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Comparative ungulate dynamics: the devil is in the detail

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Attempts to relate species differences in population dynamics to variation in life histories rely on the assumption that the causes of contrasts in demography are sufficiently simple to be derived from first principles. Here, we investigate the causes of contrasts in dynamics between two ungulate populations on Hebridean islands (red deer and Soay sheep) and show that differences in stability, as well as in the effects of variation in density and climate, are related to differences in timing of reproduction relative to seasonal variation in resource abundance. In both populations, attempts to predict changes in population size sufficiently accurately for the results to be useful for management purposes require a knowledge of the responses of different age and sex categories to changes in density and climate, as well as of population structure.

Keywords: dynamics; demography; sheep; deer

1. INTRODUCTION

Recent increases in the number of time-series long enough to provide an adequate description of population fluctuations clearly show that population fluctuations vary widely among animals with similar longevities and rates of reproduction, as well as between species with contrasting life histories (Caughley & Krebs 1983; Gaillard *et al.* 2000). For example, among grazing ungulates, populations may either show little variation in size across years, irregular oscillations, semi-regular oscillations resembling the stable limit cycles found in some smaller mammals or dramatic oscillations occasionally leading to extinction (Peterson *et al.* 1984; Fowler 1987; Coulson *et al.* 2000). While many ecological differences probably contribute to these differences (including predation, disease and human interference), the fact that stability varies widely among naturally regulated ungulate populations living in environments where human intervention is minimal and predators are absent (Boyd 1981*a*,*b*; Boussès *et al.* 1991; Clutton-Brock *et al.* 1997*a*), suggests that variation in population dynamics may often be caused by interactions between herbivore populations and their supplies.

Theoreticians have explored the possibility that contrasts in population dynamics may be consistently related to differences in life histories or in the temporal or spatial distribution of resources (e.g. Peterson *et al.* 1984; Sinclair 1989; Sæther 1997; Illius & Gordon 2000; Owen-Smith 2002). While it is likely that both these differences contribute to variation in dynamics, attempts to explain observed variation with general models assume that the causes of contrasts are sufficiently simple to be explained by general models derived from first principles (Caughley 1977). Another possibility is that contrasts in population dynamics are a consequence of detailed differences in the demographic processes affecting dynamics, driven by specific interactions between breeding systems and life-history parameters and the distribution of resources. If so, current attempts to predict variation in population dynamics using general models may meet with little success until we have a better understanding of the specific causes of contrasts in dynamics (Sutherland 1996).

In this paper, we compare the dynamics and demography of two populations of food-limited ungulates (red deer *Cervus elaphus* L. and Soay sheep *Ovis aries*) on different Hebridean islands over the same years (figure 1). We show that a detailed knowledge of demographic processes and population structure is necessary to predict changes in population size successfully and to explain the contrasts in population dynamics between the two populations.

Research on the red deer population of the north Block of Rhum has continued since 1972, when the annual 14% cull of the population of around 200 deer was terminated (Clutton-Brock *et al.* 1985*b*, 1997*a*). After 1972, numbers rose rapidly to around 300, stabilizing by 1980 although the adult sex ratio continued to change in favour of females (see figure 2*a*). Demographic processes varied between the initial period of population growth and the subsequent years when deer numbers had reached ecological carrying capacity (Albon *et al.* 2000); so, to maximize comparability with the sheep (see below), we have restricted our analysis of dynamics in the deer to the period between 1985 and 2001.

Since 1985, we have also monitored the dynamics of the Soay sheep on Hirta, the largest island of the St Kilda archipelago, *ca.* 120 km to the northwest (figure 2*b*). The sheep population was originally introduced from the neighbouring island of Soay and has been naturally regulated since 1932 (Grubb 1974*a*–*c*; Grubb & Jewell 1974; Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992). Soay sheep are derived from domestic stock that were probably

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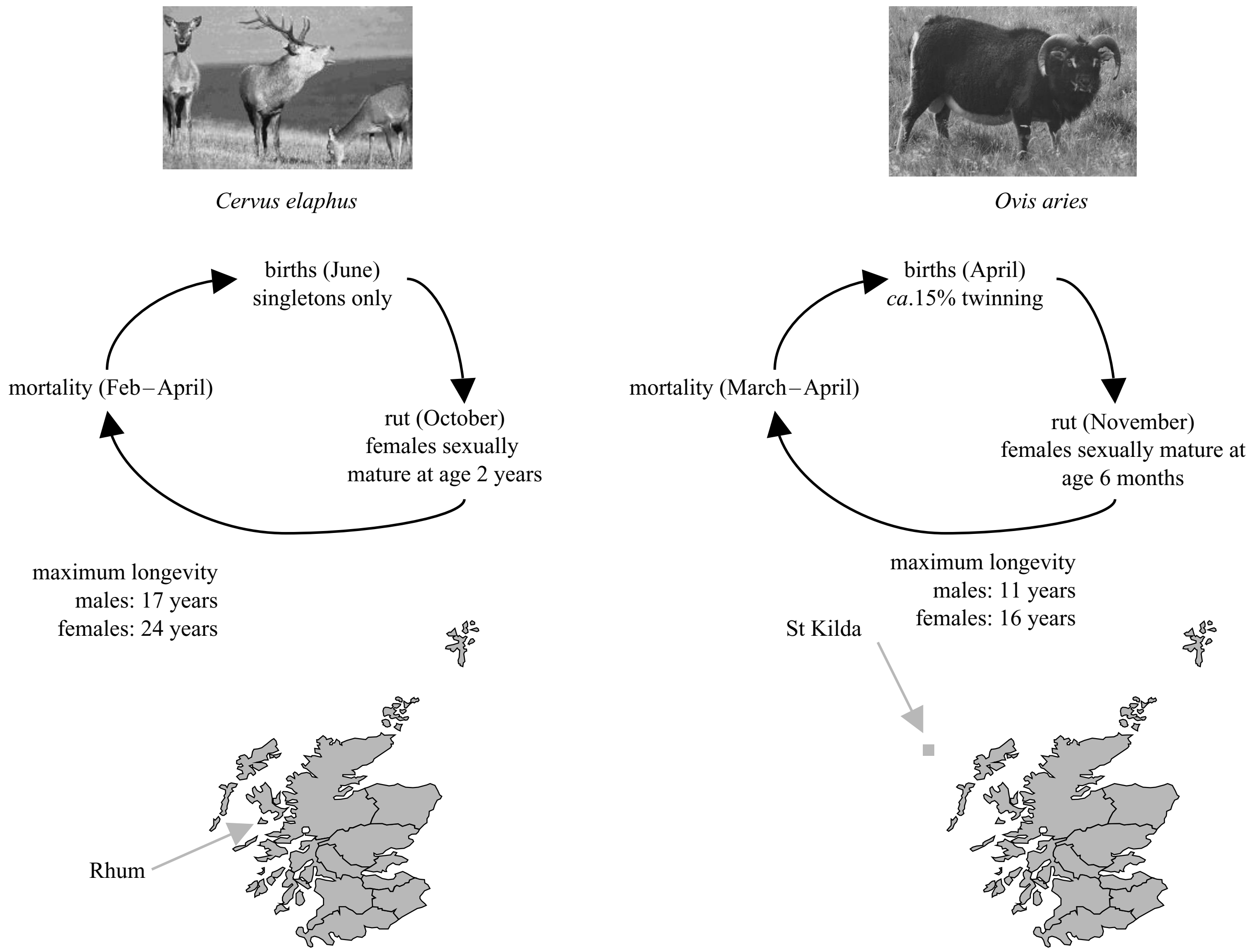

Figure 1. Summaries of the life cycles of red deer and Soay sheep.

