The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species

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The relative influences of density-dependent and -independent processes on vital rates and population dynamics have been debated in ecology for over half a century, yet it is only recently that both processes have been shown to operate within the same population. However, generalizations on the role of each process across species are rare. Using a process-orientated generalized linear modelling approach we show that variations in fecundity rates in populations of three species of ungulates with contrasting life histories are associated with density and winter weather in a remarkably similar manner. However, there are differences and we speculate that they are a result of differences in size between the species. Much previous research exploring the association between vital rates, population dynamics and density-dependent and -independent processes has used pattern-orientated approaches to decompose time-series into contributions from density-dependent and -independent processes. Results from these analyses are sometimes used to infer associations between vital rates, density and climatic variables. We compare results from pattern-orientated analyses of time-series with process-orientated analyses and report that the two approaches give different results. The approach of analysing relationships between vital rates, density and climatic variables may detect important processes influencing population dynamics that time-series methodologies may overlook.

Keywords: Soay sheep; saiga antelope; red deer; density dependence; density independence

1. INTRODUCTION

Fluctuations in the size of a population are a result of temporal variation in survival, fecundity and dispersal rates. Variation in these rates can be associated with density-dependent and -independent processes and recent research demonstrates that both processes can act within the same population (Albon *et al.* 1983; Clutton-Brock *et al.* 1987; Leirs *et al.* 1997; Stenseth *et al.* 1996*a*). However, the relative contribution of each process has been debated for over half a century (Andrewartha & Birch 1954; Leirs *et al.* 1997). Various mechanisms are likely to influence the relative role of each process on variation in vital rates and consequently on population fluctuations both within and across species. Across species there may be systematic variation with life history (Clutton-Brock *et al.* 1997; Stearns 1992). For example, density-independent factors are hypothesized to exert a stronger influence on survival rates in smaller species than in those that are larger (Stearns 1992). Within species the importance of each process may vary with latitude and habitat (Bjornstad *et al.* 1995; Stenseth *et al.* 1996*a*, 1998).

The majority of work exploring the influence of density-dependent and -independent processes on vital rates and population dynamics has used time-series analyses to detect direct and delayed density dependence and to fit an environmental covariate to explain residual variation around a deterministic model (Forchhammer *et al.* 1998; Grenfell *et al.* 1998; Lewellen & Vessey 1998).

The most commonly used method is to fit autoregressive models to logged data. The approaches estimate the effects of each process on vital rates by identifying which autoregressive time-lag or lagged weather variable most strongly influences the dynamics (Tong 1990). If a time-series of annual changes in logged population size of a large vertebrate is best described by an autoregressive model with dependence on the population size in the previous year only, then direct density dependence, acting on mortality, is inferred to be important (Royama 1992; Stenseth *et al.* 1996*b*). If the autoregressive model incorporates population size lagged by more than one year then delayed density dependence is inferred to influence the dynamics through an association between recruitment rates and population density. Similarly, examination of the estimates of lagged and non-lagged weather suggests the effects of weather on vital rates (Forchhammer *et al.* 1998).

An alternative approach is to analyse the effects of population density and density-independent factors on temporal variation in vital rates in a generalized linear modelling framework. This approach requires detailed long-term data on the proportion of individuals reproducing, surviving or dispersing.

