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Population dynamics in Soay sheep

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3.1 Introduction

A conspicuous feature of many naturally limited populations of long-lived vertebrates is their relative stability. Both in populations that are regulated by predation or culling and in food-limited populations, population size can persist at approximately the same level for decades or even centuries (Runyoro *et al.* 1995; Waser *et al.* 1995; Clutton-Brock *et al.* 1997a; Newton 1998). The persistent fluctuations shown by Soay sheep and by some other island populations of ungulates (Boyd 1981; Leader-Williams 1988; Boussès 1991) raise general questions about the causes and consequences of variation in the stability of populations (see section 1.2). How regular are they? How are they related to population density? What are their immediate causes? To what extent do fluctuations in food availability, parasite number or predator density contribute to them? And what are their effects on development and on the phenotypic quality of animals born at contrasting population density? And how much do changes in phenotype contribute to changes in dynamics?

As yet, there are very few cases where we understand either the ecological causes or the demographic consequences of persistent

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fluctuations in population size (Hanski 1987; Saether 1997). Since we are able to monitor the growth, movements, breeding success and survival of large samples of individuals as population density changes, the Soay sheep offer an opportunity to investigate the causes and consequences of changes in population size with unusual precision (see Chapter 1). While the absence of predators and the constraints on dispersal imposed by the habitat are likely to affect the relative contribution of different processes to changes in population size (see Chapter 10), the factors causing fluctuation in sheep numbers are likely to contribute to changes in population size in many other populations.

In this chapter, we start by describing the immediate causes of changes in the size and structure of the Soay sheep population on Hirta (section 3.2). Previous analyses of the population dynamics of the Soay sheep population of Hirta (Grubb and Jewell 1974) did not have access to a large enough time series to investigate the effects of variation in population density on reproduction and survival and this was an early objective of our study. Sections 3.3 to 3.5 examine how fecundity, development and survival change with population density and how climatic differences between years contribute to these effects. Variation in environmental conditions also affects early development with consequences for the subsequent growth, breeding success and survival of members of different cohorts (section 3.6). In sections 3.7 and 3.8, we describe our attempts to predict changes in the size of the population using progressively more complex models, while in section 3.9 we examine the degree of synchrony between sheep populations on the different islands of St Kilda.

3.2 Changes in population size

Numbers of Soay sheep on Hirta fluctuate widely as a result of variation in winter mortality (Fig. 1.5). Between 1959 and 1968, total numbers fluctuated from 610 to 1598 while numbers in the Village Bay population fluctuated from 174 to 404 (Grubb 1974). Between 1985 and 2000, total numbers fluctuated from 663 to 2022 and numbers in the Village Bay population from 211 to 591. Increases in population size were associated with an increase in the number of animals using

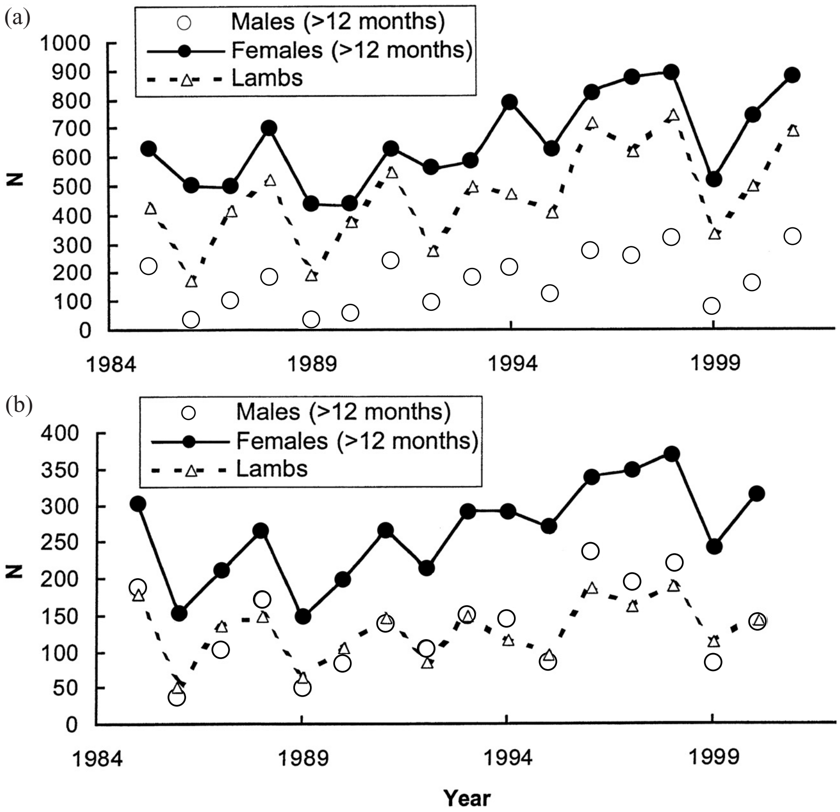


FIG. 3.1. Numbers of male and female sheep (over twelve months) and lambs (less than twelve months) (a) on the whole of Hirta (b) in the Village Bay sub-population 1985–2001. Estimates of population size for the whole island based on August counts; estimates for the Village Bay population based on censuses of marked individuals.

the most heavily populated areas rather than with an extension of the area used.

Fluctuations in numbers are more marked in some age and sex categories than others. Variation in male numbers is greater than in female numbers and variation in juvenile numbers is greater than in adult numbers (Fig. 3.1a), reflecting the increased susceptibility of males and juveniles to starvation (see sections 2.8 and 2.9).

While we counted the whole sheep population annually (see section 1.6), most of our work (like that of Jewell and his collaborators) was carried out on the Village Bay sub-population, which typically

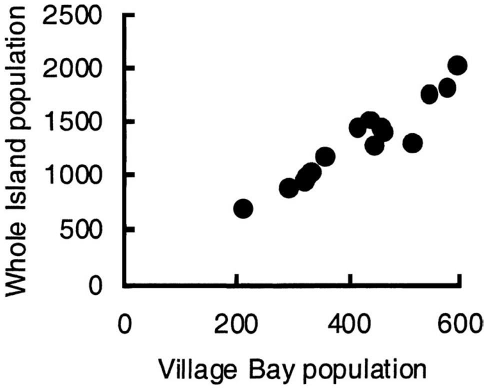
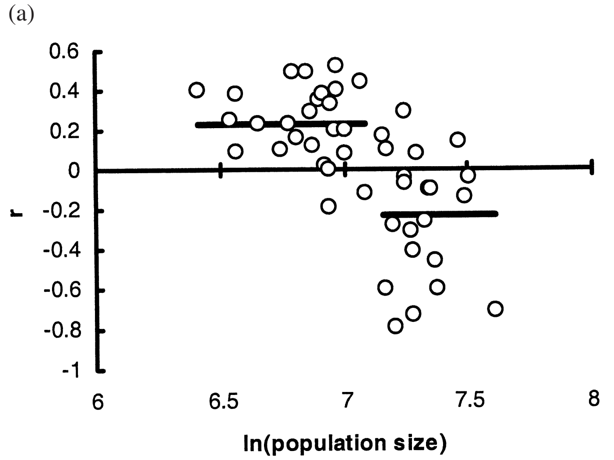


FIG. 3.2. Total number of sheep on Hirta plotted against totals for the Village Bay sub-population 1984–2002.

includes between a quarter and a third of all the animals on Hirta. Numbers of sheep using Village Bay show similar fluctuations to the whole island population (Fig. 3.1b) and their numbers are closely correlated with population size for the whole island (Fig. 3.2).

Both across the whole island and within Village Bay, year-to-year changes in population size show a pronounced threshold effect (Fig. 3.3a, b). When there are fewer than 1100–1200 animals on the island, the population increases by about 1.27 per animal per year but, when there are more than this number, it declines by an average factor of around 0.2 per animal per year. Though juvenile mortality is more variable than adult mortality, variation in adult mortality has a greater impact on changes in population size since there are more adults in the population. Adult and juvenile mortality, together with the positive covariance between them, are the key factors responsible for changes in population size (Clutton-Brock *et al.* 1991; Coulson *et al.* 1999a) (Fig. 3.4).

Years of high mortality when numbers decline are usually separated by two or three years when population size increases (Fig. 1.5), generating an alternation of boom years followed by sudden crashes. This pattern was most apparent between 1985 and 1995, when three separate years of high mortality (1985, 1988 and 1991) were each followed by two years of rapid population increase. In contrast, after the crash of 1995, numbers increased in 1996 and in 1997 and remained high in 1998 before crashing in 1999. After this, two years of increase in population size were once again followed by a crash in 2002. Similar



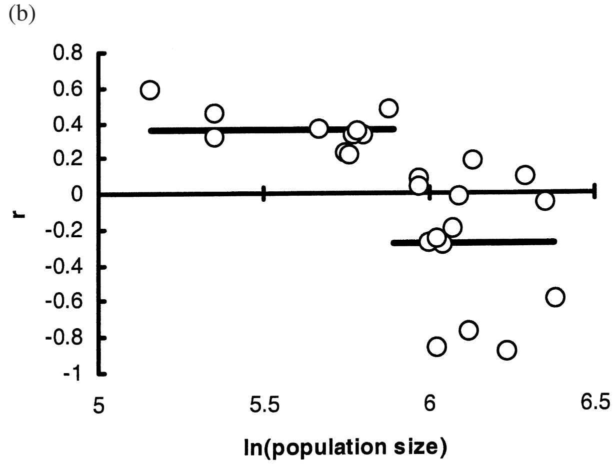


FIG. 3.3. (a) Changes in total population size on Hirta ($r = \ln [N(t+1)/N(t)]$) as a function of log density, showing the threshold population density below which population tends to increase at a density-independent rate of $r = 0.235$ and above which population tends to decline at a density-independent rate of $r = -0.213$. (b) Changes in population size in the Village Bay sub-population (as above).

variability in the timing of years of high mortality occurred between 1960 and 1968.

