

# Climate and population density induce long-term cohort variation in a northern ungulate

MADS C. FORCHHAMMER\*†, TIM H. CLUTTON-BROCK\*,  
JAN LINDSTRÖM\* and STEVE D. ALBON‡

\*Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; †Department of Population Ecology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; and ‡Centre for Ecology and Hydrology, Banchory Research Station, Hill of Brathens, Glassel, Banchory, AB31 4BY, UK

## Summary

1. Density-dependent and climatic conditions experienced by individuals before and after birth differ considerably between cohorts. Such early environmental variability has the potential to create persistent fitness differences among cohorts. Here we test the hypothesis that conditions experienced by individuals in their early development will have long-term effects on their life history traits.

2. We approached this by analysing and contrasting the effects of climate (the North Atlantic Oscillation, NAO) and population density at year of birth on cohort birth weight, birth date, litter size, age of maturity, survival and fecundity of Soay sheep, *Ovis aries* L., ewes in the population on the island of Hirta, St Kilda, Scotland.

3. Significant intercohort variations were found in life history traits. Cohorts born after warm, wet and windy (high NAO) winters were lighter at birth, born earlier, less likely to have a twin and matured later than cohorts born following cold and dry (low NAO) winters. High population densities in the winter preceding birth also had a negative effect on birth weight, birth date and litter size, whereas high postnatal densities delayed age of first reproduction.

4. High NAO winters preceding birth depressed juvenile survival but increased adult survival and fecundity. The negative influence of high NAO winters on juvenile survival is likely to be related to mothers' compromised physical condition while the cohort is *in utero*, whereas the positive influence on adult survival and fecundity may relate to the improved postnatal forage conditions following high NAO winters. High pre- and postnatal population densities decreased juvenile (neonatal, yearling) and adult (2–4 years) survivorship but had no significant effect fecundity.

*Key-words:* climatic changes, density dependence, density independence, life-history variation, North Atlantic Oscillation, Soay sheep.

*Journal of Animal Ecology* (2001) **70**, 721–729

## Introduction

The biotic and abiotic environments to which individuals are exposed may vary greatly over time and can, through phenotypic plasticity as well as microevolutionary processes, shape individual life histories (Stearns 1992). Many previous studies have documented immediate

effects of changes in environmental conditions (Sæther 1997), but it has become clear that environmental variation during individuals' early development can also have delayed, long-term effects arising from its influence on their survival and breeding performance (Albon, Clutton-Brock & Guinness 1987; Albon, Clutton-Brock & Langvatn 1992; Gaillard *et al.* 1997; Lindström 1999). Since adult body weight is a major determinant of lifetime reproductive success in many polygynous mammals (Clutton-Brock 1988), any substantial changes in early environmental conditions affecting birth weight and/or early growth may have a considerable impact on later survival and reproductive

Correspondence: Mads C. Forchhammer, Department of Population Ecology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. Fax: + 45 35321255. Tel: + 45 35321300. E-mail: mcforchhammer@zi.ku.dk

performance. For example red deer, *Cervus elaphus* L., born following warm and wet winters were consistently smaller than those born after cold and dry winters (Post *et al.* 1997) and heavier-born calves experience higher lifetime reproductive success than light-born (Clutton-Brock, Guinness & Albon 1982).

Variable environmental conditions around birth have the potential to create fitness differences among cohorts; that is, individuals born during favourable conditions may gain consistent selective advantages not shared by individuals born under less favourable conditions (Grafen 1988). In the Soay sheep population on the St Kilda archipelago (Scotland), early development of cohorts have been found to be highly density-dependent: high winter-densities led to light and early-born animals which displayed reduced growth rates that persisted into adulthood (Clutton-Brock *et al.* 1992; Robertson *et al.* 1992). Additionally, increased winter weather severity (high precipitation and strong winds) and cold springs have been shown to depress over-winter survival and population growth of Soay sheep (Grenfell *et al.* 1998; Milner, Elston & Albon 1999).

In this paper, we test the hypothesis that conditions experienced by the individual during early development will have long-term effects on life history traits. We do this by analysing the relative effects of density-dependent and climatic factors experienced by cohorts while *in utero* and during the postnatal period on birth weight, birth date, litter size and age of maturity as well as later cohort survival and fecundity in Soay sheep ewes. Thus, our paper adds to the previous studies on Soay sheep by integrating and contrasting the effects of both climate and density (see also Milner *et al.* 1999) as well as extending the previous analyses by including long-term consequences of early development on cohort-specific survival and fecundity.

Over the last 30 years, the North Atlantic regions have experienced a consistent change in winter climate (Hurrell 1996) and recent research on the atmosphere–ocean fluctuations emphasizes the role of winter climate forcing by the North Atlantic Oscillation (NAO) (Dickson 1999). At the same time, an increasing body of evidence has revealed traceable effects of the NAO in life histories of terrestrial organisms (Forchhammer 2001). Hence, given its location in the North Atlantic Ocean, the St Kilda population of Soay sheep should, in addition to the density-related influences, be particularly sensible to fluctuations in winter climate mediated by the NAO (Milner *et al.* 1999; Catchpole *et al.* 2000).

## Material and methods

### STUDY AREA AND POPULATION

The St Kilda archipelago (57°49' N, 08°34' W) is located in the North Atlantic, 70 km west of the Outer Hebrides, Scotland. The climate is maritime dominated by strong south-westerly winds and high annual precipitation.

Most winter precipitation comes as rainfall (Boyd *et al.* 1964).

The population of Soay sheep on the main island, Hirta, has not been managed in historical times and dynamics may be considered as naturally regulated (Clutton-Brock *et al.* 1991). The population displays highly persistent instability in their dynamics (Clutton-Brock *et al.* 1997) and, since 1985, repeated die-offs have occurred every 3–4 years encountering between 40 and 60% of all animals. Soay sheep are seasonal breeders: most offspring are conceived in November and born in April (Grubb 1974). Following birth, time allocated to suckling quickly falls to low levels after only 2–3 weeks (Robertson *et al.* 1992), when juveniles become increasingly dependent on available plant forage. Hence, environmental conditions experienced by the individual while *in utero* and postnatal are reflected in the density-dependent and density-independent regimes prevailing during winter and late spring/summer, respectively.