In this paper we use detailed long-term data on fecundity rates in three species of ungulates to explore whether the density-dependent and -independent processes operate in a similar manner across species. Additionally, we compare these results with those from analyses of time-series for each of the species. We used data from a population of Soay sheep (*Ovis aries*) (Clutton-Brock *et al.*
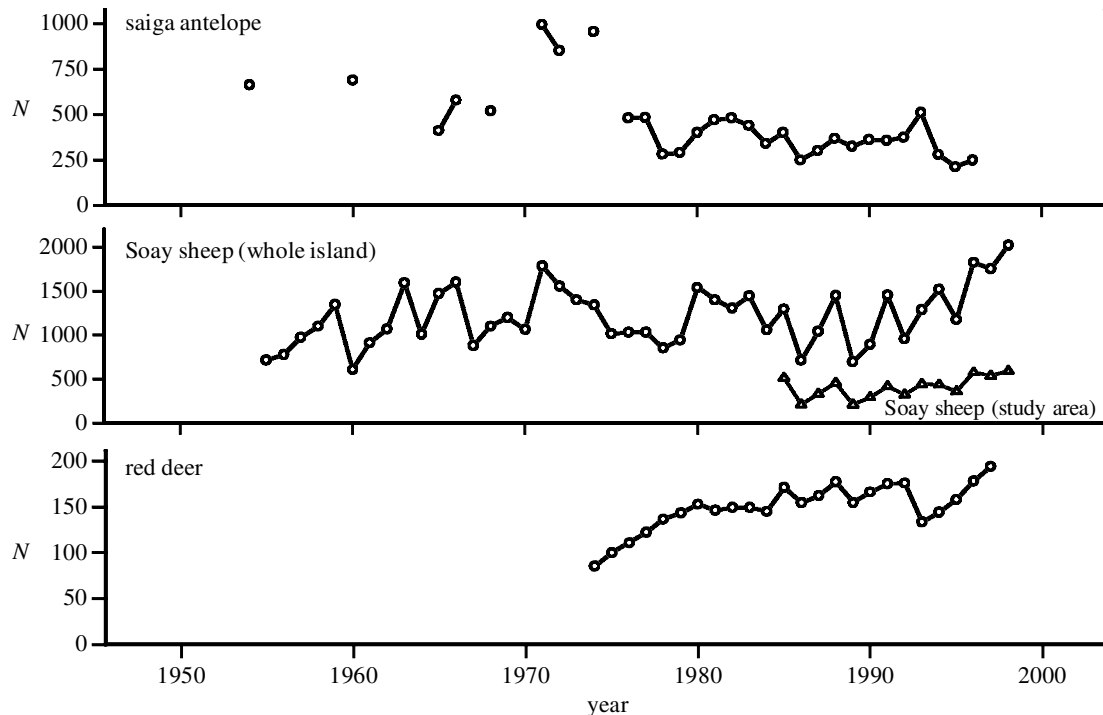
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Figure 1. Time-series data for the three species.

1991; Coulson *et al*. 1999*a*; Jewell *et al*. 1974; Pemberton *et al*. 1996), saiga antelope (*Saiga tatarica tatarica*) (Bekenov *et al*. 1998; Milner-Gulland 1997) and red deer (*Cervus elaphus*) (Clutton-Brock *et al*. 1982; Coulson *et al*. 1997). These species were selected as both detailed individual-based data and time-series are available and because Soay sheep and saiga antelope have similar life-history strategies that contrast with that of red deer. The combination of having both long time-series on abundance and long-term data on individuals is unique and provides an excellent opportunity to contrast and compare different analyses of ecological patterns and processes. We suggest that increasing our understanding of the way vital rates and population dynamics are associated with density-dependent and -independent processes requires a combination of pattern- and process-orientated approaches.

2. METHODS

(a) *Study populations*

(i) *Saiga antelope*

The saiga antelope in Betpak-dala, Kazakhstan, have been continuously monitored since 1976 (figure 1). Fecundity data have been collected from this population between 1986 and 1996 (Bekenov *et al*. 1998; Milner-Gulland 1997). The saiga antelope inhabits the semi-desert of Central Asia where it experiences a harsh and unpredictable climate with winter temperatures reaching $-30\,^{\circ}$C. The saiga is migratory, moving several hundred kilometres in large loose herds, from the winter pastures in the southern desert zone to summer pastures in the northern steppe region. Mass mortality events caused by severe winter weather are regularly observed, both amongst saiga antelope and domestic livestock. Population size is estimated

annually from aerial surveys in March–April. Fecundity rates for the saiga antelope were estimated from autopsies on individuals shot in the February prior to calving. These animals are assumed to be representative of the saiga population as a whole. (For further details, see Bannikov *et al*. 1961; Sludskii 1963; Bekenov *et al*. 1998.)

(ii) *Soay sheep*

The Soay sheep have been the focus of an individual-based study on the island of Hirta in the St Kilda archipelago from 1985 to the present (Coulson *et al*. 1999*a*; Pemberton *et al*. 1996), but have been continuously censused since 1955 (figure 1) (Grenfell *et al*. 1998). Compared to the saiga antelope, the Soay sheep experience a comparatively warm wet climate with winter temperatures rarely dropping below freezing (Jewell *et al*. 1974). Again in contrast to the saiga antelope population, being restricted to the island of Hirta they do not migrate. The population experiences frequent large mortality episodes with up to 60% of the population dying in any one year (Pemberton *et al*. 1996). Population size is estimated in October from censuses of the study area and annual fecundity rates are calculated from those individuals whose reproductive status is known.

