interaction could be illustrated by a survival surface predicted from the logistic regression model (Figure 3.3). The most important trend to note was the very much steeper decline in survival probability of light individuals relative to heavy ones as population size increased. Observed survival patterns from within the population generally supported the trends of the survival surface, including the tendency for large lambs to have lower survival than small lambs at low population densities (Table 3.4). However, this particular result should be interpreted cautiously because sample sizes from low population years were small, especially of heavy lambs born in years following severe winter mortality. Below a population size of 300, the model was based on only 37 data points, collected during 1989 and 1990.

Table 3.3 Comparison of parameter estimates for the best fitting over-winter survival models for (a) lambs, (b) adult female and (c) adult male Soay sheep, calculated using generalised linear mixed models (GLMM) and logistic regression analysis (GLM). Interactions are denoted by ' . ' between terms. Adjusted standard errors (se) allowed for a between-year effect of year-dependent variables and *F* ratios compared the mean deviance of year-dependent variables with the mean deviance due to the residual between-year effect (see text). Degrees of freedom were 1 throughout.

(a) Lamb over-winter survival model for the period 1988 -1996 (n=441).

Term	GLMM estimates	se	Wald statistic	GLM estimates	se	Change in deviance	Adjusted se	$F_{1,6}$ ratio
Constant	0.316	0.337		-0.212	0.201			
Catch date	-0.135	0.056	5.7†	-0.192	0.046	20.7***	0.103	4.35
Faecal egg count	-0.790	0.172	21.0***	-0.728	0.161	21.8***		
Body weight	4.28	0.890	25.6***	4.58	0.874	31.1***		
Sex (M)	-1.19	0.307	15.8***	-1.11	0.300	14.6***		
Population size	-0.008	0.004	11.6*	-0.007	0.002	61.4***	0.004	12.15*
NAO	-0.340	0.121	7.9*	-0.374	0.064	44.0***	0.144	9.88*
Pop . Weight	0.041	0.011	14.5**	0.042	0.010	22.6***		
Pop . Sex (M)	-0.007	0.004	4.1†	-0.008	0.003	5.9*		

(b) Survival models for adult females between 1988 and 1996 (n=676). Age was added as a two level factor of prime (1-6 years) and old (≥7 years) individuals.

Term	GLMM estimates	se	Wald statistic	GLM estimates	se	Change in deviance	Adjusted se	$F_{1,6}$ ratio
Constant	2.23	0.434		4.183	0.397			
Catch date	-0.065	0.065	1.0	-0.111	0.051	4.4*	0.102	1.11
Faecal egg count	-0.582	0.225	6.7**	-0.414	0.210	3.9*		
Body weight	6.10	1.05	33.6***	6.24	1.00	44.7***		
Ageclass (Old)	-2.29	0.422	29.5***	-2.43	0.398	39.9***		
Population size	-0.008	0.005	2.8	-0.007	0.003	6.8**	0.006	1.71
NAO	-0.646	0.280	5.3†	-0.622	0.175	28.5***	0.349	7.16*

(c) Survival models for adult males during the period 1985 - 1996 (n=372).

Term	GLMM estimates	se	Wald statistic	GLM estimates	se	Change in deviance	Adjusted se	$F_{1,10}$ ratio
Constant	0.358	0.538		0.564	0.139			
Catch date	-0.010	0.026	0.1	-0.109	0.021	36.5***	0.066	3.69†
Body weight	1.545	0.530	8.5**	1.45	0.457	10.4**		
Population size	-0.011	0.005	5.9*	-0.009	0.001	42.7***	0.003	4.32†

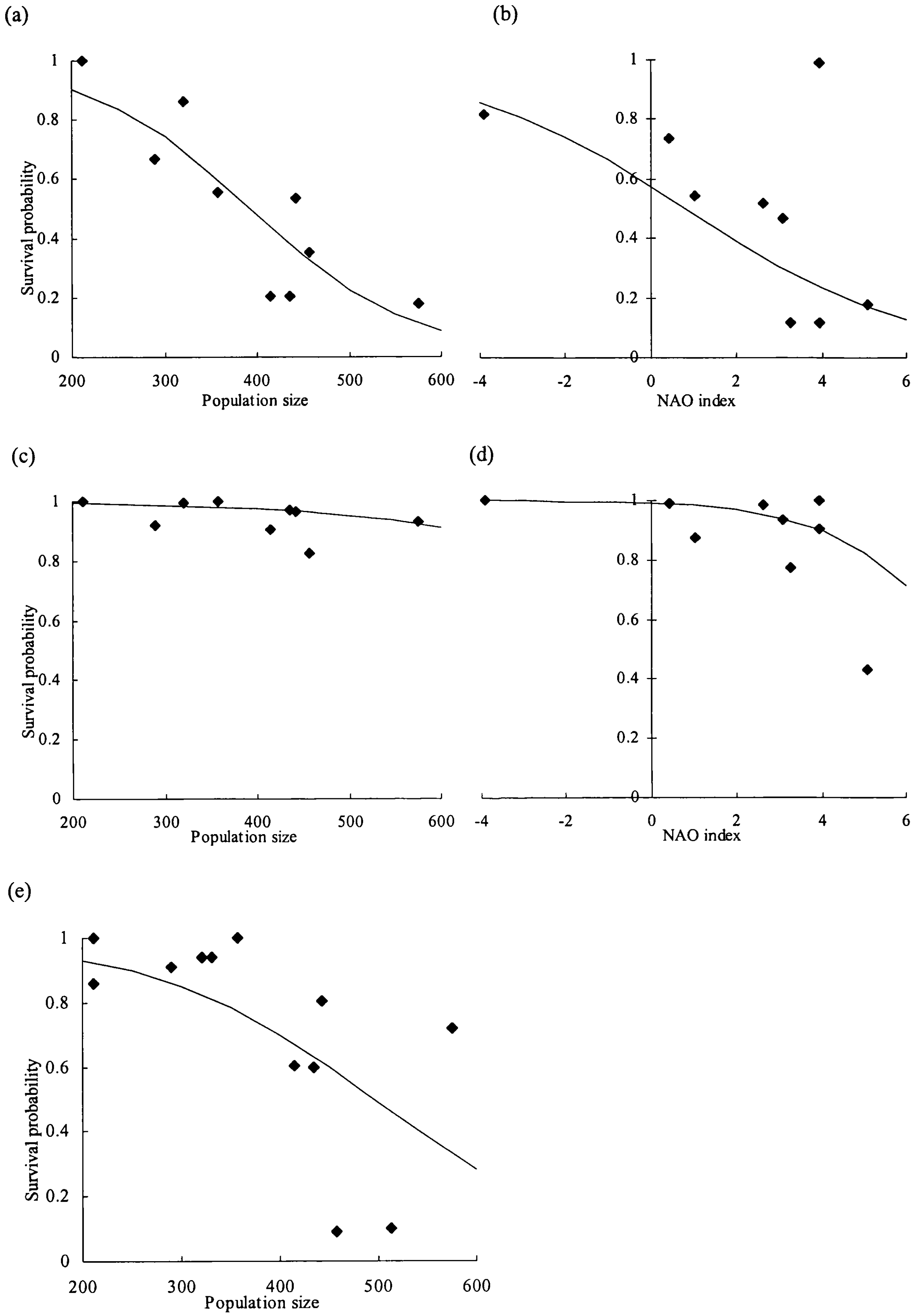

Figure 3.2 The effects of population size and NAO on survival in lambs (a,b), adult females (c,d) and adult males (e). Predicted survival probabilities are shown by the fitted lines. Points represent observed survivorships in each year, adjusted to the mean of all model variables except that varying on the abscissa. Sample sizes varied between years but, with the exception of 1989 in lambs (n=5) and 1986 and 1989 in adult males (n=5 and 6 respectively), all were greater than 10.

Figure 3.3 Fitness surface of survival probabilities predicted by the logistic regression model for lambs, illustrating the interaction between population size and body mass. The effect has been averaged across the sexes and values for faecal egg count, NAO and catch date were held constant at their means.

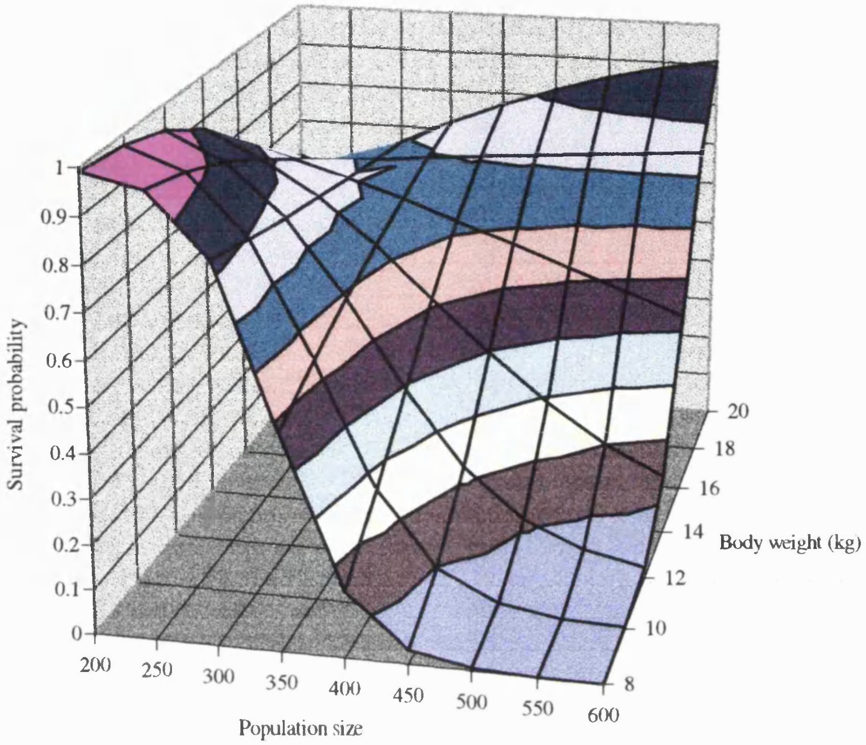

Table 3.4 Observed number of lambs surviving the winter, expressed as a fraction of the total number of individuals of that mass class entering the winter at different population sizes. The proportion of survivors is given in parentheses. Body masses have been corrected for catch date but no allowance made for other factors.

	Population size							
Mass (kg)	200-299		300-399		400-499		500-599	
8 - 9.9	0 / 0	(-)	10 / 11	(0.91)	0 / 12	(0)	0 / 7	(0)
10 - 11.9	4 / 4	(1.00)	15 / 21	(0.71)	8 / 47	(0.17)	2 / 18	(0.11)
12 - 13.9	7 / 8	(0.88)	28 / 32	(0.88)	13 / 66	(0.20)	8 / 22	(0.36)
14 - 15.9	13 / 13	(1.00)	18 / 19	(0.95)	17 / 53	(0.32)	10 / 24	(0.42)
16 - 17.9	8 / 8	(1.00)	9 / 12	(0.75)	16 / 27	(0.59)	4 / 10	(0.40)
18 - 19.9	2 / 4	(0.50)	0 / 1	(0)	5 / 7	(0.71)	3 / 4	(0.75)

Adult females

In adult females, the effect of NAO on survival was stronger than that of population size but neither had as pronounced an effect on survival as in lambs (Figure 3.2c). The effect of increasing NAO on survival was again negative, indicating that warm, wet winters with strong westerly winds reduced survival but this was only significant at the 10 % level. The weak and non-significant effect of density on adult female survival arose because there has been no major mortality event in the adult female component of the population since 1988/89. As a result there has been a considerable increase in the adult female population size throughout the 1990s.

The fit of the observed survival against the NAO in each year was good except for 1988, when survival was much lower than was predicted from its NAO index (Figure 3.2d). There was a high population density in that year and a particularly large crash occurred. However, there was less disparity between the observed survival in 1988 and that predicted for its population size (Figure 3.2c).

Body weight and ageclass were the variables with the greatest effect on over-winter survival in adult females (Table 3.3b). Again, survival chances improved with increasing body weight but there was no significant interaction between body weight and population size. Old age (≥7 years) was associated with a decrease in survival compared with individuals in their prime. A negative relationship between survival and faecal egg count also existed in adult females.

Adult males

Adult male survival over the period from 1985-1996 was influenced by a strong negative effect of population size. Survival of adult males was much more density-dependent than adult female survival, but surprisingly there was no significant effect of NAO. Body weight was the only other significant variable (Table 3.3c). Faecal egg count was not significant and there was no apparent age effect, presumably because high mortality rates meant very few males lived to old age. Again the interaction between population size and body weight observed in lambs was absent from the adult model.

COMPARISON BETWEEN MODELLING APPROACHES

There was very close agreement between parameter estimates determined by the GLMMs and those of the logistic regression analyses in all age-sex classes (Table 3.3, Figure 3.4). There was a slight disagreement between the constants of the adult female survival models, with the GLMM estimate being lower. This was the outlying point in Figure 3.4. The discrepancy arose because GLMM accords equal weight to each year, whereas logistic regression gives more weight to those years in which more individuals are present.

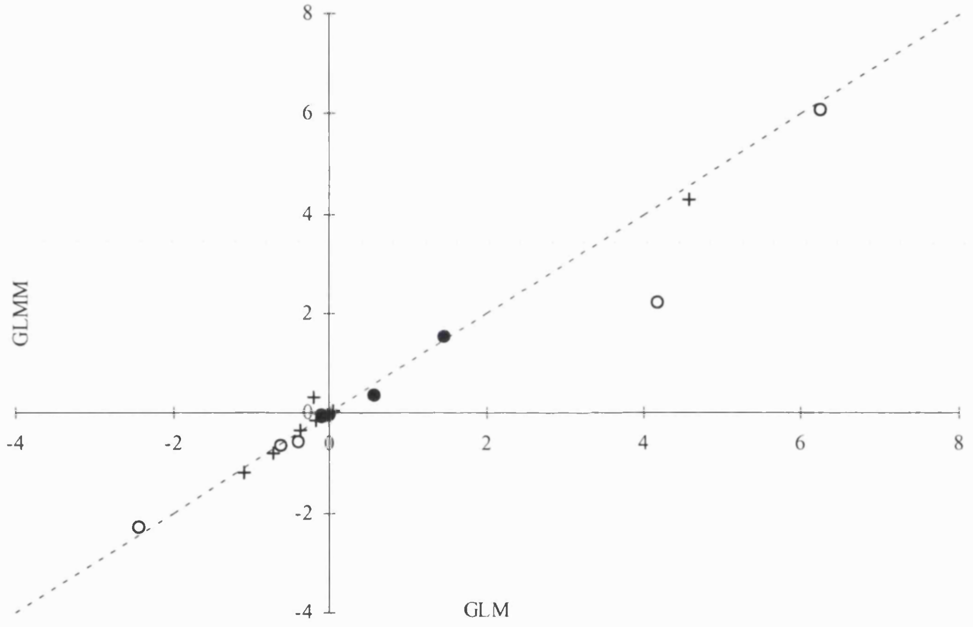

Figure 3.4 Parameter estimates made by GLMM shown in relation to those made by logistic regression (GLM) analysis in models for lambs (+), adult females (O) and adult males (●). The dashed line represents a slope of one.

More seriously, a discrepancy also arose in the standard errors of the year-dependent covariates, population size, NAO and catch date, due to the random year effect being ignored in the logistic regression model. However, once the standard errors of these terms in the logistic model were adjusted, agreement was better for population size and NAO, although worse for catch date which varied within years as well as between years. Without adjustment, the under-estimation of standard errors of the year-dependent covariates by logistic regression has important consequences for the significance of terms and could lead to incorrect inferences being drawn from the data. This was illustrated very clearly by the differences in significance as assessed by the two modelling approaches (Table 3.3).

In lambs, logistic regression analysis identified population size and NAO as having the greatest effect on over-winter survival yet neither appeared amongst the most important terms when modelled by GLMM. The individually varying parameters, body weight, faecal egg count and sex were in fact the most significant terms. Furthermore, logistic regression indicated that catch date and a population-sex interaction were significant whereas the former was only significant at the 10% level and the interaction was not significant at all, when modelled by GLMM. Similarly in adults, catch date, which was significant in the logistic regression models, was not significant in the GLMM when year was fitted as a random effect (Table 3.3). The significance of NAO and population size were also lower in the GLMMs. In the adult female model, population size which was significant in the logistic regression model was not significant at all once the random year effect was taken out (Table 3.3b). This agreed with the very weak relationship observed between adult female survival and population size in Figure 3.2c. The apparent density-dependence of adult female survival revealed by logistic regression was therefore an artefact of the analysis technique failing to take account of random year to year variation.

The differences in the relative importance of terms between the two modelling approaches could be explained by the inclusion of some random between-year variation within the year-dependent covariates. This was demonstrated by examining the contribution of these covariates towards the total between-year variation using *F*-ratios (Table 3.3). The significance of these ratios was more inkeeping with the significance of year-dependent covariates in the GLMMs. In lambs, both population size and NAO contributed significantly towards the total between-year variation. By contrast, catch date was only significant at the 10% level when compared with the residual between-year variation (Table 3.3a). In adult females, although NAO made a significant contribution towards the total between-year variation, stochastic between-year effects were more important in explaining variation than the weak effect of population size or catch date (Table 3.3b). In adult males, the effect of population size and catch date were only significant at the 10% level when compared with the residual between-year variation (Table 3.3c). This emphasised the considerable amount of year to year variation in over-winter survival, of which density-dependence, NAO and catch date were only three components.

Discussion

Our analyses have shown that both density-dependent and density-independent factors influenced survival of different components of the population. Lambs were strongly affected by both factors, with density-dependence being the stronger. In adults, survival of males was also density-dependent but to a lesser extent, whereas female survival was only weakly affected by density-independent factors and not by density-dependence at all. Juvenile survival is generally lower and more variable than adult survival and tends to be more sensitive to resource availability and changes in weather (Sinclair 1977; Fowler 1987; Owen-Smith 1990; Gaillard *et al.* 1998). My results corroborate these earlier findings.

Previous analyses of survival on St. Kilda have found that both adult male and female survival were density-dependent (e.g. Clutton-Brock *et al.* 1991; Clutton-Brock *et al.* 1997b). The lack of density-dependence of adult female survival found in this study, once stochastic between-year variation was accounted for, could be explained in terms of the difference in statistical techniques used. However, this result has probably also been exaggerated by the longer run of data now available, in particular including the winter of 1996/97 when, despite the largest population density ever, adult female survival was high. This therefore provided new evidence that on St. Kilda adult female survival was, after all, in keeping with the general principle of adult survival being buffered against density effects. Of nine long-term ungulate population studies reviewed by Sæther (1997) and a further four reviewed by Gaillard *et al.* (1998), the Soay sheep and red deer on Rum were the only populations to show a density-dependent decline in adult survival. Both are island populations, living close to their carrying capacities and are frequently resource-limited.

The influence of the North Atlantic oscillation on the survival of Soay sheep was that warm, wet and windy winters were negatively associated with survival in lambs and adult females. The lack of influence of NAO on adult male survival was surprising. If, however, the analysis of adult male survival was restricted to the period 1986-1996, the effect of NAO became highly significant (χ^2=21.3, df=1, P<0.001). Furthermore, as in the case of adult female survival, NAO was then more important than population size (χ^2=19.6, df=1, P<0.001). This switch appeared to be due to the exclusion of the high, density-dependent, winter mortality of 1985/86, despite a NAO index suitable for moderately good survival.

Although it might initially be surprising that lower survival was not associated with cold winters, the negative effect of mild, wet and windy weather could be accounted for by a decrease in time spent foraging whilst animals sheltered from gales and hailstorms (Stevenson 1994). In red deer populations in Norway, winters with high positive NAO indices were also associated with decreases in apparent numbers (Forchhammer *et al.* 1998b). However, as well as the direct negative effect on survival observed, Forchhammer *et al.* suggested that NAO also had a delayed positive effect on the population size 2 years later, operating through female fecundity which was enhanced by improved plant growth and female body condition. The influence of NAO on plant productivity on St. Kilda has yet to be examined but it seems likely that the growing season may start earlier in high NAO winters and whilst improved forage may come too late for individuals already at the end of their energy reserves, may benefit survivors. A fuller analysis of the interactions between climate, plant productivity and population dynamics is now being carried out.

One might have expected to find an interaction between population size and NAO, since environmental fluctuations tend to have greater effects at high population density (Bowyer *et al.* in press). Yet no significant interaction was found. This was also the case for over-winter survival in lambs of bighorn sheep, which was affected both by density and weather the previous spring, but the effects of weather were not mediated by changes in population density (Portier *et al.* 1998). By contrast, in the same study, the effects of winter and spring temperature on neonatal survival were found to interact with density, being more important in high density years. The analysis conducted by Portier *et al.* used logistic regression and took no account of stochastic year to year variation in survival. This raises the question of whether density and weather effects would remain significant if modelled by GLMM.

The individually varying parameters, body weight and faecal egg count were found to be the most important factors affecting survival. This was perhaps not surprising, since there was a lot of individual variability in attributes between years. Body weight was the primary factor influencing survival in all three age-sex classes studied. Although its influence on survival has long been acknowledged (Peters 1983; Calder 1984), especially in juveniles (Clutton-Brock *et al.* 1987b; Clutton-Brock *et al.* 1992; Sedinger *et al.* 1995), relatively little attention has been paid to the changing effects of body weight on survival of mature animals (Festa-Bianchet *et al.* 1997). In bighorn sheep the probability of survival was found to increase with body weight in lambs but amongst adults, significant effects were only found in old females (Festa-Bianchet *et al.* 1997). However, it should be noted that mortality of bighorns was largely due to predation, accident or disease and unlike the Soay sheep population, no evidence was found of starvation. Consequently, one would expect body weight to play a different role in survival. By contrast, under the conditions of extreme mortality due to resource shortages in some years on St. Kilda (Grubb 1974b; Clutton-Brock *et al.* 1991), heavier individuals with larger energy reserves were at an advantage. This effect is expected to be most pronounced at high densities when competition for resource is at its greatest (Lindstedt & Boyce 1985). As anticipated, a significant interaction between population size and body weight was found in lamb survival, although not in the adult population.

Our analyses have shown good agreement between parameter estimates made using logistic regression and generalised linear mixed models of over-winter survival, although standard errors of year-dependent covariates were substantially underestimated by logistic regression analysis. This concurs with findings from other areas of statistics (Glasbey 1988) that standard errors are more sensitive than regression coefficients to any change in assumptions about correlation between observations. Logistic regression, which treated the observations as independent, had considerably smaller standard errors for the covariates population size and NAO than GLMM, which treated the sample size for these covariates as the number of years and inflated their standard errors according to the unexplained between-year variation.

Fitting year, as a fixed effect, in the logistic regression analysis after the year-dependent covariates had been fitted, allowed estimation of the mean deviance. This was applied as a scaling parameter to adjust the standard errors for the year-dependent covariates. The adjustment worked reasonably well for population size and NAO. However, when the standard errors for catch date were treated in the same manner they became double those of the GLMM value. This indicated that much of the information about catch date came from within-year rather than between-year comparisons and highlighted the inability of logistic regression to deal with such terms in a satisfactory manner.

Logistic regression analysis tended to find year-dependent covariates more highly significant than GLMM leading to incorrect inferences about the relative importance of year-dependent covariates and individual variables. Some of this enhanced significance was believed to be due to the pseudo-replication effect of failing to treat year as a random effect. Logically it seems reasonable that mortality will vary substantially from year-to-year due to unrecorded factors, that the influences will be similar on all animals in the population and that, consequently, the year-dependent covariates should be measured against unexplained year-to-year variation.

Little evidence was found in any of the modelling to suggest additional unexplained differences in survival between individuals, once the fixed and random year effects had been accounted for. In part, this may be a question of power, in that there was little information in the binary survival data and therefore a lack of heterogeneity between individuals. This was exacerbated by a relatively small proportion of individuals having more than one data record (169 out of 303 adult females and 65 out of 262 adult males). Consequently unexplained differences between individuals were probably quite small and the use of individual as a random effect within GLMM was unnecessary. If a significant individual effect had been found, it would not have been possible to take account of this using logistic regression.

Therefore, of the two methods used, GLMM was preferred to logistic regression analysis in that it correctly incorporated unexplained variation between years. However, logistic regression was much faster to perform so was used for model selection. The drawback of logistic regression is that it can be non-conservative, but final fitting of models using GLMM overcame this problem. It also made good use of the robustness of the iteratively reweighted least squares algorithm for fitting logistic regression, in contrast to the Schall algorithm (Schall 1991) for fitting GLMMs whose implementation in Genstat was found to suffer from convergence problems.

An alternative approach to analysing the Soay sheep data would be integrated capture-mark-recovery analysis (Catchpole *et al.* 1998; E.A.Catchpole *et al.* in prep.). This uses the sighting history for each individual to estimate probabilities of finding animals dead or alive, along with the effect of covariates on survival. Unfortunately this methodology has yet to be developed sufficiently far to handle individual-specific covariates which are time-dependent, such as body weight. Since body weight has been demonstrated to have such a strong influence on survival in all components of the population, it was felt that the GLMM approach was more appropriate. Furthermore, the effect of recapture probabilities being other than one is to modify the intercept, but not the slope, of the logistic regression model. Year-varying recapture probabilities will therefore be contributing, along with other unrecorded effects, to the random effect for year which has been estimated in the GLMM.