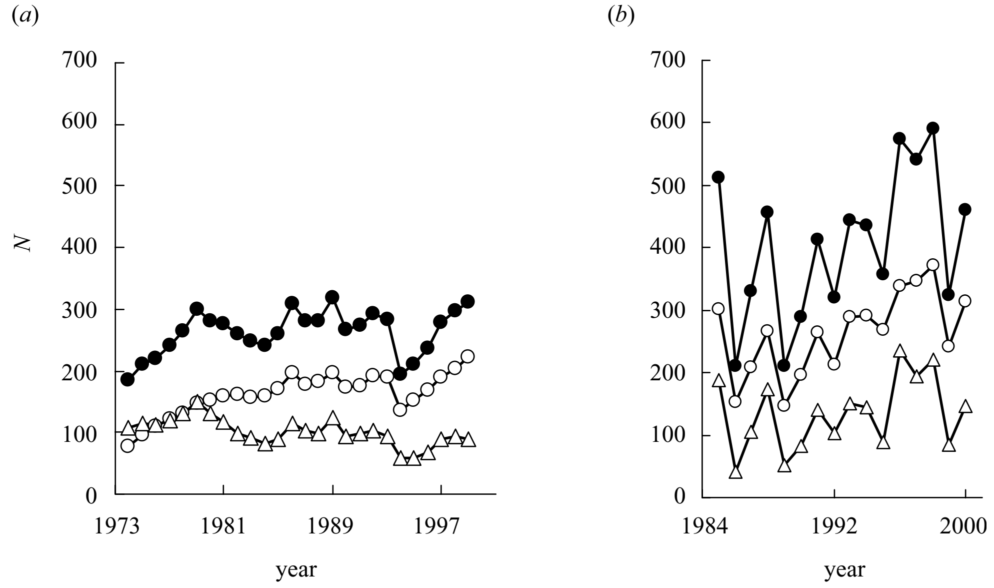

Figure 2. Time-series for (*a*) deer and (*b*) sheep numbers. Filled circles, total; open circles, total females; open triangles, total males. The ranges on the *y*-axes for sheep and deer are identical to allow comparison of the relative size of fluctuations in population size.

introduced to the Hebrides over 2000 years ago and have remained on Soay since then (Clutton-Brock 1981). Compared with most other time-series for large mammals, both of our datasets are unusual in that virtually all individuals in both populations are recognizable as individuals and their life histories have been monitored from within a few

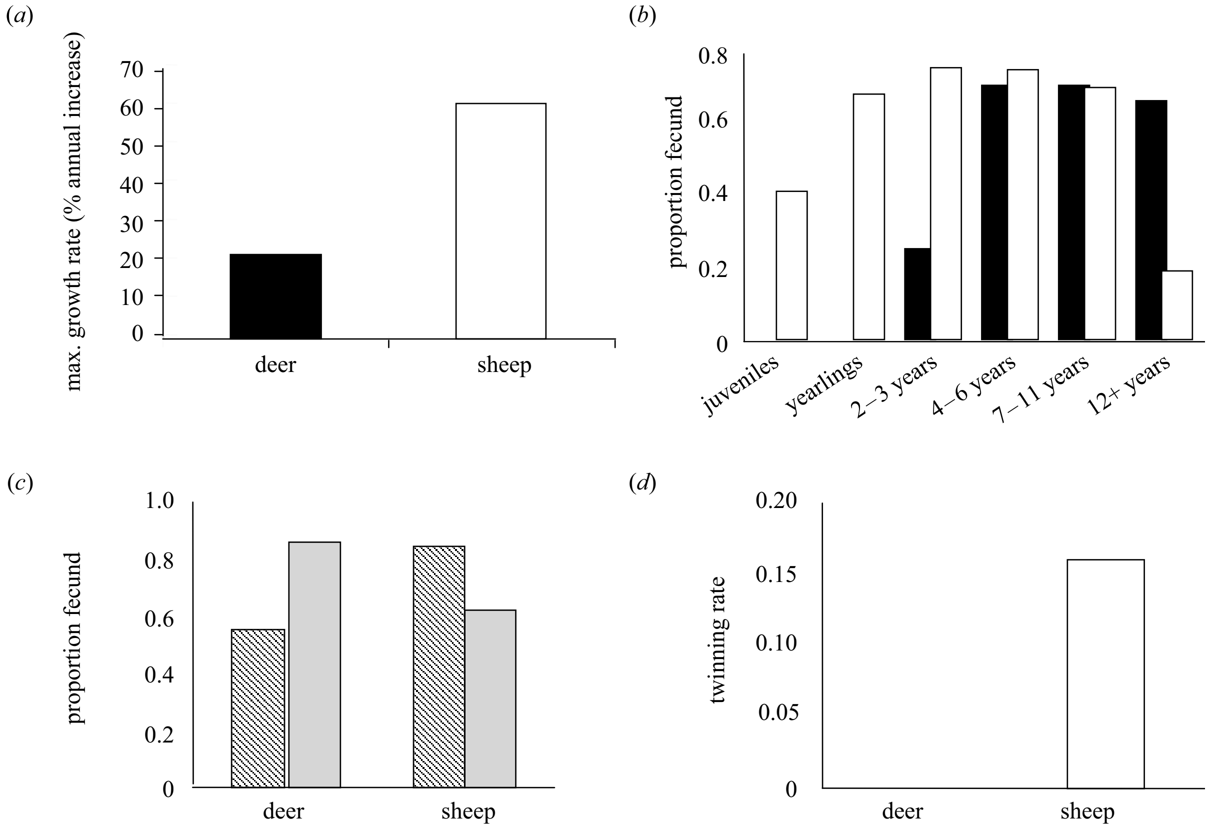

Figure 3. Fecundity in deer (black bars) and sheep (white bars). (*a*) Maximum population growth measured as the maximum percentage annual increase in population size. (*b*) Proportion of animals conceiving offspring at different ages. (*c*) Proportion of milk (hatched bars) and yeld (grey bars) females giving birth. 'Milk' are those that reared an offspring successfully until (at least) the onset of the winter in the previous year; 'yeld' are those that failed to do so either because they did not give birth or because their calf died during the summer. (*d*) Proportion of individuals bearing twins—note that red deer never twin on Rhum.

days of birth, when most lambs and calves are caught, weighed, sexed and skin-sampled for genetic analysis (Clutton-Brock *et al.* 1982*b*, 1991; Pemberton *et al.* 1996). As a result, we are able to identify the contributions of specific demographic changes to variation in population size with unusual accuracy.

The habitats occupied by the two populations at the two sites are broadly similar, with areas of herb-rich or *Agrostis*-dominated grassland at sea level grading into heather-dominated communities interspersed with flushes on the slopes of the surrounding hills (Jewell & Grubb 1974; Jewell *et al.* 1974). Densities of sheep reach higher levels than those of the deer, rising to 25 km^{-2} compared with *ca.* 15 km^{-2} in years of high density. Compared with deer, the sheep show relatively high population growth rates (figure 3*a*), partly because many females conceive for the first time at 7–8 months instead of at 2–3 years (Clutton-Brock *et al.* 1997*a*; figure 3*b*), partly because most females over a year old conceive each year (figure 3*c*) and partly because, on average, *ca.* 15% of females produce twins (figure 3*d*).

2. COMPARATIVE DYNAMICS

Between 1985 and 2001, neither the deer population on Rum nor sheep numbers on Hirta have shown a consistent temporal trend. However, while deer numbers have been relatively stable, sheep numbers have fluctuated widely between successive years. For example, while deer numbers have never declined by more than 17% in a single winter (figure 2*a*), over 60% of the sheep in autumn can die in the course of 2 months in late winter (see figure 2*b*). When high mortality occurs in the sheep, this not only removes the increment in population size that has occurred in the course of the last year, but, on average, reduces the population to less than 65% of the maximum number that has been known to survive the winter. By contrast, in the deer, winter mortality never reduces spring numbers much below 90% of observed maximum winter numbers. These contrasts in winter mortality are associated with differences in growth rate between the two populations. In the deer, numbers rarely increase by more than 10% per year; for example, it took the population 7 years to rise by 50% following the termination of culling in 1972 (see figure 2*a*). Sheep numbers, on the other hand, can increase by over 50% in the course of a single season and commonly double in the course of 2 years (figure 2*b*).