(iii) *Red deer*

The red deer have been the focus of an individual-based study on Rum from 1971 to the present (Clutton-Brock *et al*. 1982; Coulson *et al*. 1997; Pemberton *et al*. 1996). The red deer of Rum experience a similar climate to the Soay sheep population on Hirta. Like the Soay sheep they are restricted to an island and do not migrate. From 1973 the population in the north block, *ca*. 20% of the island, has been unmanaged and the deer within this area have been the focus of the ongoing long-term study. During the 1970s the population steadily

increased until it reached *ca.* 160–170 animals in the early 1980s. Since then the population has remained relatively constant in size (figure 1) (Clutton-Brock *et al.* 1982). It does not experience such severe fluctuations as seen in the Soay sheep and the saiga antelope populations. Population size is estimated in October from censuses of the study area and annual fecundity rates are calculated from those individuals whose reproductive status is known.

All of the study populations are food limited.

(b) *Life histories*

Saiga antelope, red deer and Soay sheep are not closely related. Saiga antelope and Soay sheep probably last shared a common ancestor 16–20 million years (Myr) ago, and have similar life histories (Allard *et al.* 1992; Chikuni *et al.* 1995). Saiga antelope and red deer are less closely related, last sharing a common ancestor 25–40 Myr ago (Allard *et al.* 1992), and have contrasting life histories. Both saiga antelope (Milner-Gulland 1994) and Soay sheep (Jewell *et al.* 1974) can breed in their first year and can produce twins, while the Rum red deer cannot breed until they are three years old, and may not breed until they are four years old (Clutton-Brock *et al.* 1982), and only ever produce one offspring. Soay sheep and saiga antelope are of similar sizes (adult females weigh *ca.* 25 kg and 28 kg, respectively; Fadeev & Sludskii 1982; Jewell *et al.* 1974) and are considerably smaller than red deer (70 kg; Clutton-Brock *et al.* 1982). They also do not live as long. All three species are gregarious with red deer hinds associating in matrilineal groups throughout the year (Coulson *et al.* 1997), while the Soay sheep (Jewell *et al.* 1974) and saiga antelope (Bekenov *et al.* 1998) form less cohesive social bonds. All three species rut in the autumn and calve or lamb in the following spring. Soay sheep lambing occurs earlier (April) than calving for red deer (May–June) in spite of their geographical proximity. Saiga antelope calve in May.

(c) *Analyses of yearly fecundity rates*

Separate analyses were conducted for potential first-time breeders and adults in each species. It would have been possible to distinguish other age categories in the Soay sheep and red deer as the age of each individual is accurately known. However, such accurate ageing was not possible in the saiga antelope, so to allow comparisons between the three species we distinguish only between first-time breeders and adults.

In cases where individuals could twin (Soay sheep adults and saiga calves and adults) we decomposed the multinomial response into three functions: (i) the probability of not reproducing; (ii) the probability of producing a singleton offspring; and (iii) the probability of producing twins. A generalized linear model with a multinomial error structure was then fitted to the three response variables (McCullagh & Nelder 1989). Generalized linear models with a binomial error structure (Sokal & Rohlf 1995) were used for analyses of fecundity rates when individuals could not produce twins (Soay sheep lambs and red deer). In cases where the data were considered to be overdispersed (the ratio of residual deviance to residual degrees of freedom was > 2) Williams' correction was used (Crawley 1993; Williams 1982).

Effects of the following independent terms were investigated.

(i) *Population size*

In the Soay sheep and red deer studies the number of individuals using the study area the summer prior to the rut was used.

In the saiga antelope the population counts were from aerial surveys conducted in the spring prior to birth.

(ii) *Weather variables*

The total monthly precipitations (in millimetres) and the mean monthly temperatures for each month from October to May were used. Weather data for St Kilda were collected by the UK Meteorological Office at Benbecula airport (80 km east of St Kilda) from 1985 until 1996. Unfortunately this weather station was closed in June 1996. We estimated the weather data for each missing month using the correlations between the weather at Benbecula and Stornoway airports between January 1959 and its closure. Stornoway is *ca.* 150 km away from both Benbecula and St Kilda. The average correlation coefficients between Benbecula and Stornoway airports were 0.95 for temperature and 0.84 for precipitation. The UK Meteorological Office collected weather data for Rum on Rum, and official Government weather data were used for Kazakhstan. The weather station chosen for the analysis was Tasty, situated at 69°17′ E, 44°79′ N. This weather station is situated within the saiga's winter range area, where they remain from November–December to February–March.