This study has demonstrated that the considerable between-year variation in over-winter survival of Soay sheep arose from the effects of density-dependence, density-independent climatic fluctuations, and other unaccounted for stochastic variation. The analysis emphasised the importance of including random annual effects in survival models and of taking into consideration the variation in demographic parameters expected between age and sex classes. These results also add to the growing evidence of the influence of large-scale climatic fluctuations on the structure and demographic trends of ungulates at northern latitudes.

The importance of individually-varying parameters in determining survival has also been identified. These variables were shown to have the most significant effect on survival, resulting in the differential survival of phenotypes. This differential fitness provides the raw materials for natural selection which will be addressed in the next chapter.

CHAPTER 4.

Repeated selection of morphometric traits in the Soay sheep [*]

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[*] J.M.Milner, S.D.Albon, A.W.Illius, J.M.Pemberton & T.H.Clutton-Brock (in press) Repeated selection of morphometric traits in the Soay sheep on St. Kilda. *Journal of Animal Ecology.*

Repeated selection of morphometric traits in the Soay sheep.

Summary

Long-term studies allow the outcomes of repeated selection events to be monitored. Here I investigate phenotypic selection in successive winter mortality events in the Soay sheep of St. Kilda, Scotland, between 1985 and 1996. Selection of three quantitative morphometric traits, body weight, hindleg length and incisor arcade breadth, was investigated in different sectors of the population.

Evidence from fitness differentials of positive directional selection for large size was repeatedly found in lambs and adult females. Selection in the opposing direction was only found in one year in lambs. Selection gradients showed that in most years when significant selection occurred, body weight was the focus of direct selection whereas selection of hindleg length and incisor breadth was indirect, arising from their correlation with body weight.

Selection was strongest in years of low over-winter survival and almost absent in years when survival was high. Intensity of selection was greatest in lambs, emphasising the differences in selection pressure experienced by different sectors of the population, in addition to the temporal variation in selection pressure due to population density and environmental conditions. Despite repeated positive selection of body weight, no evidence of a change in the population mean was found over the course of the study.

Introduction

An area of concern to ecologists, evolutionary biologists and conservation biologists alike is how predictable, or repeatable, selection events are. Given the wide variety of factors affecting over-winter survival, for example, further questions arise as to whether the same sectors of a population and the same phenotypes are always affected, and how selection varies with the severity of mortality.

Long term studies involving marked individuals provide unique opportunities for monitoring sequential selection events and investigating the course of evolutionary processes. Some of the best examples of natural selection of quantitative traits come from studies of birds (Price & Boag 1987) and in particular from the studies of directional and oscillating selection of beak morphology in Darwin's finches (Geospizinae) of the Galápagos islands (Grant *et al.* 1976; Boag & Grant 1981; Grant 1986; Gibbs & Grant 1987). In an area of contrasting environmental extremes, characterised by a highly variable food supply and strong intraspecific competition, body size and functional and ecological aspects of beak variation important for foraging, have experienced both positive and negative selection over the course of an El Niño event and two droughts (Boag & Grant 1981; Price *et al.* 1984; Grant & Grant 1989). By demonstrating that these traits were highly heritable (Boag 1983; Grant 1983) an understanding of the evolution and adaptive radiation of these characters has been gained.

However, phenotypic selection (an association between fitness and phenotype (Endler 1986)) of a heritable morphometric trait may be observed without any evolutionary consequences if a large component of the phenotypic variance is environmental rather than genetic (Falconer & Mackay 1996). This was the case for tarsus length in the collared flycatcher, *Ficedula albicollis* (Alatalo *et al.* 1990). Similarly, van Noordwijk *et al.* (1988) found selection against small body size in great tit (*Parus major*) nestlings acted strongly on the environmental variance that resulted from poor feeding conditions.

In this chapter, I investigate phenotypic selection in successive winter mortality events in the Soay sheep (*Ovis aries*) on St. Kilda over the period 1985-1996. These events vary considerably in severity between years due to a number of intrinsic and extrinsic factors, including population density, climatic and environmental conditions as discussed in Chapter 3. Previous studies on St. Kilda have shown selection of morphometric characters (Illius *et al.* 1995), proteins and microsatellites (Gulland *et al.* 1993; Bancroft *et al.* 1995a) in Soay sheep. Other studies have demonstrated density-dependent selection of the polymorphic traits, coat colour and horn type (Moorcroft *et al.* 1996; Clutton-Brock *et al.* 1997b). During a specific mortality event, the population crash in the winter of 1991/92, Illius *et al.* (1995) showed that differential survival favoured animals with relatively broad incisor arcades and that this character had a greater fitness advantage than body weight.

The latter analysis is expanded here, to assess whether there has been consistent directional selection across successive mortality events, and an evolutionary response to selection (Falconer & Mackay 1996). Phenotypic selection of three quantitative morphological characters, body weight, hindleg length and incisor arcade breadth, was examined. The first two represent aspects of body size whilst the latter is a trait of functional importance in foraging (Illius *&* Gordon 1987), as well as a linear measure of size. The fitness differentials of these phenotypes were explored in terms of survival. However, correlations between characters complicate the measurement of phenotypic selection (Lande & Arnold 1983) since direct selection acting on one trait also produces an indirect effect on correlated traits. I have therefore used multivariate techniques to tease apart direct and indirect selection and determine which characters are important in predicting the survival of different sectors of the population.

Materials and Methods

Study Population

As in Chapter 3, information on the survival of individual Soay sheep was taken from censuses and mortality searches. An individual was considered to have survived a winter if it was alive on 15th May the following year. In all cases 'years' ran from spring to spring so, for example, the winter of 1985 covered the period from autumn 1985 until spring 1986. Estimates of the study area population size and age/sex structure were made from census results, the population being the number of sheep entering the winter that regularly used the study area (Figure 2.4b).

Morphometric traits

The three traits, body weight, hindleg length and incisor arcade breadth were used in this analysis. In an attempt to control for the effects of catch date, body weights (and hindleg lengths in lambs) were standardised to that expected if the animals were caught on a single day (15th August).

All three morphometric variables were highly inter-correlated (Table 4.1), particularly hindleg length and body weight in lambs. In all cases, hindleg length was more closely correlated with body weight than incisor breadth. A lower correlation occurred between incisor breadth and both body weight and hindleg length in adult females. This arose because a number of females had lost teeth in old age. These individuals were not excluded from the analysis because they could help to discriminate between the effects of body weight and incisor breadth on survival.

The associations between body weight and both hindleg length and incisor breadth are shown in Figure 4.1 for lambs and adults, together with the fitted allometric relationships. There were no significant differences between the sexes either in the slopes or in the elevations of the fitted lines, except in the relationship between incisor breadth and body weight in lambs (Figure 4.1b). However, males tended to be larger than females. Considerable variation occurred in both hindleg length and incisor breadth, independent of variation in body weight, (except in the case of hindleg length in lambs) providing opportunity for selection of either trait to occur. In adult females, a number of individuals had incisor breadths considerably smaller than would have been expected for their body weight for the reasons described above.

Age and sex

Selection in lambs (individuals less than one year old) was analysed separately from yearlings (individuals aged 12 - 23 months) and adults (over two years old) because of the particular susceptibility to mortality of animals during their first winter (Clutton-Brock *et al.* 1992). Differences in survival between yearlings and adults were less marked and individuals could be grouped together in a single category without affecting the results. Data from males and females were analysed separately because of the differential survival of the sexes, lower survival in males being associated with faster growth and rutting activity (Stevenson & Bancroft 1995).

Table 4.1 Correlations between $\log_e$-transformed morphometric characters in three sectors of the population.

		df	Body weight	Hindleg length
(a) *Lambs*		435		
	Hindleg length		0.865 ***	1.00
	Incisor breadth		0.558 ***	0.531 ***
(b) *Adult females*		617		
	Hindleg length		0.578 ***	1.00
	Incisor breadth		0.268 ***	0.287 ***
(c) *Adult males*		192		
	Hindleg length		0.685 ***	1.00
	Incisor breadth		0.561 ***	0.571 ***

Analysis

Selection differentials

Standardised selection differentials, S' (Falconer & Mackay 1996) were used to investigate the degree of selection of quantitative morphometric traits during winter mortality. They were calculated as the change in the population mean of the trait before ($\overline{X}_b$) and after ($\overline{X}_a$) selection, using the following expression :

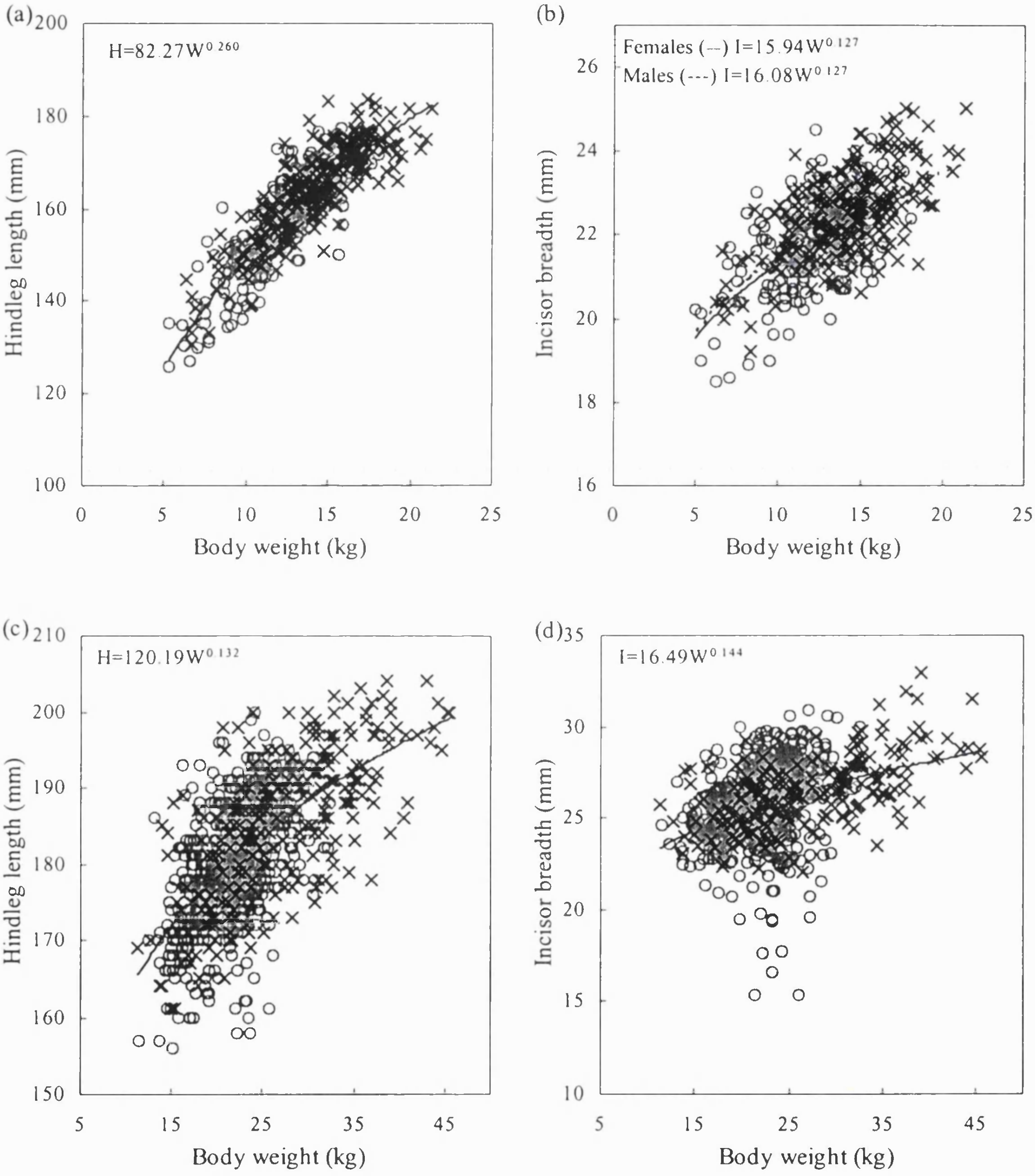
$$S' = \frac{\overline{X}_a - \overline{X}_b}{\sqrt{v_b}}$$

where v_b is the variance about the mean, before selection. Morphometric traits were transformed by natural logarithms before all analyses. The significance of S' was determined by t-tests, comparing the character means of survivors with non survivors (Endler 1986; Smith 1990). Shifts in character means were also compared between high and low density years when the population was respectively above or below a threshold of 400 animals (approximately the median population size).

Selection gradients

In an attempt to determine which of the correlated traits studied was the target of selection, multivariate selection analysis (Lande & Arnold 1983) was used on data from 1990 -1996, the years when all three characters were measured. Standardised directional

Figure 4.1 Relationships between morphometric characters in female (o) and male (x) Soay sheep, measured in August and corrected for catch date. (a), (b) lambs (r^2=0.76 and 0.36 respectively) and (c), (d) adults (r^2=0.39 and 0.12 respectively), showing fitted values according to the allometric equations given (where W is body weight, H is hindleg length and I is incisor arcade breadth).



selection gradients (β') were found from the multiple regression of relative survival on each trait, standardised to unit variance, where the relative survival of an individual was calculated as its absolute survival (0 or 1) divided by the mean absolute survival of individuals of that age/sex class (taken as the proportion of survivors (Table 4.2)). The partial regression coefficients were a measure of the intensity of selection acting on each character, without phenotypic responses due to selection on other correlated characters (Price *et al.* 1984). As such, they could be used to determine the relative importance of the traits measured (Endler 1986) and to compare between selection events. In lambs, body weight and hindleg length were too closely correlated (r=0.87, all other r<0.60) for both traits to be included in the analysis so hindleg length was dropped (Lande & Arnold 1983; Grant & Grant 1989).

Results

SELECTION DIFFERENTIALS

Body weight

Differences in mean body weight between lambs surviving winter and those dying were significant in two thirds of the years in which sample sizes were large enough for a comparison to be made (Table 4.2a). In both sexes, individuals surviving were larger than those dying in all years except 1990 and 1992, when this trend was reversed but differences were not significant. This showed that positive directional selection for increased body weight was repeatedly occurring.

In adult females, significant selection on body weight occurred in the same years as in lambs (Table 4.2b). In no year were individuals surviving significantly lighter than individuals dying, although in 1994 there was a trend in that direction. Adult females therefore also showed repeated positive selection of body weight. By contrast, in adult males there were no significant differences in body weight between survivors and non-survivors in any year, although trends were in the same direction as in other sectors of the population (Table 4.2c). Unfortunately, in many years sample sizes of adult males were too small for statistical comparison.

Table 4.2 Comparison of body weight (kg) of (a) female lambs, (b) male lambs, and over-leaf, (c) adult female and (d) adult male sheep that died with those that survived over-winter mortality. Years denote the year in which winter started, i.e. 1985 represents the winter 1985/86. All measurements were made the preceding August and corrected for catch date. The proportion of the study area population that was caught and therefore weighed, varied between years. († denotes years in which some of the individuals caught were dosed with anthelminthic treatments. These individuals have been excluded from all analyses because of the influence of treatment on survival (Gulland 1992).) *t*-tests were carried out for years in which sample sizes of those surviving and dying both exceeded five.

			1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**
Proportion population caught			0.58	0.18	0.55	0.51†	0.18†	0.40†	0.70†	0.67	0.59	0.51	0.58†	0.64
(a) Female Lambs	**Survive**	**Prop.**	0	1.00	0.80	0.21	1.00	0.94	0.23	0.87	0.47	0.18	0.84	0.42
		n	0	4	32	6	2	15	11	27	27	7	27	22
		mean	-	9.52	14.67	15.92	10.83	13.68	13.61	12.62	14.11	13.92	12.41	13.44
		var.	-	12.96	4.358	0.494	0.28	5.256	3.93	5.21	2.704	1.104	3.898	4.166
	Die	**n**	31	0	8	22	0	1	36	4	30	32	5	31
		mean	12.04	-	13.39	12.1	-	11.92	11.25	13.07	11.13	12.64	11.03	11.15
		var.	2.32	-	5.831	3.681	-	-	6.465	6.605	6.343	3.311	1.476	8.091
		t	-	-	1.51	4.74***	-	-	2.82**	-	5.23***	1.78	-	3.46***
(b) Male Lambs	**Survive**	**Prop.**	0	1.00	0.94	0	1.00	0.82	0.19	0.79	0.41	0.10	0.94	0.23
		n	0	3	36	0	3	18	4	26	18	3	15	15
		mean	-	14.3	16.39	-	14.64	16.06	16.07	13.14	16.63	13.17	13.13	16.14
		var.	-	9.078	4.804	-	9.434	5.34	8.114	6.492	4.836	5.378	10.687	3.992
	Die	**n**	34	0	2	21	0	4	17	7	26	28	1	50
		mean	13.94	-	14.13	14.71	-	17.79	13.19	14.67	14.31	13.42	12.83	13.36
		var.	12.293	-	1.033	9.122	-	9.845	8.613	6.049	6.938	7.368	-	9.649
		t	-	-	-	-	-	-	-	1.42	3.07**	-	-	2.98**

Table 4.2 (continued)

			1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
(c) Adult Females	Survive	Prop.	0.46	1.00	0.92	0.49	1.00	0.92	0.76	0.97	0.92	0.84	1.00	0.94
		n	67	25	73	31	20	47	75	105	107	91	91	154
		mean	22.19	23.29	24.16	22.73	21.56	23.49	23.37	22.24	22.54	21.9	22.4	21.81
		var.	12.73	7.35	12.66	11.81	13.04	14.25	11.58	10.5	11.72	9.57	5.64	11.98
	Die	n	78	0	6	32	0	4	24	3	9	17	0	10
		mean	21·96	-	22.55	19·84	-	20.30	20·43	17.49	19.82	22·82	-	17·76
		var.	14.47	-	6.13	10.05	-	14.86	16.11	22.7	17.01	17.95	-	9.07
		t	0.38	-	1.08	3.47***	-	-	3.52***	-	2.25*	-1.06	-	3.61***
(d) Adult Males	Survive	Prop.	0.13	1.00	0.95	0.13	0.83	0.91	0.61	0.92	0.81	0.65	1.00	0.73
		n	11	5	20	4	5	10	19	36	35	24	10	41
		mean	29.45	32.15	28.24	29.48	21.77	24.58	26	28.77	27.83	27.64	34.64	28.17
		var.	49.44	10.21	30.45	49.33	21.33	30.61	24.98	37.06	60.95	51.6	23.2	76.72
	Die	n	73	0	1	26	1	1	12	3	8	13	0	15
		mean	26.37	-	19.99	27.38	20.1	23.9	23.12	29	23.94	28.05	-	24.13
		var.	47.58	-	-	15.91	-	-	63.02	38.09	62.46	38.04	-	74.37
		t	1.38	-	-	-	-	-	1.24	-	1.27	0.17	-	1.53

Hindleg length

Significant positive selection of hindleg length was found in lambs in the same years as selection of body weight (Table 4.3). In adult females, the same pattern of differential survival favouring larger individuals was found for hindleg length as occurred for body weight, with the exception of 1993 when selection of hindleg length was not significant (Table 4.3b). In adult males there was again no evidence of selection for size in any year (Table 4.3c). The differences in leg length between survivors and non-survivors were generally less pronounced than differences in body weight.

Incisor breadth

There was significant positive selection of incisor breadth in 1991 and 1993 in female lambs and 1993 only in male lambs, corresponding with some of the years in which selection of the other traits was observed (Table 4.4a). In adults of both sexes, survivors had significantly larger incisor breadths than non-survivors in 1991 (Tables 4.4b-c), in agreement with Illius *et al.* (1995). This was also true in adult females in 1996. Both these years were years in which significant differences were found in other traits but only in the case of males in 1991 were differences greater in incisor breadth than either body weight or hindleg length, as shown by the values of the *t*-test.

BETWEEN-YEAR VARIATION IN SELECTION

At low population density over-winter survival was high (Figure 4.2-4.4) and there was no evidence of a shift in any of the character means in lambs or adult males although in adult females there was a positive shift in mean body weight (t=2.35, df=372, P=0.019). By contrast, in high population years, a distinct positive shift in character means could be seen between survivors and non-survivors in all three traits in lambs (body weight t=6.68, df=466, P<0.001; hindleg length t=6.24, df=398, P<0.001; incisor breadth t=3.12, df=341, P=0.002) and in body weight (t=3.92, df=693, P<0.001) and hindleg length (t=2.39, df=554, P=0.017) in adult females. The same was also true of body weight in adult males (t=2.05, df=279, P=0.042), detectable because of the larger sample size resulting from pooling several years' data.

The interpretation of this differential survivorship for phenotypic selection was shown by the standardised selection differentials, S', plotted against population size (Figure 4.5). Selection of both body weight and hindleg length increased with population size

Table 4.3 Comparison of hindleg lengths (mm) of (a) female lambs, (b) male lambs, (c) adult female and (d) adult male sheep that died with those that survived over-winter mortality. All measurements were made the preceding August and corrected for catch date. *t*-tests were carried out for years in which sample sizes of both survivors and non-survivors exceeded five.

			1988	1989	1990	1991	1992	1993	1994	1995	1996
(a) Female	**Survive**	**n**	6	2	15	11	27	27	7	27	22
Lambs		**mean**	169.6	156	161	161.7	158	164.5	161.9	157.6	163.4
		var.	33.15	49.45	52.46	32.61	82.42	51.66	56.06	46.67	54.24
	Die	**n**	22	0	1	34	4	30	32	5	31
		mean	155.9	-	154.1	155.3	165.1	152.8	157.1	156.1	153.1
		var.	104.48	-	-	87.82	74.56	116.98	98.99	22.13	202.59
		t	3.13**	-	-	2.14*	-	4.74***	1.18	-	3.21**
(b) Male	**Survive**	**n**	0	3	18	4	27	18	3	15	15
Lambs		**mean**	-	160.9	167.8	170.7	162.5	170.7	160.4	159.6	170
		var.	-	76.75	47.3	98.64	65.58	56.91	9.98	123.51	65.47
	Die	**n**	21	0	4	17	7	25	28	1	50
		mean	164.9	-	170.9	159.7	167.1	163.4	159.9	155	162.9
		var.	104.57	-	62.2	135.78	38.97	102.89	81.7	-	160.5
		t	-	-	-	-	1.37	2.60*	-	-	2.05*
(c) Adult	**Survive**	**n**	32	20	47	75	105	107	91	91	154
Females		**mean**	184.5	180.6	180.7	182.6	181.7	180.7	179.8	180.9	180.2
		var.	43.03	69.82	68.31	44.81	44.41	55.75	53.84	39.37	53.35
	Die	**n**	35	0	4	24	3	9	19	0	10
		mean	179.4	-	182	178.1	175	179.7	180.6	-	175.5
		var.	72.07	-	43.33	66.81	61	46.25	73.69	-	33.83
		t	2.75**	-	-	2.71**	-	0.41	-0.43	-	1.98*
(d) Adult	**Survive**	**n**	4	5	10	19	36	35	24	10	40
Males		**mean**	187.8	187.4	187.7	187.6	188.4	184.4	185.7	194.3	184.1
		var.	78.92	38.80	71.34	68.04	62.98	98.96	92.22	14.23	107.80
	Die	**n**	27	1	1	12	3	8	13	0	15
		mean	187.3	182.0	200.0	183.5	192.7	179.3	182.2	-	179.6
		var.	37.77	-	-	61.18	30.33	111.93	111.64	-	110.11
		t	-	-	-	1.37	-	1.31	1.04	-	1.43

Table 4.4 Comparison of incisor breadth (mm) of (a) female lambs, (b) male lambs, (c) adult female and (d) adult male sheep that died with those that survived over-winter mortality. All measurements were made the preceding August. *t*-tests were carried out for years in which sample sizes of both survivors and non-survivors exceeded five.

			1989	1990	1991	1992	1993	1994	1995	1996
(a) Female Lambs	**Survive**	n	0	15	10	26	27	6	25	22
		mean	-	21.74	22.55	21.73	22.31	22.23	22.11	22.12
		var.	-	0.808	0.412	0.901	0.975	0.619	1.149	0.705
	Die	n	0	0	33	4	28	31	5	31
		mean	-	-	21.84	22.45	21.66	22.05	22.14	21.57
		var.	-	-	0.804	1.13	1.71	0.884	0.333	1.473
		t	-	-	2.32*	-	2.08*	0.45	-	1.95
(b) Male Lambs	**Survive**	n	0	17	4	24	18	2	15	14
		mean	-	22.82	22.77	22.32	23.38	22.15	21.57	22.44
		var.	-	0.954	1.049	1.069	1.101	0.405	0.619	1.13
	Die	n	0	4	17	7	26	27	1	50
		mean	-	22.12	22.56	22.86	22.62	22.31	23.3	22.4
		var.	-	1.509	1.03	2.006	1.28	1.048	-	0.989
		t	-	-	-	1.11	2.26*	-	-	0.16
(c) Adult Females	**Survive**	n	8	44	68	96	103	86	82	154
		mean	26.05	25.14	26.27	26.31	26.08	25.48	26.09	25.75
		var.	5.089	5.932	4.803	4.324	3.924	2.707	3.434	3.877
	Die	n	0	4	22	2	9	16	0	10
		mean	-	25.42	25.1	24.7	25.91	26.03	-	24.44
		var.	-	8.376	2.435	2.42	3.556	3.646	-	4.063
		t	-	-	2.30*	-	0.24	-1.19	-	2.04*
(d) Adult Males	**Survive**	n	0	8	16	34	35	22	10	41
		mean	-	26.64	27.01	26.95	26.04	25.95	27.59	26.50
		var.	-	1.47	0.95	3.66	4.451	4.357	4.66	4.94
	Die	n	0	1	11	3	8	13	0	15
		mean	-	27.40	25.85	27.3	25.79	26.09	-	25.97
		var.	-	-	1.70	0.01	1.318	2.781	-	3.80
		t	-	-	2.63*	-	0.32	0.21	-	0.81

but the relationship was not linear. A threshold model, as has been applied to population growth on St. Kilda (Grenfell *et al.* 1992; Grenfell *et al.* 1998), would explain the relationship better, with no significant selection below a threshold population size of approximately 400, and significant selection above the threshold. However, the large variance in selection above the threshold means the nature of the relationship at high population density is difficult to define.