### WINTER CLIMATE

We describe annual changes in winter climate at St Kilda by using the annual winter state of the North Atlantic Oscillation (NAO). The NAO winter index expresses fluctuations in atmospheric pressures along a meridional gradient, and is quantified by the annual winter deviance from the average difference in sea-level pressures between Lisbon (Portugal) and Stykkisholmur (Iceland) (Hurrell 1995). Specifically, the NAO index for the winter before the birth of female cohort year  $t$  ( $NAO_{t-1}$ ) covers the period December <sub>$t-1$</sub>  through March <sub>$t$</sub> . By influencing the speed and direction of westerly surface winds across the North Atlantic, the NAO induces variation in temperature and precipitation in both regions (Lamb & Pepler 1987). When the atmospheric mass balance is centred over the Azores (high state of NAO), the strong across-Atlantic westerlies bring precipitation and warm temperature far north into Europe during winter. In contrast, when the NAO is in a low state (Azorean low), the westerlies are weakened and become less frequent, and the warm and wet winter weather remains over North America leaving northern Europe cold and dry (Hurrell & Van Loon 1997). For St Kilda and the Outer Hebrides, annual changes in the NAO winter index explains 61%, 56% and 23% of the variance in average winter (December–March) temperature ( $r = 0.78$ ,  $P < 0.001$ ,  $n = 32$ ), winter rainfall ( $r = 0.75$ ,  $P < 0.001$ ,  $n = 32$ ) and number of winter days with gales ( $r = 0.48$ ,  $P < 0.01$ ,  $n = 32$ ), respectively: high NAO winters are associated with warm, wet and windy winter climate whereas low NAO winters are cold and dry.

Data on the NAO winter index are from the Climate Analysis Section (National Center for Atmospheric Research, USA) and regional data from the weather station Benbecula reported in *Monthly Weather Review* 1962–93. Weather conditions in Benbecula are similar to those at St Kilda (Boyd *et al.* 1964).

MODEL PARAMETERS AND STATISTICAL  
ANALYSES

To analyse life history variation among cohorts of Soay sheep ewes, we used individual data compiled since 1985 in Village Glen, which holds 30% of the total population on Hirta. Previous studies show that dynamics of the Village Glen subpopulation closely resemble that of the total island population (Jewell, Milner & Boyd 1974; Clutton-Brock *et al.* 1991). Since 1985, over 95% of the lambs born in Village Glen have been caught and marked each year with subsequent detailed monitoring of their life histories (Clutton-Brock *et al.* 1991, 1992, 1996).

Previous analyses have shown that birth weight affects subsequent growth, survival and breeding patterns. In turn, birth weight and survival have been found to be dependent on maternal characteristics (Clutton-Brock *et al.* 1991, 1992, 1996). Hence, to evaluate the total effects of environmental conditions while female cohorts were *in utero* and during the postnatal period on their subsequent survival and reproduction it is, in addition to any direct effects, necessary to also consider any indirect influence mediated through birth weight and maternal traits. In our analyses (see below), we used the following variables.

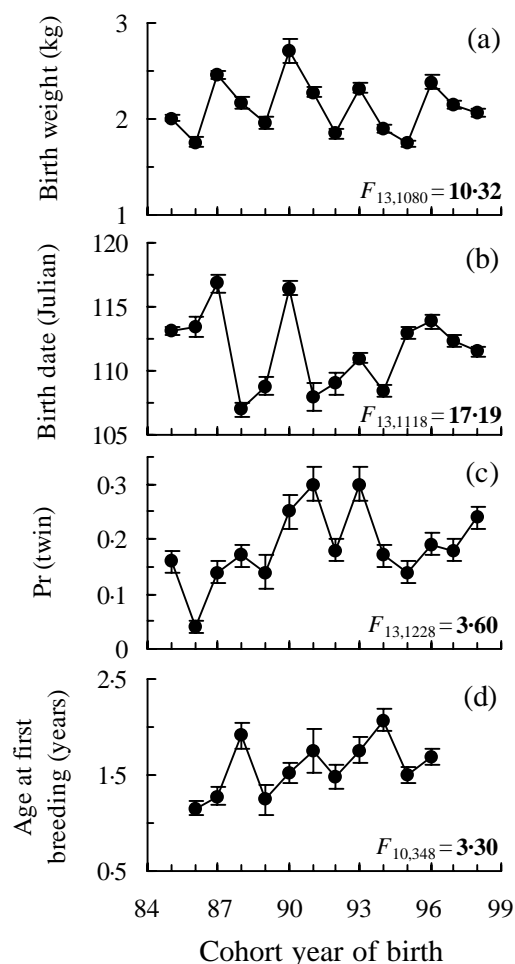
- *Maternal traits*: mother's birth weight (kg) and mother's age (years) when the lamb was born.
- *Birth weight*: live weight (kg) of the lamb when caught, corrected for age at capture (usually < 2 days) using average growth rates for lambs on Hirta.
- *Birth date*: Julian date of birth (1 January = day 1).
- Probability of being born as a twin (Pr(twin)): whether the lamb was a twin (score = 1) or singleton (score = 0).
- *Litter size*: twins or singletons.
- *Age of maturity*: age at first recorded breeding.
- *Neonatal survival*: whether the lamb did (score = 1) or did not (score = 0) survive its first month of life.
- *Survival to the age of x years*: whether the ewe did (score = 1) or did not (score = 0) survive from birth to the age of x (1–4) years; since we focus on the long-term consequences following from conditions around the birth, the survival analyses were conditional, i.e. Pr(surviving to age x|survived to x–1).
- *Probability of lambing as yearling*: whether the ewe lambed (score = 1) or not (score = 0) at the age of 1 years.
- *Fecundity at the age of x years*: number of lambs produced until the age of x (2–4) years.
- *Environmental variables*: for the cohort born in year *t* (usually in April; Grubb 1974), environmental conditions while individuals were *in utero* (November<sub>*t*-1</sub>–March<sub>*t*</sub>) were quantified by winter climate mediated through the NAO winter index (NAO<sub>*t*-1</sub>) and winter population density (*N*<sub>*t*-1</sub>). Environmental conditions during the postnatal period of cohort *t* (summer of year *t*) were quantified by spring population density *N*<sub>*t*</sub>. Winter climate conditions have been shown to have lagged influence on spring plant phenology (Inouye & McGuire 1991; Walker, Ingersoll & Webber 1995). NAO<sub>*t*-1</sub> may therefore also be considered as a postnatal environmental variable influencing cohort *t*.