The tendency for years of high mortality to be separated by two or three years of rapid population growth probably reflects the number of years necessary for a basal population of less than 1000 sheep

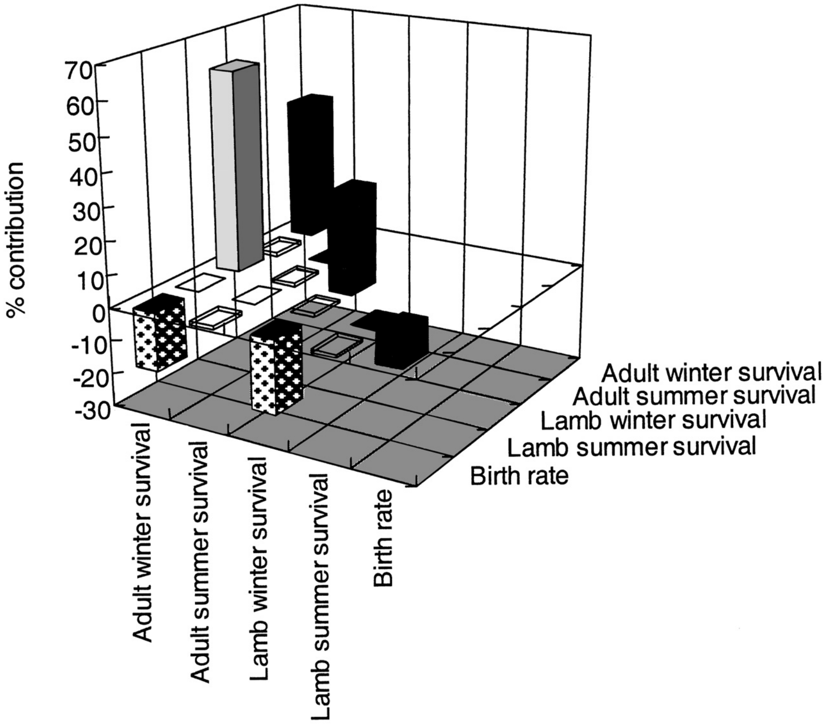


FIG. 3.4. Analysis of the key factors associated with relative changes in the size of the Village Bay population for 1986–1994 inclusive (from Coulson *et al.* 1999a). Structured demographic accounting of the variance of demographic change (Brown *et al.* 1993) was used to decompose the population fluctuations in the percentages due to changes in lamb and adult summer and winter mortality and the birth rate. The most important factors are juvenile and adult winter survival (the large black bars) and the positive co-variation between them (the large grey bar). Birth rate was not as important (the small black bar), explaining approximately 10% of the fluctuations in population size. However, birth rate did negatively co-vary with both juvenile and adult winter survival explaining 22% and 17% of the relative changes in population size respectively.

to regain a size at which heavy winter mortality is likely to recur (Clutton-Brock *et al.* 1997a). It is possible that longer intervals between crashes may have occurred between 1968 and 1985 (Fig. 1.5), but the reliability of these estimates is uncertain. Several aspects of the data from this period are surprising, including the progressive downward trend between 1971 and 1978, and we suspect that estimates of changes in population size over this period are unreliable.

3.3 Density-dependence in fecundity

Fecundity changes with population density in young and old ewes (Fig. 3.5a). The proportion of juveniles producing lambs when they are around twelve months old varies between years from less than 10% to over 80% and is low when autumn density is high (Fig. 3.5b) or winter weather conditions are wet and windy (Tavecchia *et al.* in press). Among yearlings, the proportion of individuals producing lambs at around twenty-four months shows a weak tendency to decline with increasing density (Fig. 3.5c) while, among adults, around 80% of individuals produce lambs each year, irrespective of population size (Fig. 3.3d) or reproductive status in the previous year (Fig. 3.5e). However, twinning rates decline with increasing density (Fig. 3.5f) and the incidence of abortions during late pregnancy increases.

As in bighorn sheep (Festa-Bianchet *et al.* 1998), variation in fecundity in young animals is related to variation in body weight during

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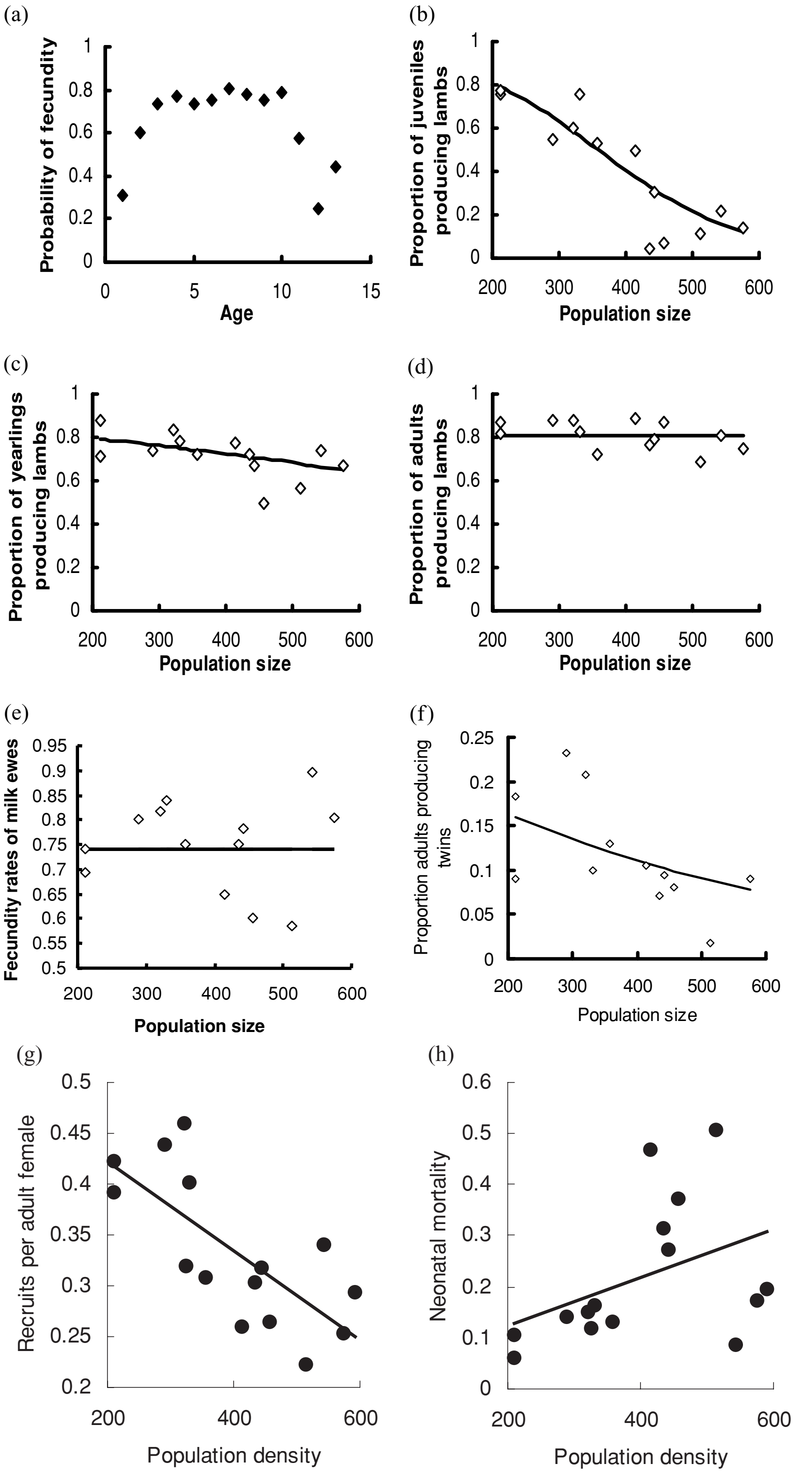
FIG. 3.5. Effects of population density on the fecundity of Soay sheep in the Village Bay population, 1986–98. Fecundity is the proportion of animals in the population that gave birth either to singleton or twin lambs in the spring while population density is the total size of the population in the Village Bay area the previous winter. As a result, after years when winter mortality is high, low fecundity is associated with high winter density but low density in the spring and summer after lambs are born. (a) Fecundity in relation to age, showing that the most parsimonious groupings of individuals are in four age classes: lambs, yearlings, adults (two to ten years) and older animals (over ten years). (b) Changes in the proportion of juveniles giving birth at approximately twelve months. (c) Changes in the proportion of yearlings giving birth at approximately twenty-four months. (d) Changes in the proportion of adults (over twenty-four months) giving birth to singleton lambs. (e) Changes in the proportion of adults (over twenty-four months) giving birth to twin lambs. (f) Changes in the proportion of females that had raised a lamb the previous year that gave birth. (g) Changes in neonatal mortality with population density the previous winter. (h) Recruits per adult. Fitted lines are from logistic regression models. Sloping lines represent a significant association between the fecundity measure and density, horizontal lines represent no significant association.


(a)
Probability of fecundity
1
0.8
0.6
0.4
0.2
0
0
5
10
15
Age
(b)
Proportion of juveniles producing lambs
1
0.8
0.6
0.4
0.2
0
200
300
400
500
600
Population size
(c)
Proportion of yearlings producing lambs
1
0.8
0.6
0.4
0.2
0
200
300
400
500
600
Population size
(d)
Proportion of adults producing lambs
1
0.8
0.6
0.4
0.2
0
200
300
400
500
600
Population size
(e)
Fecundity rates of milk ewes
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
200
300
400
500
600
Population size
(f)
Proportion adults producing twins
0.25
0.2
0.15
0.1
0.05
0
200
300
400
500
600
Population size
(g)
Recruits per adult female
0.5
0.45
0.4
0.35
0.3
0.25
0.2
200
400
600
Population density
(h)
Neonatal mortality
0.6
0.5
0.4
0.3
0.2
0.1
0
200
400
600
Population density

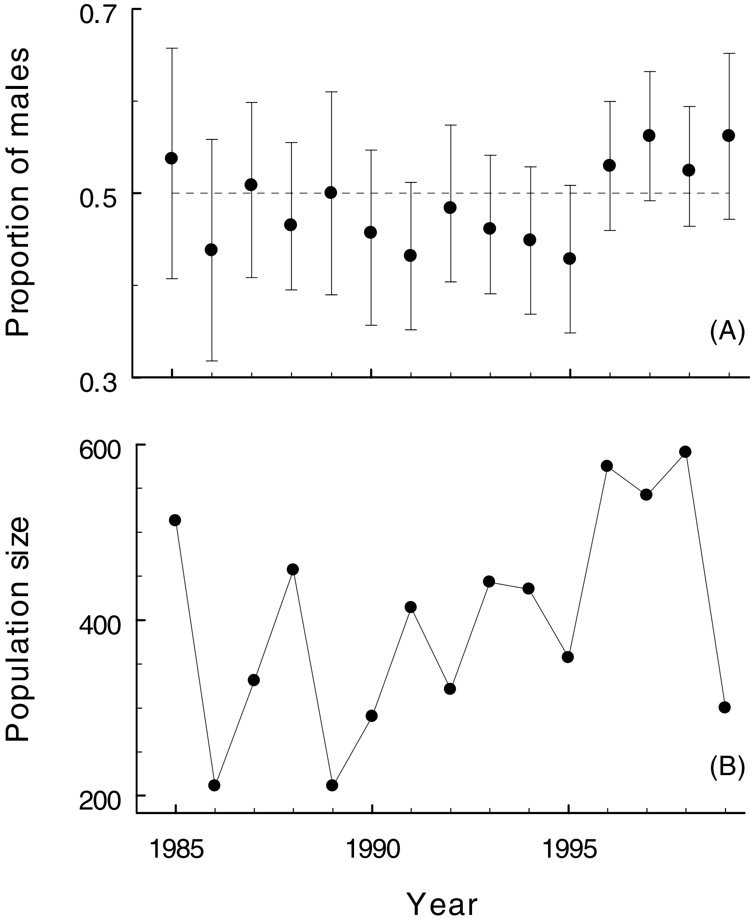


FIG. 3.6. (a) Proportion of males born in different years (±95% confidence limits (Zar 1996). (b) Population fluctuations in the Village Bay area 1985–98. (From Lindström *et al.* 2002.)

the preceding summer (see Chapter 2) (Clutton-Brock *et al.* 1996). In contrast, among adult ewes, increased weight has little effect on their probability of breeding: over 80% breed each year, irrespective of their weight and of whether or not they reared a lamb the previous year. However, twinning rates vary with body weight, ranging from 0% to 8% between years among ewes of 15–20 kg and from 23% to 38% among ewes of over 25 kg (Clutton-Brock *et al.* 1996).