Once significant weather variables were identified, interactions between them and population size were explored. Finally each term was dropped from the model, its significance assessed, and then reinstated if significant. In models with both a binomial error structure and a multinomial error structure, the best model was selected as the one that explained the most deviance in comparison to the number of degrees of freedom. In both cases the deviance is distributed as χ^2.

All generalized linear regression analyses were carried out in Genstat[TM] (Genstat Committee 1993).

(d) *Population dynamics*

We analysed the logged population counts for each of the species using a linear autoregressive regime with weather covariates fitted in an attempt to explain any remaining residual variation. The approach assumes that the population growth is linearly associated with logged population abundance. Although this assumption does not hold for the Soay sheep, it allows us to estimate the strength of density dependence and to make comparisons across the three species, and linear models give reasonable approximations for some populations with nonlinear dynamics. We do not give further details of the methods as they are frequently used to analyse ecological data. Bjornstad *et al.* (1995) provide a coherent detailed description of the fitting of linear autoregressive regimes and Forchhammer *et al.* (1998) describe how weather covariates can be incorporated into these models.

Autoregressive lags of up to three years were investigated as these lags can have biological meaning (Royama 1992; Stenseth *et al.* 1996a). Analyses were done using the TSM and TRANS-FERFUNCTION commands in Genstat[TM] 5 (Genstat Committee 1993). Only one weather covariate was fitted at a time. Weather effects were fitted unlagged, lagged by one year and lagged by two years. The most parsimonious model was selected as having the lowest corrected Akaike information criterion (AIC_c). Estimates and standard errors for the autoregressive terms and for the effects of each weather covariate were examined to determine whether the influences of past population size and weather covariates from the most parsimonious model were significant. The logged red deer time-series was non-stationary so we analysed the residuals from a model of the logged population size with year fitted as a quadratic.
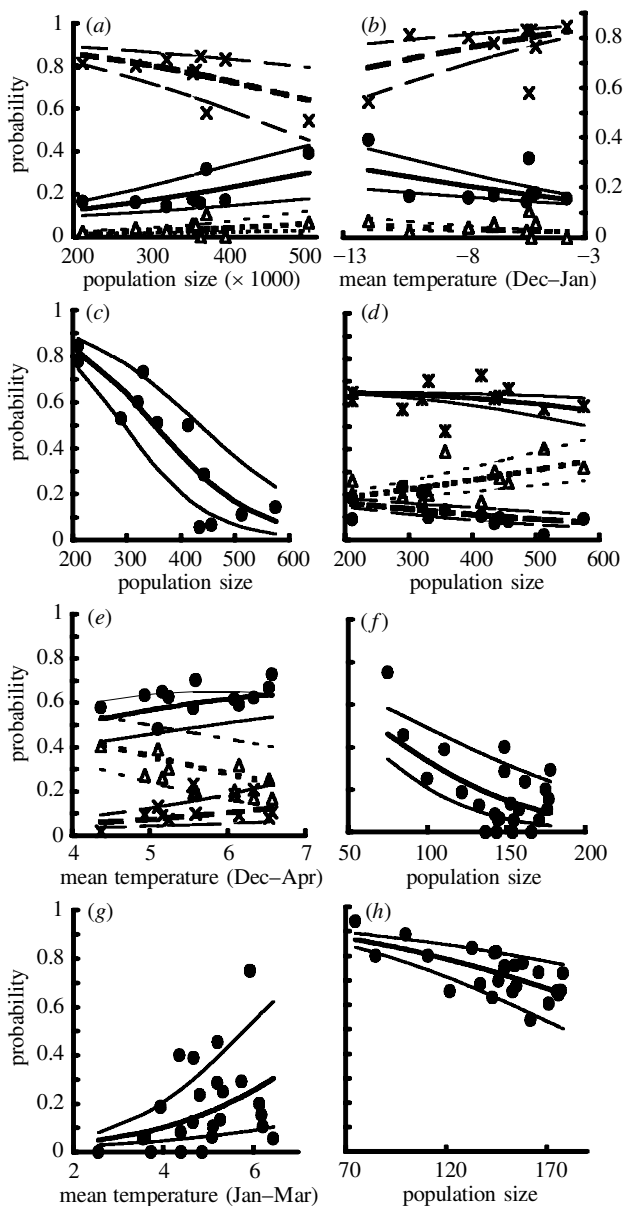
Figure 2. The associations between fecundity, population density and local winter temperature in the three species. The association between fecundity rates and (*a*) population density in saiga antelope adults, (*b*) mean December–January temperature in saiga antelope adults, (*c*) population density in Soay sheep lambs, (*d*) population density in Soay sheep adults, (*e*) mean December–April temperature in Soay sheep adults, (*f*) population density in red deer calves, (*g*) mean January–March temperature in red deer calves, and (*h*) population density in red deer adults. The triangles represent the observed proportions of females not breeding, the filled circles represent the observed proportions of females producing a singleton and the crosses represent the observed proportions of females twinning. The fitted lines are from the models described in the text. When the full model includes both population density and weather terms the term not plotted was held constant at the mean value to display the effect of the other independent variable on fecundity rates. The heavy dotted line represents the fitted proportions of females not being fecund, the heavy solid line represents the fitted proportions of females producing a singleton and the heavy dashed line represents the fitted proportion of females twinning. The lighter lines represent ± 1 s.e.m. around the model.