The correlation between survival and population density, although good in lambs (r=-0.806 in females and r=-0.817 in males), was poor in adults (r=-0.451 in females and r=-0.535 in males) with unexpectedly high survival in several years of high population density. Consequently selection was more closely related to the proportion of the population surviving than to population density itself (Figure 4.6). Selection of all three morphometric traits increased as the proportion of survivors decreased and was significantly stronger in lambs than adults for body weight ($F_{1,39}$=11.0, P=0.002) but not in hindleg length ($F_{1,29}$=1.34, P=0.256) or incisor breadth ($F_{1,25}$=0.03, P=0.854). There were no significant differences in the strength of selection between the sexes in any of the traits in either lambs (S'_w : $F_{1,17}$=0.23, P=0.640; S'_h : $F_{1,13}$=0.30, P=0.593; S'_i : $F_{1,10}$=0.37, P=0.558) or adults (S'_w : $F_{1,20}$=0.01, P=0.905; S'_h : $F_{1,14}$=0.03, P=0.876; S'_i : $F_{1,13}$=0.59, P=0.458).

SELECTION GRADIENTS

Standardised selection gradients, β', used to distinguish direct from indirect selection, showed that selection of the three traits studied was greatest for body weight in lambs, in 6 out of the 7 years for which comparisons were made (Table 4.5a). This suggests that of the traits examined, body weight, rather than hindleg length or incisor breadth, was the target of direct selection. Significant positive selection for body weight in lambs occurred in 1993 and 1996 (and at the 10% level in 1991 and 1995), whilst in 1990 there was significant negative selection for body weight. In adults, no selection could be measured in 1995 because all individuals caught the previous August survived. Otherwise a similar pattern to that observed in lambs was apparent for females, with selection being greatest for body weight in 5 out of 6 years (Table 4.5b). By contrast, in adult males there was no significant selection of body weight in any year (Table 4.5c).

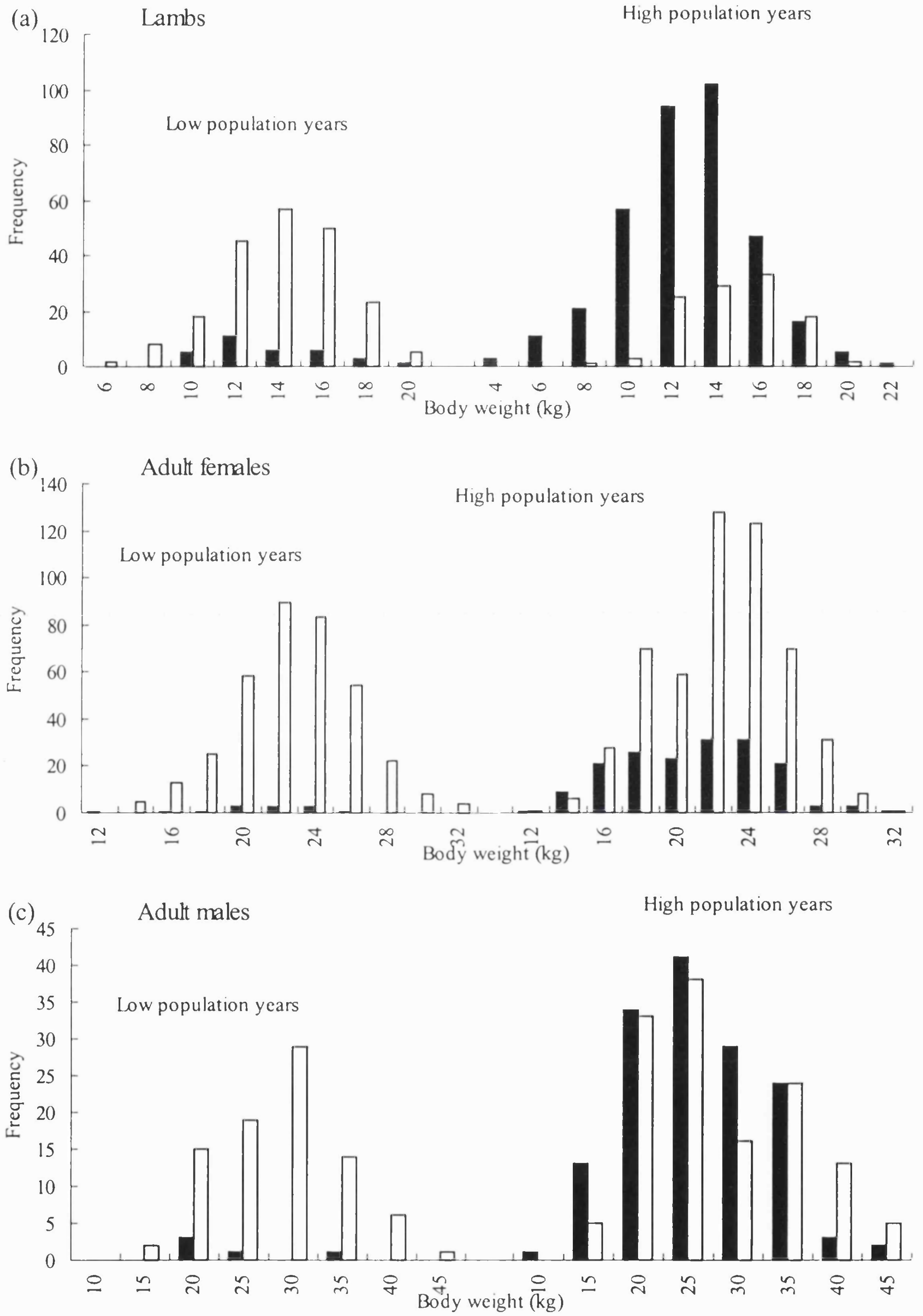
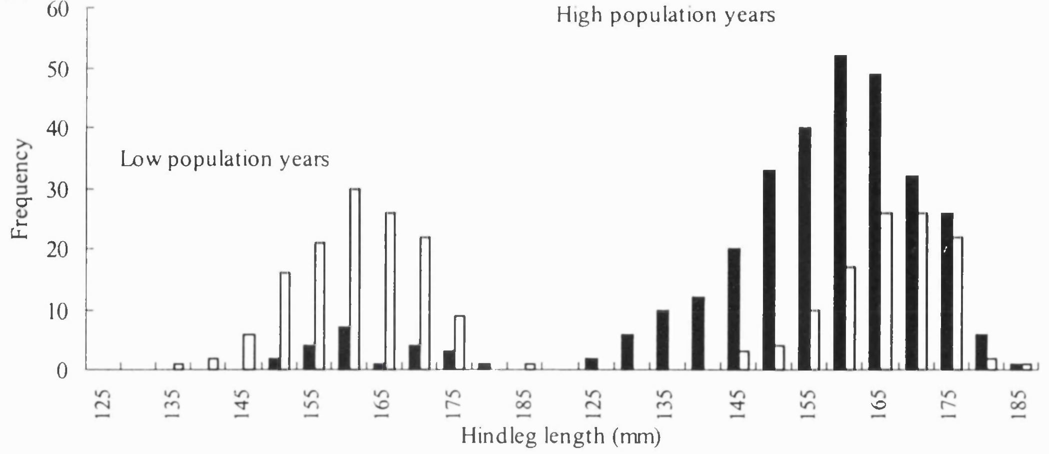
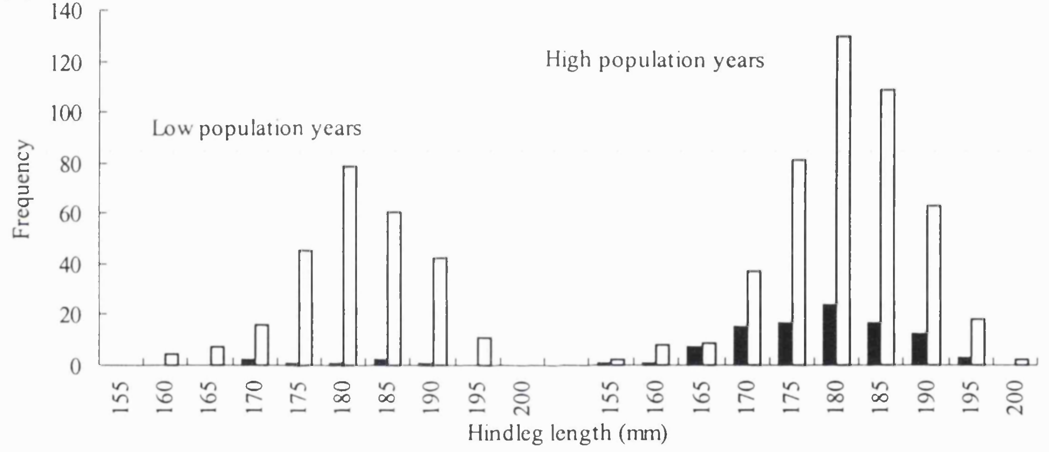


Figure 4.2 Frequency distribution of body weights corrected for catch date of (a) lambs, (b) adult females and (c) adult males during years of low (<400 individuals) and high (>400 individuals) population size. Individuals which died (■) are distinguished from individuals that survived (□) over-winter mortality.

(a) Lambs



(b) Adult females



(c) Adult males

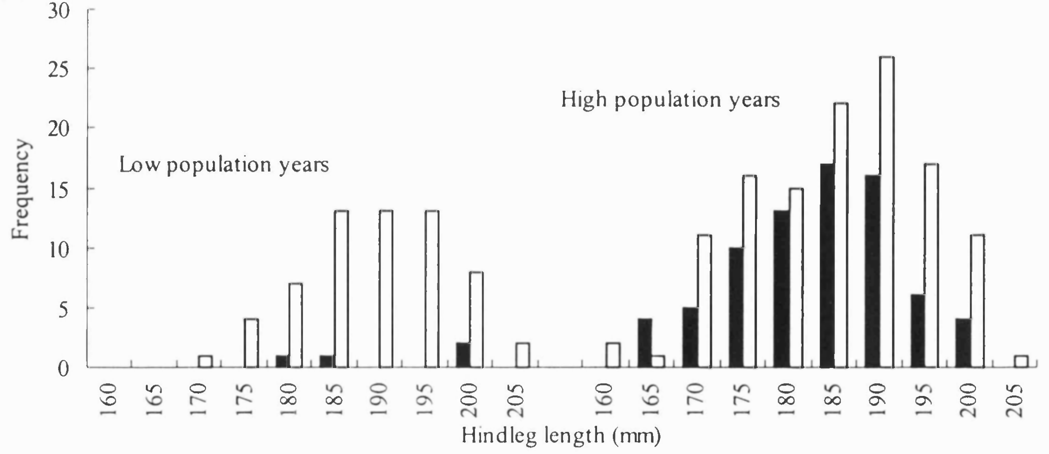


Figure 4.3 Frequency distribution of hindleg lengths of (a) lambs, corrected for catch date, (b) adult females and (c) adult males during years of low (<400 individuals) and high (>400 individuals) population size. Individuals which died (■) are distinguished from individuals that survived (☐) over-winter mortality.

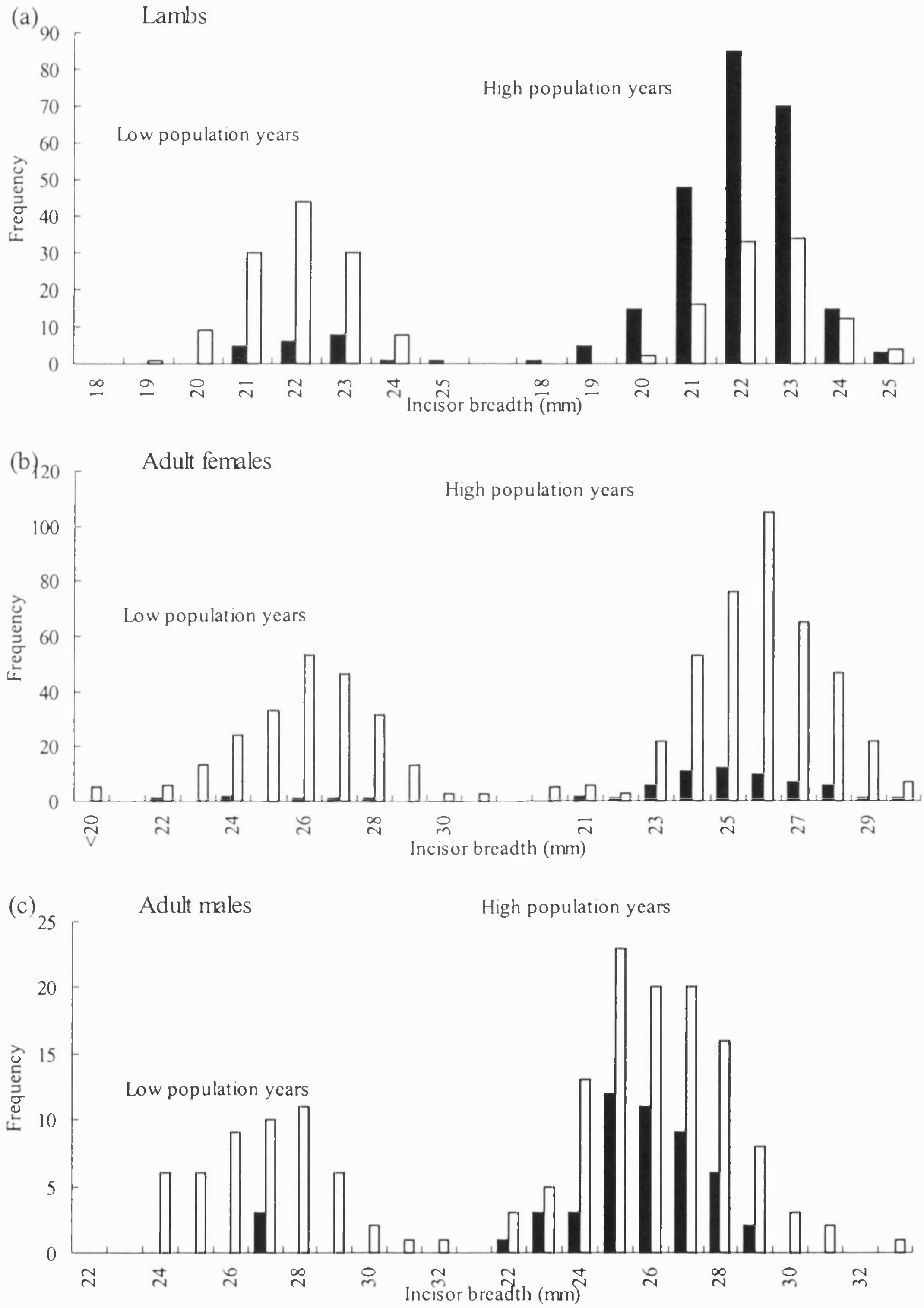


Figure 4.4 Frequency distribution of incisor arcade breadths of (a) lambs, (b) adult females and (c) adult males during years of low (<400 individuals) and high (>400 individuals) population size. Individuals which died (■) are distinguished from individuals that survived (□) over-winter mortality.

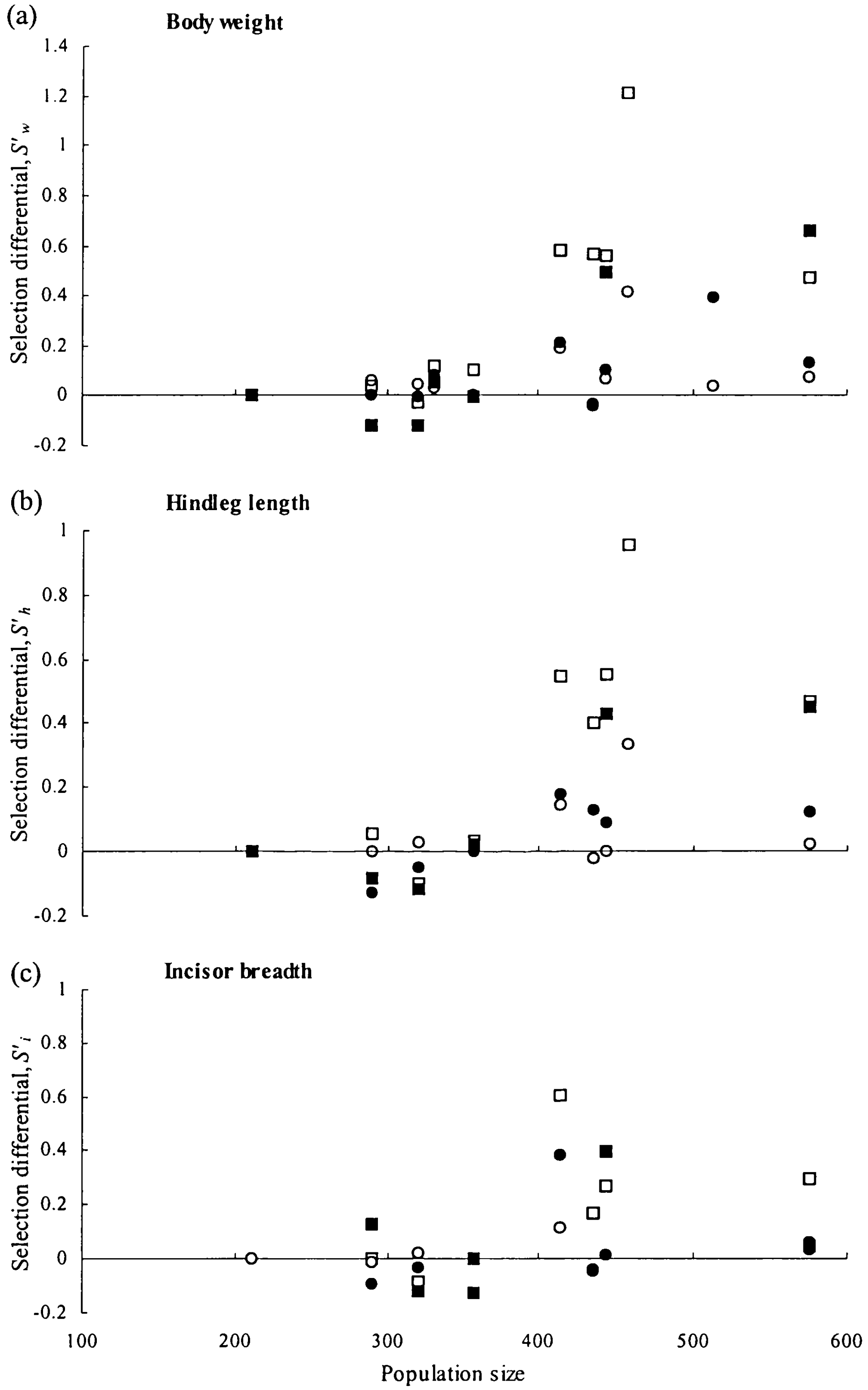


Figure 4.5 Standardised selection differentials (S') for log-transformed morphometric characters in female (□) and male lambs (■), adult females (O) and adult males (●), in relation to population density.

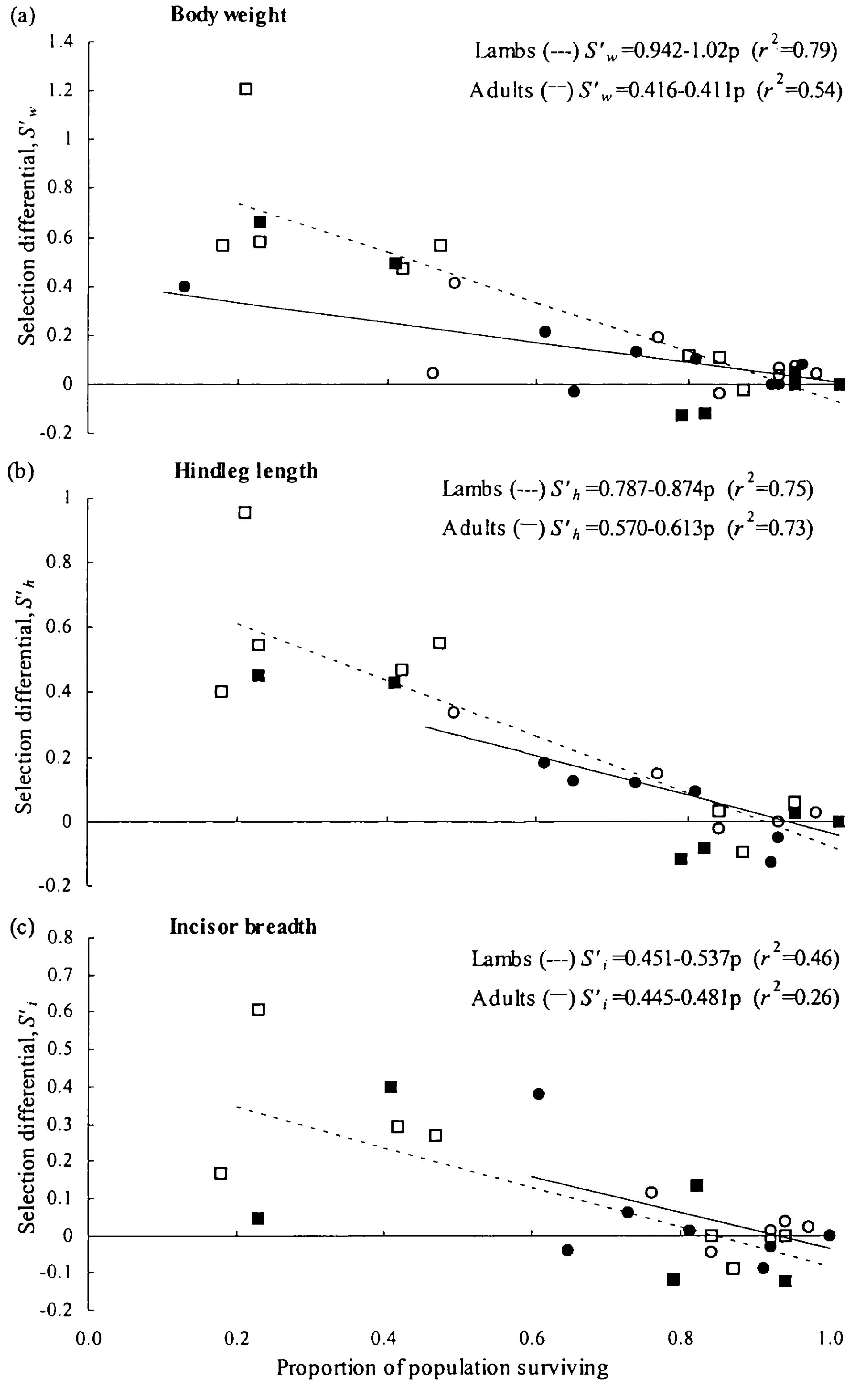


Figure 4.6 Standardised selection differentials (S) for log-transformed morphometric characters in female (□) and male lambs (■), adult females (O) and adult males (●), in relation to the proportion of each sector of the population that survived over-winter mortality (p). Fitted lines are shown for significant relationships. Differences between sexes were not significant, allowing a single common regression line to be fitted for each ageclass.

An interesting feature revealed by the selection gradients was that hindleg length in adult females never experienced significant selection (Table 4.5b), contrary to the results shown in Table 4.3b. This suggests that the apparently significant selection of hindleg length observed in lambs may also have arisen indirectly from the selection of the highly correlated trait, body weight. Furthermore, in 1993 and 1996 in adult females and in 1991 in adult males, the direction of the selection gradient for hindleg length was negative (although not significant), in contrast to the positive results obtained when selection differentials were calculated for hindleg length without taking into account the correlation with body weight.

Similarly, the direction of selection gradients for incisor breadth in all sectors of the population has been negative in most years since 1992, contrary to the direction implied by selection differentials and despite simultaneous positive selection on weight. This highlights the importance of taking correlations between characters into account. Incisor breadth was the principle character under selection in adult males in 1991. This event was the only occasion on which significant selection of any of the traits occurred in the adult male sector of the population.

Selection gradients also showed that, in agreement with the relationship between selection differentials and proportion of survivors established above, years of intense selection, when selection gradients were high, were consistent with years of low survival rates. One exception was the winter of 1994/95 when the intensity of selection in lambs was lower than would have been predicted from the small proportion of the lamb population that survived.