In mammals where adult males are larger than females, juvenile males grow faster than females before and after birth and males commonly show higher levels of mortality both before and after birth (Clutton-Brock *et al.* 1985a). As a result, female-biased birth sex ratios are sometimes found in populations where pregnant females are exposed to food shortage or harsh conditions (Clutton-Brock 1991) though these trends are by no means universal (Clutton-Brock and Iason 1986). For example, in red deer, the proportion of males born falls when winter density is high or winter weather is wet and windy (Kruuk *et al.* 1999a). In Soays, the proportion of male lambs born varies from 43% to 56% between years (Fig. 3.6). Birth sex ratios are not consistently related to weather conditions or to the mother's age or weight though there is a weak positive correlation with population density the previous autumn (Lindström *et al.* 2002). A possible functional explanation is that it is advantageous for females to produce males after years when autumn density and winter mortality are high because these will join a relatively small cohort of lambs that are likely to show high survival and breeding success (West and Godfray 1997). However, the trend is weak and it is not yet clear whether it is consistent. In bighorn sheep, too, there is little evidence of consistent variation in birth sex ratios, apart from a tendency for old mothers to produce relatively few males (Bérubé *et al.* 1996; Festa-Bianchet 1996; Gallant *et al.* 2001).

3.4 Variation in birth weight and neonatal mortality

High population density and wet, windy weather depress the average birth weight of lambs and, in conjunction, population density and weather account for 76% of variation in mean birth weight between cohorts (Forchhammer *et al.* 2001). Birth weight declines by around 200 g with every additional 100 sheep using the study area, falling from around 2.2 kg when population density the previous winter is low to 1.7 kg at high density (Clutton-Brock *et al.* 1992) (Fig. 3.7a). These results contrast with the absence of any relationship between density and birth weight in some other ungulates, including mountain goats (Côté & Festa-Bianchet 2001) and red deer (Clutton-Brock and Albon

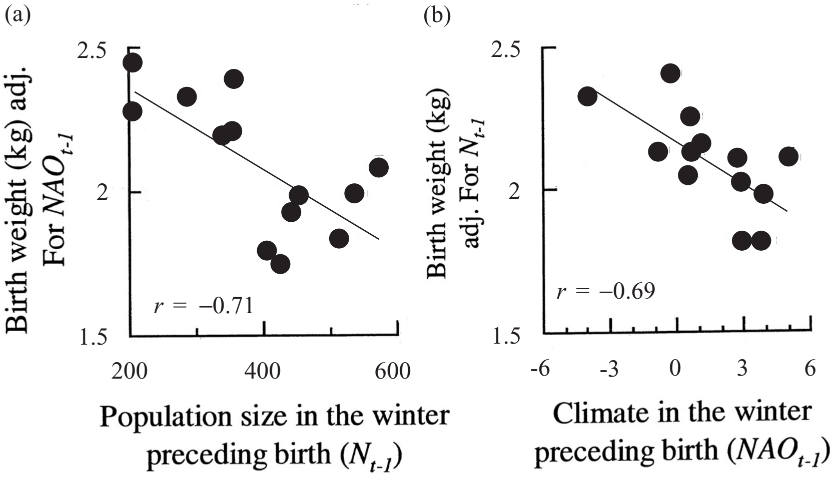


FIG. 3.7. Relationships between mean birth weight and (a) population size (N_{t-1}) and (b) climate severity (NAO_{t-1}) in the winter before birth. Correlation coefficients (r) shown in bold are significant ($p < 0.05$). Through generalised linear models taking maternal age and weight into account, the combined variation in N_{t-1} and NAO_{t-1} was found to explain 28% and 14% of the variation in cohort birth date and birth weight respectively. (From Forchhammer *et al.* 2001.)

1989). When the effects of population density have been allowed for, birth weight also falls after wet, windy winters (Fig. 3.7b). While birth weight varies with litter size, lamb sex and mother's age (section 2.7), there is no evidence that changes in density either exaggerate or reduce these effects (Clutton-Brock *et al.* 1992).

Neonatal mortality, too, varies with population density the previous winter, increasing from less than 10% when population density the previous winter is low, to around 40% when it is high (Clutton-Brock *et al.* 1992; Forchhammer *et al.* 2001) (Fig. 3.8a, b). When the effects of population density have been allowed for, neonatal mortality rises after wet, stormy winters, when the North Atlantic Oscillation (NAO) index (see Chapter 2) is high (Fig. 3.8c, d). Changes in birth weight are responsible for much of this variation, but significant effects of density and winter climate in the year before birth remain when the effects of birth weight are controlled (Clutton-Brock *et al.* 1992). As in red deer, there is no evidence of any difference in the effects of

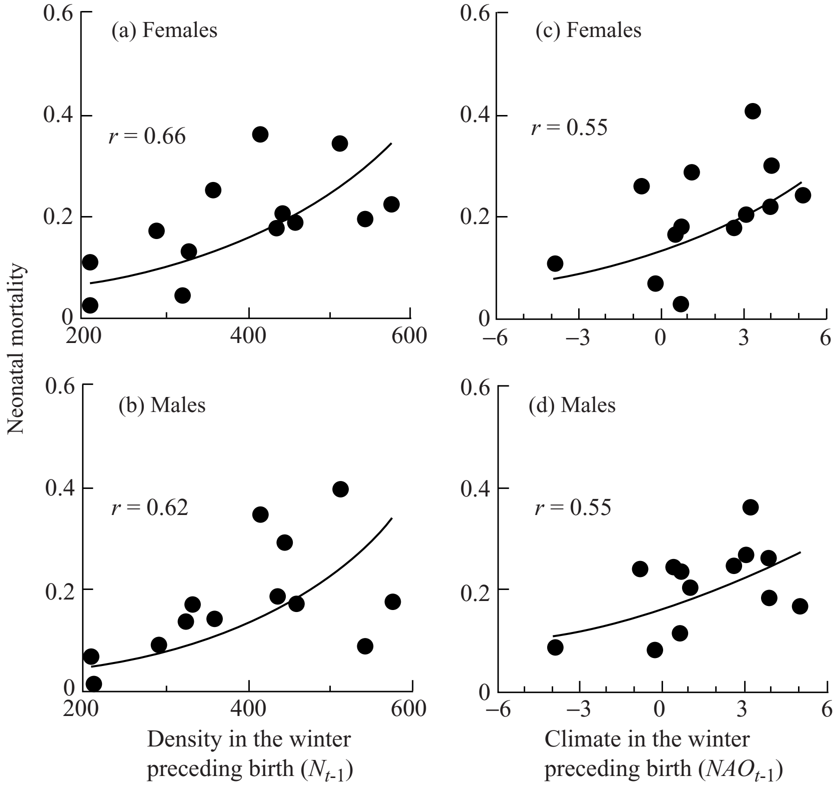


FIG. 3.8. Changes in neonatal mortality of female and male lambs with variation in density (N_{t-1}) and climate (NAO_{t-1}) in the winter preceding birth. (a) Mortality rates in female lambs plotted against N_{t-1}; (b) mortality rates in male lambs plotted against N_{t-1}; (c) mortality rates for female lambs plotted against NAO_{t-1}; (d) mortality rates for male lambs plotted against NAO_{t-1}.Correlation coefficients (r) shown in bold are significant ($p < 0.05$). Maternal age and weight, birth weight and date and twin birth were controlled for in all analyses as well as climatic variation (in a, b) or population size (in c, d). (From Forchhammer *et al.* 2001.)

density or weather on the relative survival of male and female lambs through the neonatal period.

As a result of density-dependent changes in juvenile fecundity and in neonatal mortality, rates of recruitment decline after winters when density is high (Fig. 3.9). However, this has little effect on the dynamics of the population since high winter density is associated with high

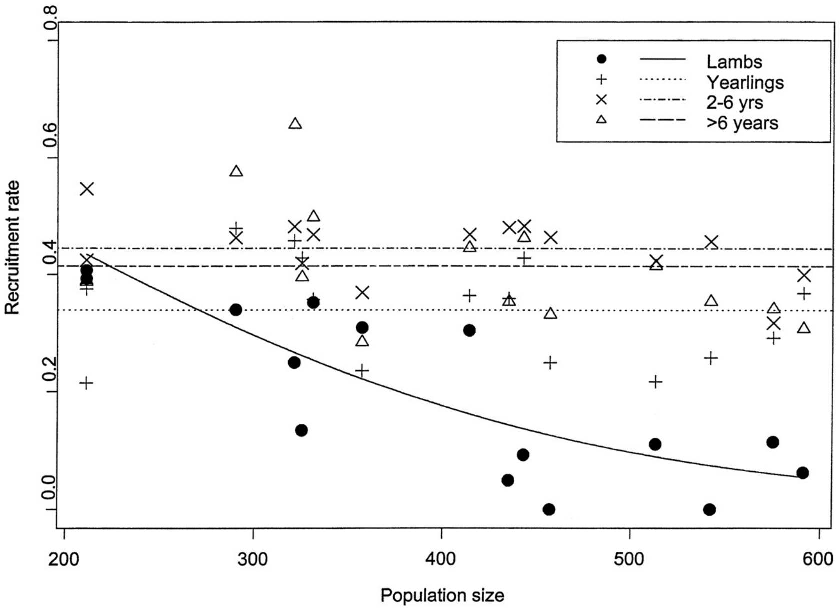
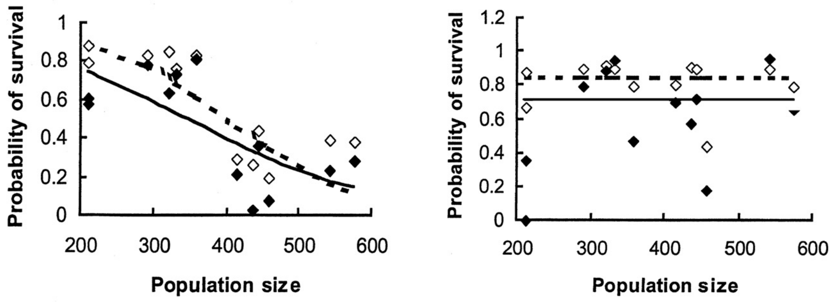


FIG. 3.9. Effects of population density in autumn on recruitment rates. Recruitment rate is the number of lambs produced that survived to six months of age per adult female. Solid points and line represent animals that were twelve months of age when they gave birth, while the three interrupted lines show recruitment rates for yearlings, two- to six-year-olds and older animals respectively.

mortality the following spring, so that reductions in birth rates occur after population density has fallen. As a result, density-dependence in fecundity may delay the rate at which the population recovers, but does little to slow the rate of increase once population size has started to rise (Clutton-Brock *et al.* 1997a).