3. RESULTS

(a) *Fecundity rates*

Fecundity rates vary among the three species. Saiga antelope are highly fecund with adults producing on average 1.7 foetuses per female per year, Soay sheep are less fecund with adults producing 0.85 lambs per female per year and red deer are the least fecund with adults producing 0.72 calves per female per year. In each of the populations individuals are grazers and are probably food limited (Bekenov *et al.* 1998; Clutton-Brock & Albon 1989; Coulson *et al.* 1997). In all species adults have higher fecundity rates than those breeding for the first time, and in all cases fecundity rates vary across years. In all species fecundity rates are more variable in first-time breeders than in adults. Red deer first-time breeders and adults and Soay sheep lambs do not twin. In contrast, saiga antelope calves and adults and Soay sheep adults can twin. Twinning rates differed between these categories: the average annual proportion of females twinning in saiga antelope calves was 0.17 (range 0–0.59), in saiga antelope adults it was 0.75 (range 0.54–0.85) and in Soay sheep adults it was 0.12 (range 0.02–0.23).

(i) *Saiga antelope*
Calves

Between 1986 and 1996 there were a total of 164 calves for which fecundity data were collected. Out of these, 34 did not breed, 107 produced a singleton calf and 23 produced twins. Sample sizes are lower than for red deer and Soay sheep with, on average, 18.2 calves sampled each year (range 5–32). Neither population density nor winter weather are significantly associated with fecundity rates.

Adults

There were a total of 381 adults for which we had fecundity data giving an average of 42.3 individuals sampled each year (range 17–85). Out of the 380 animals, 292 twinned, 75 produced a singleton offspring and 13 produced no offspring. The proportion of females that were not fecund was not significantly associated with either population density (0.745, d.f. = 1, $p > 0.05$) or any weather variables (figure 2*a,b*). However, the proportion of females that produced a singleton significantly increased with increasing population density ($\chi^2 = 7.76$, d.f. = 1, $p < 0.05$; figure 2*a*) and with decreasing mean December–January temperature ($\chi^2 = 4.2$, d.f. = 1, $p < 0.05$; figure 2*b*). The proportion of adults twinning significantly decreased with increasing density ($\chi^2 = 8.26$) and with decreasing mean December–January temperature ($\chi^2 = 5.33$, d.f. = 1, $p < 0.05$). No other weather variables were as significantly associated with fecundity rates.

(ii) *Soay sheep*
Lambs

Between 1985 and 1997 fecundity data were collected from 440 lambs, giving an average of 33.8 individuals sampled per year (range 9–56). Sample sizes were lowest in years following a population crash. Out of these 440 individuals, 240 did not breed and 200 produced a

Table 1. *A summary of the results for the three species. Estimates for each of the independent terms fitted into the generalized linear regression models with their standard errors in parentheses*

(NA represents models that were not fitted. These occur in cases where the model structure was binomial. Dashes represent terms that were not statistically significant at $p < 0.05$.)

	probability of not being fecund		probability of producing a singleton		probability of producing twins	
	population density	winter temperature	population density	winter temperature	population density	winter temperature
Soay sheep						
first breeders	NA	NA	− 0.01075 (0.00207)	—	NA	NA
adults	0.00176 (0.00073)	− 0.380 (0.117)	—	0.334 (0.167)	− 0.00310 (0.00128)	—
saiga antelope						
first breeders	—	—	—	—	—	—
adults	—	—	0.003516 (0.000882)	− 0.0881 (0.0290)	− 0.00369 (0.00138)	0.0983 (0.0449)
red deer						
first breeders	NA	NA	− 0.02181 (0.00568)	0.551 (0.206)	NA	NA
adults	NA	NA	− 0.01236 (0.00328)	—	NA	NA

singleton lamb. The data were overdispersed (ratio of residual deviance to residual degrees of freedom: 25.23:10) so Williams' correction was used. The full model only included population density ($\chi^2 =76.16$, d.f. = 1, $p < 0.001$). The proportion of fecund females declined with increasing population density (figure 2c).