We modelled the influence of early environmental conditions on cohort life history traits of ewes using generalized linear models (McCullagh & Nelder 1989) based on logistic, Poisson and Gaussian regression for binomial (Pr(twin), survival, Pr(lambing as yearling)), discrete (birth date, adult fecundity) and continuous (birth weight) response variables, respectively (Venables & Ripley 1994). From the full model, construction of the most parsimonious model was performed by standard deletion techniques and evaluation of associated Akaike information criterions (AIC) (Venables & Ripley 1994). All analyses were performed in S-plus for Windows (Mathsoft Inc. 1997).

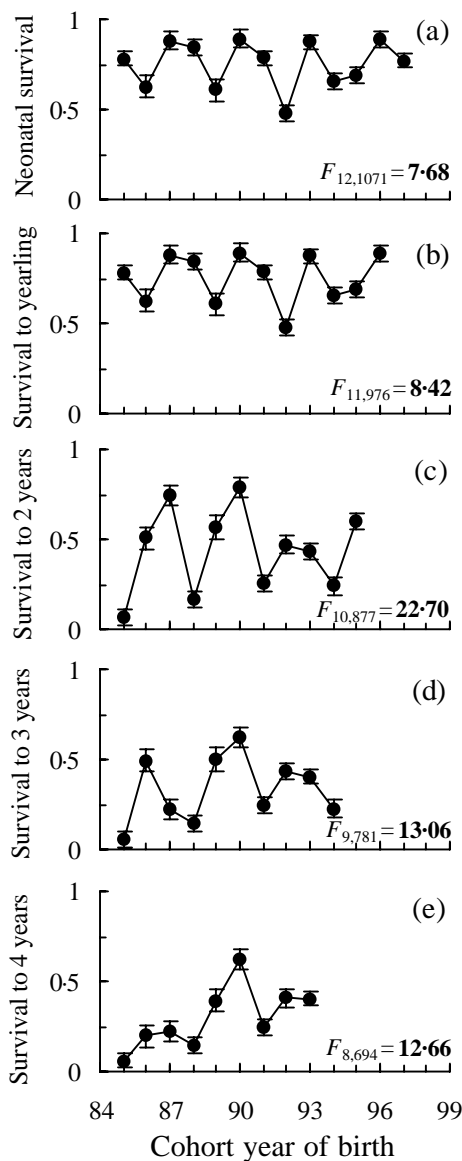
## Results

COHORT LIFE-HISTORY TRAITS IN SOAY  
SHEEP EWES

There was considerable across cohort variation in birth weight, birth date, probability of being born as a twin (Pr(twin)) and age of maturity (Fig. 1a–d). Average cohort birth weights showed a highly consistent fluctuation



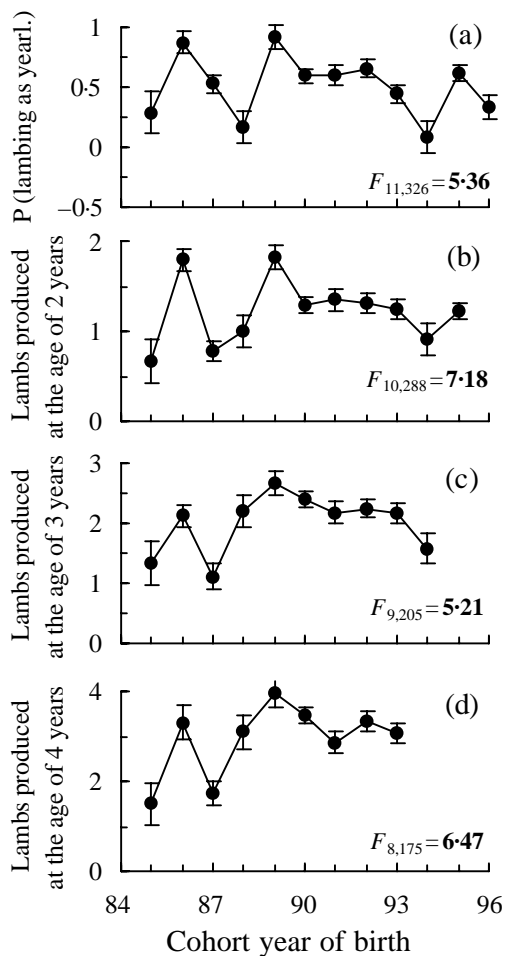
**Fig. 1.** Least-squares means ( $\pm$  SEM) by cohort of (a) birth weight, (b) Julian birth date, (c) probability of being born as a twin (Pr(twin)) and (d) age at first breeding. Bold *F*-values (Mathsoft Inc. 1997) indicate significance ( $P < 0.05$ ).