In both species, high winter mortality affects some sex and age categories more than others. To permit comparison, we have plotted mortality for different categories of animals of each species against mortality levels among mature females, defined here as 4–6 years to allow comparison between species (figure 4*a*,*b*). Relative to females of 4–6 years, juveniles, yearlings and old females show relatively high levels of mortality in both species. Yearlings show higher mortality than 4–6-year-old females in the

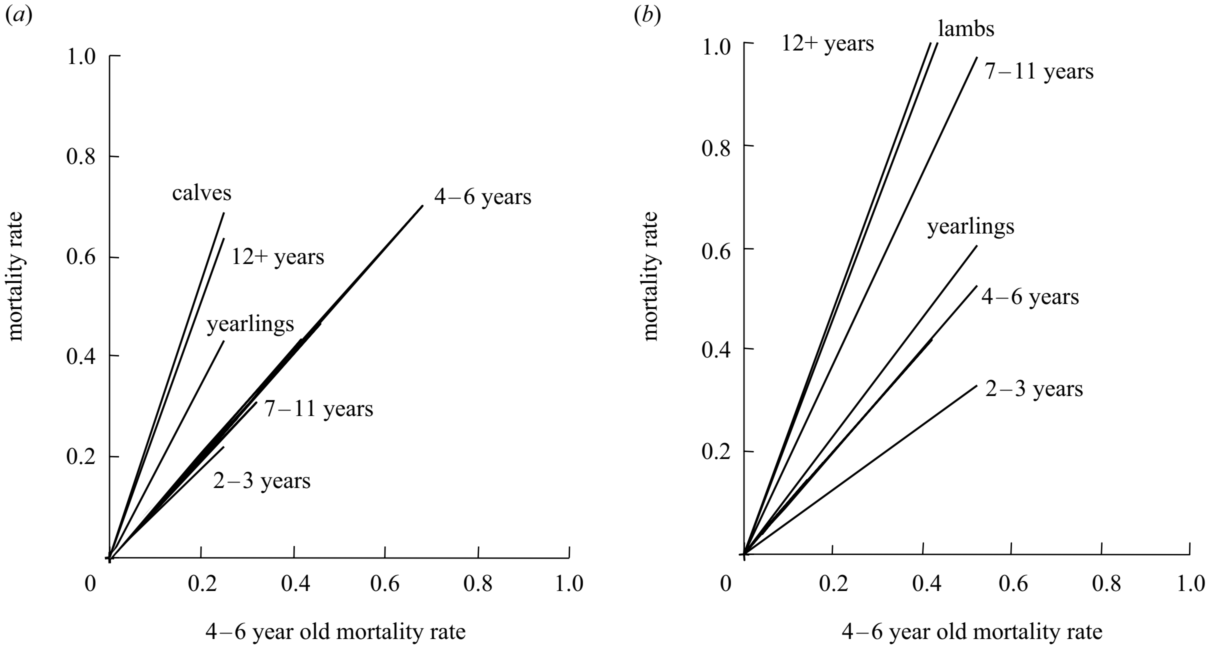

Figure 4. Mortality rates for different age categories of (*a*) female deer and (*b*) female sheep plotted against the mortality of females in their prime. Probability of mortality was the proportion of individually identified animals entering that age category that died before leaving it. All lines are forced through the origin and age categories printed next to the lines.

deer, probably because they are still growing (Clutton-Brock & Albon 1989), 2–3-year-olds show relatively low mortality in the sheep compared with the deer, perhaps reflecting the fact that growth in the sheep has largely ceased by the end of the third year of life (Jewell *et al.* 1974) while 7–11-year-old sheep show relatively high mortality as a consequence of earlier ageing.

In both species, variation in winter mortality is affected by population size (Clutton-Brock *et al.* 1982*b*; Coulson *et al.* 1997). In the deer, winter mortality increased with population density only in calves, though there is a tendency for mortality to increase in yearlings (Clutton-Brock *et al.* 1997*a*) as well as in older adults (figure 5*a*). In the sheep, only lambs and older adults were affected (figure 5*b*).

Winter weather conditions are also important (Albon *et al.* 1987; Benton *et al.* 1995). Winters in the North Atlantic region can either be wet and windy or drier and colder; these contrasts are associated with large-scale atmospheric fluctuations over the North Atlantic, called the NAO (Rogers 1984). When pressure is low over Iceland and high over the Azores (high NAO), strong westerly winds bring warm, wet weather north into Europe, and gales are common. By contrast, when pressure is high over Iceland and low over the Azores (low NAO), cold, dry weather spreads west from Siberia, and winters in northern Europe are calmer and colder. Fluctuations in NAO explain much of the variation in winter weather conditions; for example, in the Outer Hebrides, annual changes in the NAO winter index account for 61%, 56% and 23% of the variance in winter temperature, winter rainfall and number of winter days with gales, respectively (Forchhammer *et al.* 2001).

In both sheep and deer, winters of high NAO are associated with increased mortality in juveniles and older adults (figure 5*c*,*d*). Winter weather condition interacts with population density to produce high mortality in years when high population was associated with adverse weather conditions (Coulson *et al.* 2001; Forchhammer *et al.* 2001; Milner *et al.* 1999; T. H. Clutton-Brock, unpublished data). In the sheep, such years were sometimes associated with the death of over 60% of the animals entering the winter, though lambs and males of all ages were always more strongly affected than mature females (Clutton-Brock *et al.* 1991, 1997*a*).

3. VARIATION IN POPULATION STRUCTURE AND ITS CONSEQUENCES

Because relative survival differs between age categories (figure 4), the age structure of both populations varies widely between years (figure 6*a*,*b*) and these changes are not closely correlated with population density. For example, the proportion of the population made up of mature females varied from 24% to 41% between years in the deer and from 16% to 46% in the sheep (figure 6*a*,*b*); in neither species are these changes in the relative proportion of different age categories consistently correlated with density. Changes in age structure affect the number of animals that are likely to die in a particular year and so introduce an additional factor affecting fluctuations in population size. Fluctuations in population structure combined with variation in the relative mortality of different age categories contribute substantially to the magnitude of changes in population size.

Since breeding success varies between age categories, differences in survival do not necessarily reflect the extent to which particular categories of animals contribute to changes in total population size (Brown & Alexander 1991). For example, while the survival of red deer calves fluctuates more than that of mature animals, variation in the survival of mature females contributes more to fluctuations in population size (see figure 7*a*) (Albon *et al.* 2000). Similarly, despite the greater variability of changes in lamb and yearling numbers in the sheep, variation in

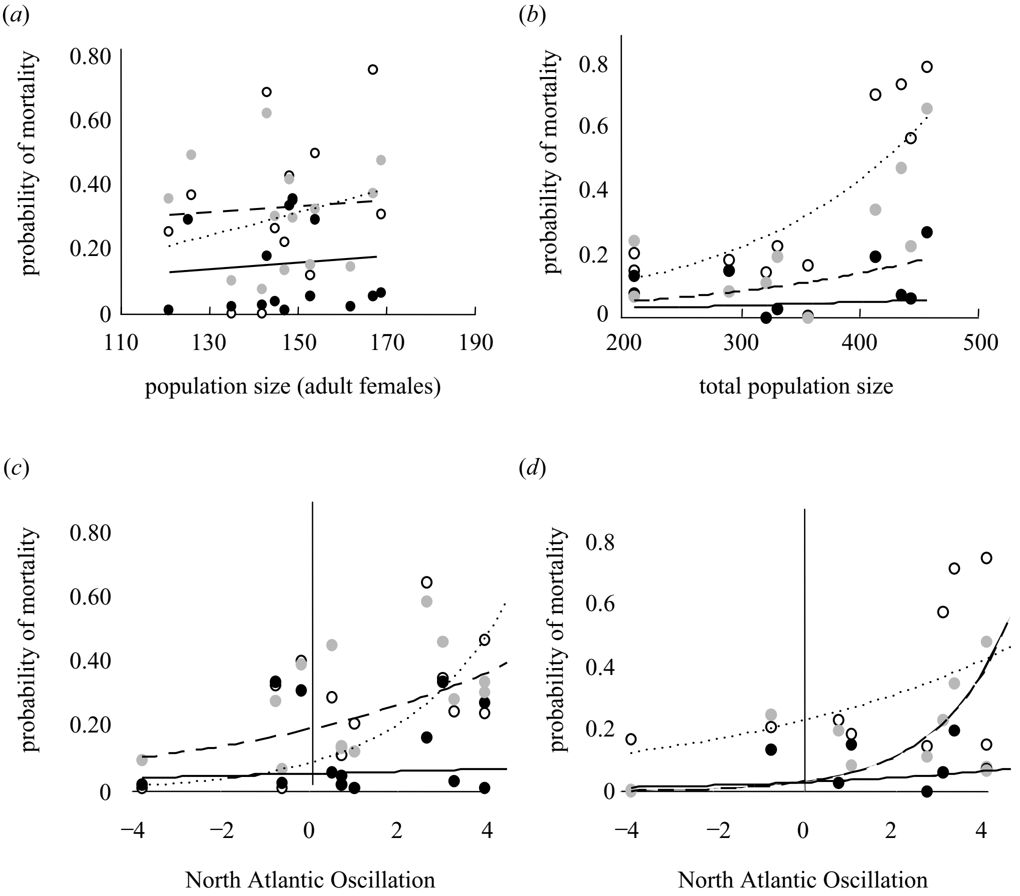

Figure 5. Effects of population density and weather on mortality in different age classes: (*a*) effects of density on deer; (*b*) effects of density on sheep; (*c*) effects of variation in the NAO on deer; (*d*) effects of NAO on sheep. Winters with high NAO values are relatively wet and windy; those with low NAO values are drier and colder. Open circles and dotted lines represent juveniles, black circles and solid lines represent prime aged adults and grey circles and dashed lines represent older adults.

adult numbers contributes more to variation in population size than changes in lamb and yearling numbers (see figure 7*b*) (Coulson *et al.* 2001). Comparing the two populations, it is clear that lambs and yearlings contribute more to changes in population size in the sheep than the deer, although both show higher mortality relative to mature females in the deer (see figure 4*a*,*b*).