Adults

Fecundity data were collected from a total of 1921 adults giving an average of 147.7 individuals sampled per year (range 99–232). Out of these, 579 did not produce any young, 1134 produced a singleton lamb and 208 twinned. The data were overdispersed. The proportion of females that were not fecund was significantly associated with population density ($\chi^2 = 4.3$, d.f. = 1, $p > 0.05$; figure 2d) and mean December–April temperature ($\chi^2 = 7.8$, d.f. = 1, $p < 0.01$; figure 2e). The proportion of females producing singleton offspring was not significantly associated with density ($\chi^2 = 0.03$, d.f. = 1, $p > 0.05$) but was significantly associated with mean December–April temperature ($\chi^2 = 4.02$, d.f. = 1, $p < 0.05$). The proportion of females twinning significantly decreased with increasing density ($\chi^2 = 6.02$, d.f. = 1, $p < 0.05$) but was not significantly associated with any weather variables.

(iii) *Red deer*
Three year olds

Between 1971 and 1997 there were a total of 355 three year olds for which we had fecundity data, giving an average 15 animals per year (range 5–24). Out of these, 61 produced a singleton offspring and 294 did not breed. The data were overdispersed so Williams' correction was used. The full model includes population size ($\chi^2 = 11.72$, d.f. = 1, $p < 0.01$) and the mean January–March temperature ($\chi^2 = 8.33$, d.f. = 1, $p < 0.01$). Fecundity rates decline with increasing

population size (figure 2f) and decreasing winter temperature (figure 2g).

Adults

We had fecundity data on a total of 2353 adults between 1974 and 1997 giving an average of 98 individuals per year (range 50–123). Out of these, 1689 produced a singleton offspring and 664 did not breed. The data were overdispersed so Williams' correction was used. The full model included only population size. Fecundity rates declined with increasing population density (figure 2h).

In none of the analyses were second-order interaction terms significant and the independent terms were never significantly correlated (largest correlation was between population density and mean winter temperature in the red deer: $r = 0.1$).

(iv) *Comparisons across species*

Density was associated with fecundity in all species and in all age classes except saiga antelope calves. Increasing density always decreased fecundity rates. In each species the same weather variable, the mean temperature during part of the winter, influenced fecundity rates; in all cases low winter temperatures decreased fecundity rates. In red deer the effect of winter temperature is only observed in first-time breeders while in saiga antelope and Soay sheep winter weather is only associated with fecundity in adults.

Regression estimates for independent terms are displayed in table 1. The regression estimates vary by nearly an order of magnitude across species and age classes. In both the Soay sheep and the red deer, the effects of density on fecundity rates are stronger in first-time breeders than in adults. In each case, in regressions where both density and winter weather influence fecundity the sizes of the estimates are similar. Fecundity

rates were most strongly influenced by density and weather in three-year-old red deer.

(b) *Population dynamics*

Examination of the autocorrelative signatures for the three populations demonstrates that the only significant autocorrelative signature occurs in the red deer population and that this represents a lag of one year. Although not significant, the autocorrelative signature with the lowest AIC_c for the Soay sheep population is an autoregressive model with a lag of one year ($AR(1)$). In contrast, but again non-significant, the best autoregressive model for the saiga antelope incorporated a lag of two years ($AR(2)$).

A more formal construction of the AR models with autocorrelative lags up to three years, incorporating weather covariates, gave the following results. For purposes of brevity we report estimates for only those models with the lowest AIC_cs.

(i) *Soay sheep*

The model with the lowest AIC_c was an $AR(1)$ model including mean December–April temperature lagged by two years. The AR estimate was not significant (estimate = 0.23, s.e. = 0.17) but the weather estimate was (estimate = 0.08, s.e. = 0.03).

(ii) *Saiga antelope*

The model with the lowest AIC_c was an $AR(1)$ model including mean December–January temperature lagged by one year. The AR estimate was not significant ($AR(1)$ estimate = 0.37, s.e. = 0.24) but the estimate for lagged weather was (estimate = 0.045, s.e. = 0.012).