EVOLUTIONARY RESPONSE

Having demonstrated significant positive selection of body weight over a number of years, in both lambs and adult females, with only one significant, and less intense, selection event in the opposing direction in lambs, one might expect to detect a long-term shift in the population mean of this trait. However, modelling change in body weight against time from 1985 to 1996, no evidence was found to support this (Figure 4.7). Once age, sex and population size had been controlled for ($F_{6,2125}$=584.5, P<0.001) no additional variation in weight could be accounted for by time ($F_{1,2125}$=0.86, P=0.354). However, estimates of the heritability of body weight suggested that it was significant

Table 4.5 Standardised directional selection gradients (β' ± standard error) for correlated morphometric characters in (a) lambs, (b) adult females and (c) adult males. Values indicate the relative intensity of selection, comparable between traits and between selection events. In lambs body weight and hindleg length were too closely correlated for both to be included in the analysis. All characters have been $\log_e$ transformed.

(a)		β' ± se		
	n	**Body weight**	**Incisor breadth**	R^2
1990	36	-0.163 ± 0.071 *	0.113 ± 0.072	0.09
1991	64	0.653 ± 0.339 †	0.118 ± 0.282	0.08 *
1992	60	-0.034 ± 0.070	-0.098 ± 0.070	0.03
1993	99	0.598 ± 0.152 ***	-0.144 ± 0.140	0.17 ***
1994	65	0.224 ± 0.372	-0.110 ± 0.371	0
1995	46	0.117 ± 0.063 †	-0.108 ± 0.062 †	0.05
1996	114	0.608 ± 0.176 ***	-0.285 ± 0.175	0.08 **

(b)			β' ± se		
	n	**Body weight**	**Hindleg length**	**Incisor breadth**	R^2
1990	48	0.091 ± 0.047 †	-0.052 ± 0.054	0.000 ± 0.051	0.02
1991	89	0.169± 0.069 *	0.017 ± 0.071	0.078 ± 0.062	0.11 **
1992	96	0.029 ± 0.017 †	0.024 ± 0.019	-0.001 ± 0.016	0.06 *
1993	112	0.114 ± 0.037 **	-0.050 ± 0.035	-0.019 ± 0.030	0.06 *
1994	98	-0.022 ± 0.051	0.019 ± 0.050	-0.036 ± 0.044	0
1995	82	-	-	-	-
1996	164	0.075 ± 0.026 **	-0.015 ± 0.025	0.017 ± 0.020	0.07 **

(c)			β' ± se		
	n	**Body weight**	**Hindleg length**	**Incisor breadth**	R^2
1990	9	-0.036 ± 0.163	-0.189 ± 0.219	0.070 ± 0.242	0
1991	27	0.214 ± 0.163	-0.070 ± 0.183	0.392 ± 0.167 *	0.18†
1992	36	0.021 ± 0.058	-0.051 ± 0.061	0.009 ± 0.063	0
1993	43	0.137 ± 0.133	0.067 ± 0.128	-0.121 ± 0.106	0.01
1994	33	-0.253 ± 0.220	0.244 ± 0.197	-0.007 ± 0.178	0
1995	10	-	-	-	-
1996	55	0.150 ± 0.180	0.022 ± 0.159	-0.052 ± 0.114	0

but low (Chapter 5). Any response to selection would therefore be slow, particularly since, as will be shown in the next chapter, a lot of the variance in body weight was of environmental rather than genetic origin.

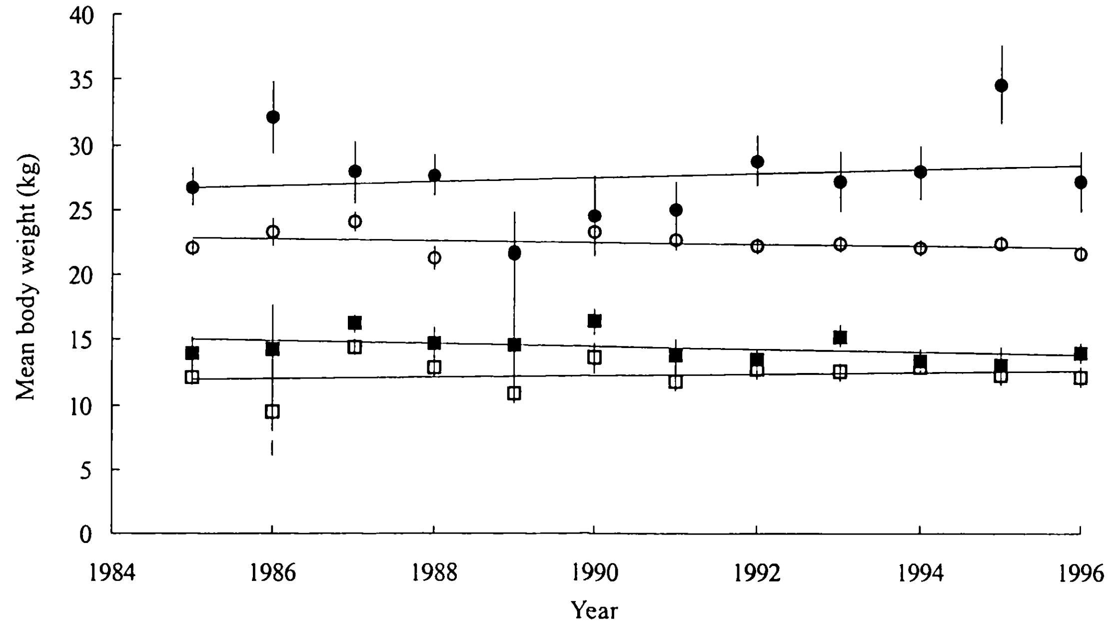


Figure 4.7 Changes in mean body weight (corrected for catch date) in female (□) and male lambs (■), adult females (O) and adult males (●) during the period 1985 to 1996. 95% confidence intervals are marked. Change in body weight (*W*) is described by the expression *W*=*c*-0.004pop where *c* is 14.20 for female lambs, 16.32 for male lambs, 24.01 for adult females and 28.93 for adult males.

Discussion

This analysis shows clear, strong evidence for repeated phenotypic selection of body weight in lambs, and to a lesser extent in adult female Soay sheep on St. Kilda. Standardised selection gradients indicated that although there was also apparent selection of the correlated traits, hindleg length and incisor breadth, these traits were subject to indirect selection whilst body weight (or some unmeasured character with which weight is highly correlated) was the target of direct selection. However, due to the small genetic component of variation in body weight no significant evolutionary response to repeated selection was detected. It may be that over a longer time period a response would be detectable.

The fact that body weight should be important in determining over-winter survival of Soay sheep is neither new (Grubb 1974b; Clutton-Brock *et al.* 1992; Stevenson 1994; Bancroft *et al.* 1995a; Clutton-Brock *et al.* 1997b) nor surprising when one considers fasting endurance theory (Lindsted & Boyce 1985; Millar & Hickling 1990) or energetics models (Searcy 1980; Brown *et al.* 1993). However, that it should be more important than incisor arcade breadth contradicts the findings of Illius *et al.* (1995), who argued for the functional importance of incisor breadth in determining food intake rates at times of low forage availability, and supported it with evidence of superior survival of relatively large-mouthed individuals after body weight had been controlled for. In the current analysis the only evidence that this might be the case was from adult males in 1991/92 when incisor breadth, not body weight, was the target trait of selection.

However, careful examination of the original 1991/92 data set revealed some misclassifications in the survival outcomes of some individuals. Re-analysis with the corrected data set did not support the initial findings but showed that although incisor breadth had a strong effect on its own, it was not significant after controlling for body weight. If incisor breadth was more important than body weight in determining survival, one might expect the group of adult females with missing teeth and therefore small incisor arcades relative to their body weight, to show lower levels of survival than other females of similar body weight but this was not the case.

At times of high sheep population the standing biomass of vegetation is at a minimum (Grubb 1974b). The hypothesis presented by Illius *et al.* (1995) was that individuals with the broadest incisor arcades would be able to maximise their bite size and hence food intake rate (Gordon *et al.* 1996) when grazing on very short swards. However, this theory does not account for the fact that under the heavy grazing pressure associated with high population density, the sward in late winter is very heavily dominated by bryophytes (Gwynne & Boyd 1970; M.J.Crawley, unpublished data) able to exploit a time of competitive release from grass species. Histological analysis of faecal samples from St. Kilda shows a peak in bryophyte intake in March, accounting for as much as 30% of epidermal fragments (Milner & Gwynne 1974). A trade-off may therefore exist between large bite size at the expense of high bryophyte intake of low nutritional value (Prins 1981) and smaller bite size with the ability to select more highly nutritious food items (Gordon & Illius 1988). Indeed in recent years, when population size was high, selection on incisor breadth tended to be negative in all age and sex classes (Table 4.5) after controlling for body weight.

Large body size has long been recognised as important in enhancing survival of terrestrial vertebrates during periods of resource shortage in seasonal environments (Millar & Hickling 1990). The fasting endurance hypothesis (Lindsted & Boyce 1985) provides a mechanism to explain the differential survival observed on St. Kilda where at the end of winter none of the island's plant communities can provide sufficient nutrients to support the sheep (Milner & Gwynne 1974) and animals die of malnutrition (Gulland 1992). Comparing across species, larger individuals have proportionally greater fat reserves relative to body weight (Calder 1984) and are able to metabolise somatic sources at a lower weight specific rate (Lindsted & Boyce 1985) whilst their daily energy requirements are proportionally lower (Kleiber 1961). If the same holds within a species, during periods of shortage the smallest individuals will deplete their reserves first (Millar & Hickling 1990). However, larger size will only be favoured when losses incurred during fasting can be recouped later and the absolutely greater food requirements of a large body size can be met. When food is generally limited, as may be the case on small islands, individuals of smaller body size may be at an advantage because they are better able to survive and reproduce under such conditions (Lomolino 1985). On St. Kilda there was no evidence of a long-term change in body size despite temporal fluctuations in selection pressures caused by short-term perturbations in environmental conditions and population size. This suggests that an optimal body size may have already been reached.

Body weight is composed of two elements, body size and condition. There is no reliable measure or index of condition in live animals because Soay sheep are unusual in depositing little subcutaneous body fat compared with domestic breeds (McClelland *et al.* 1976). However, indirect evidence suggested that it was the condition element of body weight rather than body size that experienced selection. If body size was under-going selection one would expect hindleg length to have shown equally strong selection as body weight. Furthermore, the lower heritability and repeatability of body weight than hindleg length indicated a larger proportion of environmental variance (including a proportionally greater measurement error) within the body weight phenotypes. This can be attributed to variation in condition (Lindstedt & Boyce 1985) since body fat is the most variable constituent of body mass (Pond 1978). Condition is known to be highly dependent on environmental conditions, in particular food availability (Choquenot 1991), and is often used to explain part of the variability of size from variation in environmental conditions (van Noordwijk *et al.* 1988). However, the possibility that some other fitness trait such as disease resistance, which also has implications for body condition, is the underlying variable under selection, cannot be ruled out.

The lack of evolutionary response could result from opposing selection occurring at some other phase of the life history or on some other unmeasured trait that is correlated with body weight. Survival is only one component of fitness but similar analysis conducted on female fecundity data have also shown selection pressures favouring heavier maternal body weights (Clutton-Brock *et al.* 1997b). This would therefore reinforce the trend towards increased body weight rather than counteract it.

Selection was most intense when survival was lowest, both when comparing between sectors of the population and between years. This observation was in agreement with the result of Price *et al.* (1984) for selection of beak dimensions in Darwin's finches. The differences in selection pressure found between sectors of the population highlights the importance of assessing the responses to selection separately for each age or sex class (Fowler 1987; Gaillard 1998). In particular lambs were more strongly affected by selection than adults, explained by the greater influence on survival of phenotypic variation within growing animals (Clutton-Brock 1988). This is in keeping with the general rule that juvenile survival is highly sensitive to limiting factors whether caused by population density or by stochastic environmental factors (Gaillard *et al.* 1998).

Although the strongest selection was detected when population density was high, as found by Moorcroft *et al.* (1996) and Clutton-Brock *et al.* (1997b) on St. Kilda, high population density did not necessarily lead to strong selection if environmental conditions were favourable for survival. This mirrors the relationship between population growth and sheep density in which at high densities the population can increase, decrease or remain constant, depending on environmental conditions (Grenfell *et al.* 1998). It also emphasises the importance of environmental stochasticity in determining population dynamics (Sæther 1997), as shown in Chapter 3.

This chapter therefore highlights the temporal variation in intensity of selection due to the effects of density and stochastic environmental variation on survival, as well as the variation between age and sex classes. I have shown that the same phenotypes and same sectors of the population were consistently affected by phenotypic selection, but the implications of this for the evolution of body size were moderated by the low heritability of body weight. Heritabilities of all the traits will be discussed more fully in the next chapter.

CHAPTER 5.

Variance components and heritabilities of morphometric traits in the Soay sheep.*

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* J.M.Milner, S.Brotherstone, J.M.Pemberton & S.D.Albon (submitted) Variance components and heritabilities of morphometric traits in a wild ungulate population. *Evolution*.

Variance components and heritabilities of morphometric traits in the Soay sheep.*

Summary

Using maximum likelihood procedures and an 'animal model' approach, I have estimated the heritabilities and variance components of three morphometric traits in the Soay sheep (*Ovis aries*) on St. Kilda, Scotland. The traits, body weight, hindleg length and incisor arcade breadth, have previously been shown to experience selection to differing extents.

Using a genealogy containing over 1800 dams and nearly 1000 sires, estimated by genetic paternity techniques, I demonstrate that all traits have low but significant heritabilities.

Body weight was found to have a lower additive genetic coefficient of variation than either of the other traits and it is argued that, as predicted by Fisher's fundamental theorem, this was due to the importance of body weight for fitness, in terms of survival and fecundity. Consequently additive genetic variation had been depleted during successive selection events.

Maternal effects caused heritabilities in females to be over-estimated but there was no significant maternal effect in male offspring.

Introduction

Individual phenotypic variation is widespread among species living in the wild. Such variation allows selection to take place. But a genetic component to this variation is also required for subsequent generations to show an evolutionary response to natural selection (Endler 1986). If, however, a trait has been under unidirectional selection for many generations, there may be little remaining additive genetic variation. This is the basis of Fisher's fundamental theorem, explaining the low heritability of fitness traits (Fisher 1930). The heritability of a trait should therefore be inversely related to its importance for fitness (Gustafsson 1986) and correspondingly, the degree of selection it is under.

In Chapter 4, body weight was shown to experience repeated direct positive selection among lambs of both sexes and adult females, due to differential over-winter survival. By contrast, the correlated quantitative traits, hindleg length and incisor arcade breadth, experienced indirect selection, although in a single selection event there was evidence of direct selection of incisor breadth in adult males. One would therefore predict that, since the population is isolated, preventing variation entering the population by immigration, body weight should have lower additive genetic variation and consequently a lower heritability, than the other two traits. This population has been the subject of a long-term study (Clutton-Brock *et al.* 1991) and has a well recorded genealogy. It is therefore one of few wild mammal populations in which evolutionary predictions can be addressed using a quantitative genetic approach.

To date, the application of quantitative genetic theory to evolutionary studies of species in the wild has been limited, particularly amongst endothermic vertebrates, when compared with its use in animal breeding. Exceptions tend to come from studies of genetic components of variation, heritability and selection of quantitative traits in bird populations, for example in Darwin's finches (Geospizinae) on the Galápagos islands (Grant *et al.* 1976; Boag & Grant 1981; Grant 1986), and tend to use traditional analysis techniques (see review by Boag & van Noordwijk 1987).

Methods of estimating heritabilities traditionally used by ecologists, such as offspring-parent or sib regression (Boag & Grant 1978; van Noordwijk *et al.* 1988; Falconer &

Mackay 1996) using least-squares, make a number of assumptions, many of which are not valid in wild populations (Cheverud & Dittus 1992). For example, it is assumed that there is no assortative mating, that populations are in Hardy-Weinberg equilibrium, that there is no inbreeding or selection, that parents are randomly sampled from the population and that genetic means and variances are constant over generations. Furthermore, such methods require data of a balanced design.

Although it is unlikely that assortative mating occurs in the Soay sheep on St. Kilda (Paterson & Pemberton 1997), the other assumptions of traditional heritability analyses are probably violated. Being a small, island population some degree of inbreeding would be expected (Falconer & Mackay 1996). Furthermore it is known that not all individuals make an equal contribution to the next generation, particularly amongst males. Paternity analysis has shown that male reproductive success is markedly skewed with most males producing zero or one offspring whilst a few individuals produced more than 15 offspring (Coltman *et al.* in prep.). Consequently the data are unbalanced which, together with over-lapping generations and incompletely nested half- and full-sib progenies, made analysis by traditional least-squares methods virtually impossible (Shaw 1987). Maximum likelihood procedures and an 'animal model' approach (Henderson 1972; Kennedy 1989; Meyer 1991), which makes far fewer assumptions have therefore been used. This also allowed us to take account of selection of parents and to make more effective use of the unbalanced data. All data, including those from distant relatives and over several generations could be used, helping to improve the accuracy of the heritability estimates (Cheverud & Dittus 1992). By using a multivariate analysis technique, heritability estimates of several traits could be made simultaneously, taking correlations between traits into consideration (Meyer 1991).

Despite an awareness of the problems associated with trying to fit ecological data to traditional methods, raised as long ago as the late 1960s (Hartley 1967) and reiterated with the advent of maximum-likelihood techniques (Shaw 1987), there are few examples in the literature of the use of such techniques outside the field of plant and animal breeding (Knott *et al.* 1995). Exceptions tend to come from botanical or invertebrate studies under experimental conditions (e.g. Waser *et al.* 1995; Montalvo & Shaw 1994; Knott *et al.* 1995). Maximum-likelihood techniques have only been used to evaluate heritabilities in one study of a wild mammal, a population of Toque macaques

(*Macaca sinica*) in Sri Lanka (Cheverud & Dittus 1992) whilst the use of animal models has been largely restricted to the animal breeding community (but see Knott *et al.* 1995). This seems to be the first time an animal model has been used to analyse genetic variation in a wild population.

In this chapter a full, sex-specific analysis of the heritable variation of three morphological traits, body weight, hindleg length and incisor arcade breadth in the Soay sheep is conducted. I determine whether, as anticipated, the additive genetic variation varies inversely with the strength of selection experienced by each trait. I also investigate whether traits are equally heritable in both males and females, and discuss the implications in terms of natural and sexual selection of body size.

Materials and Methods

Study population

The genealogy of the study area population of Soay sheep has been built up by successive years of tagging lambs at 2-3 days old, during April and early May. The mother's identity is recorded at the time and paternities assigned subsequently using genetic techniques (see below).

Measurements of the morphometric traits investigated here were all made on animals caught in Augusts between 1988 and 1997 (Clutton-Brock *et al.* 1992; Illius *et al.* 1995). Many animals (56% of females and 25% of males) have been caught in more than one year, providing repeated measures from the same individual.

Genetic determination of paternities

Locus-specific protein and microsatellite markers were used to investigate paternity for lambs born between 1987 and 1997, to sampled mothers (Coltman *et al.* in prep.). Individuals were genotyped at 15-17 loci (Pemberton *et al.* 1996) and candidate fathers for each lamb were identified from all tagged rams known to be alive during the preceding rut. Using the parentage-inference software Cervus 1.0 (Marshall *et al.* 1998), a log-likelihood ratio, or LOD score, was calculated for each candidate father of each lamb. Criteria for inferring paternity to the ram with the highest LOD score with 95%

and 80% confidence, were obtained by simulation. A comparison was made between heritabilities estimated using pedigree files based on 'relaxed' and 'strict' paternity assignments in which there was 80% and 95% confidence, respectively.

Of 1870 individuals of known parentage used in the relaxed pedigree file, 1823 had known dams and 945 had sires estimated with 80% confidence. A further 330 'base' animals of unknown parentage were also present, through which more distant relationships could be established. The strict pedigree file was slightly smaller having 1842 individuals with at least one known parent. Of these, the same 1823 individuals with known dams were present and 383 individuals had paternities estimated with 95% confidence. Consequently the strict pedigree file included many more missing values for paternity. In addition 287 base animals of unknown parentage were present.

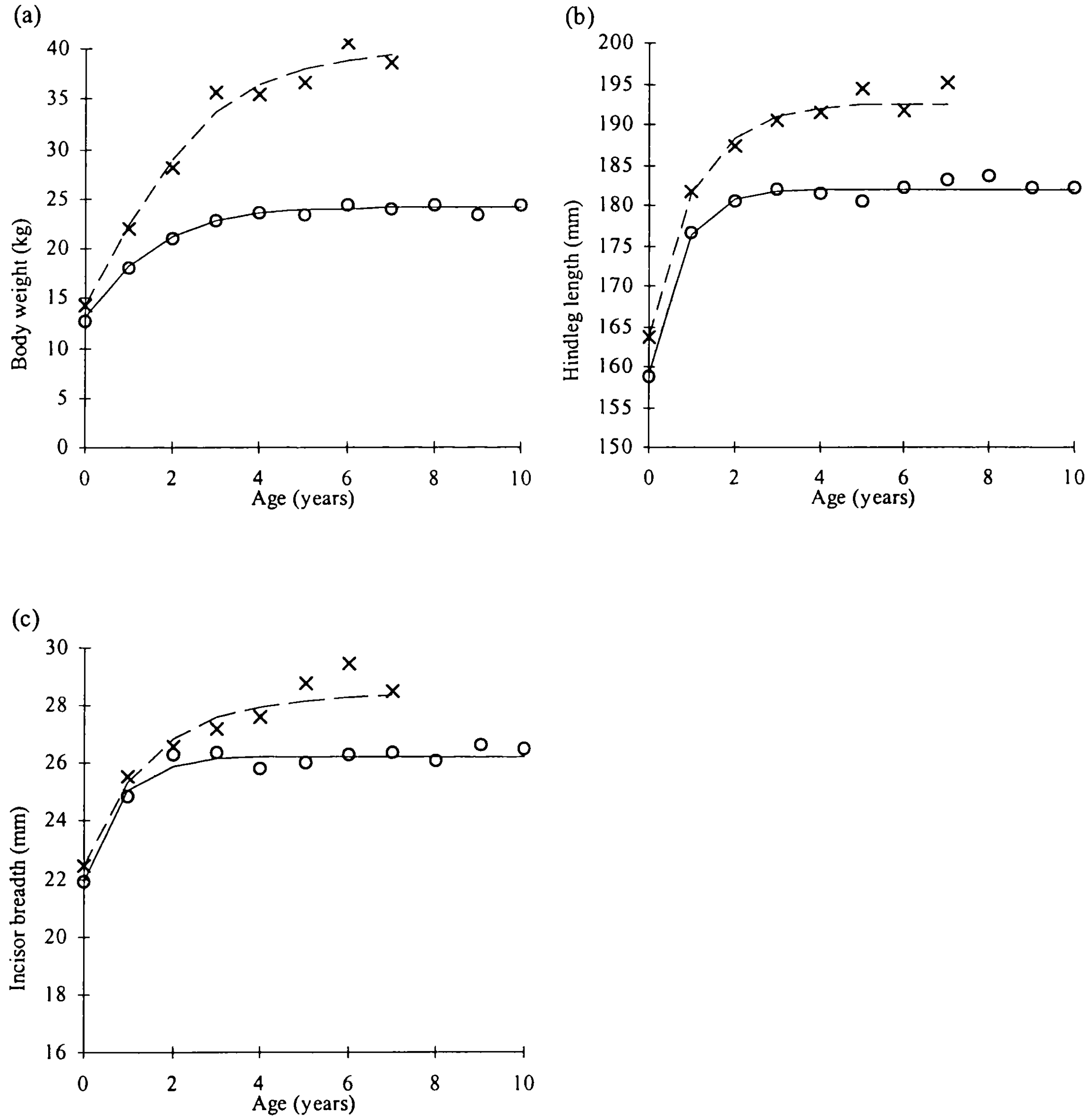
Analysis

Morphometric model fitting

General linear models (GLM), using a least-squares approach (McCullagh & Nelder 1989), were used to determine which terms explained the greatest amount of variation in each of the morphometric traits. The explanatory variables identified by the GLMs were fitted as fixed effects in the heritability analysis, so enabling the effects of these terms to be controlled for. Analyses were carried out independently for each sex. The inclusion of terms in the GLMs was investigated by sequentially dropping, and re-fitting terms if significant, until the models included only those terms whose elimination would significantly decrease the explanatory power.

Age, which explained the greatest proportion of the variance in all three traits, had a non-linear relationship with the traits and therefore could not be fitted in the GLM without transformation. Age-related variation was removed using growth curves (Figure 5.1) from which age-specific fitted values for the traits were derived. Hindleg length and incisor arcade breadth reached an asymptotic mature size relatively early in life. Exponential growth curves were fitted for these traits. By contrast, a Gompertz growth curve was found to be more appropriate for body weight (Fitzhugh 1975) where mature size was reached later and in males appeared to continue to change through out life.

Figure 5.1 Growth curves for the three morphometric traits a) body weight, b) hindleg length and c) incisor arcade breadth in female (_o_) and male (--x--) Soay sheep. Fitted points were the observed age-specific population means. Body weight was described by the Gompertz curve $a + ce^{-e(-b(\mathrm{age} - m))}$ where $a = 2.92$ and 4.65, $c = 21.21$ and 35.33, $b = 0.814$ and 0.622, and $m = -0.37$ and 0.413 for females and males respectively. Exponential curves, $a + br^{\mathrm{age}}$, were fitted for hindleg length and incisor breadth where for hindleg length $a = 181.98$ and 192.58, $b = -23.01$ and -28.90, and $r = 0.241$ and 0.389 for female and male hindleg lengths respectively, and for incisor breadth $a = 26.19$ and 28.37, $b = -4.27$ and -5.93, and $r = 0.268$ and 0.512 for females and males respectively.