As a result of both these effects, models which assume a constant age structure and ignore the contrasting effects of density and climate on survival and reproduction in different age categories, fail to predict changes in population size accurately (see figure 8). For example, stochastic, unstructured models of variation in sheep numbers account for only 21% of variation in population size (figure 8*c*) (Grenfell *et al.* 1992, 1998), while the inclusion of variation in age structure and in the responses of different age and sex categories in age-structured Markov models raises the proportion of the variation accounted for to nearly 90% (figure 8*d*) (Coulson *et al.* 2001). The age structure of the deer population does not vary so widely between years so that the contrast in accuracy between structured and unstructured models is less pronounced in the deer (see figure 8*a*,*b*).

4. COMPARATIVE EFFECTS OF DENSITY AND CLIMATE ON RECRUITMENT

In both species, the rate of recruitment to the population (which is a function of the number of females breeding and the proportion of calves surviving to weaning) is related to density as well as to density independent factors. In the deer, the fecundity of adult females ($\geqslant 3$ years) decreases with increasing population density (figure 9*a*). During the early years, when population size was still increasing, changes in age at first breeding contributed extensively to this trend while, in later years, the proportion of animals breeding for the first time at 3 years was consistently low and did not vary with population size (figure 9*b*). In both periods, female deer that had successfully reared calves (milk hinds) showed reduced fecundity when numbers were high, while the fecundity of those that had failed to do so was unaffected by density (figure 9*c*,*d*). This contrast between milk and yeld hinds is caused by differences in body mass that are known to affect fertility (Mitchell & Brown 1974; Albon *et al.* 1983*b*, 1986); female deer that have reared calves continue to suckle them until the early winter and, compared with yeld hinds, show lower body masses and fecundity in the autumn rut

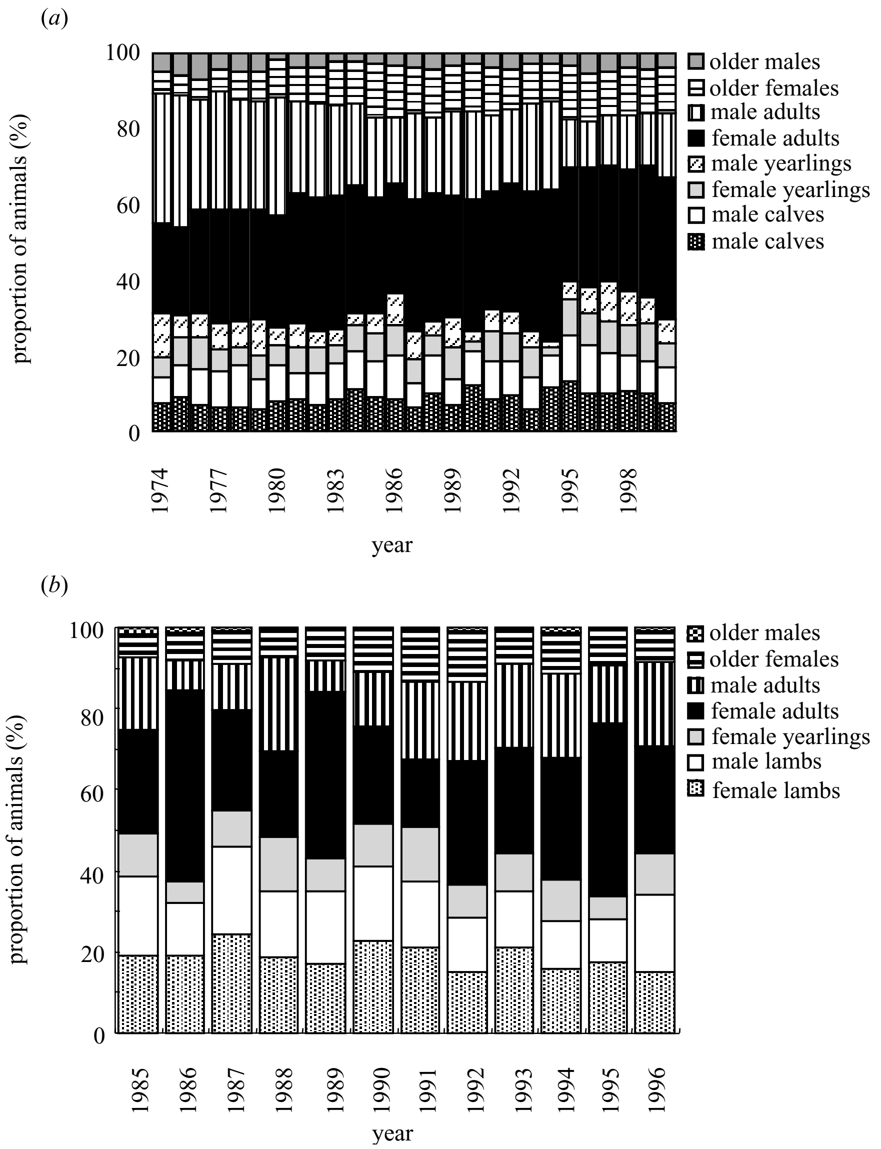

Figure 6. Age structure in different years for (*a*) deer and (*b*) sheep. The figure shows the proportion of animals of different ages in different years. Population structure varies more between years in the sheep.

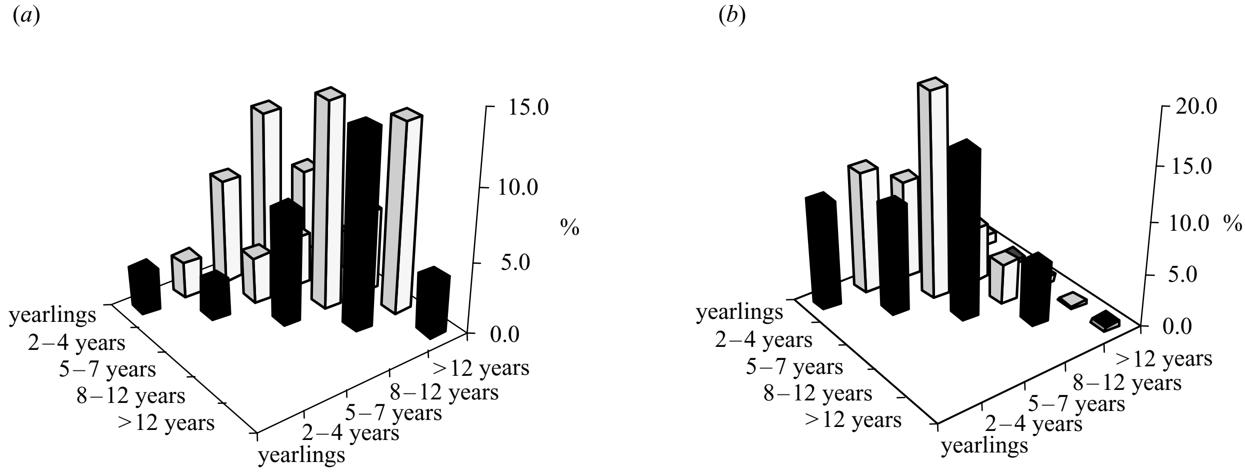

Figure 7. Contributions of different age classes to the relative change in population size in (*a*) deer (*b*) sheep. Columns show the extent to which particular age classes (and the covariation between them) contribute to relative changes in population size between successive years. Black columns on the centre diagonal represent the percentage contribution of each class to the relative change in population size over the study period (see Coulson *et al.* 1999; Albon *et al.* 2000). The off-diagonals (pale bars) represent the percentage contribution of the covariation between different age classes to the relative change in population size.