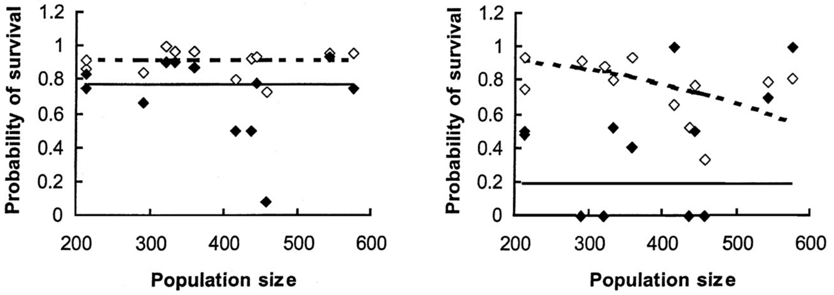
3.5 Winter mortality

Winter mortality of juveniles and older adults varies with population density (Fig. 3.10a–d). Lambs of both sexes are usually the first to die, followed by yearling and adult males and adult females while, among adults, older individuals typically die before animals in their prime (Clutton-Brock *et al.* 1997a). While high mortality only is confined to years when summer density is high, the sheep do not always show high mortality when numbers are high. For example, sheep numbers



(a) Juveniles

(b) Yearlings



(c) Adults

(d) Older adults

FIG. 3.10. Effects of population density on the survival of Soay sheep in the Village Bay population, 1986–98, showing survival plotted against total population density. Open symbols and dotted lines represent values for females, closed symbols and solid lines, values for males. The most parsimonious grouping of individuals for analyses of survival group animals in eight age classes: female juveniles, male juveniles, female yearlings, male yearlings, female adults (two to six years), male adults (one to six years), older females (over six years) and older males (over six years). (a) Changes in survival of juveniles; (b) changes in survival of yearlings; (c) changes in survival of female and male adults; (d) changes in survival of older females and males. (From Coulson *et al.* 2001.)

in the winter of 1997/8 were 542 in the study area and 1751 on the whole island but, despite the unusually large size of the winter population, winter mortality was below 10% (Fig. 1.5). However, in the following winter (1998/9), around 50% of sheep using the Village Bay area died between January and April. These two years differed in winter weather and in values of NAO: in the winter of 1997/8, NAO values were low while in 1998/9, NAO values were high, gales were frequent and rainfall was high. High NAO values are associated with depressed survival in most age categories (Fig. 3.11) and appear to predict survival better than low winter temperature, probably because the sheep are well protected from the cold by their thick fleeces (Milner *et al.* 1999b; Coulson *et al.* 2001). Wet, stormy weather has two separate consequences. First, the fleeces become sodden and individuals have to expend large amounts of energy to avoid hypothermia. Second, individuals seek shelter to escape the weather and are prevented from foraging. These two processes are associated with negative energy budgets which, if prolonged, cause individuals in poor condition to die of starvation.

The relative effects of population density and winter weather on survival differ between age categories (Milner *et al.* 1999b; Clutton-Brock and Coulson 2002). In juveniles, population density exerts a stronger influence than winter weather, while in yearlings and adults winter weather exerts a stronger effect than density (Figs. 3.10 and 3.11). In addition, the timing of the critical climatic changes differs between the sexes. Male mortality is closely related to NAO values between December and March as is the mortality of female juveniles and older females (Fig. 3.11a–d). In contrast, the mortality of female yearlings and prime age females is more closely related to rainfall in February and March than to NAO between December and March (Fig. 3.11e, f).

Shortage of resources in winter is the principal cause of high mortality (see Chapter 4), though energy expenditure may also be affected by climatic variation and parasite load (Chapter 5). Plant biomass in spring is closely associated with population growth in the following year and is negatively correlated with sheep numbers the previous August (see Chapter 4). Estimates of the energy requirements of sheep in the Village Bay sub-population in winter, based on observed changes in plant biomass and estimated energy requirements of the sheep, suggest that the availability of vegetation per head during the winter is insufficient to cover the animals' requirements once female numbers in summer exceed 300 sheep, and predict a rapid decline in body weight, which is marked when total autumn numbers exceed 450 or female numbers exceed 200 (Clutton-Brock *et al.* 1997a) (Fig. 3.12). If animals die once they have exhausted their fat

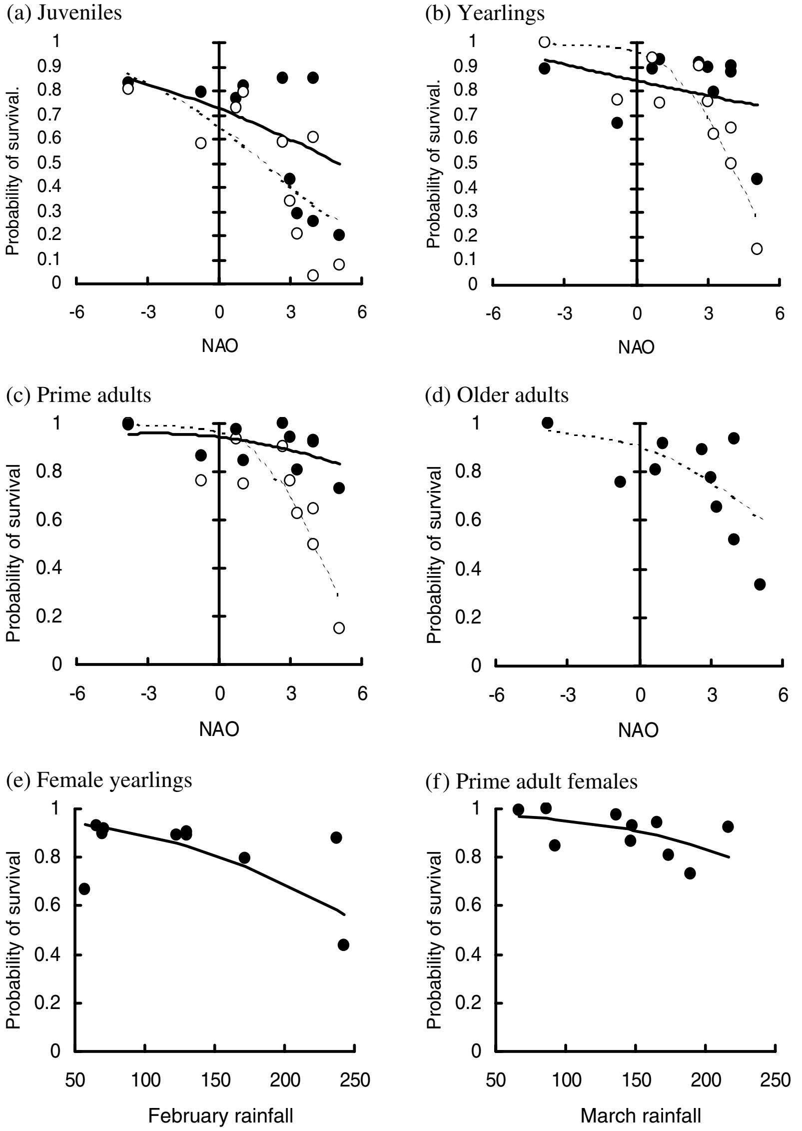


FIG. 3.11. Comparative effects of weather on the over-winter survival of different sex and age classes. (a) Changes in the survival of male and female juveniles with NAO between December and March. (b) Changes in survival of male and female yearlings with NAO between December and March. (c) Changes in survival of prime-aged adults (two to six years) with variation in NAO. Open symbols and solid lines represent females; solid symbols and broken lines represent males. Lines are from logistic regression mark–recapture–recovery models. (d) Changes in survival of older adults with variation in NAO between December and March. (e) Changes in survival of female yearlings with February rainfall (mm). (f) Changes in survival of prime-aged females in March rainfall (mm).

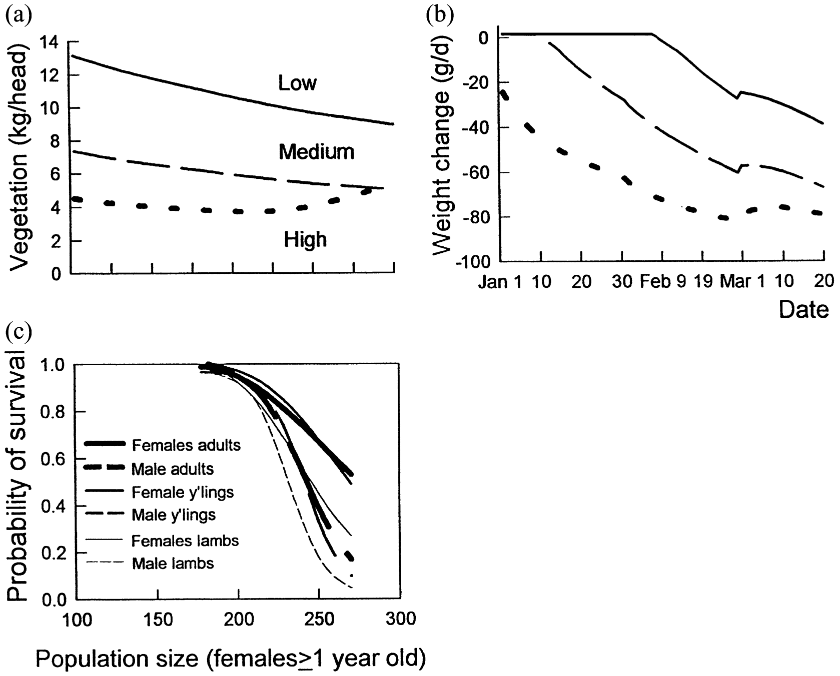


FIG. 3.12. Energetic predictions of food availability and survival. (a) Predicted amount of vegetation available per head of sheep in Village Bay, Hirta, between January and March under low (solid line), medium (wide dashed line), and high (narrow dashed line) population density (from Clutton-Brock *et al.* 1997a). The high rates of mortality at high population density cause an increase in available vegetation per head, slightly mitigating the rate of weight loss. (b) Predicted patterns of weight loss in adult females. (c) Predicted proportions of each class surviving winter plotted in relation to total population. Males are unable to regain body reserves after rutting at high population densities and are then more likely to die than females, while juveniles of both sexes have lower body reserves than older animals. The results were obtained by initialising the model to a starting population of 400 sheep, in the ratio 0.5:0.2:1 females and 0.5:0.2:0.2 males (the ratios are for lambs: yearlings: adults) and then running the simulation for 100 years.

reserves, these patterns predict an increase in mortality from starvation as total autumn population size rises above 400 or female numbers rise above 180 (Clutton-Brock *et al.* 1997a). Summer conditions, in contrast, appear to have little effect on mortality. August standing crop declines as sheep density rises (see Chapter 4) and the growth rate of lambs and the body weight of females in August decline with increasing density (Clutton-Brock *et al.* 1992, 1997a). However, the magnitude of these changes is small and they principally affect growth in the year *after* a population crash.