The goodness of fit of the growth curves was supported by almost identical fitted values derived when a cubic smoothing spline (Hastie & Tibshirani 1990) for age was fitted. Furthermore, if age classes were fitted for each year of age, so making no inference about the shape of the relationship between age and the traits, heritability estimates were similar to those presented in this paper. By contrast, if age was fitted as a quadratic term, very different heritability estimates were derived due to the disproportionate effects of the relatively few points from older animals which had high leverage. This highlighted the importance of finding a satisfactory age-specific growth curve before carrying out the variance component estimation.

Other covariates considered for inclusion in the GLMs were an index of parasite burden (see Chapter 2) and catch date, which to some extent controlled for daily weight gain in August (Chapter 2). Birth year or 'cohort' and year of measurement, which allowed for year to year changes in environmental conditions, measurers and population density, were fitted as categorical variables. Birth type (twin or singleton) and coat colour (light or dark) were fitted as two level factors. Horn type was also a two level factor, in females polled individuals were distinguished from those with normal and scurred or deformed horns, and in males in which polled animals do not occur, normal horned individuals were distinguished from scurred. When modelling incisor arcade breadth, the number of missing teeth was also included as a covariate.

Genetic correlations & heritability estimates

A multivariate restricted maximum likelihood (REML) procedure which allowed for unequal design matrices and missing observations, was used to estimate genetic correlations and variance components of the three traits simultaneously (PEST and VCE software by Groeneveld, Kovac & Wang, University of Illinois, 1993). An 'animal model' was used, such that the phenotype of the individual was written in terms of its additive genetic value, and other fixed and random effects as follows :

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Pc} + \mathbf{e}$$

where $\mathbf{y}$ was a vector of the records on individuals, $\mathbf{b}$ was a vector of the fixed effects, $\mathbf{a}$ was a vector of the additive genetic effect, $\mathbf{c}$ was a vector of the permanent environmental random effect and $\mathbf{e}$ was a vector of residual effects. X, Z, and P were design matrices relating records to the appropriate fixed or random effects (Southwood & Kennedy 1990). The significant explanatory variables determined by GLM were fitted as fixed effects. The additive genetic random effect allowed for a related breeding population by using an additive genetic relationship matrix created from the pedigree file. This incorporated information from all known relatives, of both sexes, correctly weighted for relatedness. The permanent environmental effect grouped repeated measurements from the same individual to determine the environmental variance between individuals that arose from long-term or non-localised conditions.

Consequently the total phenotypic variance (V_T) was partitioned into three components, the additive genetic variance (V_A), the environmental variance (V_E) and the residual variance (V_R) which included non-additive genetic effects and variance arising from measurement errors:

$$V_T = V_A + V_E + V_R$$

Heritabilities (h^2) were calculated as the ratio of the additive genetic variance to the total phenotypic variance (Falconer & Mackay 1996):

$$h^2 = V_A / V_T$$

whilst the ratio of the environmental variance to the total phenotypic variance was c^2 (Henderson 1972):

$$c^2 = V_E / V_T.$$

Heritability estimates tend to have an upward bias if maternal effects are ignored because resemblance between mother and offspring due to the shared maternal environment and the mother's nutritional condition can be mistaken for resemblance due to genetic effects (Falconer & Mackay 1996). Therefore, to investigate the influence of maternal environmental effects on heritability estimates the analysis was re-run with an additional environmental random effect for dam. This divided the total phenotypic variance into four components, including the variance due to the maternal effect V_M. The data files were restricted to include only those individuals whose dam was known. The significance of the maternal effect was assessed by comparing the model deviances with and without dam fitted as a random effect.

Genetic correlations between traits, arising chiefly from pleiotropy (Falconer & Mackay 1996), were determined by the same analysis package, using the strict paternity pedigree data. Phenotypic correlations (r_P), the total observed correlation of phenotypic values, were calculated from the phenotypic covariances between traits estimated by VCE as follows:

$$r_P = \mathrm{cov}_P / \sigma_{Px}\sigma_{Py}$$

where cov_P was the phenotypic covariance between traits x and y, and σ_{Px} and σ_{Py} were the phenotypic standard deviations of traits x and y.

Approximate standard errors of the variance components were also estimated by REML. However, for most of the multivariate analyses, especially those of males (Table 5.3), the approximation to the second derivative was not good enough to yield useful estimates of the standard errors. This arose with smaller sample sizes and when the strict pedigree file was used because fewer pedigree connections could be made. The reliability of the standard errors also has implications for the significance of heritabilities which were determined by *t*-tests.

Repeatability

Repeatability gives an index of the constancy of multiple measurements from a single individual (van Noordwijk *et al.* 1988) by expressing the proportion of the between-individual variance that was due to permanent differences, both genetic and environmental (Falconer & Mackay 1996). Repeatability (r) was estimated from the sum of the heritability (h^2) and c^2, so represented an upper limit to possible heritability values:

$$r = h^2 + c^2 = (V_A + V_E) / V_T$$

Coefficients of variation

It has been argued that heritabilities do not provide a good means of comparing genetic variation between traits or populations and that standardising genetic variances by the trait means rather than the total phenotypic variance is more appropriate (Houle 1992). Consequently the additive coefficient of variation (CV_A) was calculated for each sex, to compare the potential of each trait to respond to selection.

$$CV_A = 100\sqrt{V_A}/\bar{x}$$

where $\bar{x}$ was the trait mean (Houle 1992).

Results

Morphometric model fitting

In all cases, age was the principle term accounting for the variation in the three morphometric traits (Table 5. 1). In males, absolute growth of all three traits was faster than in females (Figure 5.1) and males had significantly larger body weights (t=4.32, df=1775, P<0.001), incisor arcade breadths (t=2.81, df=1567, P=0.005) and, within yearly age classes, hindleg lengths (t=7.76, df=7, P<0.001). Males also continued to grow for longer than females. The asymptotic hindleg length of males was only reached at about 6 years of age and those of body weight and incisor breadth were never reached. By contrast, females tended to reach their asymptotic incisor breadth as 2 year-olds and reached adult leg length at about 3-4 years of age, although body weight continued to increase slightly with age.

Cohort and year were also highly significant in all trait models except for year in the female hindleg length model (Table 5.1). Characteristics of both the year of birth and year of measurement, particularly in terms of population density and whether or not it was a crash year, had a large influence on birth weights and subsequent development and growth rates (Robertson *et al.* 1992). Birth type had a marked effect on all traits with singletons being larger than twins. Parasite burden had a negative effect on body weight (Gulland 1992) but in the longer term could also inhibit growth and so accounted for variation in other morphometric characters too. Body weight has previously been shown to differ between females of different coat colour and horn type (Clutton-Brock *et al.* 1997b) and although the underlying reason for this is not clear, it was not surprising to find a significant influence of coat colour on all these morphometric traits and horn type on some of them. Missing teeth had a negative influence on incisor arcade breadth (Table 5.1).

All the GLMs explained a high proportion of the trait variation (Table 5.1), especially the models for body weight (r^2 >0.80). Observed phenotypic means were in good agreement with the fitted lines (Figure 5.1) suggesting that I had realistic models with which to look for family resemblance in traits.

Table 5.1 General linear regression models for the three morphometric traits a) body weight, b) hindleg length and c) incisor breadth, for each sex. Mean square (m.s.) values show the effect of adding each term last to the model. Age-specific fitted values derived from the growth curves in Figure 5.1 were fitted as a proxy for age in all models. Faecal egg count was transformed by natural logarithms.

Females	df	ms	*F*	*P*	**Males**	df	ms	*F*	*P*
(a) Body weight			$r^2=0.82$					$r^2=0.88$	
Catch date	1	35.46	7.22	0.007	Catch date	1	173.18	19.24	<0.001
Age	1	4474.0	910.58	<0.001	Age	1	2389.2	265.49	<0.001
Twin	1	343.37	69.88	<0.001	Twin	1	456.88	50.77	<0.001
Faecal egg	1	184.97	37.65	<0.001	Faecal egg	1	159.45	17.72	<0.001
Year	9	13.16	2.68	0.004	Year	9	62.74	6.97	<0.001
Cohort	18	11.91	2.42	<0.001	Cohort	12	62.92	6.99	<0.001
Coat colour	1	74.80	15.22	<0.001	Coat colour	1	40.23	4.47	0.035
Residual	1043	4.91			Residual	563	8.99		
Total	1075	26.62			Total	589	75.34		
(b) Hindleg length			$r^2=0.69$					$r^2=0.68$	
Age	1	54858.1	1069.5	<0.001	Catch date	1	827.30	11.43	<0.001
Twin	1	6796.0	132.49	<0.001	Age	1	11472.6	158.46	<0.001
Faecal egg	1	729.10	14.21	<0.001	Twin	1	3276.3	45.25	<0.001
Cohort	18	250.09	4.88	<0.001	Faecal egg	1	980.16	13.54	<0.001
Coat colour	1	385.70	7.52	0.006	Year	9	177.57	2.45	0.010
Horn type	1	353.91	6.90	0.009	Cohort	12	243.18	3.36	<0.001
Residual	1052	51.16			Coat colour	1	616.14	8.51	0.004
Total	1075	163.87			Residual	563	72.48		
					Total	589	224.38		
(c) Incisor breadth			$r^2=0.67$					$r^2=0.77$	
Age	1	111.9	557.76	<0.001	Age	1	310.65	205.89	<0.001
Twin	1	18.91	9.49	0.002	Twin	1	24.15	16.01	<0.001
Year	8	9.84	4.93	<0.001	Faecal egg	1	16.99	11.04	<0.001
Cohort	18	8.90	4.46	<0.001	Year	7	4.18	2.77	0.008
Coat colour	1	29.81	14.95	<0.001	Cohort	9	5.56	3.69	<0.001
Miss. teeth	1	397.89	199.59	<0.001	Coat colour	1	15.96	10.58	<0.001
Residual	924	2.00			Horn type	1	25.76	17.07	<0.001
Total	954	6.13			Miss. teeth	1	9.81	6.50	0.011
					Residual	488	1.51		
					Total	510	6.46		

Correlations between traits

Phenotypic correlations between the three traits were similar in each sex (Table 5.2). Genetic correlations were less similar, especially in the case of incisor breadth. Hindleg length and body weight showed a high degree of phenotypic and genetic correlation in both sexes. This explained the observed indirect selection of hindleg length when direct selection of body weight occurred (Chapter 4). The phenotypic correlations between body weight and incisor arcade breadth and between incisor breadth and hindleg length were lower but the genetic correlations were not consistent. In females there was only a moderate genetic correlation between body weight and incisor breadth, yet in males these traits were highly genetically correlated. A similar, though less extreme, pattern was apparent between incisor breadth and hindleg length, with males again showing a higher genetic correlation than females. Since the standard errors were low, these appear to be genuine differences between the sexes.

Table 5.2 Phenotypic (above the diagonal) and genetic (below the diagonal) correlations between traits in each sex. Correlations were determined by variance component estimation using the strict paternity pedigree data. Standard errors (in parentheses) are approximate.

	Females				**Males**			
Trait	n	Body weight	Hindleg length	Incisor breadth	n	Body weight	Hindleg length	Incisor breadth
Body weight	1075		0.68 (0.02)	0.30 (0.03)	584		0.61 (0.03)	0.27 (0.04)
Hindleg length	1075	0.74 (0.09)		0.31 (0.03)	584	0.78 (0.10)		0.31 (0.04)
Incisor breadth	953	0.27 (0.17)	0.17 (0.17)		505	0.95 (0.10)	0.53 (0.17)	

Heritabilities & repeatabilities

The heritability estimates (h^2) for the three traits ranged from 0.09 for body weight in males to 0.32 for hindleg length in males using the relaxed paternity pedigree files and from 0.18 to 0.39 for the same traits using the strict data set (Table 5.3). As predicted, the heritabilities of body weight were lower than those of hindleg length and incisor breadth. In all cases heritabilities were lower than might have been expected for morphometric traits (Mousseau & Roff 1987) but, with the exception of body weight in males estimated using the relaxed pedigree data, all were significantly different from zero.

Table 5.3 Variance components and heritability (h^2) estimates for morphometric traits in females and males, calculated using pedigree files with paternities determined with a) 80% confidence (relaxed) and b) 95% confidence (strict). The total phenotypic variance was the sum of the additive genetic variance (V_A), the permanent environmental variance (V_E) and the residual variance (V_R). The repeatability (r) equalled (V_A + V_E) / V_T.

a) Relaxed paternity pedigree containing 2200 individuals

Trait	V_A (se)	V_E (se)	V_R (se)	h^2 (se)	c^2 (se)	r
Females (1076 data records from 502 individuals)						
Body weight	0.94 (0.36)	2.97 (0.38)	1.79 (0.07)	0.16^{**} (0.06)	0.52 (0.06)	0.69
Hindleg length	21.5 (6.42)	43.5 (5.99)	7.13 (0.28)	0.30^{***} (0.08)	0.60 (0.07)	0.90
Incisor breadth	0.43 (0.10)	0.29 (0.09)	1.12 (0.04)	0.23^{***} (0.05)	0.16 (0.05)	0.39
Males (590 data records from 386 individuals) ‡						
Body weight	0.81 (0.48)	3.71 (1.02)	4.73 (0.27)	0.09 (0.05)	0.40 (0.07)	0.49
Hindleg length	24.4 (9.10)	34.7 (6.59)	18.5 (1.30)	0.32^{***} (0.09)	0.45 (0.08)	0.76
Incisor breadth	0.38 (0.14)	0.22 (0.13)	0.88 (0.05)	0.26^{***} (0.05)	0.15 (0.06)	0.41

b) Strict paternity pedigree containing 2129 individuals

Trait	V_A (se)	V_E (se)	V_R (se)	h^2 (se)	c^2 (se)	r
Females (1075 records from 501 individuals) ‡						
Body weight	1.30 (0.41)	2.62 (0.39)	1.78 (0.07)	0.23^{**} (0.07)	0.46 (0.07)	0.69
Hindleg length	27.7 (7.72)	37.7 (6.68)	7.13 (0.27)	0.38^{***} (0.10)	0.52 (0.10)	0.90
Incisor breadth	0.45 (0.10)	0.26 (0.10)	1.13 (0.04)	0.24^{***} (0.05)	0.14 (0.05)	0.38
Males (584 records from 381 individuals) ‡						
Body weight	1.62 (0.77)	2.95 (0.93)	4.64 (0.27)	0.18^{*} (0.09)	0.32 (0.09)	0.50
Hindleg length	30.2 (9.16)	29.5 (8.49)	18.5 (1.15)	0.39^{***} (0.11)	0.38 (0.11)	0.76
Incisor breadth	0.47 (0.10)	0.13 (0.13)	0.88 (0.06)	0.32^{***} (0.07)	0.09 (0.08)	0.40

‡ reliability of standard errors uncertain.

The heritabilities estimated using the pedigree files based on strict paternity data were slightly higher than those based on relaxed pedigrees in both sexes, and particularly in male body weight. However, all the heritabilities estimated using the relaxed pedigree fell within the standard errors of the estimates made using the strict pedigree file (although only just in the case of body weight). This suggested that either the paternities estimated at only 80% were adequate for this heritability analysis because sample sizes were large, or that the paternities in which there was at least 80% confidence were in fact more accurate than this. The total phenotypic variances were very similar whether the strict or relaxed paternity pedigrees were used (Table 5.3). Differences in the heritability estimates came about from higher additive genetic variances and lower environmental variances using the strict pedigree files whilst residual variances were essentially the same in both cases.

The heritabilities of body weight in males, and in females when estimated using the relaxed pedigree, were low compared with the other traits. This arose from a combination of low additive genetic variance with a large residual variance component in males, and a relatively large environmental variance in females. The additive genetic variance component was smaller in males than females whilst the total phenotypic variance of male body weight was much greater than that of female body weight. This led to lower and less significant estimates of the heritability of male body weight than female body weight, although estimates based on the strict pedigree fell within the range of the standard errors. Neither of the other two traits showed differences in heritability between the sexes.

The repeatability of measures of hindleg length were high and of body weight, reasonably high (Table 5.3), indicating low variation in these traits between consecutive measures from the same animal. Incisor breadth had lower repeatabilities and was characterised by the highest residual variance components. The latter trait would have benefited the most from a greater number of multiple measurements. The low heritability of incisor breadth resulted not from a low additive genetic variance but from the large residual variance component in both sexes. In the case of female hindleg length and body weight and, to a lesser extent, male hindleg length, low heritabilities arose from large environmental variance components.

Coefficients of variation

Presenting the additive genetic variance as the additive genetic coefficient of variation, rather than the heritability, highlighted the differences in the genetic variation both between traits and between sexes (Table 5.4). Coefficients of variation would be expected to be approximately three times larger for volumetric morphological traits than for those of linear dimensions (Houle 1992). In fact the CV_A s for body weight were closer to double those of hindleg length and incisor arcade breadth, showing that the additive genetic variance of body weight was low relative to the other two traits. This was the case in both sexes and particularly marked in males when the relaxed pedigree

Table 5.4 The additive coefficients of variation (CV_A) for the three morphometric traits calculated using the variance components estimated by both the relaxed and strict analysis.

	Females CV_A		**Males CV_A**	
Trait	relaxed	strict	relaxed	strict
Body weight	5.06	5.95	4.37	6.18
Hindleg length	2.67	3.03	2.83	3.15
Incisor breadth	2.65	2.72	2.53	2.82

file was used.

There was good agreement between the CV_A values calculated using the relaxed and strict data in females, but in males agreement was less good, particularly for body weight. This made it difficult to interpret the difference in CV_A between the sexes. The low CV_A for male body weight calculated using the relaxed data implied that the low heritability of male body weight arose from a genuine lack of additive genetic variance in this trait, rather than a high residual variance. However, this was contradicted by the higher value calculated using the strict data set which implied there was little difference in the amount of additive genetic variance in body weight between the sexes. This discrepancy was similar to the result found from the heritability estimates suggesting that the apparent difference between sexes arose from the use of the relaxed paternity pedigree.

Maternal effects

As anticipated, when the maternal environmental effect, M (the ratio of the maternal effect variance to the total phenotypic variance), was taken into consideration, the heritability estimates for both females and males were generally lower (Table 5.5). However, the heritability of female body weight remained the same despite a significant maternal effect. Comparing the maternal effect between the sexes, it was apparent that females experienced a strong effect whilst there was no significant maternal effect on traits in male offspring. This was reflected by a significant change in deviance caused by dropping the dam random effect from the female model (χ^2=23.8, df=1, P<0.001)

Table 5.5 Variance components and heritability estimates (h^2) made when the maternal effect (M) was taken into consideration. The pedigree file based on the strict paternity pedigree was used. Total phenotypic variation was divided into four variance components, the additive genetic variance (V_A), the permanent environmental variance (V_E), the maternal effects variance (V_M) and the residual variance (V_R).

Trait	V_A (se)	V_E (se)	V_M (se)	V_R (se)	h^2 (se)	M (se)
Females (947 records from 449 individuals and 232 dams) ‡						
Body weight	1.30 (0.47)	1.48 (0.42)	0.80 (0.25)	1.80 (0.08)	0.24** (0.09)	0.15*** (0.04)
Hindleg length	20.0 (8.66)	32.9 (7.73)	16.2 (5.07)	7.37 (0.34)	0.26* (0.11)	0.21*** (0.06)
Incisor breadth	0.30 (0.10)	0.14 (0.08)	0.21 (0.07)	1.06 (0.05)	0.17** (0.06)	0.12** (0.04)
Males (575 records from 375 individuals and 218 dams) ‡						
Body weight	1.10 (0.45)	2.86 (0.57)	0.45 (0.44)	4.67 (0.25)	012* (0.05)	0.05 (0.05)
Hindleg length	15.3 (10.1)	36.1 (8.09)	8.14 (4.89)	18.6 (1.21)	0.20 (0.13)	0.10 (0.06)
Incisor breadth	0.43 (0.09)	0.15 (0.07)	0.00 (0.02)	0.89 (0.05)	0.29*** (0.10)	0.00 (0.01)

‡ reliability of standard errors uncertain.

whereas there was no significant change when dam was dropped from the male model (χ^2=2.44, df=1, P>0.1).

Examination of the variance components in females revealed that when the maternal effect was added, the residual variance components remained similar (comparing Table 5.5 with Table 5.3b). Much of the maternal effect variance came from the variance previously attributed to the environmental component and in the case of body weight all came from the environmental component.

Discussion

This analysis showed that hindleg length and incisor breadth had low but highly significant heritabilities in both sexes of Soay sheep. The heritability of body weight was less significant and in males was only significant when the strict paternity pedigree file was used. Heritabilities were highest for hindleg length and, as predicted, lowest for body weight. However, in females, especially once the maternal effect was taken into consideration, heritability estimates of all three traits were very similar, but the additive genetic coefficients of variation showed that body weight nevertheless had a much lower additive genetic variance.

Although morphological traits are generally considered to be only loosely associated with fitness, compared with life history traits (Mousseau & Roff 1987), some morphological traits will nonetheless have a large influence on fitness. For example, morphological beak traits in Darwin's finches (Geospizinae) have a functional relationship with fitness through foraging efficiency (Grant *et al.* 1976; Grant 1985). Despite this, beak size and shape traits were found to be highly heritable (Boag & Grant 1978; Boag 1983). However, additive genetic variation could be maintained within the population by immigration, opposing selection at other stages of the life history (Price & Grant 1984) and, in the longer term, by oscillating rather than directional selection (Gibbs & Grant 1987).

Similarly within the Soay sheep, body weight is a morphometric trait which has a large influence on the fitness components, survival (Clutton-Brock *et al.* 1992; Bancroft *et al.* 1995a) and fecundity (Clutton-Brock *et al.* 1996; Clutton-Brock *et al.* 1997b). But in contrast to the finches, evidence from the relationship between body weight and female fecundity suggests that selection occurring at this stage of the life cycle may reinforce, rather than oppose, the trend of positive selection for larger size (Clutton-Brock *et al.* 1997b). Consequently additive genetic variation may have been depleted by successive selection events. Furthermore, because the population is totally isolated, genetic variation can not be maintained by immigration.

The morphometric trait, hindleg length, experiences indirect selection due to its close correlation with body weight (Chapter 4). This suggests that it is less closely associated with fitness than body weight and was consistent with the finding of a higher degree of genetic variability and a higher heritability for hindleg length than for body weight. The laws of dimensionality would predict that body weight should have an additive genetic coefficients of variation three times greater than that of the linear traits, hindleg length and incisor breadth, for the same degree of genetic variation (Houle 1992) yet this was not the case in either sex. Incisor arcade breadth was a morphological trait with a functional relationship with bite size and food intake rate (Gordon *et al.* 1996). It might therefore be expected to have a close association with fitness. However, there was no evidence of its repeated selection and heritability estimates and additive genetic coefficients of variation of incisor breadth were very similar to those of hindleg length.

A similar argument of erosion of additive genetic variation resulting from repeated selection events could be invoked to explain differences in the heritability of body weight between the sexes. Since Soay sheep are sexually dimorphic and male reproductive success is assumed to be closely linked to body size (Trivers 1972; Clutton-Brock *et al.* 1979), one might expect male body size to be subject to both sexual and natural selection whilst female size is only subject to natural selection. Evidence from observations during the rut on St. Kilda indicate that the level of rutting activity is linked to body weight at all ages (I.R.Stevenson pers. comm.). However, although the heritability of male body weight was found to be lower than females, differences were not sufficiently marked to fully support this hypothesis. A detailed investigation of the sexual selection of male body weight has yet to be carried out.

The heritabilities estimated in this study were low compared with those found for other morphometric traits. Mosseau & Roff (1987), conducting a comparison between the heritabilities of morphological and life history traits in populations of wild, outbred stock, found a mean heritability of 0.46 for 570 morphological traits. This compared with a mean heritability of 0.26 for life-history traits. My estimates are more in keeping with those expected for life-history traits. Although the heritability estimates used in Mosseau & Roff's study were derived from parent-offspring regressions whereas I used maximum likelihood techniques, studies in which the two approaches have been used on the same data set suggest good agreement (Cheverud & Dittus 1992; Knott *et al.* 1995), at least in cases where data are not extremely unbalanced.

Low heritabilities of each trait probably arose from differing combinations of high residual or environmental variance and, as discussed above, low additive genetic variance. Heritabilities in small populations have a tendency to be lower than those in large populations due to gene fixation (Falconer & MacKay 1996). However, it has been shown that despite being small and isolated, the Soay sheep population on St. Kilda has remarkably high allozyme heterozygosity (Bancroft *et al.* 1995b).

In animal and plant breeding programmes, environmental conditions can be strictly controlled so minimising the environmental variance component (Alatalo *et al.* 1990). By contrast, in natural populations, environmental variation tends to be much greater, increasing the total phenotypic variance relative to the additive genetic variance, and so reducing heritabilities (Ricklefs & Peters 1981). In this study, a high environmental variance of all traits was indicated by values for c^2, the ratio of the permanent environmental variance to total phenotypic variance, which exceeded the heritabilities. This is contrary to the implications of a study by Weigensberg & Roff (1996). They showed the assumption that natural heritabilities would be overestimated by laboratory determinations, due to a reduction in environmental variability, to be unfounded. No significant differences were found between 189 heritability estimates made under laboratory conditions and 165 field estimates.