(iii) *Red deer*

The model with the lowest AIC_c was an $AR(1)$ model including winter temperature lagged by two years. Both the $AR(1)$ and the winter weather estimates were significant (estimate = 0.68, s.e. = 0.18 and estimate = 0.28, s.e. = 0.1, respectively).

4. DISCUSSION

Our analyses of inter-annual variation in fecundity rates demonstrate that in all three species fecundity rates are associated with both density and weather in similar manners. In all three species both high density and the same weather variable, cold winter temperature, depress fecundity rates. These results are surprising because there are variations in the life-history strategies between the species, the way the data are collected and the areas in which the species occur. However, as well as the similarities in the ways that density and weather are associated with fecundity rates, there are also differences. In the adult age classes, winter weather has an influence on fecundity rates only in the saiga antelope and Soay sheep. Differences between species are also noticeable in the first-breeding-age classes when there is no obvious pattern in the way fecundity rates are associated with density and weather. Time-series analyses gave results that only partially support results from the analyses of fecundity.

Density and winter weather had effects of similar magnitude in analyses of fecundity rates in adults of both the saiga antelope and the Soay sheep. In contrast, only density was associated with fecundity in red deer adults. This suggests that the effects of density-independent processes are stronger in smaller species (Stearns 1992). Adult saiga antelope and Soay sheep are considerably smaller than red deer, having a higher surface-area-to-volume ratio. A consequence of this is that more energy is required to maintain a constant body temperature (Clutton-Brock *et al.* 1997). Being smaller results in saiga antelope and Soay sheep being more susceptible to the vagaries of winter weather than red deer.

Within all species density was associated with survival in the adult age class with all regression estimates being similar in size; a comparison of the estimates and their standard errors shows that there are no significant differences in the ways that the populations responded to density. Competition between individuals for high-quality forage is probably the mechanism leading to the associations between fecundity rates and density (Illius & Gordon 1999). In the Soay sheep and red deer this competition is intraspecific, in the saiga antelope it is a mixture of intra- and interspecific with livestock (Bekenov *et al.* 1998).

Although the magnitudes of the effects of density and winter weather were similar in the Soay sheep and the saiga antelope, the way that each process influenced fecundity varied. Fecundity rates changed in the Soay sheep because the proportion of both twins and singletons produced decreased, while in the saiga antelope the change in fecundity rates was due to only a change in the twinning rates. These differences are probably a result of variation in the life-history strategies of the species. However, in both species fecundity rates are higher than those observed in red deer and in most other ungulate species. So why do the saiga antelope and Soay sheep have such high fecundity rates? Both populations demonstrate sporadic, periodic population crashes. Detailed analyses of the sheep data have shown that these population crashes are a result of interactions between the population density, the weather and the age structure of the population; high density does not always result in a population crash (Coulson *et al.* 2000; Grenfell *et al.* 1998). The same is likely to be true of the saiga antelope. As the distribution of weather events and the density of the population are unpredictable we suggest that individuals will optimize their fitness by attempting to breed in each year. In contrast, red deer maximize their lifetime reproductive success by not breeding every year (Clutton-Brock *et al.* 1996).

Comparison of the effects of density and weather on fecundity rates in first breeders is harder to interpret. Fecundity rates in saiga antelope are not associated with either variable. However, there is variation in these rates over time. These differences are presumably associated with cohort effects, individual covariates, sampling error or the smaller sample sizes. The data did not allow us to test for cohort or individual effects in all three species. In both the Soay sheep and the red deer, fecundity rates are more strongly associated with density in first breeders than in adults. In both cases, first breeders will be subordinate to adults and this could limit their access to high-quality grazing (Clutton-Brock *et al.* 1982; Jewell *et al.* 1974). Within the sheep another process affects fecundity: lambs

born at high population density are lighter than those born at lower density and their weight influences whether they successfully reproduce (Clutton-Brock *et al.* 1996).

The differences in the ways that fecundity rates in each of the species respond to density-dependent and -independent processes may be a result of factors other than variation in their life-history strategies. First, the saiga antelope are hunted (Bekenov *et al.* 1998; Milner-Gulland 1994, 1997) while the sheep and red deer within the study areas are not. One effect of hunting could be to decrease the density of saiga antelopes. Second, the data are collected in different ways. Within the Soay sheep and red deer populations all individuals are individually recognizable (Coulson *et al.* 1997, 1999a). All breeding events are recorded so in each year every mother–offspring pair is known. The fecundity rates are extremely accurate. In contrast, fecundity rates within the saiga antelope population are calculated from autopsies of females that are shot in February (Bekenov *et al.* 1998). The number of foetuses within each mother is then counted. It is possible that our estimates of saiga fecundity are inflated because some foetuses may be reabsorbed between February and birth. Unfortunately there are no data on live births in the saiga population to test this. These differences between the three populations make our finding that fecundity rates, density and weather are associated in similar ways even more surprising.