**Fig. 2.** Least-squares mean ( $\pm$  SEM) by cohort of survivorship of (a) neonates, (b) yearlings, (c) 2-year-old, (d) 3-year-old and (e) 4-year-old Soay sheep ewes. Bold  $F$ -values (Mathsoft Inc. 1997) indicate significance ( $P < 0.05$ ).

with smaller females born every third year and heavier lambs born in intervening years (Fig. 1a). More irregular, but still significant fluctuations were observed in cohort birth dates, Pr(twin) and age of maturity (Fig. 1b–d).

Similarly, both juvenile and adult survival fluctuated consistently over the study period with maximum survival every 3–4 years (Fig. 2a–e). Note that within a cohort, survival to yearling is dependent on surviving as neonatal, and survival to 2 years is dependent on surviving as neonatal and yearling and so forth. Given this, it is even more surprising that being born in years with high juvenile survival does not necessarily suggest high survival rate to adulthood. For example, ewes born into cohort 1985 had a 78% chance surviving to yearling (Fig. 2a–b) but only a 6–7% chance of surviving to adult (2–4 years) (Fig. 2c–e). In contrast, cohort 1986 had lower juvenile survival (62%) but higher chance



**Fig. 3.** Least-squares means ( $\pm$  SEM) by cohort of (a) probability of lambing as yearling and number of lambs produced at the age of (b) 2 years, (c) 3 years and (d) 4 years. Bold  $F$ -values (Mathsoft Inc. 1997) indicate significance ( $P < 0.05$ ).

of surviving to adult (20–51%) than the 1985 cohort (Fig. 2), suggesting that a given set of early environmental conditions may have different short- and long-term consequences.

Average fecundity also varied significantly among cohorts: low fecundity during earlier years of life (Fig. 3a–b) was followed by low fecundity in later years (Fig. 3c–d).

#### THE INFLUENCE OF EARLY ENVIRONMENTAL CONDITIONS

##### *Birth weight, birth date, twin births and age of maturity*

Birth weight, birth date, the probability of being born as twin and age of maturity were all affected by both density-dependent and climatic conditions in the cohort year of birth. Cohorts born after warm, wet winters with high occurrence of strong winds (high  $NAO_{t-1}$  indices) were smaller, born earlier, had less probability of being born as a twin and matured later than cohorts born following cold, dry winters with fewer days with gales (low  $NAO_{t-1}$ ) (Table 1a–d).

**Table 1.** The most parsimonious generalized linear models of (a) birth weight, (b) birth date, (c) the probability of being born as a twin (Pr(twin)) and (d) age of first reproduction of cohorts of Soay sheep ewes born between 1985 and 98. For each independent variable in the most parsimonious model is given: regression coefficient  $b_i$  (SEM), change in model deviance ( $\Delta$  deviance) explained by the term when fitted last, percentage of total (null) deviance explained by the term's  $\Delta$  deviance and significance level ( $P$ , two-tailed)

Independent term	$b_i$ (SEM)	$\Delta$ deviance	% of total deviance	$P^a$
<b>(a) Birth weight<sup>b</sup></b>				
Mother's age	0.1043 (0.0082)	52.8	20.9	< 0.0001
Litter size	-0.6333 (0.0514)	49.9	19.8	< 0.0001
$N_{t-1}$	-0.0017 (0.0002)	23.5	9.4	< 0.0001
$NAO_{t-1}$	-0.0529 (0.0087)	12.0	4.7	< 0.0001
<b>(b) Birth date<sup>b</sup></b>				
$NAO_{t-1}$	-0.3465 (0.1183)	415.8	16.7	0.002
$N_{t-1}$	-0.0074 (0.0028)	290.3	11.7	0.01
Mother's birth weight	0.7824 (0.4414)	139.8	5.6	0.07
<b>(c) Pr(twin)<sup>b</sup></b>				
Mother's age	0.3078 (0.0432)	56.8	9.6	< 0.0001
$N_{t-1}$	-0.0033 (0.011)	8.4	1.4	0.003
Mother's birth weight	0.4045 (0.1648)	6.1	1.0	0.01
$NAO_{t-1}$	-0.0208 (0.0423)	0.24	< 1	0.62
<b>(d) Age of first reproduction<sup>b</sup></b>				
$N_t$	0.0027 (0.0004)	16.5	21.2	< 0.0001
$NAO_{t-1}$	0.0058 (0.0017)	3.8	4.9	0.003

<sup>a</sup>Significance of regression coefficients were tested against the  $F$ -distribution for birth weight, birth date and age of first reproduction, but against  $\chi^2$ -distribution for Pr(twin). <sup>b</sup>The full model included the following independent variables: [mother's age, mother's birth weight, litter size,  $NAO_{t-1}$ ,  $N_{t-1}$ ] for birth weight ( $n = 769$ ) and birth date ( $n = 543$ ), [mother's age, mother's birth weight,  $NAO_{t-1}$ ,  $N_{t-1}$ ] for Pr(twin) ( $n = 567$ ) and [mother's age, mother's birth weight, litter size, birth weight,  $NAO_{t-1}$ ,  $N_{t-1}$ ,  $N_t$ ] for age of first reproduction ( $n = 361$ ).

Similarly, cohorts experiencing high population densities while *in utero* ( $N_{t-1}$ ) were born smaller, earlier and more often as singletons than cohorts exposed to low densities while *in utero* (Table 1a–c). There was no effect of  $N_{t-1}$  on age of maturity, but high population densities during the postnatal period ( $N_t$ ) delayed the age of maturity (Table 1d).

Combined,  $NAO_{t-1}$  and  $N_{t-1}$  explained 14% and 28% of the intercohort variation in birth weight and birth date, respectively, and  $NAO_{t-1}$  and  $N_t$  combined explained 26% of the intercohort variation in age of maturity (Table 1).

Also evident from our analyses was the substantial maternal effect on life history traits: older and/or heavy-born mothers produced heavier offspring born later and more often twins than younger and lighter-born mothers (Table 1a–c). No significant maternal effect was found on intercohort variations in age of maturity.