Of the three traits examined, hindleg length showed the greatest environmental variance, in terms of the largest c^2 values. It seems probable that this was the cause of the low heritability of leg length rather than a lack of genetic variance. The amount of environmental variance of body weight was slightly lower than in hindleg length although one might have expected the reverse situation. Van Noordwijk *et al.* (1988) pointed out that although many studies have shown that a considerable part of the total phenotypic variance of body size in birds is genetic, body weight, which includes a condition component, is often used to explain variation in size due to environmental conditions (see also Alatalo *et al.* 1990). Within the Soay sheep, marked year to year variation in environmental conditions (Grenfell *et al.* 1998) caused variation in body weight through changes in body condition. Such changes are generally highly dependent on food availability (Choquenot 1991). Hindleg length, on the other hand, remained relatively constant from year to year, accounting for its higher repeatability measures than body weight. The greater environmental variance of hindleg length than body weight implied a higher between-individual variance of hindleg length once environmental factors such as year and cohort had been accounted for.

The range of measures observed for body weight were proportionally greater than the other two traits. Consequently measurement error, which contributed to the non-permanent environmental or residual variance, was proportionally greater for weight than for hindleg length. Gutfill and wetness of fleece were factors affecting weight that could not be controlled for (Illius *et al.* 1995) and added to the error in this measure. The residual variance was therefore a contributing factor towards the lower repeatability and heritability of body weight. The greater variance in male body weights than female weights meant this effect was exacerbated in males. Incisor breadth had an even higher residual variance, accounting for its low heritability. This probably arose partly from the smaller sample sizes of incisor breadth which has only been measured since 1990, and partly from measurement error. Measurement of this trait involved two stages, first taking a dental impression and then measuring the impression, so increasing the opportunity for random errors to occur.

In females, a highly significant maternal effect was found in all three traits but, by contrast, no significant maternal effect was detected in males. This reflected differences in the social behaviour of the sexes. Females tend to be hefted within matrilineal groups (Grubb 1974a) and consequently female offspring grew up under the same environmental conditions as their mothers. By contrast, male offspring dispersed from their natal group, usually forming yearling male groups within their mothers' range at first and then joining all male groups in other parts of the study area (Grubb 1974a). Although one would expect the mother's nutritional condition to affect early development of male and female offspring equally, the fact that males continue growing for many years after dispersal may mean that environmental conditions in the bachelor groups may have a greater influence on traits than maternal effects.

This study is the first to use the animal model approach to make a detailed assessment of the components of phenotypic variance of morphometric traits in a wild population. It has shown that the additive genetic variance of body weight, a trait subjected to repeated directional selection, was lower than that of other morphometric traits that have a smaller influence on fitness.

CHAPTER 6.

Influences of morphometric traits on foraging choices in the Soay sheep on St. Kilda

Influences of morphometric traits on foraging choices in the Soay sheep on St. Kilda

Summary

Foraging behaviour was observed in a sample of Soay sheep at the end of winter and in mid-summer, in 1996 and 1997. The spatially heterogeneous sward of gaps and tussocks presented choices between quality and quantity of forage enabling two opposing foraging hypotheses to be tested: (1) incisor arcade breadth allows small mouthed individuals to graze selectively from tussocks whilst large mouthed individuals can have high intake rates from gaps (2) metabolic requirements of light weight individuals can be best met from high quality gaps but those of heavy individuals can not be met by grazing low biomass gaps.

At the end of winter, when tussocks were dominated by standing dead matter, all sheep showed a strong preference for grazing gaps. Neither body weight nor incisor arcade breadth were significant in explaining individual variation in gap selectivity. By contrast, in summer, sheep showed a weak preference for gap over tussock. There was an interaction between sex and body weight, such that small females favoured grazing of gaps more than heavier females and males. In addition, gap selectivity indices in summer were positively related to whether or not an individual survived the following winter.

Observed individual variation in gap selectivity was interpreted in terms of body weight and diet quality. Analysis of faecal nitrogen content supported the same argument, in that young and light individuals had significantly higher faecal nitrogen levels than older and heavier individuals. This suggests that young and light individuals select higher quality diets than old and heavy ones. In addition, faecal nitrogen levels were higher in summer when diet quality was higher than at the end of winter.

Introduction

During the population crash of Soay sheep on St. Kilda in the winter of 1991/92, differential survival occurred. This was thought to favour individuals with relatively broad incisor arcade breadths (Illius *et al.* 1995), although it has subsequently been shown that only in adult males was incisor breadth more important than body weight in explaining the observed mortality (Chapter 4). The hypothesis proposed to explain the differential survival was that broad mouthed individuals had higher food intake rates (Gordon *et al.* 1996) on the short swards, characteristic of high population winters.

However, because broad mouthed animals also tend to be large animals (Illius *et al.* 1995; Chapter 4) they have absolutely higher energy demands, and because during low population years sward height and structure are markedly different (S.D.Albon, pers. comm.), it was felt that there may be opposing fitness advantages of small mouth size or body size under alternative grazing conditions.

This study was set up to investigate the influences of mouth and body size on grazing efficiency under the contrasting environmental conditions of high and low population years. Unfortunately, the anticipated population crash of the winter 1996/97 did not occur, despite a record number of sheep using the study area (575 individuals at the start of winter). However, the spatially heterogeneous vegetation on St. Kilda (Gwynne *et al.* 1974) nonetheless provides an opportunity to test two opposing foraging hypotheses and hence establish a mechanism to explain the observed survival patterns.

The hypotheses tested were:

(1) individuals with broad incisor arcades are suited to grazing on short, vegetative swards where they can maintain high intake rates because of their large bite size. Meanwhile, animals with small incisor breadths feed more selectively on high quality items taken from taller swards that have a high proportion of standing dead or reproductive material.

(2) small bodied individuals with relatively high metabolic requirements, feed more from short vegetative swards where high quality forage is accessible. Large individuals which can not meet their total daily energy requirements on short swards are displaced and feed less discriminatively on longer vegetation.

The theories behind these hypotheses, described more fully in Chapter 1, have been developed at the interspecific level (Bell 1970; Jarman 1974; Demment & van Soest 1985; Gordon & Illius 1988). They are based on allometric differences in gut capacity (Demment 1982) and mouth size (Clutton-Brock & Harvey 1983; Illius & Gordon 1987) relative to body size and metabolic rate. In particular, large ungulates are capable of tolerating poorer quality diets than are small ones, by virtue of their relatively greater digestive capacity which enables longer gut retention times (van Soest 1982). By contrast, small ungulates need high quality diets to sustain their relatively higher metabolic rates but have lower total energy requirements (Kleiber 1961; Peters 1983). However, interspecific relationships are not necessarily applicable at the intraspecific level (Calder 1984; Belovsky 1987). Considerably less attention has been paid to the influence of intraspecific differences in individual phenotype on foraging behaviour and diet selection (Partridge & Green 1985; but see Gordon *et al.* 1996).

Sheep are selective grazers (Nicholson *et al.* 1970; Grant *et al.* 1985), showing a strong preference for green grass leaves over low quality dead material and reproductive stems (L'Huillier *et al.* 1986). The diet selected is therefore likely to result from a trade-off between quantity and quality whilst maximising herbage intake rate (Stephens & Krebs 1986; Wilmshurst *et al.* 1995). Intake rate will be determined by sward characteristics such as height and density, as well as by characteristics of the animal (Allden & Whittaker 1970). Consequently, the optimal outcome will vary between individuals depending on factors such as age, sex, body weight, incisor breadth (Gordon *et al.* 1996), parasite burden (Hutchings *et al.* 1998) or reproductive status (Parsons *et al.* 1994),and the foraging environment (Demment & Greenwood 1988).

To understand individual variation in foraging efficiency and the relevance of the interspecific foraging hypotheses at the intraspecific level, I examined diet selectivity on St. Kilda. Grazing at the end of winter, when the availability of forage is limited and many animals may die of starvation (Grubb 1974b; Clutton-Brock *et al.* 1991), is compared with behaviour in mid-summer, when forage is abundant.

Materials and Methods

STUDY AREA

Sheep population

This study was carried out on sample of individuals from the Soay sheep study population. All individuals regularly used the area inside the head dyke in Village Bay (Figure 2.3).

Most sheep are born in April so during the summer observation periods, 'lambs' were approximately 3 months old, 'yearlings' were approximately 15 months old and 'adults' were all animals over 2 years old. During the winter observation period, animals approaching the end of their first winter were 11 -13 months old and so will be called 'yearlings' to avoid confusion with new-born lambs. All sheep over the age of 21months were considered as 'adults'.

Vegetation

The distribution of the Soay sheep is non-random with respect to vegetation community, higher sheep densities being associated with the most productive communities (Milner & Gwynne 1974; M.J.Crawley *et al.* unpublished). Favoured grazing occurs within the head dyke in Village Bay, in the relatively fertile area formally cultivated by the St. Kildans. This area is characterised by a spatially heterogeneous sward, composed of tall tussocks with a high proportion of standing dead material, and short, heavily grazed inter-tussocks or gaps (Gwynne *et al.* 1974; Figure 6.1). The tussocks have developed because of the growth form and lower palatability of *Agrostis capillaris*, which is avoided by the sheep. Consequently dead material also accumulates, accentuating the tussocks, especially in winter (Table 6.1, Figures 6.1a). Shoots of the preferred graze species, *Festuca rubra* and *Poa humilis*, are present at higher biomass in tussocks than gaps in all seasons (Table 6.1), but remain less grazed because of their relative inaccessibility amongst the standing dead material (Figure 6.2). Between the tussocks are heavily grazed gaps, dominated by *Holcus lanatus*, but also containing the preferred and perennial grass species *Festuca rubra, Anthoxanthum odoratum* and to lesser extent *Poa humilis*. There is also a higher proportion of dicotyledenous plants such as *Trifolium repens* in gaps and bryophytes, particularly *Rhytidiadelphus squarrosus*, are

Table 6.1 Composition of gaps and tussocks within the head dyke in Village Bay. Mean dry masses (DM) (and variances) are given for 12 harvested plots of 0.04 m^2. Dry mass of grass includes all grass species. Mass of standing dead matter and proportion of grass accounted for by the palatable species, *Festuca rubra* and *Poa humilis*, are also shown. Data from M.J.Crawley (unpublished).

		Live grass (g DM)	Proportion of palatable spp.	Bryophytes (g DM)	Standing dead (g DM)
Mar. 96	Gap	2.97 (1.91)	0.24 (0.01)	4.26 (14.8)	4.39 (6.41)
	Tussock	8.38 (6.29)	0.25 (0.03)	0.72 (0.77)	19.9 (35.6)
Aug. 96	Gap	3.38 (5.59)	0.23 (0.02)	2.37 (4.02)	1.69 (3.40)
	Tussock	16.7 (35.8)	0.21 (0.02)	0.16 (0.04)	11.2 (88.7)
Mar. 97	Gap	2.16 (1.16)	0.18 (0.04)	4.81 (16.1)	1.87 (1.35)
	Tussock	4.00 (2.60)	0.40 (0.02)	0.57 (0.36)	20.4 (24.1)
Aug. 97	Gap	3.17 (4.77)	0.52 (0.17)	3.13 (12.6)	0.82 (1.85)
	Tussock	14.1 (26.9)	0.27 (0.02)	1.18 (2.33)	7.18 (52.7)

abundant (Gwynne & Boyd 1970). Bryophytes are especially dominant at the end of winter when they are able to exploit a time of release from competition with grass species (M.J.Crawely *et al.* unpublished). During the summer, when plant productivity exceeds consumption, sheep are less able to maintain the open gaps, many of which develop into an 'intermediate' class (Figure 6.1b).

DATA COLLECTION

Morphometric measurements

The morphometric measurements used were body weight, hindleg length and incisor arcade breadth, measured from animals caught in August as described in Chapter 2. Unfortunately no body weight data were available for late winter when weights were at their annual low (Doney *et al.* 1974), so for all analyses of winter data, morphometric measures from the previous August were used. However, since individuals were found to have consistent deviations from average growth curves, previous August values gave an acceptable indicator of relative size. Age and sex specific growth curves (Chapter 5) were also used to calculate the 'proportional weight' as the observed August weight divided by the August weight predicted by the growth curves. This gave an indication of whether an individual was relatively under- or over-weight for its age and sex.

Figure 6.1 Photographs of the vegetation within the head dyke in (a) March and (b) July, showing the marked seasonal differences in sward structure and quality.

(a)

(b)

Parasite burden

Faecal strongyle egg counts were used as an index of gastrointestinal parasite burden (Gulland & Fox 1992; Chapter 2). Again for late winter analyses, data from the previous August were used.

Foraging behaviour

Foraging behaviour was investigated in a sample of individuals of different age and sex classes within the head dyke in Village Bay. Observations were made in the late winter / early spring (March-April) and summer (July-August) of 1996 and 1997 (Table 6.2). Grazing preferences were monitored by counting the number of bites taken from patches of tussock, gap or intermediate during a period of 5 minutes continuous grazing. Between two and five replicates were collected for each individual (Table 6.2). In the winter of 1997, a number of animals died before the observation period finished, especially yearlings. Observations of lambs were only made in the summer of 1997. The grazing choice data was complimented by information on the relative occurrence or 'availability' of each of the patch types as measured by walking a transect between the start and end points of the area grazed during the 5 min. period, and recording which patch type was present at each step.

It should be noted that in this chapter, late winter is taken as March and April of the calendar year. For example the late winter observation period of 1996 was March - April 1996, whereas in other chapters this period would be considered as the end of winter 1995 which covers the period from October 1995 to March 1996.

Faecal analysis

During March 1997 and July 1997, a minimum of three faecal samples per season were collected fresh from each observed individual. These were then frozen and subsequently freeze dried (Savant RVT400) since oven drying can have a radical effect on nitrogen content (Le Du & Penning 1982). Dried samples were ground using a Glen Creston mill (Stanmore, U.K.) and digested by the sulphuric-peroxide modification of the Kjeldahl procedure (Rowland & Grimshaw 1985; Grimshaw *et al.* 1989). Ammonium-nitrogen content was determined by the indophenol-blue method (Hinds & Lowe 1980; Grimshaw *et al.* 1989) using an automated continuous flow system (Burkard Scientific SFA2).

Table 6.2 Details of study animals during each observation period. Body masses were measured in August so those of individuals observed during the late winter were taken from the previous year.

		No. individuals		Mean no. reps. / individual		Mean (var.) body mass (kg)		Total no. observn
		Females	*Males*	*Females*	*Males*	*Females*	*Males*	
Wint. 96	*Yearlings*	4	4	4.3	3.8	12.0 (6.07)	13.4 (1.81)	32
	Adults	7	4	3.4	3.5	23.2 (4.01)	34.7 (34.5)	38
Sum. 96	*Yearlings*	6	8	2.3	2.4	16.8 (4.69)	20.7 (8.37)	33
	Adults	15	9	2.3	2.3	23.6 (2.85)	38.1 (25.1)	55
Wint. 97	*Yearlings*	5	5	4.0	3.0	11.8 (3.84)	16.2 (5.63)	38
	Adults	19	13	4.6	4.4	19.8 (10.4)	29.4 (104)	145
Sum. 97	*Lambs*	4	5	4.0	4.0	14.0 (1.30)	12.8 (7.00)	36
	Yearlings	5	5	3.4	3.6	15.9 (4.59)	20.8 (8.80)	35
	Adults	8	7	3.8	3.6	21.4 (4.22)	34.2 (54.2)	55

Over 85 % of faecal nitrogen is derived from endogenous metabolic and microbial sources (Mason 1969; van Soest 1982) and consequently the usefulness of faecal nitrogen for predicting dietary nitrogen has been questioned, especially for diets with high tannin contents (Hobbs 1987; Robbins *et al.* 1987; Wehausen 1995). However, I use faecal nitrogen content for comparative purposes only, as an indicator of the relative digestibility of the diet selected by individuals within a single population (Prache *et al.* 1998). This approach avoids some of the problems associated with using faecal nitrogen predictively to estimate diet quality (Hobbs 1987; Leslie & Starkey 1987). Furthermore, unlike browsing ungulates, sheep on St. Kilda graze predominantly on tannin-free monocotyledons (Milner & Gwynne 1974; McLeod 1974; Hofmann 1989; Irwin *et al.* 1993).

Under controlled experimental conditions, 12 Scottish blackface wethers, of uniform liveweight and treated with an anthelminthic (Ivermectin, Ivomec, Meck Sharp & Dohneto) to clear parasites, were all fed the same diet of grass hay (Hadjigeorgiou 1996) No significant individual variation in faecal nitrogen was found ($F_{11,35}$=1.54, P=0.16). This suggests that individual variation in faecal nitrogen observed from my field studies arose from differences in body weight, age, sex, parasite burden or differences in quality of diet consumed.

Figure 6.2 A tussock in early April, showing a few new shoots of grass protruding from amongst the standing dead material.

Analysis

Bite rate (bites/s) was calculated as the total number of bites taken from gap, tussock and intermediate swards during each 5 min. observation period, divided by the exact length of observation time in seconds.

Diet selectivity was assessed by preference ratios (Crawley 1983) for gap relative to tussock, using log ratio analysis (Elston *et al.* 1996). Data from the intermediate vegetation type were excluded. The log ratio of bites (R_b) and availability (R_a) were calculated as follows:

$$R_b = \log\left(b_g / b_t\right) \qquad \text{and} \qquad R_a = \log\left(a_g / a_t\right)$$

where b_g and b_t are respectively the number of bites of gap and tussock eaten and a_g and a_t are the availability of gap and tussock respectively. In cases where bites of tussock or the availability of tussock were zero, half a unit was transferred from the gap to the tussock side of the equation, in order that the logarithm could be taken. These ratios were also used to calculate a gap selection index (I_g), as follows:

$$I_g = \log \frac{(b_g/b_t)}{(a_g/a_t)} = R_b - R_a$$

This index is distributed approximately normally. An index of zero indicated no selection, gap and tussock being grazed in relation to their availability. Positive values indicated gap was being selected at higher levels than expected from its relative abundance and negative values indicated avoidance of gap.

Since repeated observations were made from each individual, analysis was carried out by restricted maximum likelihood (REML) (Robinson *et al.* 1982), which allowed the identity of the individual to be fitted as a random effect. This is the means by which REML takes account of non-independent samples from the same individual (Thompson & Welham 1993). The relationships between gap selection index and the parameters age, sex, body weight, incisor breadth, hindleg length, parasite burden and gap availability (R_a) were modelled for each season because of the very marked seasonal differences. Similar models were derived for bite rate and faecal nitrogen content. Terms were dropped from the analysis using a series of sub-models nested within the full model and change in deviance were used to assess the significance of each term dropped, with degrees of freedom equal to the difference in degrees of freedom between the full and sub-model. A new full model was then created that excluded the weakest non-significant term and the process was repeated. This was continued until only significant terms remained within the full model. Deviance was distributed approximately as χ^2. The goodness of fit of the model was assessed at the stratum level by comparing the stratum variances of the final model with the stratum variances of the null model in which no fixed effects were fitted.

Results

Seasonal differences in forage availability and grazing preferences

Marked structural and compositional differences existed between the sward at the end of winter and in mid-summer (Figure 6.1; Tables 6.1 & 6.2). Green grass biomass of both gaps and tussocks was greater in summer than late winter in both years, although the seasonal difference in total grass biomass of gaps was only significant at the 10% level whereas it was highly significant in tussocks (t=1.60, df=46, P=0.058 for gap; t=8.30, df=46, P<0.001 for tussocks). The opposite was true of the standing dead matter and seasonal differences were significant in both gap and tussock (t=-2.02, df=46, P=0.025 for gap; t=-4.96, df=46, P<0.001 for tussocks). The proportional cover of gap was greater in late winter, when the tussocks had been grazed back, than in summer (Figure 6.3). This was most pronounced in March 1997 due to a higher over-winter sheep population (575 sheep) than in the winter of 1995/96 (357 sheep). In both summers, the intermediate patch type accounted for about half of all available vegetation (47.2% and 61.1% in 1996 and 1997 respectively).

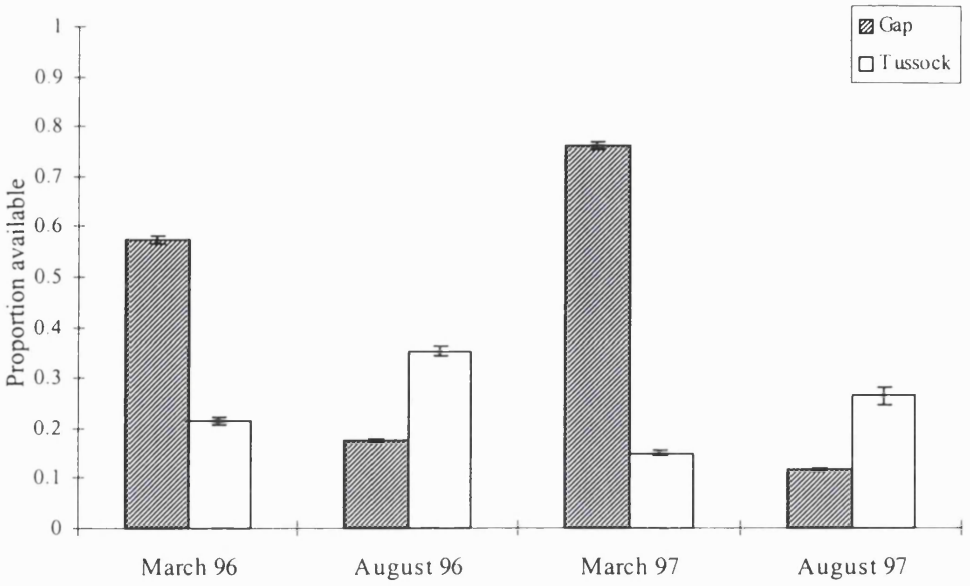
At the end of winter all sheep showed a marked preference for grazing gap rather than tussock (Figure 6.3). The proportion of gap consumed was greater than its relative availability whilst the reverse was true for tussock. Consequently, once the relatively greater abundance of gap (indicated by availability indices (R_a) greater than zero) had been accounted for, the mean gap selection index (I_g) was significantly greater than zero (t=17.1, df=252, P<0.001; Table 6.3; Figure 6.4). There was a significant positive relationship between I_g and R_a in late winter (Table 6.5a).

By contrast, in summer there was much weaker evidence for a selective preference of gap over tussock at the all-individual level. Gap and tussock were consumed in approximately the proportions at which they occurred (Figure 6.3) but the mean values of I_g were, nonetheless, still significantly greater than zero (t=2.46, df=222, P=0.015), indicating that selection for gap was occurring (Table 6.3; Figure 6.4). However, the main effect relationship between I_g and R_a was not significant in summer (Table 6.5b).

Bite rate

The preference for gap at the end of winter could be explained if higher nutrient intake rates were maintained on the gaps than in tussocks, despite their much lower standing biomass (Table 6.1). By modelling bite rate, it was found that as the log ratio index of bites from gap (R_b) increased, bite rate increased in both seasons (Table 6.4). In other words, bite rate was faster when eating gap than tussock. Bite rates were also significantly faster in late winter than summer (Table 6.3; $F_{1,474}$=32.94, P<0.001), corresponding to the increased grazing of gap in late winter. Faster bite rates may compensate for smaller bite sizes due to lower sward biomasses in winter.

(a) Proportions available



(b) Proportions eaten

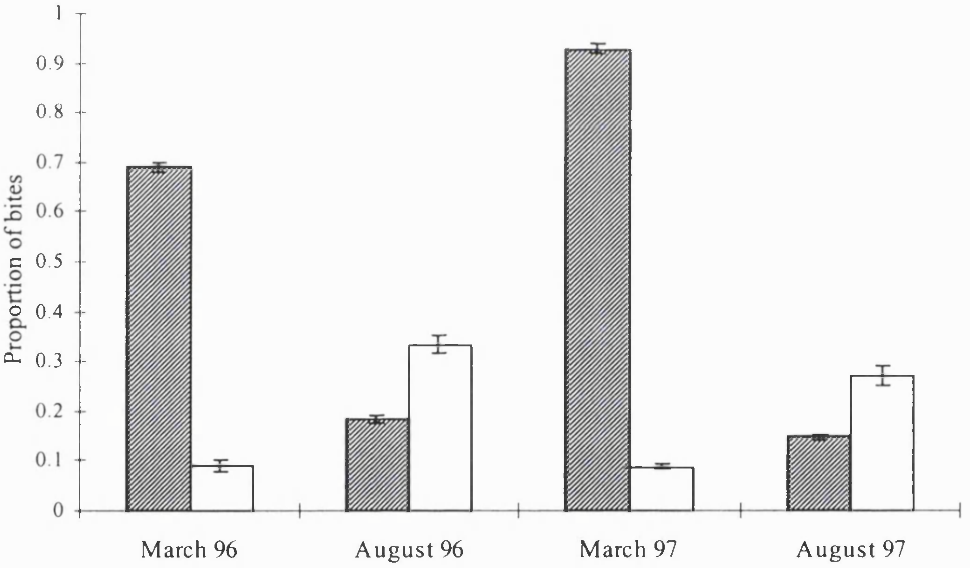


Figure 6.3 Average proportions of gap and tussock (a) available and (b) eaten in each of the observation seasons. The presence of the intermediate vegetation type accounts for the difference between the sum of the proportions of gap and tussock and one.

Table 6.3 Means (and variances) of observed gap selection indices (I_g) and bite rates (bites s^{-1}) for different age and sex classes during each of the observation periods.