Sex differences in energy requirements and expenditure probably account for much of the variation in mortality between age and sex categories. Juveniles and adult males would be expected to show higher mortality and earlier death dates than adult females as a result of their lower fat reserves at the onset of winter (Clutton-Brock *et al.* 1997a). They may consequently be more likely to be affected by conditions during the first half of winter while mature females, which are able to regain weight lost during lactation in the autumn months, may be more susceptible to variation in conditions in late winter. In addition, the energetic costs of gestation rise sharply in late winter (see Chapter 2). Another reason why population density may have less impact on mature females is that they are commonly the last animals to die, with the result that variation in population size in late winter is substantially lower than at the onset of winter and competition for resources is reduced (Clutton-Brock *et al.* 1997a).

Variation in the susceptibility of different age categories to high winter density has important consequences for population demography and dynamics. Though juvenile mortality is more variable than adult mortality, variation in adult mortality has a greater demographic impact, partly because adults constitute a larger proportion of the population and partly because their subsequent survival and breeding success is higher than that of juveniles (Fig. 3.4). Juvenile and adult mortality rates are positively correlated and the co-variation between them is also important in influencing the population dynamics (Fig. 3.4).

The age structure of the population in autumn also affects levels of winter mortality. The proportion of juveniles, prime adults and older animals in the population varies between years as a result of variation in mortality in previous years (Fig. 3.13). When the population includes relatively large numbers of juveniles and older adults, levels of winter mortality are likely to be high (see section 3.8). Since crashes remove many older animals, they also reduce natural mortality in

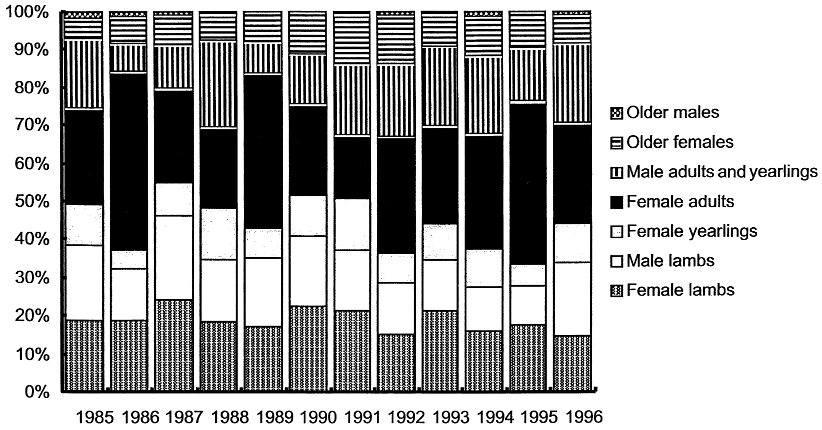


FIG. 3.13. Age structure in different years. The figure shows the proportion of animals of different ages in different years. (From Clutton-Brock and Coulson 2002.)

the winter immediately following a crash, leading to an increase in age-related natural mortality as the number of years since a crash increases.

Higher mortality rates in males also have important consequences. When sheep numbers are low after crashes, there are up to eight or nine females per male among adults. In contrast, the adult sex ratio is close to parity in summers when population density is high (Fig. 3.14). Fluctuations in the adult sex ratio have repercussions for the rutting behaviour of males and the distribution of mating success across age classes (see Chapters 6 and 9).

3.6 Cohort variation in growth, survival and reproductive performance

As in many other vertebrates (Lindström 1999), conditions during early development generate differences in the growth between cohorts in the sheep. Lambs born after winters of high density or high NAO are lighter as yearlings and adults (Clutton-Brock *et al.* 1992; Forchhammer *et al.* 2001). Both density and climate appear to exert direct effects on growth. When the influence of birth weight is controlled for, cohorts born after winters when population density is high

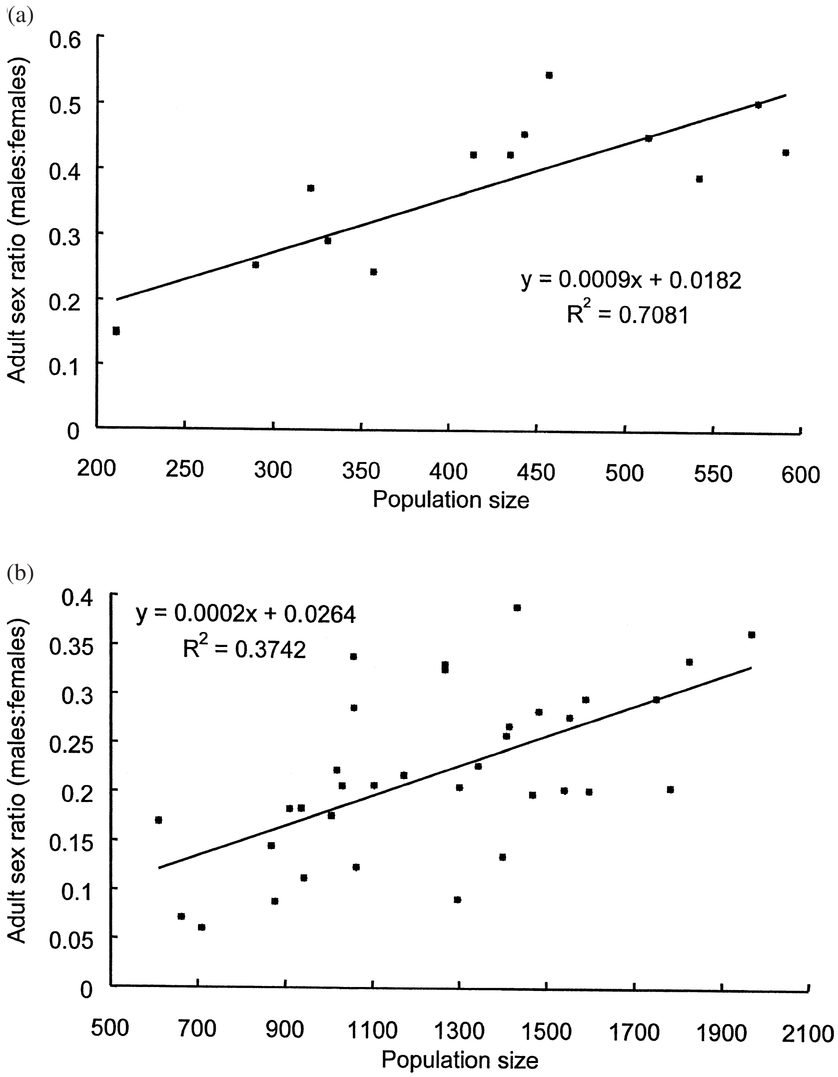
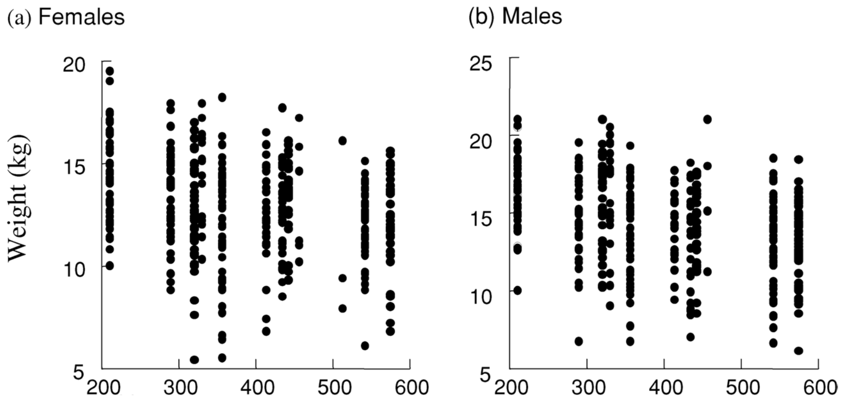


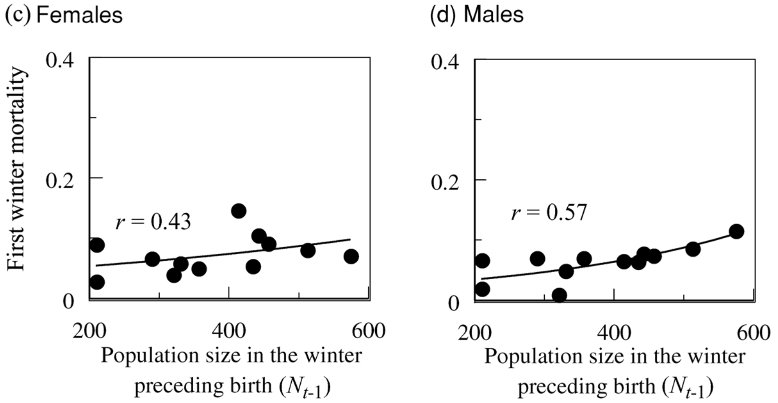
FIG. 3.14. Sex ratio (males:females) among adults (more than one year old) (a) in the Village Bay population in October 1985–98 and (b) the whole island population (1955–99) in relation to population size at the same time.

show lower body weights at four months in both sexes (Fig. 3.15a, b) and repeated weighing of lambs during the first weeks of life confirms that growth rate is depressed (Robertson *et al.* 1992). This is probably because population density depresses the biomass of live



(a) Females

(b) Males



(c) Females

(d) Males

FIG. 3.15. Variation in growth and survival between cohorts. (a, b) Changes in weight at four months in females and males plotted on population size in the winter preceding birth. (c, d) Changes in mortality of lambs in their first winter, plotted on population size in the winter preceding birth. Both analyses control for the effects of maternal age and weight, birth weight and date, capture date, twin birth and NAO were controlled using generalised linear models. (From Clutton-Brock *et al.* 1992; Forchammer *et al.* 2001.)

grass in spring (see Chapter 4) which is, in turn, closely related to the daily weight gain of lambs during their first four months of life (Robertson *et al.* 1992; see also Côté and Festa-Bianchet 2001). Light-born juveniles weigh less at subsequent ages than heavy-born ones (Chapter 2), and the average weight of cohorts at four, sixteen and twenty-eight months declines with increasing density in the winter before birth (Forchhammer *et al.* 2001) (Fig. 3.15a, b). Variation in early development is also correlated with the growth and weight of adults (Forchhammer *et al.* 2001).