### Survival

Cohorts born following warm wet, winters with much wind (high  $NAO_{t-1}$ ) had reduced neonatal and yearling survivorship as compared to cohorts born after cold dry and calm winters (low  $NAO_{t-1}$ ) (Table 2a–b). In contrast, cohorts born after high  $NAO_{t-1}$  displayed significantly increased adult (2–4 years) survivorship compared to cohorts born after low  $NAO_{t-1}$  (Table 2c–e).

High population density while *in utero* ( $N_{t-1}$ ) was found to have a significant negative effect on survivorship of juveniles (neonates, yearlings) and adult 2-year-olds only, whereas high postnatal densities ( $N_t$ ) had a significant

negative effect on survivorship of adult aged 2–4 years only (Table 2).

Fluctuations in winter severity ( $NAO_{t-1}$ ) before birth explained around 3% and between 2 and 12% of the intercohort variation in survival of juveniles and adults (2–4 years), respectively (Table 2). Annual changes in winter density ( $N_{t-1}$ ) explained 3–7% and 1% of the intercohort variation in survival of juveniles and 2-year adults, respectively, whereas changes in spring/summer density ( $N_t$ ) explained 4–9% of the intercohort variation in survival of 2–4-year-old ewes (Table 2). Overall heavier-born ewes had higher juvenile and adult survivorship than lighter-born ewes and explained between 8 and 27% of intercohort variation in survivorship (Table 2).

### Fecundity

Cohorts born after high  $NAO_{t-1}$  winters produced more offspring as adults (2–4 years) than cohorts born following low  $NAO_{t-1}$  winters (Table 3). Whereas high population density in the summer following birth ( $N_t$ ) decreased the probability of lambing as yearlings, neither population densities in the winter before birth ( $N_{t-1}$ ) or  $N_t$  had any detectable effect on adult fecundity (Table 3). Variations in the state of the NAO explained 4–16% of the intercohort variation in adult fecundity (Table 3). Timing of first reproduction was also important, explaining up to 46% of the intercohort variation in adult fecundity. Delayed first-time reproduction decreased the total number of offspring produced as 2–4-year-olds (Table 3).

**Table 2.** The most parsimonious generalized linear models of survival of Soay sheep ewes: (a) neonatal survival (cohorts 1985–97) and survival to (b) yearling (1985–96), (c) 2 years old (1985–95), (d) 3 years old (1985–94) and (e) 4 years old (1985–93). For abbreviations see Table 1

Independent term	$b_i$ (SEM)	$\Delta$ deviance	% of total deviance	$P^a$
<b>(a) Neonatal survival<sup>b</sup></b>				
Birth weight	1.9407 (0.1763)	188.8	26.7	< 0.0001
NAO <sub><i>t</i>-1</sub>	-0.1190 (0.0437)	20.3	2.9	0.005
$N_{t-1}$	-0.0019 (0.0009)	17.6	2.5	0.03
<b>(b) Survival to yearling<sup>b</sup></b>				
Birth weight	1.8343 (0.1804)	174.7	27.1	< 0.0001
$N_{t-1}$	-0.0039 (0.0012)	43.1	6.7	0.001
NAO <sub><i>t</i>-1</sub>	-0.0741 (0.0453)	2.7	< 1	0.09
<b>(c) Survival to 2 years<sup>b</sup></b>				
Birth weight	1.3301 (0.1508)	96.5	12.5	< 0.0001
$N_t$	-0.0097 (0.0011)	74.5	9.7	< 0.0001
NAO <sub><i>t</i>-1</sub>	0.2380 (0.0610)	15.8	2.1	0.0001
$N_{t-1}$	-0.0032 (0.0011)	8.7	1.1	0.003
<b>(d) Survival to 3 years<sup>b</sup></b>				
NAO <sub><i>t</i>-1</sub>	0.3773 (0.0572)	71.5	10.1	< 0.0001
$N_t$	-0.0062 (0.0010)	65.2	9.1	< 0.0001
Birth weight	1.1556 (0.1463)	58.9	8.5	< 0.0001
<b>(e) Survival to 4 years<sup>b</sup></b>				
NAO <sub><i>t</i>-1</sub>	0.4097 (0.0629)	74.2	11.9	< 0.0001
Birth weight	1.0949 (0.1536)	51.5	8.3	< 0.0001
$N_t$	-0.0028 (0.0011)	29.0	4.7	0.005

<sup>a</sup>Significance of regression coefficients were tested against the  $\chi^2$ -distribution. <sup>b</sup>The full model included the following independent variables: [mother's age, mother's birth weight, birth weight, litter size, NAO<sub>*t*-1</sub>,  $N_{t-1}$ ,  $N_t$ ] for neonatal survival ( $n = 848$ ) and survival to yearling ( $n = 769$ ), 2 years ( $n = 691$ ), 3 years ( $n = 609$ ) and 4 years ( $n = 490$ ).

**Table 3.** The most parsimonious generalized linear models of fecundity of Soay sheep ewes: (a) probability of giving birth as yearling (cohorts 1985–96) and cumulative number of lambs produced as (b) 2 years old (1985–95), (c) 3 years old (1985–94) and (d) 4 years old (1985–93). For abbreviations see Table 1

Independent term	$b_i$ (SEM)	$\Delta$ deviance	% of total deviance	$P^a$
<b>(a) Probability of lambing as yearling<sup>b</sup></b>				
$N_t$	-0.0080 (0.0016)	31.8	8.2	< 0.0001
Birth weight	0.3072 (0.2079)	2.2	< 1	0.13
<b>(b) Number of lambs produced at 2 years<sup>b</sup></b>				
Age of first reproduction	-0.7537 (0.1153)	55.4	45.5	< 0.0001
NAO <sub><i>t</i>-1</sub>	0.0616 (0.0300)	4.3	3.5	< 0.0001
Birth weight	0.0446 (0.0871)	0.3	< 1	0.009
<b>(c) Number of lambs produced at 3 years<sup>b</sup></b>				
Age of first reproduction	-0.4372 (0.0782)	35.3	33.4	< 0.0001
NAO <sub><i>t</i>-1</sub>	0.0702 (0.0272)	9.9	9.4	0.009
<b>(d) Number of lambs produced at 4 years<sup>b</sup></b>				
Age of first reproduction	-0.3289 (0.0663)	26.9	25.3	< 0.0001
NAO <sub><i>t</i>-1</sub>	0.0835 (0.0249)	17.5	16.5	0.0006