		Mean (var.) I_g		Mean (var.) bite rate	
		Females	*Males*	*Females*	*Males*
Winter 96	*Yearlings*	2.22 (2.61)	0.91 (1.52)	0.95 (0.02)	0.92 (0.03)
	Adults	2.23 (3.07)	1.85 (1.78)	0.93 (0.02)	0.91 (0.02)
Summer 96	*Yearlings*	0.39 (0.92)	0.10 (0.40)	0.90 (0.02)	0.89 (0.02)
	Adults	0.30 (0.98)	-0.12 (1.13)	0.92 (0.01)	0.86 (0.01)
Winter 97	*Yearlings*	1.15 (0.84)	1.59 (2.56)	1.00 (0.02)	1.06 (0.02)
	Adults	1.33 (1.46)	1.29 (1.78)	1.11 (0.02)	1.04 (0.03)
Summer 97	*Lambs*	0.32 (5.95)	-0.39 (1.84)	0.96 (0.02)	0.96 (0.02)
	Yearlings	1.17 (1.93)	0.20 (0.86)	0.99 (0.01)	0.97 (0.01)
	Adults	0.18 (1.47)	0.27 (1.16)	1.02 (0.02)	0.98 (0.01)

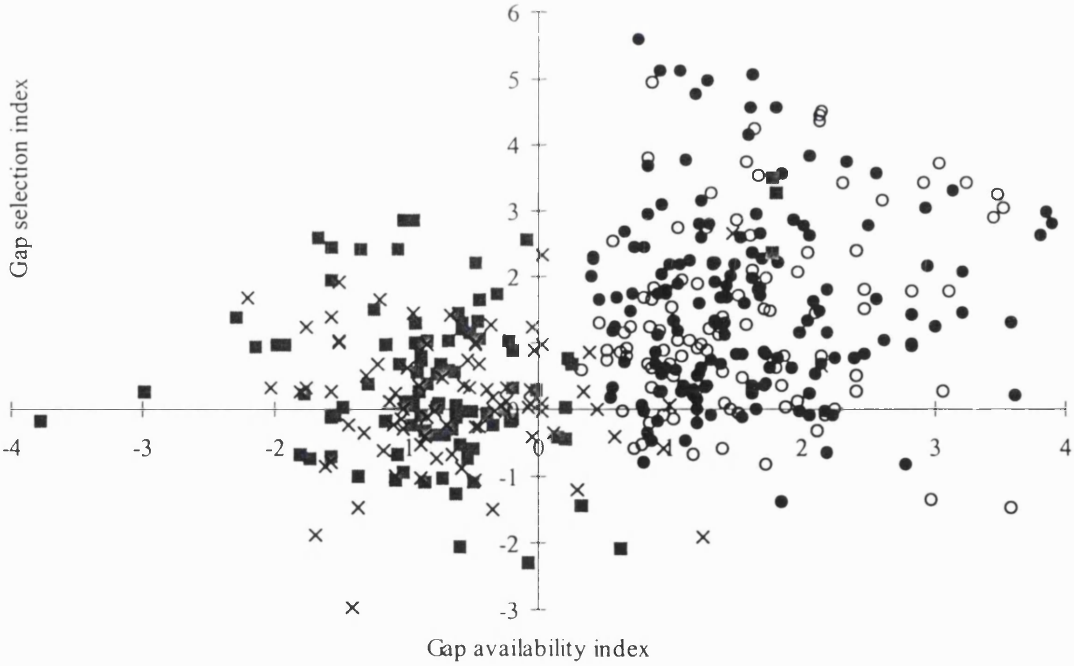


Figure 6.4 Gap selection index in relation to the gap availability ratio in late winter (● females and O males) and summer (■ females and X males). Data are from both 1996 and 1997. Each observation point for every individual is shown.

My model also showed that bite rate varied between individuals with older animals having significantly faster bite rates than younger ones, in both seasons (Table 6.4). There was no significant main effect of sex on bite rate. In summer there was no significant difference in bite rate between yearlings and adults but lambs had particularly low bite rates which could be explained in terms of their lack of experience in selecting bites, or their lower intake requirements (Partridge & Green 1983). In late winter a negative relationship between incisor arcade breadth and bite rate was found which interacted significantly with sex (Table 6.4a). As incisor breadth increased, bite rate decreased more in males than in females.

Table 6.4 REML models for bite rate in (a) late winter and (b) summer. Age was fitted as a two level factor of (i) yearlings and (ii) adults in late winter, and (i) lambs and (ii) yearlings and adults together, in summer. R_b is the log ratio of bites of gap eaten. Individual was fitted as the random effect. The change in deviance is distributed as χ^2.

(a) Late winter : n = 253

% variation explained : between individuals = 54.1 %, within individuals = 55.0 %.

Term	Parameter estimates	se	df	Change in deviance
Constant	0.869	0.026		
R_b	0.019	0.004	1	18.5 ***
Date	0.006	0.001	1	141.2 ***
Year (97)	0.273	0.024	1	86.6 ***
Age (yearling)	-0.059	0.030	1	3.90 *
Sex (M)	-0.008	0.023	1	0.10
Incisor breadth	-0.001	0.006	1	3.76
Date . Year (97)	0.003	0.001	1	7.63 **
Incisor b . Sex (M)	-0.015	0.007	1	4.62 *

(b) Summer : n = 223

% variation explained : between individuals = 43.0 %, within individuals = 34.1 %.

Term	Parameter estimates	se	df	Change in deviance
Constant	0.823	0.025		
R_b	0.022	0.004	1	24.6 ***
Date	0.015	0.002	1	47.3 ***
Year (97)	0.136	0.017	1	49.3 ***
Age (adults)	0.047	0.022	1	4.35 *
Date . Year (97)	-0.008	0.003	1	7.30 **

Individual differences in grazing preferences

There was considerable variability in gap selectivity. This was both between and within individuals, making between individual variation difficult to detect (late winter $F_{54,198}$= 1.53, P=0.019; summer (yearlings and adults) $F_{55,122}$=1.51, P=0.031). From hypothesis (1) one would predict a positive relationship between incisor arcade breadth and the gap selection index (I_g) whereas from hypothesis (2) one would expect a negative relationship between body weight and I_g. However, it was apparent from the seasonal trends that at the end of winter, the good quality grass within tussocks was so inaccessible that most individuals rarely grazed from tussocks at that time of year. Consequently the power to discriminate between individuals was poor, so it was not surprising to find that neither incisor breadth nor body weight had a significant affect on I_g in late winter. None of the other individual parameters, hindleg length, age, sex and parasite burden, were significant either, but date and the gap availability index (R_a) both had positive relationships with I_g (Table 6.5a). R_a also interacted with the proportional body weight such that relatively under-weight individuals responded more strongly to the availability of gap than over-weight animals (Figure 6.5). At high gap availability under-weight animals selected significantly more gap than over-weight animals (t=2.65, P<0.01), whilst at lower gap availability the trend was reversed and less extreme (t=1.81, P<0.10).

No association was found between gap selectivity index in winter and survival. In winter 1996 none of the sample died, whilst in winter 1997, the gap selection index of survivors and non-survivors were not significantly different (t=0.05, df=40, P=0.96), despite nearly a third of individuals dying. The winter model was only able to explain 17% of the between individual variation in gap selectivity (Table 6.5a) suggesting that the main factors responsible for differences in grazing selectivity had not been revealed.

In summer, evidence was found to support hypothesis (2) amongst females. There was a significant negative effect of body weight on I_g such that small females showed a strong preference for gap whilst large individuals showed no particular preference (Table 6.5b). There was no relationship between male body weight and selectivity for gap so consequently there was a significant sex-weight interaction (Figure 6.6). The relationship between female body weight and I_g arose from a particularly strong relationship in the summer of 1997 whilst a similar situation was not apparent in

Table 6.5 REML models of the gap selection index (I_g) for (a) late winter, and (b) summer, in yearlings and adults. R_a is the log ratio of gap availability. The proportional weight is : (observed August weight) / (expected age-, sex-specific August weight). Individual was fitted as the random effect. Interactions are denoted by ' . ' between terms. Change in deviance is distributed as χ^2.

(a) Late winter : n = 253

% variation explained : between individuals = 16.6 %, within individuals = 5.55 %.

Term	Parameter estimates	se	df	Change in deviance
Constant	1.471	0.095		
R_a	0.321	0.113	1	8.33 **
Date	0.020	0.005	1	14.5 ***
Proportional weight	-0.436	0.725	1	1.20
R_a . Prop.weight	-1.837	0.757	1	5.81*

(b) Summer (yearlings & adults) : n = 168

% variation explained : between individuals = 33.8 % within individuals = 7.49 %.

Term	Parameter estimates	se	df	Change in deviance
Constant	-0.569	(0.311)		
R_a	0.578	(0.201)	1	1.40
Date	0.008	(0.024)	1	8.79 **
Year (97)	0.169	(0.173)	1	2.51
Sex (M)	0.242	(0.208)	1	0.19
Body weight	-0.109	(0.031)	1	3.42
Survival (survivors)	0.577	(0.280)	1	4.12 *
R_a . Year (97)	-0.552	(0.230)	1	5.62 *
Date. Year (97)	0.066	(0.032)	1	4.29 *
Sex (M) . Weight	0.097	(0.033)	1	7.24 **

summer 1996. During the summer of 1997 there was a particularly high proportion of palatable grass species present in the gap, providing almost twice the biomass of palatable grass available in the previous summer (Table 6.1).

The summer grazing selectivity model also showed that there was a positive relationship between survival over the following winter and grazing selectivity (Table 6.5b). Survivors had significantly higher gap selection indices than non-survivors (t=2.19, df=71, P=0.031) suggesting a fitness advantage in grazing from gaps in summer.

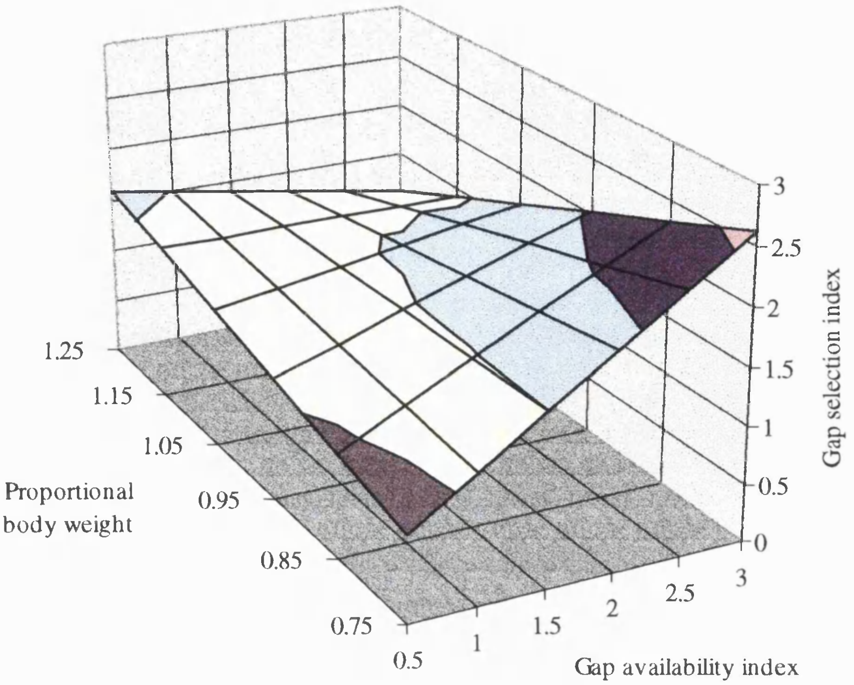


Figure 6.5 Model of the gap selection index for late winter showing the predicted surface explained by the interaction between the gap availability index and proportional body weight (observed August weight / expected August weight).

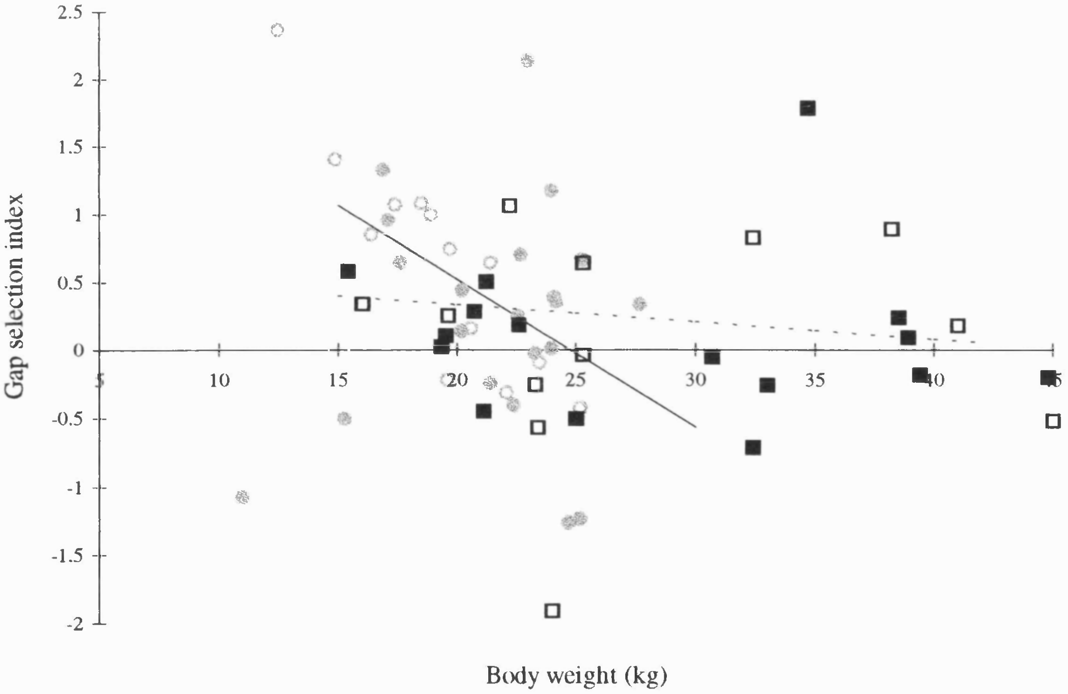


Figure 6.6 Fitted lines from the model of the gap selection index in summer (—— females; -----males) showing the observed data points (mean value for each individual) for females ● 1996 and ○ 1997, and males in ■ 1996 and □ 1997.

Faecal Analysis

The nitrogen content of faecal samples collected at the end of winter tended to be lower than in those collected during summer, in all age classes (Table 6.6; Figure 6.7). In both seasons, young and light weight individuals had higher faecal nitrogen levels than older and heavier animals (Table 6.7). The relationship between weight and faecal nitrogen was described by an exponential curve which was steeper at the end of winter than in summer (Figure 6.7; season-weight interaction $F_{1,242}=9.29$, $P<0.001$). There were no significant differences in faecal nitrogen content between the sexes after controlling for body weight. Parasite burden, as determined by faecal egg count, had a significant positive relationship with faecal nitrogen content (Table 6.7). As date increased at the end of winter, faecal nitrogen content increased, whilst during the summer, faecal nitrogen content decreased with time. Consequently there was a significant interaction between date and season.

Table 6.6 Mean (and variance) of faecal nitrogen content (% FN) determined from samples collected during the late winter and summer observation periods, for each age and sex class, in 1997.

		Females		*Males*	
		n	% FN	n	% FN
Wint. 97	*Yearlings*	14	1.98 (0.18)	16	1.94 (0.18)
	Adults	61	1.76 (0.27)	58	1.47 (0.14)
Sum. 97	*Lambs*	14	2.44 (0.13)	18	2.46 (0.33)
	Yearlings	15	2.42 (0.13)	12	2.29 (0.14)
	Adults	21	2.29 (0.10)	23	2.37 (0.06)

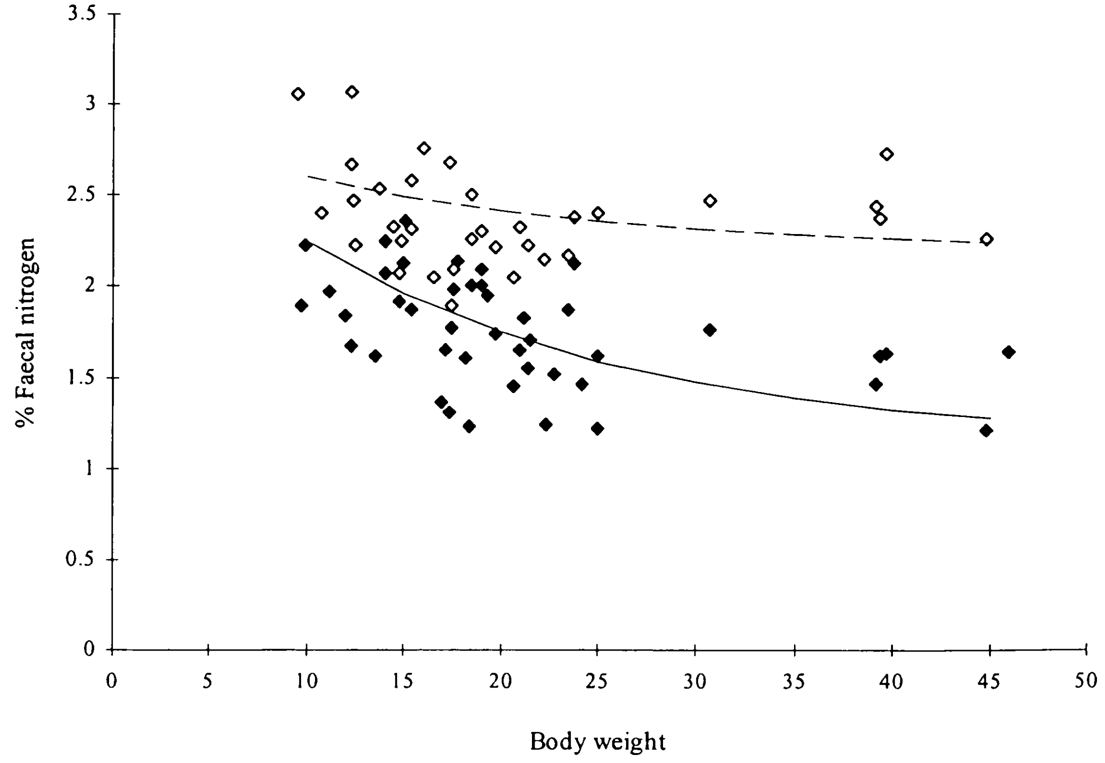
One interpretation of the observed trends is that diets were better quality in summer than winter, and that faecal nitrogen content declined as body weight increased due to the poorer quality diets of large bodied animals than small bodied individuals. If this argument holds, one may expect to find a positive relationship between faecal nitrogen and diet selectivity, once factors such as age, size and parasite burden have been controlled for. Consequently the residuals from the model in Table 6.7 were fitted in a new model of the gap selection index I_g (Table 6.8). Only data from 1997 were available so both seasons were modelled together. As predicted, positive deviations from the

Table 6.7 REML model for faecal nitrogen content in March and July / August of 1997. Individual and chemical analysis batch number were fitted as random effects. Fitted values (*Ewt*) from the exponential curve $Ewt=A+B*0.941^{wt}$ where A=1.265 or 2.190 and B=1.522 or 0.575 in winter or summer respectively, and *wt* was the August body weight, were fitted to account for the non-linear relationship between body weight and faecal nitrogen. Interactions are denoted by ' . ' between terms. Change in deviance is distributed as χ^2.

n=217, % variation explained : between individuals = 50.9 %, between batches = 56.2 %, within individual and batch = 11.9 %.

Term	Parameter estimates	se	df	Change in deviance
Constant	3.140	(0.259)		
Date	0.019	(0.004)	1	9.39 **
Season (summer)	-0.312	(0.767)	1	11.3 ***
Age	0.055	(0.020)	1	7.30 **
Ewt	1.336	(0.246)	1	23.3 ***
Faecal egg count	0.121	(0.038)	1	9.41 **
Date . Season (sum.)	-0.030	(0.009)	1	11.2 ***

Figure 6.7 The relationship between faecal nitrogen content and body weight in late winter and summer. Fitted lines are from the model in Table 6.7 (—— winter; – – – summer) and points are individual means of the observed data from ♦ winter and ◊ summer.



modelled faecal nitrogen content were significantly associated with an increased selectivity of gap (χ^2=7.07, df=1, P<0.010). This reinforces the proposed link between selectivity of grazing, faecal nitrogen content and diet quality. Furthermore, a greater proportion of the between-individual variation in gap selectivity was explained by this model than either of those in Table 6.5.

In addition, the effects of parasitism became far more pronounced when individual deviations in faecal nitrogen content were taken into account (Table 6.8). Faecal egg count interacted strongly with both age and sex, such that parasitised females avoided tussocks more than parasitised males and parasitised lambs and yearlings avoided tussocks more than parasitised adults. This implied that adult males were the least likely age and sex class to exhibit the predicted avoidance of tussocks as parasite burden increased (M.R.Hutchings *et al.*, unpublished).

Table 6.8 REML model of the gap selection index (I_g) for 1997, using both late winter and summer data and including the residual values from the faecal nitrogen model in Table 6.7 (resid FN). Age was fitted as a three level factor, (i) lambs, (ii) yearlings and (iii) adults. Individual was fitted as a random effect. Interactions are denoted by ' . ' between terms. Change in deviance is distributed as χ^2.

n = 318, % variation explained : within individuals = 17.4 %, between individuals = 40.8 %

Term	Parameter estimates	se	df	Change in deviance
Constant	-0.010	0.467		
R_a	0.268	0.134	1	0.46
Season (summer)	-1.002	0.335	1	8.65 **
Age (yearling)	1.038	0.458	2	1.48
(adult)	1.139	0.470		
Sex (M)	-0.140	0.230	1	1.37
Proportional weight	0.101	0.802	1	0.001
Faecal egg count	1.294	0.305	1	0.16
Resid FN	1.690	0.622	1	7.07 **
R_a . Season (summer)	-0.473	0.196	1	5.67 *
R_a . Prop weight	-1.489	0.475	1	9.59 **
Faecal egg . Age (y)	0.368	0.305	2	21.2 ***
(adult)	-1.173	0.403		
Faecal egg . Sex (M)	-0.997	0.237	1	15.3 ***

Discussion

Grazing preferences

An important finding from this study was that gap selection indices in summer were significantly higher in survivors of the following winter, than in non-survivors. This suggested that there was a fitness advantage associated with choosing to graze gap over tussock, in summer. However, whether this was due to selection of a higher quality diet or higher forage intake rates, or some combination of the two could not be determined. A knowledge of bite sizes and total daily intake would be needed to address this question. No differences were found between gap selection indices of survivors and non-survivors during winter. It therefore seems that summer may be a more important time of year for the expression of individual foraging strategies, rather than winter when all individuals are heavily constrained by forage availability.

In addition, this study suggests that of the two opposing foraging hypotheses presented, the body weight hypothesis (2) was more applicable to the Soay sheep on St. Kilda than the incisor arcade breadth hypothesis (1). Support for hypothesis (2), that small animals feed preferentially on high quality forage from gaps, came from the higher gap selectivity index of females in summer 1997. This could be explained either by the selection of a high nutrient diet by small females, in order to sustain their relatively higher metabolic rates (Kleiber 1961), or by the displacement of larger animals which are unable to support their absolutely greater metabolic demands for food on short swards (Clutton-Brock *et al.* 1982; Illius & Gordon 1987). The lack of support for hypothesis (2) from males or in other seasons may have arisen because the methodology was too crude to detect trends against the considerable environmental noise and high within-individual variability. In addition, in summer, the high availability and consumption of the 'intermediate' patch type meant that about 50% of bites were excluded from analysis. However, evidence from the faecal nitrogen analysis, discussed below, also supported hypothesis (2).

No evidence was found to support hypothesis (1) that individuals with broad incisor arcade breadths grazed more from gaps than individuals with narrow incisor arcades. This may have arisen because sheep, being relatively small ungulates are able to feed selectively (Grant *et al.* 1985), regardless of incisor arcade breadth. Gordon & Illius

(1988) suggested that ungulate species below about 100 kg body weight could feed with sufficient selectivity not to require adaptation of the dental arcade. In addition, in late winter when the gaps are dominated by bryophytes, the advantages of a large incisor arcade breadth, in terms of intake rate, may be counteracted by the difficulty in avoiding a high intake of bryophytes which have a low nutritional value (Prins 1981).

Marked seasonal differences in grazing selectivity were apparent, reflecting the changes in sward characteristics between late winter and summer. Protein content and digestibility are negatively related to sward maturity (van Soest 1982) with immature plants in low-biomass areas such as the gaps, tending to be of better nutritional quality than mature, high-biomass vegetation (Fryxell 1991). Furthermore, animal intake rates tend to be higher on short, heavily grazed swards than lightly grazed swards (Parson *et al.* 1983; Wallis de Vries & Daleboudt 1994). Since sheep preferentially select the sward that maximises herbage intake (Black & Kenney 1984), it was unsurprising to find that sheep favoured gaps in both seasons, but particularly in late winter. As mastication time decreases with declining bite mass (Newman *et al.* 1994), an increased bite rate may compensate for small bite sizes (Forbes 1988). However, bite sizes of Soay sheep, grazing under experimental conditions, were not significantly larger on low quality reproductive swards than on short vegetative swards, despite the reproductive swards being taller (Pérez-Barbería & Gordon submitted). This was presumably because sheep did not bite deeply into the reproductive sward, in order to avoid the pseudostem horizon (Barthram 1981). Furthermore, the long time taken to select good quality bites from tussocks in late winter apparently reduced the intake rate sufficiently for most animals to avoid them at that time of year (Ungar & Noy-Meir 1988).