Differences in early development are associated with variation in mortality during the first winter of life. Cohorts that show relatively low birth weight suffer relatively high mortality throughout their first year of life (Forchhammer *et al.* 2001). After the effects of birth weight have been allowed for, cohorts exposed to high population density during the winter before birth tend to show relatively high mortality in their first winter, especially among males (Fig. 3.15c, d). In contrast, NAO values during the winter before birth are not consistently related to juvenile mortality. (These results differ from an earlier analysis (Clutton-Brock *et al.* 1992), which found no significant effect of population density during the winter preceding birth on subsequent mortality, but did not control for climatic effects.)

The effects of variation in early development extend into the breeding lifespan. Cohorts exposed to high population density *in utero* show relatively high mortality as yearlings and two-year-olds (Forchhammer *et al.* 2001). Subsequently, the effects of population density in the winter before birth disappear, but cohorts that experience high density in their first summer (N_t) show relatively high adult mortality while cohorts born after winters with high NAO indices show expected levels of mortality as juveniles but reduced mortality as adults (Forchhammer *et al.* 2001). Finally, conditions during early development are related to variation in fecundity. The proportion of juveniles that conceive during their first summer and give birth at around twelve months of age varies between cohorts from around 20% to over 80% (see section 2.6). Cohort differences in the age of females at first breeding are not consistently related to population size in the winter before their birth (Fig. 3.16a). However, females breed later when the winter preceding their birth is characterised by high NAO (Fig. 3.16b) or when population density is high in the summer that they are born (Fig. 3.16c). In addition, yearlings born in summers when population density is high produce relatively few lambs, though this effect disappears in adult females. In conjunction, population size in the first summer and NAO in the previous winter account for 81% of intercohort variation in age at first breeding (Forchhammer *et al.* 2001).

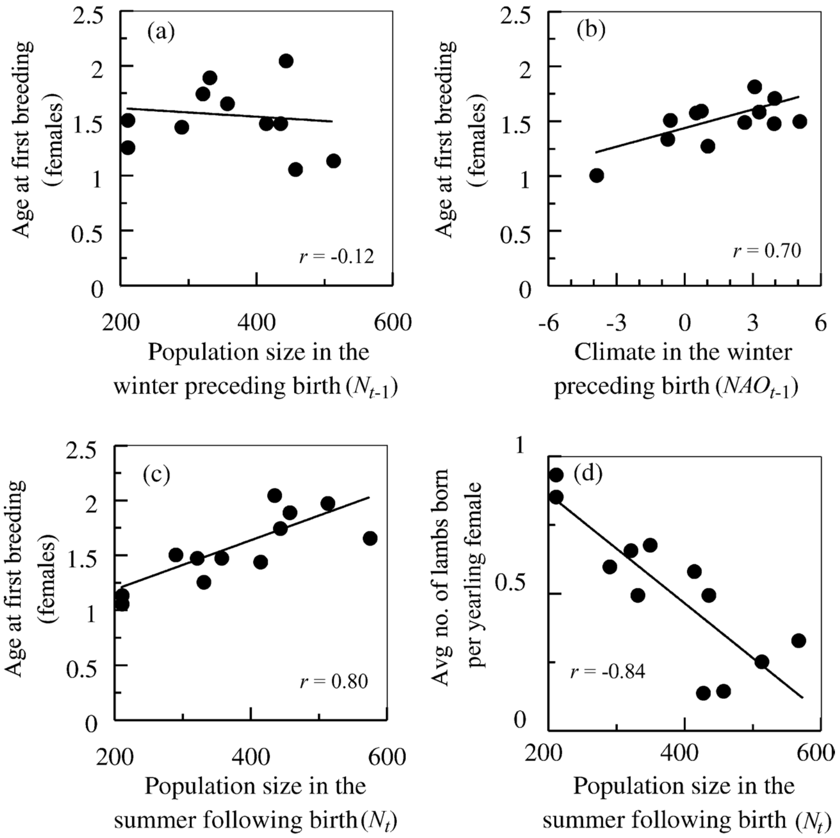


FIG. 3.16. Variation in fecundity between cohorts. (a) Relative age at first breeding in females plotted on population size in the winter preceding birth (N_{t-1}). (b) Relative age at first breeding plotted on NAO values in the winter preceding birth (NAO_{t-1-}). (c) Relative age at first breeding plotted on population size following birth (N_t). (d) Average number of lambs born per yearling female plotted on population size in the summer following birth (NE). Correlation coefficients shown in bold are significant ($p < 0.05$). (From Forchhammer *et al.* 2001.)

What consequences do the differences in survival and fecundity between cohorts have for the dynamics of the population? Since weight at four months exerts a strong effect on survival through the first winter, density-dependent changes in growth could, in theory, play a major role in generating instability if cohorts of lambs produced at high density had insufficient reserves to survive their first winter (Clutton-Brock *et al.* 1992). However, in practice, the demographic effects of these changes in growth are slight. While changes in birth weight are probably responsible for part of the reduction in neonatal survival at high density, the latter has little effect on changes in population size since neonatal survival usually falls *after* winters when population density and mortality are both high (Clutton-Brock *et al.* 1991). As a result, increases in neonatal mortality may delay population recovery after years of high mortality but probably have little effect on the magnitude of population crashes (Clutton-Brock *et al.* 1997a). Similarly, birth weight and weight at four months are lowest in summers that *follow* crashes rather than those that *precede* them, so that density-related changes in growth affect survival in the first winter *following* a winter when mortality is high. Since mortality is generally low in these years, the principal effect of these changes in growth may again be to reduce the rate at which the population recovers.

3.7 Modelling the impact of density-dependence

Like most other attempts to predict animal numbers, we initially constructed a simple deterministic model of the dynamics of the sheep population based on our measures of the effects of density on fecundity and survival between 1985 and 1995 and structured for different age and sex categories (Grenfell *et al.* 1992). Over this period, there was a nonlinear relationship between annual survival (S) and total population size and density-dependence was strongly *over-compensatory* (Grenfell *et al.* 1992). Over-compensatory mortality has been demonstrated in a number of relatively short-lived organisms (Hassell *et al.* 1976; Peterson *et al.* 1984) but is unusual in longer-lived species (Fowler 1981, 1987; Clutton-Brock and Coulson 2002). The dynamics of over-compensatory density-dependence in seasonally reproducing populations have already been explored (Hassell *et al.* 1976; May 1976; Bellows 1981) and we began by using a simple model from the literature on insects, expressing the density-dependent survival pattern by the following standard function (Bellows 1981).

$$S = \frac{d}{1 + (aN)^b} \tag{3.1}$$

Here, the parameters d, a and b respectively control the level of density-independent mortality, the threshold population size ($1/a$) above which density-dependent mortality occurs, and the strength of density-dependence, which is overcompensating for $b > 1$ (Maynard Smith and Slatkin 1973; Bellows 1981).

We used the model to explore the demographic consequences of the effects on density on fecundity and survival in the sheep. Since lambs reproduce in their first year of life and the survival curves of males and females are qualitatively similar in shape (Fig. 2.15), the dynamics of the population can be captured by adding across sex and age classes to produce the following model of dynamics (Bellows 1981; Grenfell *et al.* 1992).

$$N_{t+1} = \lambda S_t N_t = \frac{\lambda d N_t}{1 + (a N_t)^b} \tag{3.2}$$

In Equation (3.2) a, b and d are survival parameters, as described above, averaged over the age and sex variations in survival. The other component of the model is the annual rate of increase of the population due to reproduction, λ. This parameter is calculated as $\lambda = (f + 1)$, where f is the average individual reproductive rate; the product λd therefore represents the maximum net annual increase in population, allowing for density-independent mortality.

This model illustrates the potential impact of over-compensatory density-dependence on the dynamics of the Hirta sheep population. The dynamics of the model depend on an interaction between the degree of over-compensatory mortality (b) and the net density-independent rate of increase of the population (λd) (Bellows 1981). As b increases above unity, the model moves from a stable equilibrium through periodic population cycles of increasing complexity, to an irregular, chaotic pattern of crashes (Grenfell *et al.* 1992). To compare the degree of over-compensation in the sheep population with values observed from previous studies, Fig. 3.17a plots b against λd for lamb yearlings and adults, in comparison with the equivalent figures from a range of insect studies (Bellows 1981). It shows that the degree of over-compensatory density-dependence found in the Soay population in some periods is unusually high: the values of b observed

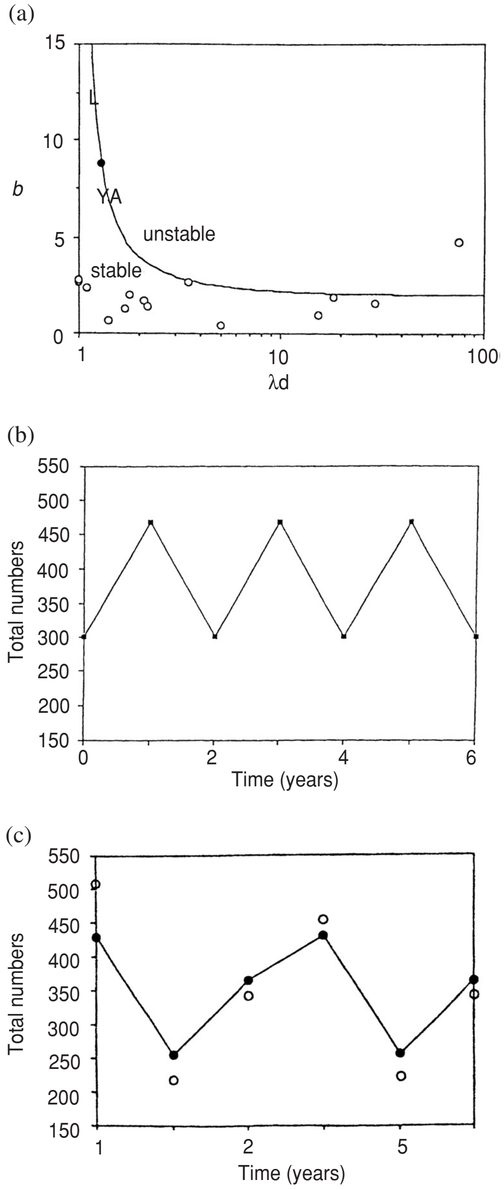


FIG. 3.17. (a) Local stability boundary for equilibria of the simple non-age-structured model (Equation (3.2)) (Bellows 1981) in terms of the degree of over-compensatory density-dependence (*b*) and the average net reproductive rate (λd). The *b* estimate for sheep (•) was calculated by averaging parameter estimates from the survival curves for each age class; the corresponding λd estimate refers to the average net reproductive rate of Soay sheep (Grenfell *et al.* 1992). Equivalent estimates for insect populations (Bellows 1981) (○) are included for comparison. (b) Biennial fluctuations in population size predicted by a more complex age-structured model of the sheep population with moderate levels of *b* ($b = 10$) (Grenfell *et al.* 1992). (c) Triennial fluctuations predicted by the same model with high levels of *b* ($b = 50$). Observed changes in sheep numbers are shown by the open circles.

for different age and sex categories of sheep (running from 6.08 for adult females to 16.31 for male lambs) is much higher than in most insect populations, where the observed upper limit is around $b = 5$ (Bellows 1981). Thus even though the reproductive rate of the sheep is relatively low, the level of over-compensation is still sufficiently high to generate the possibility of unstable dynamics. With moderate values of b, biennial cycles can be expected (Fig. 3.17b) while triennial cycles resembling those observed in the sheep will occur if b values are extremely high (see Fig. 3.17c, where $b = 50$).