<sup>a</sup>Significance of regression coefficients were tested against the  $\chi^2$ -distribution for probability of lambing as yearling and against the  $F$ -distribution for the other dependent variables. <sup>b</sup>The full model included the following independent variables: [mother's age, mother's birth weight, birth weight, born as twin, NAO<sub>*t*-1</sub>,  $N_{t-1}$ ,  $N_t$ ] for probability of lambing as yearling ( $n = 341$ ) but did also include [age of first reproduction] for number of lambs produced at the age of 2 years ( $n = 257$ ), 3 years ( $n = 213$ ) and 4 years ( $n = 182$ ).

## Discussion

Our study demonstrates that the life history variations across cohorts of Soay sheep ewes (Figs 1–3) are significantly influenced by early environmental conditions experienced by cohorts *in utero* and during their postnatal period. Changes in population densities and climate were both found to be important components

influencing birth weight, birth date, litter size and age of maturity (Table 1) as well as inducing, directly and indirectly through birth weight, persistent long-term cohort variations in survival and fecundity of ewes (Tables 2, 3).

In general our results add to the increasing body of evidence demonstrating similar short-term and long-term effects of early environmental conditions on life

history traits of several other ungulate species (*Cervus elaphus* L.: Albon *et al.* 1987, 1992; Post *et al.* 1997; Loison & Langvatn 1998; Rose *et al.* 1998; Kruuk *et al.* 1999; *Capreolus capreolus* L.: Gaillard *et al.* 1997, 1998; *Alces alces* L. and *Odocoileus virginianus* Zimmermann: Mech *et al.* 1987; Sæther *et al.* 1996; Post & Stenseth 1998; *Ovis canadensis* L.: Festa-Bianchet, Gaillard & Jorgenson 1998; Portier *et al.* 1998; *Tragelaphus strepsiceros* Pallas: Owen-Smith 1990). For Soay sheep, our analyses are in accordance with earlier findings, which have demonstrated that following increased population density preceding birth ( $N_{t-1}$ ) consistently resulted in lighter and earlier born lambs (of both sexes) (Clutton-Brock *et al.* 1992; Robertson *et al.* 1992). Additionally, as shown by Clutton-Brock *et al.* (1992), we found that the negative effect of  $N_{t-1}$  on neonatal survival was caused directly by increased density-dependent mortality as well as indirectly by a density-dependent decline in birth weight (Table 2a). Finally, recent analyses by Milner *et al.* (1999) on interannual survival of Soay sheep, documented, similar to our results (Table 2), that lamb survival was negatively influenced by both high winter population density and high NAO winters but positively affected by body weight, which in turn is largely determined by birth weight (Clutton-Brock *et al.* 1992).

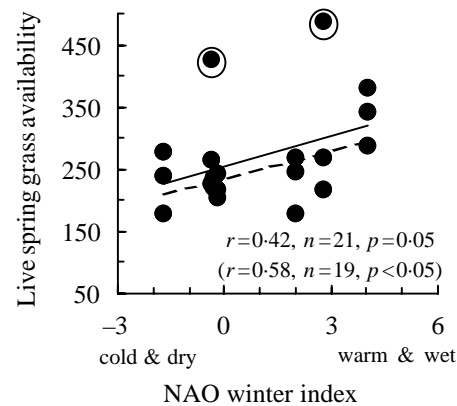
Our results do, however, also present novel aspects of the contrasting effects of density- and climate-related factors operating when the cohort is *in utero* vs. those operating after birth.

#### EFFECTS OF DENSITY-DEPENDENT CONDITIONS AROUND BIRTH

With respect to density-dependence in survival, we found that short-term (juvenile: neonatal and yearling) survivorship was influenced solely by density experienced *in utero* ( $N_{t-1}$ ), but long-term (adult: 2–4 years) survivorship mainly by postnatal densities ( $N_t$ ) (Table 2). We also found that age of maturity (but not later fecundity, Table 3) was negatively influenced by  $N_t$  only (Table 1d). Hence, adding to previous studies (Clutton-Brock *et al.* 1991, 1992; Grenfell *et al.* 1992; Milner *et al.* 1999) this study shows that although cohorts born in crash years (high  $N_{t-1}$  and low  $N_t$ ) experience initial negative density-dependence in life history traits, their long-term life history perspectives are good with earlier reproductive start and higher adult survivorship than those of cohorts born in peak years (low/intermediate  $N_{t-1}$  and high  $N_t$ ). A similar density-dependent long-term relationship has been documented in Soay sheep rams: cohorts born in years with low density experienced significantly higher lifetime breeding success than those born in high density years (Coltman *et al.* 1999).

#### EFFECTS OF CLIMATIC CONDITIONS AROUND BIRTH

High NAO winters (warm, wet and windy) preceding birth of cohorts had a negative short-term effect on



**Fig. 4.** Relationship between NAO $_{t-1}$  and the relative availability of live grass spring/summer year  $t$  (measured between 1986 and 1992). 'Warm and wet' and 'cold and dry' specify average winter temperature and rainfall in relation to the state of the NAO. Grass availability are adjusted for sheep numbers in winter using fully factorial ANOVA with year of live grass availability estimation as factor and population size as covariate (Mathsoft 1997). The dashed line and correlation coefficient given in brackets are associated with the regression excluding the two circled outliers.

juvenile survival of cohorts (Table 2a,b), but a positive long-term effect on adult (2–4 years) survival (Table 2c–e). This dichotomy may relate to two different aspects of the influence of the NAO. On one hand, increased occurrence of wet and windy weather has been shown to deteriorate physical conditions of sheep considerably (McIlroy 1989). Because ewes are at their lowest physiological energy budget balance during winter (Clutton-Brock *et al.* 1997), increased occurrence of rain and gales during high NAO winters severely compromise the condition of pregnant ewes and, hence, their foetus. Therefore, the negative short-term effect of the NAO documented in this study may relate to conditions cohorts experience *in utero* through their mothers' compromised condition.