The preference for gaps in summer, on St. Kilda, may have only been weak because the the costs of searching for the less abundant gaps (approximately 10% of the sward) outweighed the cost of grazing from the intermediate and tussock patches, for most individuals. In summer it may be that the intermediate patch type represents a good compromise between bite size, abundance and food quality. Unfortunately bite size data were not collected during the study on St. Kilda, but need to be known if the trade-offs between diet quality and quantity are to be fully understood.

Faecal nitrogen content

As with the grazing preferences, there were striking seasonal differences in faecal nitrogen content between late winter and summer. In addition, there was a significant decline in faecal nitrogen as body weight increased. Diet quality arguments could be invoked to explain both these observations, although other factors may also be involved.

From my original hypothesis (2), one would predict that small animals should select a higher quality diet than large animals and consequently would have a higher faecal nitrogen content, if it can be assumed that faecal nitrogen is a good indicator of diet quality (Holecheck *et al.* 1982; Leslie & Starkey 1987; Irwin *et al.* 1993). This argument was supported by an observed decrease in faecal nitrogen as consumption of grass stems increased and agreement between an individual sheep's faecal nitrogen content and a visual assessment of individual variation in the number of bites of leaves and stems eaten (Prache *et al.* 1998). The significance of deviations from the weight-specific faecal nitrogen relationship in the gap selectivity model also supported the relationship between diet quality and faecal nitrogen content. However, evidence from the foraging observations only supported hypothesis (2) for one sex, in one season, yet the faecal nitrogen trend was observed for both sexes in both seasons. Alternatively, large animals have greater gut capacities (Demment & van Soest 1985) allowing longer retention of digesta and increased digestive efficiency (Illius & Gordon 1991), which may have implications for the concentration of nitrogen excreted in the faeces.

Individual variation in faecal nitrogen also results from variation in metabolic excretion (Langlands *et al.* 1963) and parasite infection (Poppi *et al.* 1986). Consequently it was not surprising to find a highly significant effect of faecal egg count on faecal nitrogen content. Infection impairs gastric dietary protein breakdown resulting in enhanced excretion of nitrogen in the faeces of infected animals (Poppi *et al.* 1986; Fox *et al.* 1989). However, this effect may be counteracted to some extent by the reduced level of food intake caused by strongyle infection, resulting in a slower gastrointestinal transit rate (Gregory *et al.* 1985; Fox *et al.* 1989) and consequently lower excretion of endogenous nitrogen (Wehausen 1995).

There are a number of possible explanations for the observed higher faecal nitrogen content in summer than winter. The simplest is that diet quality is lower in winter and therefore faecal nitrogen content is lower (Leslie & Starkey 1985; Irwin *et al.* 1993). The interaction between season and date could then be explained by an improvement in forage quality as March progresses towards the start of the growing season. By contrast, during summer a decrease in faecal nitrogen could be caused by declining forage quality with time, as the sward matures and the number of reproductive stems increases (Prache *et al.* 1998).

However, ruminants tend to have lower voluntary food intake rates in winter (Hughes *et al.* 1962; Milne *et al.* 1978) because poorer quality forages with high cell wall contents have low passage rates (White *et al.* 1981). The resulting lower throughput rates cause less sloughing off of cells from the intestine walls, which contribute to the endogenous nitrogen component of faeces (van Soest 1982; Wehausen 1995). In addition, the anatomy of the gastrointestinal tract may also change in response to seasonal differences in diet quality (Weckerly 1987; Aagnes & Mathiesen 1996). However, the implications of this for nitrogen retention are not clear.

Tannins increase the concentration of nitrogen in the faeces (Robbins *et al.* 1987). This could also be a contributing factor to the higher faecal nitrogen contents in summer, irrespective of diet quality, because although tannins are virtually absent in grasses (McLeod 1974; Robbins *et al.* 1987), both tannins and phenolics are present in heather. The diets of Soay sheep on St. Kilda have a low heather content in March and April (Milner & Gwynne 1974) and therefore sheep would have a low tannin intake. By contrast, in the summer heather accounts for about a quarter of all epidermal fragments in faecal samples (Milner & Gwynne 1974), so increasing the faecal nitrogen content relative to late winter. However, it should be noted that faecal cuticle analysis is not considered a reliable method of assessing diet composition (McInnis *et al.* 1983).

This study has shown very strong differences in seasonal foraging behaviour and faecal nitrogen contents which I relate to seasonal differences in forage availability and quality. Individual variation in foraging behaviour in summer was related to body weight in females but no relationship was found with incisor arcade breadth. In addition, a survival advantage of increased gap selectivity in summer was found. Individual variation in grazing selectivity was harder to explain in winter, when no fitness advantages were found. The positive link between gap selectivity and faecal nitrogen content was explained in terms of selection for a high quality diet. This, together with the relationship between summer diet selection and survival, suggest that individual variation in grazing strategy has fitness implications for the individual.

CHAPTER 7.

Discussion

Discussion

Summary of major findings

Natural selection

My most important accomplishment in this thesis has been to demonstrate the natural selection of body weight in the Soay sheep of St. Kilda. I provide evidence that the three conditions necessary for natural selection to occur (Endler 1986) are present within the Soay sheep population. First, there is substantial individual variation in body weight (Figure 4.1, Tables 4.2 and Table 5.3). Second, two pieces of evidence support the fitness differences between phenotypes. In Chapter 3, I showed that there was a strong positive relationship between body weight and survival in all age, sex classes, and in Chapter 4 that significant differences existed between body weights of survivors and non-survivors. Evidence of phenotype fitness differences also comes from other papers which show the relationship between body weight and both the survival (Clutton-Brock *et al.* 1992; Bancroft *et al.* 1995a) and fecundity (Clutton-Brock *et al.* 1996; Clutton-Brock *et al.* 1997b) of Soay sheep. Third, the inheritance of body weight in both sexes was demonstrated in Chapter 5.

In addition, I demonstrate that the intensity of selection varies with population density (Chapter 4). Despite considerable advances in the study of density-dependent natural selection in model systems such as bacteria or *Drosophila* (reviewed by Mueller 1997), there are still very few cases in which it has been shown in a wild mammal population (Endler 1986; but see Moorcroft *et al.* 1996; Clutton-Brock *et al.* 1997b). My study is perhaps the only example of density-dependent selection of a morphometric trait in a free-living population.

Repeated selection

In Chapter 1, I set out three specific objectives that I aimed to address in this thesis. The first was to establish whether differential survival favoured the same individuals in repeated selection events or whether opposing selection occurred under different environmental conditions. This was addressed in Chapter 4, in which I demonstrated that indeed the same phenotypes were consistently favoured by phenotypic selection, and the same sectors of the population were repeatedly affected. Although a trend towards reduced survival of large lambs in low population years was apparent (e.g. in 1990 and 1992 in male lambs and in 1992 only in female lambs; Table 4.3), the number of individuals dying in these years was so low that *t*-tests could not be calculated or were not significant. No similar trends were observed amongst the adult population. The reduced survival of large lambs under low density conditions therefore had little impact at the population level, across the years. With the exception of Price *et al.*'s (1984) demonstration of recurrent selection of beak morphology in Darwin's medium ground finch (*Geospiza fortis*), this study is one of few instances in which repeated selection of a trait has been described in a natural population.

Heritability

The second objective was to determine whether the traits were heritable and whether an evolutionary response could be expected. In Chapter 5, I showed that all three morphometric traits had low but significant heritabilities, if the strict paternity pedigree was used. An evolutionary response would therefore be expected, especially since no evidence of significant opposing selection was found and since selection acting on female fecundity also favours increased maternal body weight (Clutton-Brock *et al.* 1997b).

The response to selection (R) can be predicted as the product of the selection differential (S) and the heritability (h^2).

$$R = h^2 S \quad \text{or} \quad R = h^2 S' \sqrt{v}$$

where S' is the standardised selection differential and v is the variance of the population before selection (Endler 1986; Falconer & Mackay 1996). In principle, the response to selection needs to be re-calculated for every generation since gene frequencies, and therefore heritabilities, change between generations and the rate of selection varies with time (Chapter 4). However, in practice, changes in gene frequencies will not be apparent for several generations and so the response is usually maintained with little change over five, ten or more generations (Falconer & Mackay 1996). In Chapter 4, standardised selection differentials were calculated for $\log_e$ transformed body weights. The mean S'

across the whole Soay sheep population and all years of the study was about 0.23. This is equivalent to a selection differential of 1.1 kg and if we assume a mean heritability of body weight of 0.20 (Chapter 5), the predicted response would be an increase in mean body weight of about 0.22 kg since 1985. This is insufficient to detect by regression, especially given the measurement errors of body weight and that the increase is unlikely to be evenly distributed. It is therefore not surprising that in Chapter 4 no increase in body weight was detected over the 12 years.

Only rarely is it possible to detect an evolutionary response to natural selection in the short-term. Darwin (1859) believed natural selection was working ‘daily and hourly on every slight variation’, yet the changes can not be observed ‘until the hand of time has marked the long lapse of ages’. However, there is an example from Darwin’s finches of the Galápagos, of measurable selection on beak depth in *Geospiza fortis* in just two years (Grant 1986). Selection was more intense than observed in the Soay sheep and was combined with much higher heritabilities of beak traits to give a very rapid response.

Foraging behaviour

The third objective of my study was to relate individual variation in foraging behaviour to differences in body or mouth size, and so establish a mechanistic explanation for the observed survival patterns. Despite considerable unexplained variation in grazing selectivity both within and between individuals (Chapter 6), I was able to show a positive relationship between grazing selectivity in summer and survival over the following winter. This suggests that individuals that preferentially grazed high quality, but low biomass, gap in summer were at a fitness advantage.

Individual phenotype did not have a large effect on foraging behaviour at the end of winter when good quality forage was scarce and nearly all individuals selectively grazed in the gaps. By contrast, in the summer, there was a negative relationship between body weight and selectivity for gap in adult females in 1997. This, together with higher faecal nitrogen levels in small individuals, supported the hypothesis that small animals select higher quality diets than large ones (Jarman 1974; Demment & van Soest 1985). No relationships were established between grazing behaviour and incisor arcade breadth, suggesting that body weight was more important than incisor breadth in determining foraging patterns. This evidence ties in with that presented in Chapter 3 and 4, to complete the picture of the relationships between body weight, foraging behaviour and survival.

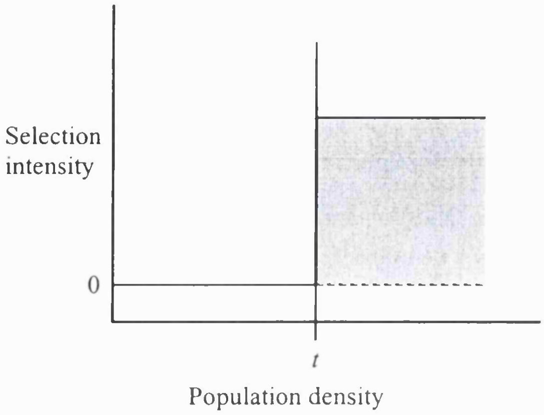
Other findings

Non-linearity of selection

My study has also highlighted the variation in selection pressure acting on different age and sex classes of population, as well as at different population densities. This may be important in that temporal changes in selection pressures can preserve genetic variation in traits that influence fitness (Anderson 1994). I found a non-linear relationship between population density and selection but because so few examples of density-dependent selection occur in the literature (Endler 1986), it is not possible to determine how usual this is. However, it was perhaps unsurprising to find very little selection occurring in years of low population density when survival was high. Furthermore, Price *et al.* (1984) found that the intensity of selection for large beak and body size in Darwin's medium ground finch (*Geospiza conirostris*) was greatest when survival was lowest, comparing between years and between sectors of the population.

The relationship between survival of Soay sheep and density is non-linear (Grenfell *et al.* 1998), whilst the relationship between selection and the proportion of the population surviving is linear (Figure 4.6). Therefore, one might expect the relationship between density and selection to reflect the pattern observed for survival. Examination of Figure 4.5 suggests that this is indeed the case. A schematic representation of the relationship is given in Figure 7.1 showing a 'broken-stick' model. However, there remains considerable uncertainty both about the shape of the relationship at the transition point between low and high population densities, and the threshold value (assumed to be a whole island population of approximately 1200 sheep in survival models (Grenfell *et al.* 1998)). More information from populations at or near the threshold size is required to parameterise the selection intensity model. In addition, as seen from the data points in Figure 4.5, the selection intensity is much more variable above the threshold than below it, depending on the severity of the winter. Similarly, Grenfell *et al.* (1998) found that at

Figure 7.1 Schematic diagram to show the relationship between the intensity of selection and population density, where *t* is the threshold density. Above *t* the intensity of selection increases by an amount that is dependent on environmental conditions so could lie anywhere within the shaded area.



high densities, the population size could increase, decrease or remain constant depending on environmental conditions.

Density and density-independent effects on survival

As indicated by the discussion above, environmental conditions, as well as population density, are known to have an important effect in determining over-winter survival rates of Soay sheep (Grenfell *et al.* 1998). In this thesis, I determine the relative importance of these two types of factor for survival, together with characteristics of the individual (Chapter 3). It transpired that individual phenotype was more important than either population density or climate in determining survival patterns. Although not explicitly stated in other studies (Gaillard *et al.* 1993; Jorgenson *et al.* 1997), this does also seem to be the case.

Whilst a number of authors have commented on the differences in survival of juveniles and adults in response to both density and environmental stochasticity (Sauer & Boyce 1983; Fowler 1987; Owen-Smith 1990; Gaillard *et al.* 1998), fewer have indicated the relative importance of each. From those that have (Douglas & Leslie 1986; Owen-Smith 1990; Jorgenson *et al.* 1997; Portier *et al.* 1998), no consistent pattern emerges as to whether it is density or density-independent climatic factors that regulate survival rates of ungulate populations. Sæther (1997) concludes that a combination of stochastic variation in the environment and population density influence population dynamics. It seems that the balance between density and density-independent effects may vary between species, populations and local environmental carrying capacities.

Analysis techniques

This thesis has also provided a testing ground for some new analysis techniques. As computer processing time reduces, the use of complex statistical techniques is becoming increasingly realistic, opening up many new avenues of analysis to be explored. For the survival analysis presented in Chapter 3, I used generalised linear mixed modelling (GLMM), so called because it includes a mix of both fixed and random terms. This enabled random year to year variation in survival to be taken into account. It is a new, robust and, as yet, under-used technique which enabled the analysis of the entire adult Soay sheep data set. With it, I was able to show that the use of repeated records from the same individual over a number of years did not bias the results. Even more importantly, a comparison between the results obtained using GLMM and logistic regression analysis showed that the estimates of significance of terms that varied only between years, were flawed and seriously exaggerated. This shows the importance of including random effects in models and to some extent brings into question the validity of studies in which these effects have been ignored. It consequently has implications for all sorts of ecological studies in which the variation of some terms has a different structure to that of others.

In Chapter 5, I also used a new analysis technique for estimating heritabilities, which despite featuring in the animal breeding literature since the late 1980s (Kennedy 1989), has never been applied to a wild vertebrate population before. This is somewhat surprising considering the benefits of the mixed, multivariate 'animal model' approach in populations that are under-going selection and where data sets are unbalanced (Groenevald *et al.* 1992; Knott *et al.* 1995). Ecological data sets are rarely able to satisfy the assumptions of least-squares methods of heritability estimation (Shaw 1987). Consequently, there strikes me as being considerable potential for the application of animal models in ecology, particularly in quantitative genetic studies of populations where there is long-term monitoring of known individuals.

Evolutionary implications

Evolution of body size

This thesis has shown clear evidence for the natural selection of body weight. Although no evolutionary response has been detected over the last 12 years, this must have implications for the evolution of body size in Soay sheep. Many hypotheses have been put forward to explain the evolution of body size. Those relevant to the discussion of increasing body size predicted on St. Kilda include Cope's Rule that animal taxa tend to evolve towards larger body size (Damuth 1993), Bergmann's Rule explaining large body size at northern latitudes (McNab 1971; Searcy 1980) and the fasting endurance hypothesis (Lindstedt & Boyce 1985; Millar & Hickling 1990; Chapters 1 & 4). The island rule, which accounts for gigantism in insular small mammals and dwarfism in large mammals (van Valen 1973; Lomolino 1985), would predict that Soay sheep should become smaller due to limiting food resources. Underlying all these hypotheses are mechanisms based on energetics and the allometry of body size and metabolic rate (McNab 1971; Western 1979; Damuth 1993; Brown *et al.* 1993), competition and predation (Hutchinson & MacAurthur 1952; Schoener 1970).

Alternatively, if feeding efficiency is subject to natural selection, there is the potential for selection of body size to be based on foraging efficiency (Belovsky 1987). Demment and van Soest (1985) provide a nutritional explanation for body size patterns in large herbivores based on digestive efficiencies. In the course of this study, I have been able to identify that natural selection of body weight is occurring and propose a mechanism by which this could operate. I link over-winter survival with grazing behaviour in summer and the selection of short vegetative forage. In addition, circumstantial evidence of survival patterns enables a link to be made between body size, selection and foraging if the fasting endurance hypothesis is invoked.

I have been unable to resolve whether it is body weight itself, body condition (a component of body weight) or some other character that is closely correlated with weight, that is under selection. The lack of evidence of direct selection of hindleg length (Chapter 4) suggested that condition or fat stores, rather than skeletal size, may confer the selective advantage on heavy animals. Body condition has fitness advantages for survival and fecundity. Fat reserves play an important role in survival, especially in seasonal environments, as advocated by the fasting endurance hypothesis (Chapters 1 & 4; Lindstedt & Boyce 1985). Although body weight has an important effect on fecundity (Albon *et al.* 1983; Jorgenson *et al.* 1993), it may well be that body condition is the component responsible for this. Certainly, condition has been shown to affect female fertility in sheep (Gunn & Doney 1975) and fertility is related to kidney fat index in red deer (Albon *et al.* 1986). In addition, body condition could be related to other fitness traits such as natural immunity or resistance to parasites and disease, but as yet no data are available to test this in the St. Kilda population.

Evolution of foraging efficiency

Since natural selection acts to maximise energy intake (Stephens & Krebs 1986), we would expect foraging efficiency to be under very strong selection pressure. This could explain why amongst large herbivores we see many different anatomical adaptations to diet (Demment & van Soest 1985; Janis & Ehrhardt 1988; Hoffman 1989). The search for evidence of the natural selection of foraging efficiency in the Soay sheep has only just begun with this study.

In terms of satisfying Endler's (1986) three conditions of natural selection, my results suggest that there is some individual variation in foraging behaviour, or more specifically, in grazing selectivity. This was also demonstrated by Prache *et al.* (1998). However, I have been largely unsuccessful in determining what factors explain the variation, especially in winter. Sex, age and body weight accounted for a small proportion of it whilst incisor arcade breadth was not significant at all (Chapter 6). I have also been able to demonstrate a fitness advantages of grazing selectivity in summer, when the gap selection index was positively related to survival during the following winter. No connection was derived between either grazing selectivity or faecal nitrogen content in winter and survival. Similarly, no evidence was found of a relationship between winter food supply and moose (*Alces alces*) calf survival amongst Norwegian populations (Sæther *et al.* 1996). By contrast, density-dependent calf survival of wild reindeer herds (*Rangifer tarandus*) was mediated by winter forage availability (Skogland 1985). The fitness advantages of grazing behaviour may, however, also be closely related to fecundity but this was not assessed in this study (Langvatn *et al.* 1996; Sæther & Heim 1993). Further work needs to be carried out on the fitness advantages of foraging behaviour.

At the outset of this project, it was thought that countervailing selection of incisor arcade breadth may act during summer and non-crash winters when vegetation is abundant and sheep must graze selectively to maintain diet quality. This was based on pre-1995 experiences when it was assumed that non-crash winters were also low population density winters. The situation on St. Kilda during recent winters has been markedly different from expectation, in that the population has increased continually since the last minor crash in the winter of 1994/95. Consequently the population has reached record levels without crashing, and as a result vegetation conditions have been more similar to those of crash winters than non-crash winters. This means that it has not been possible to carry out the planned comparison of grazing behaviour between abundant and sparse vegetation conditions. Although the effect of countervailing selection of incisor breadth on reproductive fitness has not been tested, the argument for countervailing selection during over-winter mortality in non-crash years does not stand up to close scrutiny. Firstly, there was no evidence of enhanced survival of small mouthed individuals either in low population density years, or any other (Table 4.4). This was partly because there were so few deaths in low density years. Secondly, although in most cases we do not know the cause of death of individuals dying in low population years, it is generally not starvation. It is therefore inappropriate to invoke the same foraging and diet quality arguments to explain observed survival patterns as used in crash years.

However, having said this, some interesting and unexpected results came to light in Chapter 4 when the correlation between traits was taken into consideration. When standardised selection gradients were calculated (Table 4.5), a general result of direct selection for increased body weight was found. Since body weight and incisor breadth are positively correlated (Table 4.1), we would expect indirect selection of incisor arcade breadth to be positive. However, in five of the seven winters studied in lambs and 3 winters in adults, indirect selection of incisor breadth was negative, despite positive selection of body weight. Although these trends were not significant, it does suggests that something other than what had been predicted is going on. The implication is that under high population density conditions, a narrow incisor breadth relative to body weight may in fact be advantageous. As suggested in Chapter 4, this could possibly be explained if large mouth size was associated with high intake rates of bryophytes, which have a low nutritional value (Prins 1981).

Future Research

The previous sections of this discussion have raised a number of further questions worth investigating. In particular, what is the functional mechanism underlying the fitness advantage of large body weight? Are body condition and energy reserves the crucial factors that account for the superiority of heavy animals? What non-nutritional factors, such as disease resistance, affect body condition and how important are these in determining fitness? How do the fitness advantages of grazing selectivity vary with population density? These are all issues that should be addressed if a more comprehensive understanding of the natural selection observed on St. Kilda, is to be achieved.

In addition, one wonders whether the observed directional selection over the past 12 years is part of a much longer trend or whether it has arisen as a result of climate change. An interesting starting point may therefore be to conduct a comparison between the morphometrics of the Soay sheep now, and data collected on St. Kilda during the 1960s. Over this longer time period, evolutionary changes should be easier to detect. Unfortunately body weight data collected during the two periods are not directly comparable because animals tend to have been caught at different times of year. In cases where animals have been caught at the same times of year, such as those caught in cleits at night in November, they are currently processed immediately whereas during the 1960s, sheep were kept in the cleit over night and weighed the next morning (P.A. Jewell, pers. comm.). Consequently body weights from the 1960s may appear lower because of less gutfill at weighing. However, if appropriate correction factors are applied, statistical comparisons should nonetheless be possible.

A collection of bones, including skulls and long bones, was made on Hirta between 1959 and 1979 (J.Clutton-Brock *et al.* 1990). In addition, skulls and leg bones of all carcasses found of sheep tagged since 1985 have also been kept. This material would therefore provide an excellent opportunity to investigate changes in skeletal size over the past 30-40 years. This may help to understand whether it is skeletal size or body condition that is under selection.

Finding a suitable measure of body condition for Soay sheep would greatly help in disentangling the effects of skeletal size and condition. As discussed in Chapter 4, Soay sheep deposit very little subcutaneous body fat (McClelland *et al.* 1976) but as ultrasound equipment becomes more sophisticated, and portable, it may yet be possible to measure other fat deposits. This could provide a very important variable which would be clearly related to survival and fecundity, but which may also be more easily related to foraging efficiency. In addition, condition is likely to be related to disease resistance. The relationship between parasite resistance, condition and survival needs to be better understood, if we are to rule out alternative explanations of my results, such as selection for disease resistance.

Foraging behaviour during the summer appeared to be the time of year when individual variation was important. Since protein and energy levels are likely to be below maintenance for most, if not all, individuals in the late winter (Milner & Gwynne 1974; Clutton-Brock *et al.* 1997a), there is less scope for individual variation. By contrast, in summer, those sheep foraging particularly efficiently will be in a position to build up large energy reserves enabling them to survive the winter. Summer therefore seems to be the season in which more attention should be focused. A comparison of foraging behaviour under the vegetation conditions of high and low population density summers would be particularly useful.

Individual variation in foraging behaviour was poorly explained. Since there are apparent fitness advantages associated with grazing selectivity, there is an obvious need for a better understanding of what determines individual foraging choices. The methods used here were apparently too crude to detect clear patterns of individual behaviour. However, grazing trials carried out under more controlled, experimental conditions with artificial swards maybe useful. The disadvantage of such trials is that they tend to be short-term and so the long-term fitness benefits of various strategies can not be monitored. A desirable alternative would be to manipulate the natural swards, but the World Heritage Site status of St. Kilda, together with a number of logistical problems mean that in practise this is not a feasible option.

Having demonstrated the natural selection of body weight in Soay sheep arising from differential survival, a complementary study now needs to be carried out for fecundity.

A preliminary investigation suggests that selection for increased body weight also occurs through female fecundity (Clutton-Brock *et al.* 1997b), but this needs to be clarified for all sectors of the population and under the contrasting conditions of different years. In addition, the influence of male body weight on reproductive success has never been assessed, but has very important evolutionary implications because of the potential role of body weight in sexual selection as well as natural selection.

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