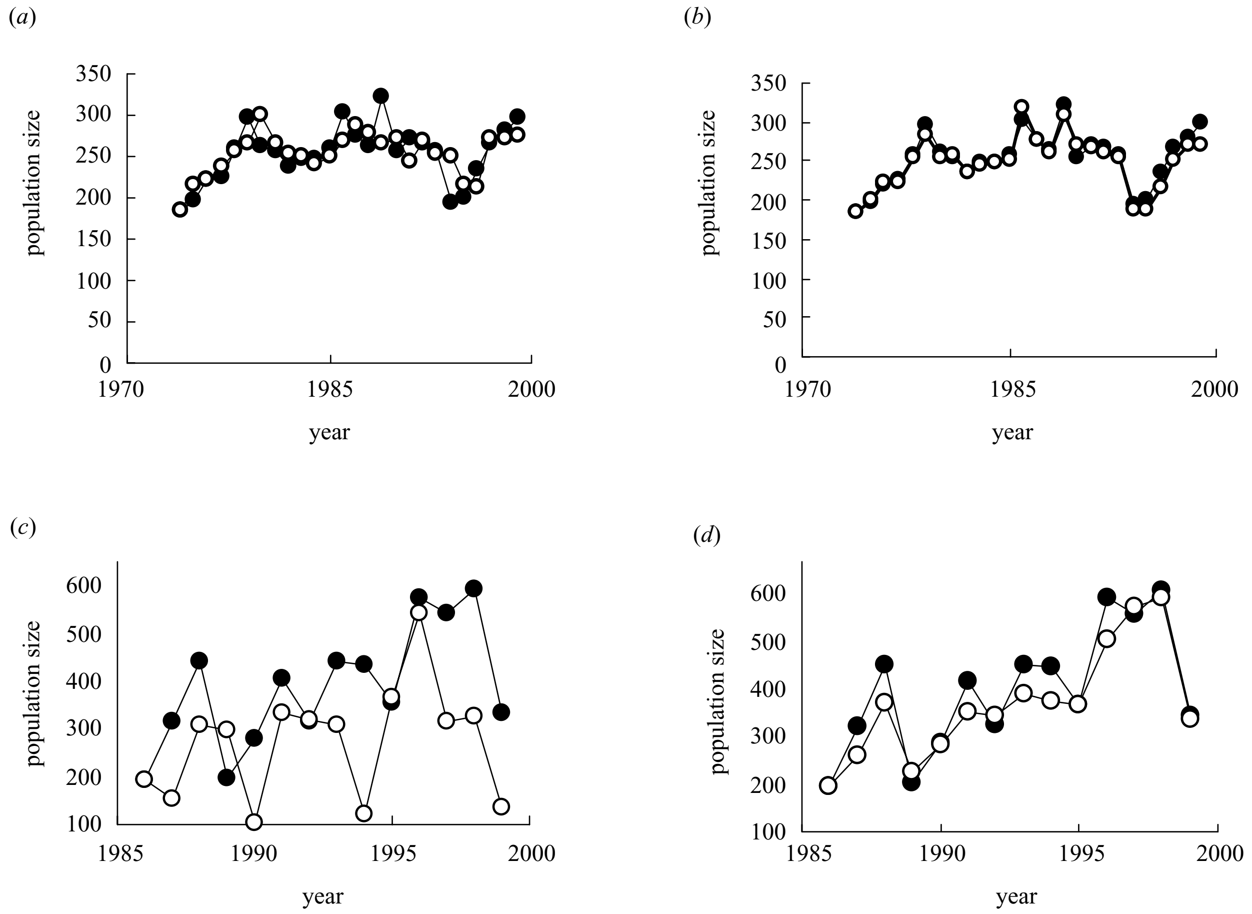

Figure 8. Accuracy of predictions derived from contrasting population models for (*a*,*b*) deer and (*c*,*d*) sheep. Black circles represent the observed population size and open circles predicted population sizes derived from (*a*,*c*) time-series models fitted to count data and winter weather (see Grenfell *et al.* (1998) for sheep; Coulson *et al.* (2000) for deer) and (*b*,*d*) age-structured Markov models that incorporate the effects of variation in age structure (see Coulson *et al.* (2001) for sheep; Coulson *et al.* (1999) for deer).

(Mitchell *et al.* 1976). Variation in the birth rate was also affected by winter weather—relative to population density, fewer milk hinds bred after wet, windy winters, probably partly because a higher proportion of animals failed to conceive and partly because more embryos were aborted or resorbed in the course of the winter (Albon *et al.* 1986; Kruuk *et al.* 1999).

In the sheep, there is a weaker relationship between density and fecundity overall (figure 10*a*) though, as in the deer, the proportion of animals that produced offspring in their first year after reaching breeding age showed a more marked decline (figure 10*b*). In contrast to the deer, females that had reared lambs successfully the previous season were *more* likely than 'yeld' females to give birth again (figure 10*c*), presumably reflecting a difference in phenotypic quality. A similar pattern has been demonstrated in bighorn sheep (Festa-Bianchet 1998).

The contrasting effects of previous reproduction on fecundity in the two species probably reflect differences in the timing of breeding and the duration of parental investment (Clutton-Brock *et al.* 1997*a*). Female deer that have reared calves through the summer months (milk hinds) are of substantially lower mass than those that have not done so. By contrast, female sheep that have reared one or two lambs through the summer regain lost condition after June, when lactation virtually ceases, and enter the winter at similar masses to those that have raised young.

Variation in recruitment rate also has contrasting effects on the population dynamics of the two populations. In the deer, density dependent changes in age at first breeding and in the fecundity of milk hinds begin to depress recruitment at relatively low population densities (see figure 9). As a result, density dependent changes in recruitment slow population growth, contributing to population stability (Clutton-Brock *et al.* 1982*b*, 1997*a*). By contrast, density dependent changes in fecundity have relatively little effect on population growth rates in the sheep (figure 10). Although birth rate and neonatal survival are depressed at high densities, these effects are relatively slight (Clutton-Brock *et al.* 1997*a*). Moreover, changes in fecundity usually occur in the year *after* a winter of high mortality (Clutton-Brock *et al.* 1997*a*) and consequently do little to slow the rate of population growth, though they may delay recovery of the population (Clutton-Brock *et al.* 1997*a*).

5. COMPARATIVE EFFECTS OF DENSITY AND CLIMATE ON DEVELOPMENT

Contrasts in the timing of reproduction also affect the impact of density and climate on early development and neonatal mortality in the two species. In both the deer and the sheep, environmental factors affecting foetal growth generate differences in birth mass between cohorts, which exert an important influence on subsequent growth, sur-