These calculations prompt the question why Soay sheep should show such high levels of over-compensatory mortality (Grenfell *et al.* 1992; Clutton-Brock *et al.* 1997a). Their relatively high fecundity (generated by their ability to conceive at less than a year old and the relatively high incidence of twins) is almost certainly important, for it permits sheep numbers to rise by over 60% in a single summer, producing a situation where, in some years, the number of animals entering the winter is substantially greater than the food supply can support (Clutton-Brock *et al.* 1997a). The effects of high fecundity are augmented by the lack of any significant decline in fecundity during periods of population increase. Density-dependent changes in the proportion of females lambing at twelve months, in twinning rate and in average recruitment per female (Fig. 3.9) are largely confined to breeding seasons following winters of high mortality and consequently have little effect on the rate of population growth. The reason underlying this lack of sensitivity of fecundity to rising density (which contrasts with many other large mammals: see Fowler 1987) is probably that female sheep wean their lambs by midsummer, when food supplies are still abundant, with the result that they can regain weight lost during lactation by the end of the summer and enter the rut at body weights similar to those of females that have not reared lambs (see Chapter 2). Comparisons show no differences in body weight in August between adult females that have raised singleton lambs and those that have failed to breed while females that have reared twins are significantly heavier than other categories (Clutton-Brock *et al.* 1997a).

3.8 Incorporating the effects of climate and age structure

It is clearly important to incorporate density-independent effects in any attempt to predict variation in sheep numbers for climate variation has important effects on survival (see section 3.5). As in our previous model (see section 3.7), we started by relating population growth rate to population size for the whole population, in this case using data for all years between 1955 and 1999. Figure 3.18a plots instantaneous population growth rate ($r_t = x_{t+t} - x_t$) against the log of population size in the previous year $t(x_t)$ showing the close relationship between population size and population growth rate, as well as the presence of marked variation in survival at high population densities. A plot of x_{t+1} against x_t (Fig. 3.18b) reveals this pattern in more detail and shows that population growth rates are positive below a threshold population of around 1100 individuals ($x_t \cong 7$) while, above this level, population growth rate tends to be negative, though there is much variation (Fig. 3.3). We modified the balance of noise and density-dependence using a threshold auto-regressive model (Grenfell *et al.* 1998); Fig. 3.18b illustrates this fitted to separate linear auto-regressive models above and below the threshold. At low densities, the model indicates a variable increase in population size while, at high densities, the population can increase, remain constant or fall, depending on density-independent factors. Simulation of the model, incorporating the influence of density-independent factors and random noise, captures the essence of both the growth rate pattern (Fig. 3.18c) and the map of x_{t+1} on x_t (Fig. 3.18d). Like our previous model, this emphasises that the system sometimes shows strong overcompensatory density-dependence but, at other times, mild winter weather conditions allow the sheep to escape the consequences of high winter density and low food availability.

Since the effects of population density and climatic variation on mortality vary between age and sex categories (see section 3.5) it is also important to incorporate variation in the age structure of the population in predictive models (Coulson *et al.* 2001). Age-structured models which incorporate differences in population structure as well as variation in the responses of different sex and age categories to population density and winter weather predict changes in population size with considerably more accuracy than models that ignore these differences (Fig. 3.19). For example, stochastic, unstructured models of variation in sheep numbers account for little more than 20% of variation in population size (Grenfell *et al.* 1992, 1998), while the inclusion of variation in sex and age structure and in sex and age-specific

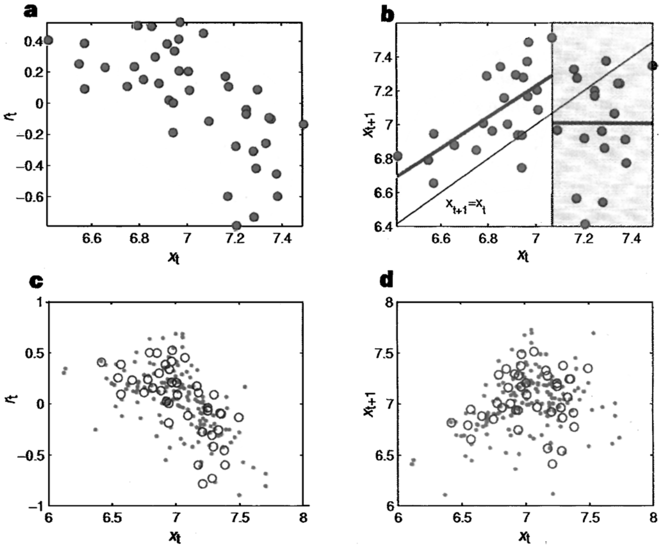


FIG. 3.18. Modelling population size for the whole of Hirta. (a) Plot of annual population growth rate $r_t = x_{t+1} - x_t$ against log population size (x_t). (b) Fit of an univariate SETAR threshold model to the scatter plot of x_{t+1} against x_t. The threshold, $x_t = C = 7.066$, and the linear relationship above and below it, were estimated by a least-squares fit to the data; see Grenfell *et al.* (1998) for more details. Shaded area denotes the regime above the threshold, blue lines show the best-fit model and the diagonal black line is at $x_{t+1} = x_t$. (c) Comparing the observed r_t versus x_t plot (circles) with 150 iterates of the best-fit model with added noise (dots), as defined in **Table 1**; a transient of 250 years was run off before recording the points. (d) The same comparison as (c), but plotted as x_{t+1} against x_t.

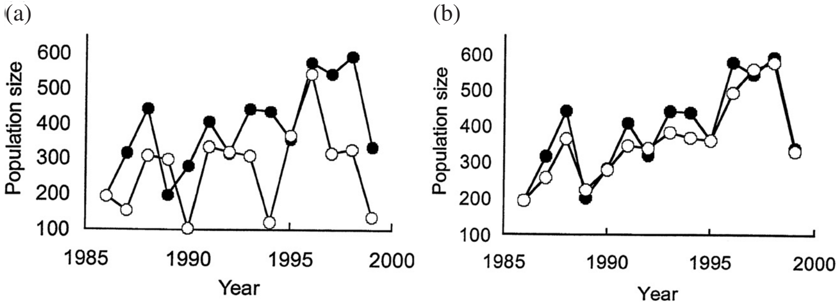


FIG. 3.19. Observed (solid points) and predicted (open points) values of population size indifferent years using (a) an age-structured Markov model and (b) a time series model.

responses to density and weather (Fig. 3.19) raises the proportion of variation accounted for to nearly 90% (Coulson *et al.* 2001).

3.9 Synchrony in dynamics between populations

Where density-independent factors exert a strong influence on population dynamics, separate populations in the same area should show synchronous changes (Moran 1953). Numbers of black-faced sheep on Boreray have been counted approximately every other year between 1955 and 2000 and, as expected, their numbers are closely correlated with the number of Soay sheep on Hirta (Fig. 3.20). Moran (1953) showed that the expected correlation between populations in the absence of density-dependence equals the correlation between environmental perturbations so, with no density-dependence, the expected environmental correlation would equal the observed correlation between populations ($r = 0.685$). In fact, our analysis shows that, because of relatively strong effects of density on the system (Royama 1992), closer environmental correlation than that observed would be necessary to generate the level of correlation between the sheep populations on the two islands (Grenfell *et al.* 1998).

To identify the specific climatic changes responsible for generating synchronous dynamics in the two populations, we investigated the effects of including a range of different weather variables in our model, including mean monthly temperature, mean monthly precipitation and the total number of hours with wind over 34 knots during the months of March and April (Grenfell *et al.* 1998). Our eventual model (which included a negative effect of March gales on population growth rate above and below the density threshold and a positive effect of April temperature on population growth rate below the threshold) suggested that known climatic effects could account for around 30% of the observed inter-island correlation (Grenfell *et al.* 1998). Correlations with sheep numbers on the smaller island of Soay are less close, possibly because of the difficulties of censusing sheep numbers accurately there. Recent studies of other northern ungulates also suggest that variation in winter weather associated with the NAO can synchronise fluctuations in separate populations. For example, fluctuations in caribou and musk ox populations on opposite coasts of

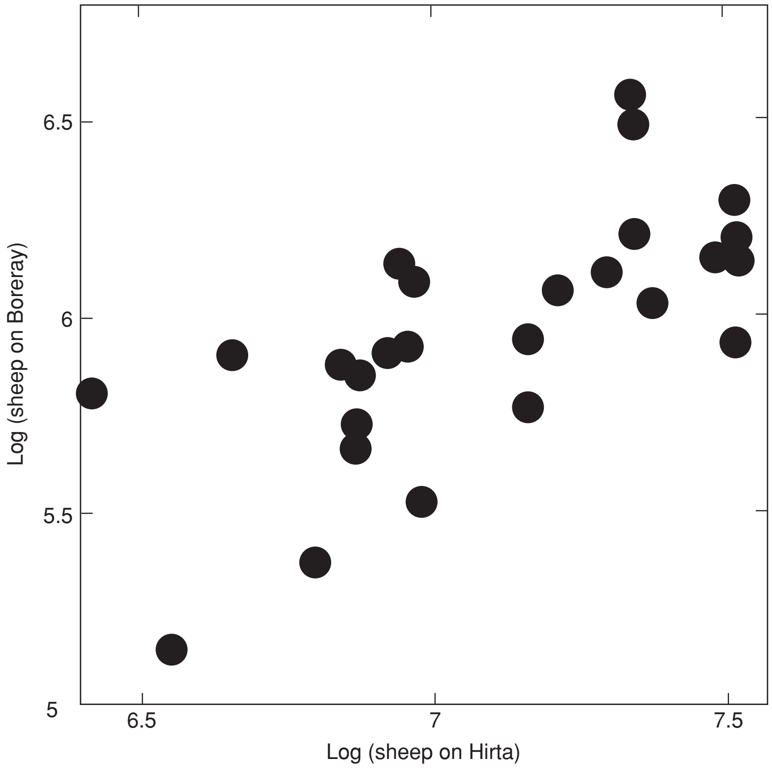


FIG. 3.20. Log number of black-faced sheep on Boreray plotted on estimates of log number of Soay sheep on Hirta. The association between the logged population sizes is significant (Pearson $r = 0.685$, 95% bootstrap confidence limits: 0.447–0.838) To permit easy comparison with the models, we calculated the correlation coefficient (see text) after replacing replicate Boreray counts for a given year with their maximum. This assumes that the maximum of repeated population counts is likely to be the best estimate, but using the *mean* of replicated counts gives a similar correlation.