Our results differ slightly from previous analyses of fecundity in the sheep and deer (Kruuk *et al.* 1999; Post *et al.* 1997). Post *et al.* (1997) report a positive association between fecundity and density for hinds that successfully raised a calf in previous years, yet did not find a significant association between potential first-time breeders and density. However, our analyses differed: we analysed a larger data set, used a binomial error structure in contrast to Post *et al.*'s correlations and did not consider the North Atlantic Oscillation. Kruuk *et al.* (1999) did not consider winter temperature in their analyses of fecundity rates and only included weather variables found to be significantly associated with variation in the birth sex ratio. As temperature and rainfall are correlated their results support our findings.

Across all three species, the only AR model with a significant lag was found in the red deer population. Ecologists often interpret such lags to suggest that direct density dependence is associated with the population dynamics by acting on survival rates (Forchhammer *et al.* 1998). A detailed analysis of the key factors associated with relative changes in the population size of red deer only partially supports this (Albon *et al.* 2000). When the red deer population increased during the 1970s the birth rate was the most important vital rate associated with change in population size, however, once the population stopped increasing from the early 1980s onwards, adult winter survival became the most influential vital rate. Survival rates in red deer adults and calves are associated with population density (Albon *et al.* 2000; Coulson *et al.* 1997). It is probably the importance of adult winter survival in more recent years that resulted in the significant lag of one year. However, the most important vital rate associated with the relative change in size of the Soay sheep population is lamb and adult over-winter survival (Coulson *et al.* 1999a) and over-winter survival in some

age classes is significantly associated with population density (Catchpole *et al.* 2000; Coulson *et al.* 2000; Milner 1999), so we expected to observe a significant density-dependent effect in the sheep population. The fact that we did not observe a significant lag may suggest that simple AR models may not always be powerful enough to detect density-dependent processes.

Density-dependent and -independent processes have been shown to be associated with over-winter survival (Catchpole *et al.* 2000; Coulson *et al.* 1997), birth weight (Coulson *et al.* 1998), birth sex ratio (Kruuk *et al.* 1999) and fecundity (Post & Stenseth 1999) in both sheep and deer. However, different weather variables appear to influence different vital rates. For example, in the Soay sheep high rates of fecundity are associated with high winter temperatures. In contrast, high rates of survival are associated with dry Marches (Catchpole *et al.* 2000; Coulson *et al.* 2000). Wet winters tend to occur in warm years (correlation coefficient between December–March mean temperature and total precipitation for Benbecula = 0.36, $n = 39$, $p < 0.01$, year range 1959–1997). Consequently, environmental conditions that favour high survival rates depress fecundity rates. A similar effect is observed in the red deer (Coulson *et al.* 1997, 1999b). These differences suggest that dynamics of populations are the result of the effects of subtle interactions between density and weather on vital rates and the contribution of each vital rate to changes in population size. The weather variable that is most strongly associated with variation in a vital rate is presumably a function of the time of year when most energy is invested in survival and fecundity. Also, the importance of each vital rate, and consequently density-dependent processes, and which weather variable is most strongly associated with the dynamics, can vary over time and may be associated with how close the population is to carrying capacity (Albon *et al.* 2000). Time-series analyses are limited in their ability to detect these subtle interactions and therefore may fail to capture the true role of density and environmental variation on population dynamics. However, much ecological data consists of time-series of population size. Attempts are still made to infer mechanisms from the analysis of time-series data, however, with the current methodologies available, this should be strongly cautioned against. We suggest that process-orientated analyses of vital rates should be used to construct population models and the dynamics these models generate should be compared with observed dynamics described by pattern-orientated methods (see Bjornstad *et al.* (1998) for an example).

Our results demonstrate very similar associations between fecundity rates, density and weather in three contrasting ungulate species. These analyses have expanded on previous analyses of fecundity rates in Soay sheep and red deer and are the first analyses of fecundity rates in saiga antelope. We hope that as long-term fecundity and weather data become available for other ungulate species, the associations we report are supported. Our analyses also demonstrate that our understanding of how populations fluctuate can be enhanced by combining analyses of vital rates with results from time-series analyses and suggest that this approach is likely to uncover intricate interactions.

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