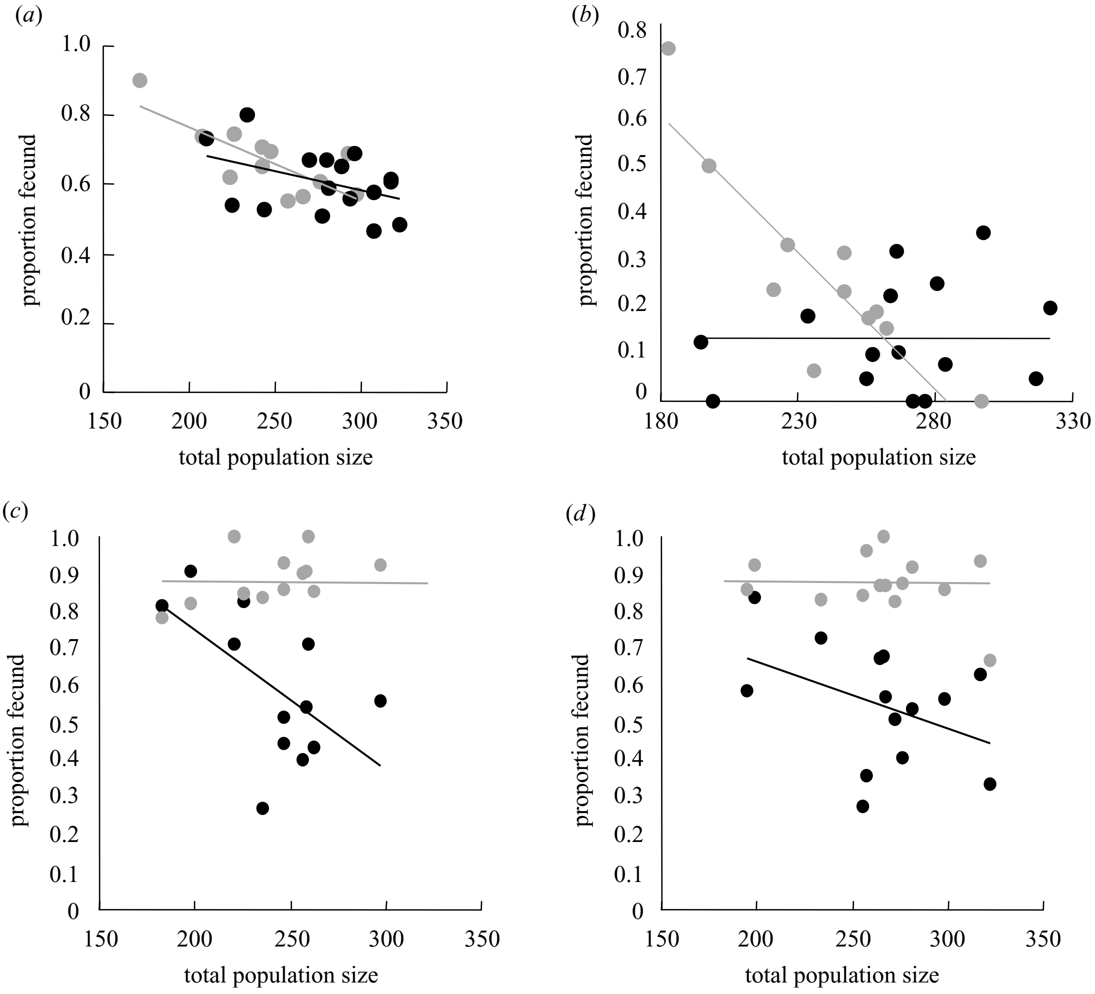

Figure 9. Changes in fecundity in red deer: (*a*) proportion of all adults that produced calves; (*b*) proportion of 3-year-old females that produced calves in early years (grey) and later years (black); (*c*,*d*) proportion of multiparous females that produced calves in (*c*) the early years (1973–1984) and (*d*) later years (1985–2001); black, females that had reared a calf to 6 months the previous season); grey, those that had failed to do so.

vival and breeding success (Albon *et al.* 1983*a*,*b*; Clutton-Brock & Albon 1989; Forchhammer *et al.* 2001). In the deer, birth mass is unaffected by population density (figure 11*a*) but varies with temperature in April and May, the last 2 months of gestation (figure 11*b*) (Albon *et al.* 1983*a*,*b*). By contrast, in the sheep, high population density depresses birth mass (figure 11*c*) while variation in climatic conditions in spring has no consistent effect (figure 11*d*). Like differences in the effects of environmental variation on fecundity, these contrasts are probably a result of differences in reproductive timing. Because of their relatively long gestation period (32 weeks), red deer bear their young in late May or June, so that the last 2 months of gestation occur in April and May, when grass growth is variable and can be strongly influenced by seasonal fluctuations in temperatures (Clutton-Brock & Albon 1989). As a result, spring temperatures are the dominant factor affecting birth mass and neonatal mortality in the deer. By contrast, the shorter gestation period of the sheep (21.5 weeks) and their earlier breeding season means that the last 2 months of gestation (February, March) precede the principal onset of spring growth, so that food availability and maternal condition are influenced to a greater extent by the effects of population density and climatic factors on food availability and energy expenditure during the winter months.

The effects of density and winter weather on the two species generate contrasting differences in survival and breeding performance between cohorts. In the deer, neonatal mortality is density independent and is affected principally by temperature and rainfall before and immediately after birth (Clutton-Brock & Albon 1989). Density independent variation in birth mass generates density independent differences in growth and breeding success between cohorts that persist throughout the lifespans of their members; females born below average mass remain below average mass as adults and produce small calves throughout the whole of their lives (Albon *et al.* 1987; Clutton-Brock *et al.* 1988). These differences are substantial; the average mass of calves produced over their lifetime by members of cohorts born between 1970 and 1979 varied by 40%, ranging from 5.0 kg to more than 7.0 kg (Clutton-Brock & Albon 1989). Cohorts that produce small calves show consistently high levels of calf loss, and offspring survival during the first 2 years of life varied between cohorts of mothers from less than 10% to over 60% (Clutton-Brock & Albon 1989). In the sheep, where birth mass is depressed by population density as well as

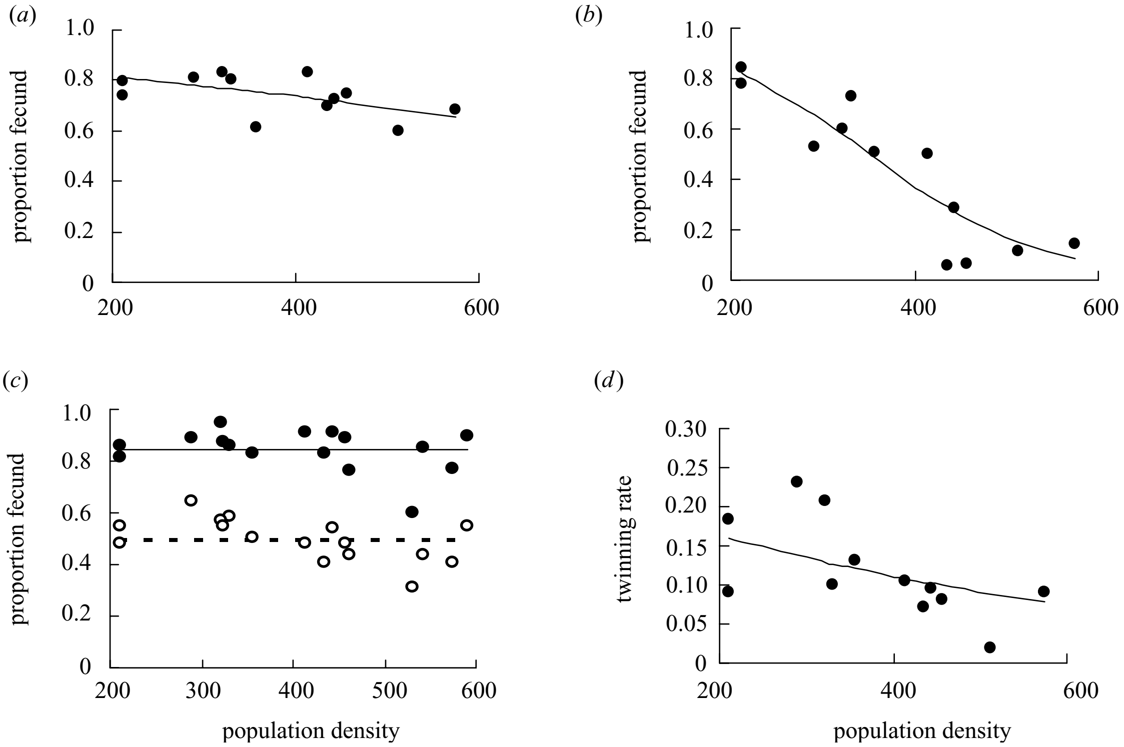

Figure 10. Changes in fecundity in sheep: (*a*) proportion of females of breeding age (12 months and older) that produced lambs (all potential breeders); (*b*) proportion of juveniles (12 months) that produced lambs (first time breeders); (*c*) proportion of mature females (>12 months) that had raised at least one lamb the previous season (all adults excluding first time breeders) (black circles, 'milk ewes') and those that had failed to do so (open circles, 'yeld ewes'). Dashed line; series 3; solid line, series 4. (*d*) All adults.

by wet winter weather, cohorts show density dependent differences in neonatal mortality, growth and fecundity (Forchhammer *et al.* 2001). However, the demographic effects of these differences are reduced, for individuals born after a winter when population density and mortality were high join a cohort with access to superabundant food supplies, which can offset their initial disadvantages.

While variation in early development exerts strong effects on the subsequent life histories of individuals in both populations, as in other vertebrates, these have limited impact on population dynamics in both species. In the deer, this is because cohort variation is density independent, so that, although the occasional sequence of 'good' or 'bad' cohorts may generate variation in population size (Albon & Clutton-Brock 1988), the demographic impact of cohort variation is limited. In the sheep, where birth mass and cohort performance vary with population density, cohort variation might be expected to have larger demographic effects. However, partly because cohorts conceived at high density commonly experience low density during their first year of life and show compensatory growth, and partly because years of high mortality are relatively frequent (and so interrupt runs of 'good' and 'bad' cohorts—see above), the demographic effects of variation in development between cohorts are slight. This will not always be the case and cohort effects may have important consequences for population dynamics in species where early development varies with density and population size is comparatively stable.