On the other hand, the reported long-term positive effect of high NAO winters may relate to favourable postnatal environmental conditions induced by high NAO winters. Winter conditions are known to influence spring/summer plant phenology (e.g. Inouye & McGuire 1991; Walsh *et al.* 1997) where, for example, plants in Norway respond annually to increasingly higher NAO winters by blooming earlier and for a longer period (Post & Stenseth 1999). A similar relationship between warm, wet winters and forage availability may be present on Hirta: high NAO winters increased live spring/summer grass availability with up to 25% (Fig. 4). Weather-induced increases in spring forage quality have been reported previously to increase juvenile survival in several other ungulate species (Owen-Smith 1990; Gaillard *et al.* 1997; Portier *et al.* 1998).

Lamb growth rates are positively related to increased forage biomass (Robertson *et al.* 1992) and high fecundity of ewes is associated with super-abundance of forage in summer (Clutton-Brock *et al.* 1991). Therefore,

the improved spring/summer forage conditions following high NAO winters may be an important component in determining cohort quality, because fecundity of cohorts also increased if born following high NAO winters (Table 3).

Whether attributable to density-dependence and/or density-independence, the 'weeding out' of inferior phenotypes at early stages in the same cohort has been demonstrated to produce the aforementioned short-term vs. long-term dichotomy in ewe survivorship. In red deer, for example, cohorts that suffered high juvenile mortality subsequently showed significantly higher adult survival (Rose *et al.* 1998). However, although initial removal of inferior phenotypes in Soay sheep cohorts following high NAO winters and/or high population densities may interact with the aforementioned dichotomous influence of the NAO, two observations speak against this. First, decreased juvenile survival (0–1 years) did not increase subsequent adult survival (2–4 years) ( $r_{\text{survival } 0-2 \text{ years, survival } 2-6 \text{ years}} = -0.12$ ,  $n = 9$ ,  $P > 0.75$ ). Secondly, as would be expected through a 'weeding out' mechanism, increased density-dependent stress around birth (high  $N_{t-1}$ ,  $N_t$ ) did not produce a long-term positive relationship with survival (Table 2).

Recent climatic research suggests that the NAO probably plays a major role in the last 2–3 decadal warming of the Northern Hemisphere (Hurrell 1996). Therefore, the documented influence of the NAO on Soay ewe cohort variations may give us an indication of the specific effect of large-scale changes in climate, e.g. global warming, on life histories of long-lived, iteroparous organisms. Coinciding with a significant increase of the mean surface temperature throughout the Northern Hemisphere, the NAO index has, since 1969, increased significantly until reaching a century-long extreme maximum in 1995 (Hurrell 1996). In the last decade of the NAO's latest increasing phase, cohorts of ewes born between 1985 and 1995 were born lighter and matured later (Table 1), but displayed higher adult survivorship and fecundity (Tables 2, 3). Hence, as reported previously for red deer in Norway (Post *et al.* 1997, 1999), the forecasted global warming may produce populations of smaller but more long-lived and fecund female cohorts.

### Acknowledgements

We thank the National Trust for Scotland and the Scottish Natural Heritage for permission to work on St Kilda and for their help. We also thank the Royal Artillery for their logistic assistance. Important contributions to this work were made by the many volunteers who helped collecting data since the project start in 1985. Thanks to Tim Coulson, Dave Coltman, Loeske Kruuk and two anonymous referees for their comments on earlier drafts of this manuscript. This study has been funded by grants from the National Environmental Research Council, the Science and Engineering Research

Council, the Royal Society, and by the Danish National Science Research Council (SNF) to M.C.F. and the European Union (TMR) to J.L.