Greenland are synchronous and are correlated with changes in NAO (Post and Forchhammer 2002).

3.10 Discussion

As in many other northern ungulates (Fowler 1987; Clutton-Brock and Albon 1989; Saether 1997; Gaillard *et al.* 1998; Post and Stenseth 1998), late winter mortality is the most important cause of changes in population size in the sheep. Young of the year, males and old females are particularly likely to die (Saether 1997; Loison *et al.* 1999b). Though mortality is less variable in adults than juveniles, changes in adult mortality contribute more to changes in population growth since adults form a larger portion of the population (Fig. 3.4).

Variation in mortality is affected both by population density and by density-dependent factors: high mortality of adults is largely restricted to years when summer numbers exceed 1100–1200, although favourable winter weather conditions can allow a large summer population to escape high winter mortality. The immediate cause of fluctuations in winter mortality is starvation combined with variation in energy requirements resulting from climatic differences. Chapter 4 examines the effects of sheep density on primary production and food availability. In addition, density-dependent changes in parasite numbers exacerbate the effects of food shortage on the sheep and accentuate fluctuation in their growth and survival (see Chapter 5).

While there is no inherent cyclicity in sheep numbers, there is some regularity in the rise and fall of the population. It usually requires at least three breeding seasons for a population that has suffered heavy mortality to regain a level where the next population size reduction is likely to occur (1100–1200). As a result, years of high winter mortality are usually separated by at least two intervening years of low mortality (Fig. 1.5). This pattern is most clearly seen in changes in the number of adult females, and is least obvious in the changes in the number of juveniles and males (Fig. 1.5), presumably because juveniles and males are more susceptible to starvation than females (Figs. 3.10 and 3.11), so that fluctuations in climate can generate high mortality even when population density is relatively low. Interactions between population density and climatic factors have been recorded in other northern ungulates (Douglas and Leslie 1986; Loison and Langvatn 1998; Post and Stenseth 1998, 1999; Post and Forchhammer 2002) though they do not always lead to persistent fluctuations in population size. Climatic factors in winter interact with population density to affect survival in Scottish red deer populations, while summer weather conditions have relatively little effect (Albon and Clutton-Brock 1988). In coastal populations, wet, stormy weather has a greater effect on mortality than winter temperatures (Albon and Clutton-Brock 1988) and values of

NAO predict changes in winter mortality (Albon *et al.* 2000). In mainland red deer populations, where winter temperature varies more widely, mid-winter temperatures exert stronger effects (Albon *et al.* 1992) and similar effects occur in continental populations (Loison and Langvatn 1998). Like young sheep, juvenile red deer are more susceptible than adults to variation in population density combined with adverse winter weather and males are more susceptible than females, leading to consistent correlations between population density and the adult sex ratio (Clutton-Brock *et al.* 1997a) though the extent of sex differences varies between populations (Loison and Langvatn 1998).

So why does the fecundity of female sheep not decline with increasing density as it does in many other ungulates, including red deer (Clutton-Brock *et al.* 1997a)? The likely answer is that Soay lambs develop rapidly and, by the time they are six weeks old, they obtain most of their food themselves (Jewell *et al.* 1974; Robertson *et al.* 1992). In combination, the relatively early breeding season of the sheep and the rapid development of their offspring allow female sheep that have reared lambs successfully to regain condition between June and August, when food supplies are super-abundant so that, by the rut, successful breeders do not differ in body weight from animals that have failed to rear lambs (Clutton-Brock *et al.* 1997a). As a result, the link between population density, food availability, body condition and fecundity is broken, and female sheep are almost as fecund in years when population density is high as in other years (Fig. 3.16). In ungulates with longer lactation periods, like bighorn sheep and red deer, mothers are unable to regain condition before the October rut so that high density or harsh weather are more likely to affect weight in the rut (Clutton-Brock *et al.* 1997a; Festa-Bianchet *et al.* 1998). Where these differences in weight at the onset of the breeding season are relatively small (as in bighorn sheep), they may have little effect on subsequent fecundity or survival (Festa-Bianchet *et al.* 1998). In contrast, where they are large (as in red deer) they can affect the probability that females will conceive in the autumn rut as well as their survival through the following winter (Clutton-Brock *et al.* 1983).

Extrinsic factors too, may be important, too. By preventing dispersal, the isolation of the St Kilda sheep population may lead to higher local densities and increased opportunities for instability. Rodent populations in fenced enclosures commonly attain artificially high population densities and may also show high mortality (Finnerty 1980; Cockburn 1998). Dispersal is necessarily reduced in island populations, preventing the gradual leakage of subordinate animals into inferior habitat and leading to increased levels of mortality *in situ*. However, the contrast in population stability between the red deer populations of Rum and the Soay sheep of Hirta shows that the constraints on dispersal imposed on the sheep do not, on their own, account for the persistent instability of population size (Clutton-Brock *et al.* 1997a).

The relatively fluid social organisation of the sheep may also contribute to their unusual dynamics. Dominance interactions and displacements are rare among females and there are no obvious social divisions within the population, apart from those between hefts (see Chapter 2). In other ungulates, including red deer, dominance relationships are often well defined among females as well as males, and subordinates or intruders are commonly displaced from resources by dominant members of the group (Thouless 1986). Consistent dominance relationships may focus the effects of rising population density on particular animals or groups, generating a more graded response to rising density and greater variance in dates of death (Clutton-Brock *et al.* 1997a). Since early deaths reduce the total food requirements of remaining animals, increased variance in death date may increase the food available to survivors, contributing to a reduction in late-winter mortality and tending to increase the stability of population size.

Early development appears to exert an important influence on many aspects of growth, development, survival and breeding success of the sheep as it does in many other mammals (Lindström 1999). High population density in autumn is associated with relatively early birth dates and light birth weights the following spring and cohorts born after wet, stormy winters (high NAO) tend to be born lighter than those born after cold, dry winters (Fig. 3.7). Population density and climatic factors in the year before birth affect juvenile survival and growth during the first year of life partly through their influence on birth weight (see Chapter 2) and similar effects are found in other northern ungulates (Anderson and Linnett 1998; Portier *et al.* 1998) though they are not universal (see Côté and Festa-Bianchet 2001). Both density and climatic factors also appear to have independent effects on growth and survival for, after the influence of birth weight is controlled for, cohorts born after winters when population density is high show low survival through their first summer, low body weights at four months and, in males, relatively low survival during the first winter (section 3.6). In addition, cohorts of females that experience high density in the first year of life are less likely to breed in their first year.

Our analysis of cohort effects sheds some light on the causal pathways underlying the effects of density and climate on development. Sheep density in winter depresses the availability of live grass in late winter and spring (Chapter 4.5); this may constrain prenatal growth rates, leading to low birth weights which, in turn, contribute to neonatal mortality. In some animal populations, high NAO values in winter are associated with improved performance or survival the following spring, possibly because relatively mild, wet winters are associated with reduced snow cover or with an earlier onset of plant growth in spring (Douglas and Leslie 1986; Saether *et al.* 1996; Forchhammer *et al.* 1998a, b; Post and Stenseth 1999). The contrasting tendency for wet, windy weather in winter to depress birth weight, neonatal survival and juvenile fecundity in the sheep probably occurs because the energetic costs adverse conditions depress fat reserves and prevent conception. Food availability during the first summer may be the principal factor affecting juvenile development and reductions in food availability caused by high sheep density in the first year of life probably account for the reduction in the survival and fecundity of juveniles when density is high.

Our results suggest that delays in the effects of rising population density on fecundity and survival in the sheep are responsible for allowing summer numbers to rise above winter carrying capacity. Combined with scarcity of shelter, high parasite load and no possibility of dispersal, competition for limited resources during late winter leads to intermittent, savage reductions in population size. This explanation of the dynamics of Soay sheep resembles the conclusions of recent studies of population dynamics in other resource-limited herbivore populations, which emphasise the capacity of lags or delays in density to generate fluctuations in numbers (Saether 1997).

It is sometimes suggested that lagged responses to rising density and persistent fluctuations in population size are an inevitable consequence of the absence of predators (Messier 1994; Saether *et al.* 1996; Saether 1997). In contrast, our work suggests that delays in density-dependent changes in the sheep are a consequence of their unusually rapid development and of the timing of reproductive events. Comparisons with the dynamics of the resource-limited red deer population on Rum over the same period suggest that fecundity and recruitment may respond more quickly to changes in density in the deer because critical stages of growth extend into periods of the year when resources are limiting (see Chapter 10). While the presence of predators may often reduce fluctuations in the density of their prey (Messier 1994), stability may vary widely among resource-limited populations of herbivores as a result of contrasting responses to population density and weather generated by differences in reproductive timing and life-histories (Clutton-Brock and Coulson 2002). Indeed, it would not be surprising if similar differences in life-history were also important in affecting the population dynamics of species subject to high rates of predation.

While this chapter has been principally concerned with the causes of fluctuations in mortality and in population size, the unusual dynamics of the sheep have many important consequences. Changes in sheep numbers affect the structure of plant communities (see Chapter 4) as well as the numbers of parasites (Chapter 5). The sex differences in mortality that occur in years when mortality is high generate consistent fluctuations in the adult sex ratio (Fig. 3.14) which affect the distribution of mating success in males and the intensity of sexual selection (see Chapter 6). Intense competition for resources in crash years also exposes effects of variation in phenotype and genotype which are difficult to detect in more clement circumstances and increases the intensity of natural selection on a wide range of phenotypic and genotypic characters (see Chapters 7 and 8). Finally, fluctuations in mortality increase the costs of reproduction (Fig. 2.14) and affect the relative fitness of different reproductive strategies (see Chapter 9).