6. SEX DIFFERENCES IN SURVIVAL

So far, we have focused exclusively on the dynamics and demography of females. However, in both populations, high population density and adverse winter conditions affect the growth and survival of males more than females (Clutton-Brock *et al.* 1985*b*, 1997*a*). In the deer, where males are *ca.* 8% heavier than females at birth, sex differences in survival occur during gestation. As population density increases, the proportion of males at birth declines among offspring born to yeld hinds and, when these effects are allowed for, birth sex ratios decline after wet winters (Kruuk *et al.* 1999). Since the effects of density and weather occur after conception, they are presumably a consequence of variation in rates of abortion or resorption rather than of variation in the sex ratio at conception. By contrast, birth sex ratios in the sheep do not vary consistently either with population density or with winter climate (Lindström *et al.* 2002), perhaps because sex differences in birth mass are smaller (*ca.* 4%).

Neonatal mortality does not vary between the sexes in either species (Clutton-Brock *et al.* 1985*a*, 1992) while mortality is higher in males than females both during the first 2 years of life and in prime-aged animals (Clutton-Brock *et al.* 1985*a*, 1991, 1992) (figure 12*a*,*b*). Sex differences in mortality tend to be more pronounced in the sheep and, after years when mortality is high there can be eight times as many mature females as males among the survivors (figure 12*c*,*d*). In younger animals, this is prob-

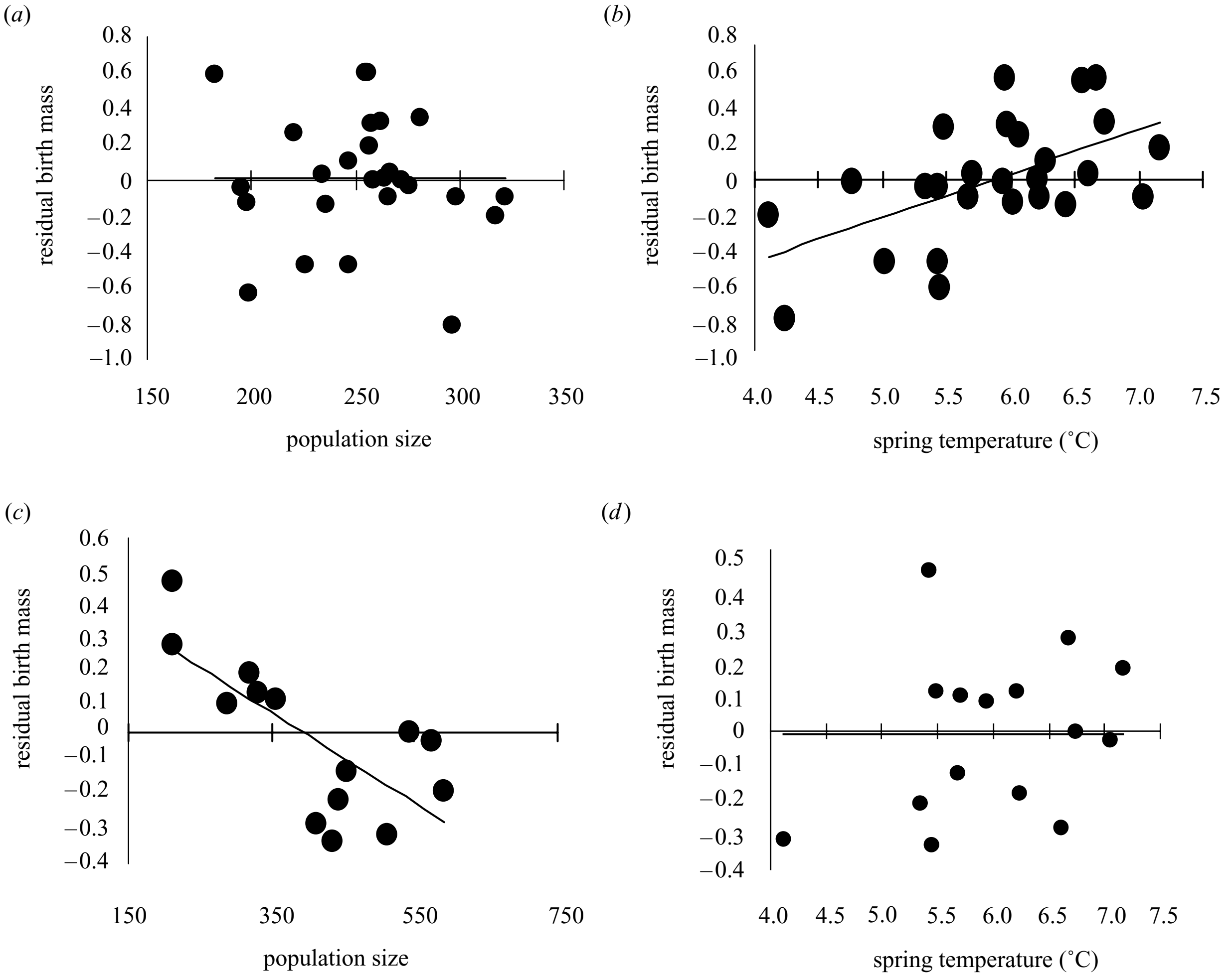

Figure 11. Birth mass of calves and lambs. Effects of (*a*,*c*) population size and (*b*,*d*) spring temperature on birth mass in (*a*,*b*) deer and (*c*,*d*) sheep. Spring temperature was measured as the mean average daily temperature in April and May. The *y*-axis (residual birth mass) shows the difference between the mean birth mass of each cohort and the population mean for the study period of both populations. Solid lines derived from linear regression models.

ably partly because male lambs and yearlings are actively involved in the rut (Coltman *et al.* 1999*a*,*c*) and consequently enter the winter in comparatively poor condition, often with relatively high parasite loads (K. Wilson, B. T. Grenfell, J. G. Pilkington, H. E. G. Boyd & F. M. D. Gulland, unpublished data). By contrast, differences in relative mortality of mature males between the two species are related to the timing of the rut; the relatively early (October) rut of the deer allows males to regain some of the mass lost during the mating season before midwinter, while male sheep (which rut in November and December) have little opportunity to regain condition before the onset of the regular period of starvation in late winter.

7. SEX DIFFERENCES IN DISPERSAL

The sexes also show contrasting patterns of dispersal in the two species. While most female deer remain in the area where they are born throughout their lives (Clutton-Brock *et al.* 1982*a*; Coulson *et al.* 1997), males commonly disperse between the ages of 2 and 4 years, and better grown adolescents are more likely to do so than smaller animals (Clutton-Brock *et al.* 2002). High population density increases the proportion of males that disperse and discourages immigrants, contributing to female biases in high density populations. By contrast, both male and female sheep remain in their natal area (heft) though neither associate closely with their relatives (see § 1).

Density dependent increases in mortality and emigration among males relative to females generate consistent relationships between population density and the adult sex ratio that affect the intensity of male competition and the distribution of mating success (Rose *et al.* 1998; Coltman *et al.* 1999*c*). In the deer, high population density is associated with a progressive bias towards females in the population sex ratio (figure 12*c*). This leads to increases in the proportion of males (especially of younger males) that hold harems (Clutton-Brock *et al.* 1997*b*) and to a reduction in the period for which individual males hold harems. In the sheep, males conceived at high population density and born immediately after a year when mortality is high enter a population that is heavily skewed toward females (figure 12*d*) and show relatively high mating success in their first and second years of life (Coltman *et al.* 1999*a*–*c*).