### References

- Albon, S.D., Clutton-Brock, T.H. & Guinness, F.E. (1987) Early development and population dynamics in red deer. II: Density-dependent effects and cohort variation. *Journal of Animal Ecology*, **56**, 69–81.
- Albon, S.D., Clutton-Brock, T.H. & Langvatn, R. (1992) Cohort variation in reproduction and survival: implications for population demography. *The Biology of Deer* (ed. R.D. Brown), pp. 15–21. Springer Verlag, Berlin.
- Boyd, J.M., Doney, J.M., Gunn, R.G. & Jewell, P.A. (1964) The Soay sheep of the island of Hirta, St Kilda. A study of a feral population. *Proceedings of the Zoological Society of London*, **142**, 129–163.
- Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S. N. & Albon, S. D. (2000) Factors influencing Soay sheep survival. *Applied Statistics*, **49**, 453–472.
- Clutton-Brock, T.H., ed. (1988) *Reproductive Success*. The University of Chicago Press, Chicago.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer – behaviour and ecology of two sexes*. The University of Chicago Press, Chicago.
- Clutton-Brock, T.H., Illius, A.W., Wilson, K., Grenfell, B.T., MacColl, A.D.C. & Albon, S.D. (1997) Stability and instability in ungulate populations: an empirical analysis. *American Naturalist*, **149**, 195–219.
- Clutton-Brock, T.H., Price, O.F., Albon, S.D. & Jewell, P.A. (1991) Persistent instability and population regulation in Soay sheep. *Journal of Animal Ecology*, **60**, 593–608.
- Clutton-Brock, T.H., Price, O.F., Albon, S.D. & Jewell, P.A. (1992) Early development and population fluctuations in Soay sheep. *Journal of Animal Ecology*, **61**, 381–396.
- Clutton-Brock, T.H., Stevenson, I.R., Marrow, P., MacColl, A.D., Houston, A.I. & McNamara, M. (1996) Population fluctuations, reproductive costs and life history tactics in female Soay sheep. *Journal of Animal Ecology*, **65**, 675–689.
- Coltman, D.W., Smith, J.A., Bancroft, D.R., Pilkington, J. & Pemberton, J.M. (1999) Cohort effects on lifetime breeding success and the opportunity for selection in Soay rams. *American Naturalist*, **154**, 730–746.
- Dickson, B. (1999) All change in the Arctic. *Nature*, **397**, 389–391.
- Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J.T. (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, **152**, 367–379.
- Forchhammer, M.C. (2001) Terrestrial ecological responses to climate change in the Northern Hemisphere. *Climate Change Research – Danish contributions* (eds A.M.K. Jørgensen, J. Fenger & K. Halsnæs). GAD, Copenhagen, in press.
- Gaillard, J.-M., Boutin, J.-M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.-D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.
- Gaillard, J.-M., Liberg, O., Andersen, R., Hewison, A.J.M. & Cederlund, G. (1998) Population dynamics of roe deer. *The European Roe Deer: the biology of success* (eds R. Andersen, P. Duncan & J.D.C. Linnell), pp. 309–335. Scandinavian University Press, Oslo.
- Grafen, A. (1988) On the uses of data on lifetime reproductive success. *Reproductive Success* (ed. T.H. Clutton-Brock), pp. 454–485. University of Chicago Press, Chicago.
- Grenfell, B.T., Price, O.F., Albon, S.D. & Clutton-Brock, T.H. (1992) Overcompensation and population cycles in an ungulate. *Nature*, **355**, 823–826.



- Grenfell, B.T., Wilson, K., Finkenstädt, B.F., Coulson, T.N., Murray, S., Albon, S.D., Pemberton, J.M., Clutton-Brock, T.H. & Crawley, M.J. (1998) Noise and determinism in synchronised sheep dynamics. *Nature*, **394**, 674–677.
- Grubb, P. (1974) Population dynamics of the Soay sheep. *Island Survivors: the ecology of the Soay sheep of St Kilda* (eds P.A. Jewell, C. Milner & J.M. Boyd), pp. 242–272. Athlone Press, London.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.
- Hurrell, J.W. (1996) Influence of variations in extratropical wintertime teleconnections in Northern Hemisphere temperature. *Geophysical Research Letters*, **23**, 665–668.
- Hurrell, J.W. & Van Loon, H. (1997) Decadal variations in climate associated with the North Atlantic Oscillation. *Climatic Change*, **36**, 301–326.
- Inouye, D.W. & McGuire, A.D. (1991) Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae): implications for climate change. *American Journal of Botany*, **78**, 997–1001.
- Jewell, P.A., Milner, C. & Boyd, J.M., eds (1974) *Island Survivors: the ecology of the Soay sheep of St Kilda*. Athlone Press, London.
- Kruuk, L.E.B., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999) Early determinants of lifetime reproductive success differ in male and female red deer. *Proceedings of the Royal Society London B*, **266**, 1655–1661.
- Lamb, P.J. & Pepler, R.A. (1987) North Atlantic Oscillation: concept and an application. *Bulletin of the American Meteorological Society*, **68**, 1218–1225.
- Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology and Evolution*, **14**, 343–348.
- Loison, A. & Langvatn, R. (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia*, **116**, 489–500.
- Mathsoft Inc. (1997) *S-plus 4.0 Release 2 for Windows*. Mathsoft Inc., Seattle.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London.
- McIlroy, S.H. (1989) Rain and windchill as factors in the occurrence of pneumonia in sheep. *Veterinary Record*, **125**, 79–84.
- Mech, L.D., McRoberts, R.E., Peterson, R.O. & Page, R.E. (1987) Relationship of deer and moose populations to previous winter's snow. *Journal of Animal Ecology*, **56**, 615–627.
- Milner, J.M., Elston, D.A. & Albon, S.D. (1999) Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology*, **68**, 1235–1247.
- Owen-Smith, N. (1990) Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology*, **59**, 893–913.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Yoccoz, N. (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis Canadensis*). *Journal of Zoology*, **245**, 271–278.
- Post, E. & Stenseth, N.C. (1998) Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology*, **67**, 537–543.
- Post, E. & Stenseth, N.C. (1999) Climate variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322–1339.
- Post, E., Stenseth, N.C., Langvatn, R. & Fromentin, J.-M. (1997) Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society London B*, **264**, 1317–1324.
- Robertson, A., Hiraiwa-Hasegawa, M., Albon, S.D. & Clutton-Brock, T.H. (1992) Early growth and suckling behaviour of Soay sheep in a fluctuating population. *Journal of Zoology*, **227**, 661–671.
- Rose, K.E., Clutton-Brock, T.H. & Guinness, F.E. (1998) Cohort variation in male survival and lifetime breeding success in red deer. *Journal of Animal Ecology*, **67**, 979–986.
- Sæther, B.-E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution*, **12**, 143–149.
- Sæther, B.-E., Andersen, R., Hjeljord, O. & Heim, M. (1996) Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology*, **77**, 1493–1500.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Venables, W.N. & Ripley, B.D. (1994) *Modern Applied Statistics with S-Plus*. Springer, New York.
- Walker, M.D., Ingersoll, R.C. & Webber, P.J. (1995) Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology*, **76**, 1067–1083.
- Walsh, N.E., McCabe, T.R., Welker, J.M. & Parsons, A.N. (1997) Experimental manipulations of snow-depth: effects of nutrient content of caribou forage. *Global Change Biology*, **3**, 158–164.

Received 27 August 2000; revision received 13 February 2001