8. DISCUSSION

Our comparison of the population dynamics and demography of the deer and sheep emphasizes five main

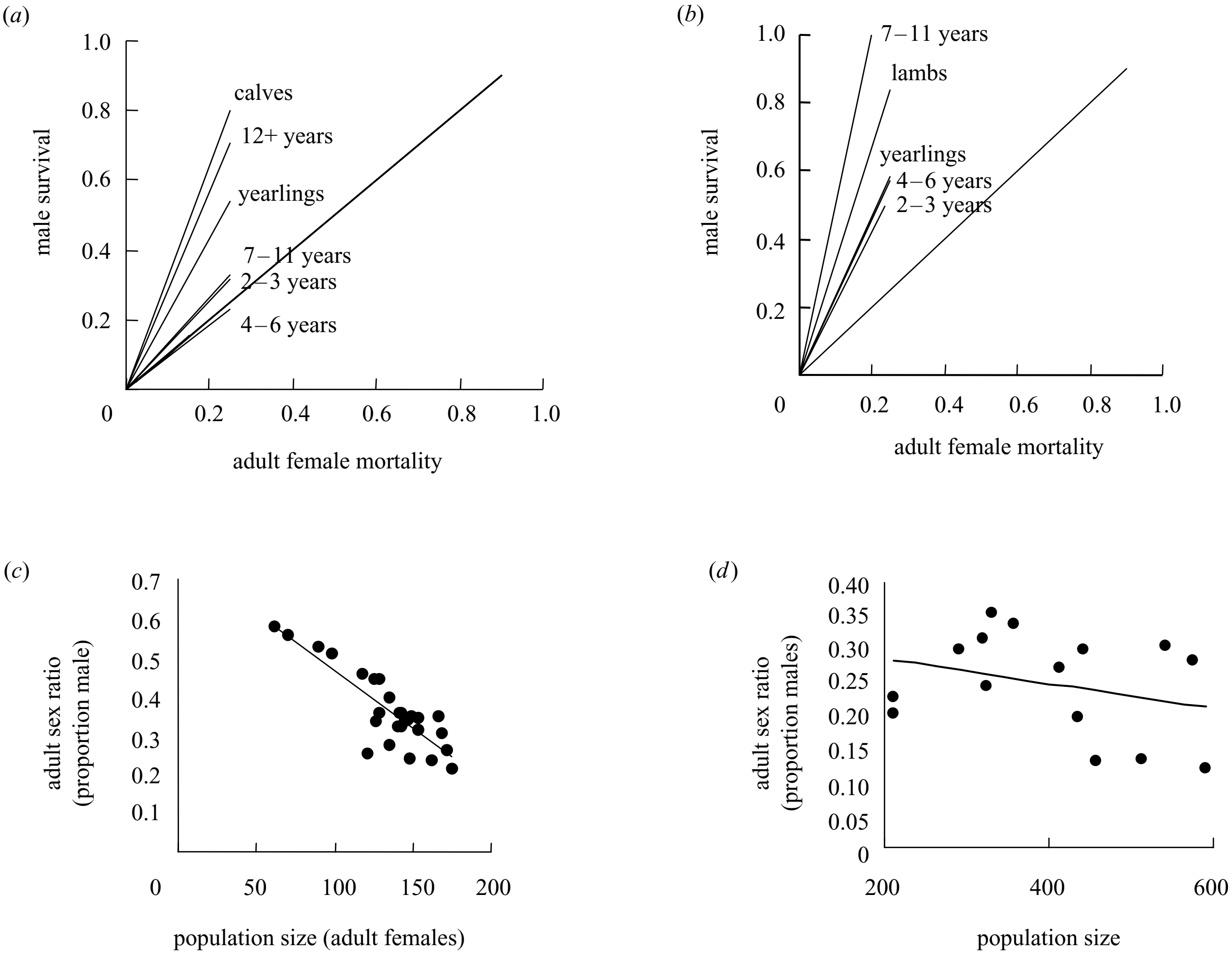

Figure 12. Mortality of males: (*a*) mortality of different age categories of male deer plotted on the mortality of 4–6-year-old female deer; (*b*) mortality of different age categories of male sheep plotted on the mortality of 4–6-year-old female sheep; (*c*,*d*) adult sex ratios in spring plotted on population size the previous autumn for deer and sheep. In both cases, population size was the number of individuals entering the winter while the sex ratio was estimated the following spring.

points. Changes in population density as well as in climatic variation commonly affect young and old animals more than those in their prime, and males more than females (see figure 5). Similar differences in the effect of environmental variation on different age and sex categories have been observed in a wide range of other ungulates (Caughley 1977; Fowler 1987; Gaillard *et al.* 2000). However, as our analysis shows, variation in the numbers of different categories of animals and in their reproductive potential mean that differences in survival do not necessarily reflect the extent to which different categories of animals contribute to changes in population size (see figure 7). In both our study populations, variation in the survival of mature animals contributed more to changes in population size than juvenile survival.

Our comparisons of the demographic processes operating in the deer during the initial period, when density was increasing, with similar processes after the population had ceased to increase, emphasize the extent to which demographic processes change during different stages of population and the need to control for these effects in comparisons between species (see figures 5 and 9). During the period of population growth in the deer, changes in density had a larger impact on variation in recruitment than winter weather conditions, while the situation was reversed after the population had ceased to increase (Albon *et al.* 2000). Variation in birth rate also accounted for a larger proportion of the observed changes in recruitment during the period of population growth than in the subsequent period while the relative contribution of adult survival rose in later years.

Our results show that differences in the potential rate of reproduction underlie the contrasts in stability between the two populations. The higher rate of recruitment in the sheep, combined with the lack of density dependent changes in the early stages of population growth, permits sheep populations close to ecological carrying capacity to increase by over 50% in the following summer (when resources are not limiting) and to enter the following winter at levels that cannot be sustained by winter food supplies, generating over-compensatory mortality that reduces population size to a level below ecological carrying capacity (Clutton-Brock *et al.* 1992, 1997*a*; Grenfell *et al.* 1992). As might be expected, the extent of winter mortality is not controlled by population density alone and is affected both by climatic factors in winter and by the age structure of the population (Grenfell *et al.* 1998; Coulson *et al.* 2001). The potential for overcompensation to occur is greater in the sheep than the deer, where population size rarely increases by more than 15% in a single season so that the population's capacity to exceed winter carrying capacity is constrained. Consequently, both population size and over-winter mortality do not vary as widely as in the sheep. As might be expected, maximum values of over-winter mortality appear to be larger in ungulates characterized by high potential rates of increase than in species showing lower values of *R*. Recent studies have recorded substantial fluctuations in population size in several other ungulates with high potential rates of increase (Boyd 1981*a*; Boussès *et al.* 1991; Milner-Gulland 1994; Coulson *et al.* 2000).

Finally, our analyses emphasize that the effects of high potential rates of increase on population stability are mediated by specific aspects of species ecology. In particular, it is clear that the timing of reproductive events, relative to seasonal changes in food abundance and energetic needs, exert important effects on the demographic impact of variation in population density and climate. For example, it is only because lambs are weaned so early in the summer that female sheep are able to recoup the energetic costs of lactation before the onset of winter, with the result that fecundity escapes from the effects of rising density (figure 10), generating high rates of population increase at relatively high population densities (figure 2*b*) and leading, eventually, to over-compensatory mortality (Clutton-Brock *et al.* 1997*a*). Differences in the timing of reproductive events between the two species are probably responsible for contrast in the effects of reproductive success on subsequent breeding performance (see figures 9 and 10) as well as in the contrasting effects of density and winter on differences in birth mass, neonatal survival and breeding success between cohorts (see figure 11). In addition, specific aspects of the ecology of the two populations affect the impact of demographic changes on population dynamics. In both populations, there are substantial differences in early development between cohorts but, for different reasons, this variation has few consequences for population dynamics. In the deer, this is because cohort differences are density independent so that, although they may produce short-term changes in population performance and size, these have few protracted effects. In the sheep, cohort differences are density dependent but their impact on survival and growth usually occurs immediately *after* years of high mortality and is also quickly eroded by subsequent fluctuations in density. In species that combine the early birth date of the sheep with the protracted lactation of the deer, cohort effects might both be density dependent and have an important impact on population dynamics.

General models of population dynamics have played an important heuristic role in predicting the effects of demographic change on dynamics. However, our results suggest that predictions of change in population size accurate enough to be used for management purposes will need to be based on more specific models that incorporate the effects of variation in age structure and in the responses of different age and sex categories to changes in population density and climate. General attempts to account for variation in population dynamics between populations and species will need to recognize the effects of relatively detailed differences in environmental seasonality, development, reproductive timing and population substructure on demographic processes as well as on their impact on population size. At the moment, a detailed understanding of the effects of variation in demography on dynamics is available for very few mammals (Fowler 1987; Gaillard *et al.* 2000) and the extent of these effects is unclear. The immediate need is to explore the demography and dynamics of a wider range of species.

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GLOSSARY

NAO: North Atlantic Oscillation