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

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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 on fecundity.

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

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
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 over their counterparts 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). 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 & Robertson 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 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 density-dependent and density-independent regimes prevailing 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<sub>t</sub>) covers the period December<sub>t</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 & Peppler 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 < 0.01, 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 female sheep 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 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 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−March) 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...
Birth weight, birth date, maternal and paternal age and size during the previous year, and the condition of the ewe at mating were all significant factors in determining the probability of being born as a twin. 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 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 of surviving to adult (20–51%) than the 1985 cohort (Fig. 2a–e), suggesting that differences in early environmental conditions (4-year-old Soay sheep) may affect body condition. Mathematical models indicated significant differences in body condition (P < 0.05) among groups of different ages and genders. Given this, it is clear that factors such as nutrition and health are crucial in determining the survival of young sheep. Moreover, the influence of early environmental conditions on survival to adulthood is likely to have long-term consequences, as those born in years with high juvenile survival may not necessarily survive to adulthood. This suggests that early conditions are important in determining long-term survival. Therefore, it is crucial to understand the factors influencing survival in young sheep, as they may have significant impacts on the population dynamics of the species. Mathematical models can be used to predict survival rates and help inform conservation efforts.
Cohort variations in Soay ewes

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 $\chi^2$ deviance and significance level ($p$, two-tailed).

<table>
<thead>
<tr>
<th>Independent term</th>
<th>$b_i$ (SEM)</th>
<th>$\Delta$ deviance</th>
<th>% of total deviance</th>
<th>$P^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Birth weight$^a$</td>
<td>0.0141 (0.0082)</td>
<td>52.8</td>
<td>20.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Litter size</td>
<td>-0.6333 (0.0514)</td>
<td>49.9</td>
<td>19.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$N_t$</td>
<td>0.0017 (0.0002)</td>
<td>23.5</td>
<td>9.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>NAO$_t$</td>
<td>-0.0529 (0.0087)</td>
<td>12.0</td>
<td>4.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(b) Birth date$^b$</td>
<td>-0.3465 (0.1183)</td>
<td>41.5</td>
<td>16.7</td>
<td>0.02</td>
</tr>
<tr>
<td>NAO$_t$</td>
<td>0.0074 (0.0028)</td>
<td>290.3</td>
<td>11.7</td>
<td>0.01</td>
</tr>
<tr>
<td>$N_t$</td>
<td>-0.7824 (0.4414)</td>
<td>139.8</td>
<td>5.6</td>
<td>0.07</td>
</tr>
<tr>
<td>Mother’s birth weight</td>
<td>-0.0033 (0.011)</td>
<td>8.4</td>
<td>1.4</td>
<td>0.03</td>
</tr>
<tr>
<td>(c) Pr(twin)$^b$</td>
<td>0.3078 (0.0432)</td>
<td>56.9</td>
<td>9.6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>NAO$_t$</td>
<td>-0.0033 (0.011)</td>
<td>8.4</td>
<td>1.4</td>
<td>0.03</td>
</tr>
<tr>
<td>Mother’s birth weight</td>
<td>0.4045 (0.1688)</td>
<td>6.1</td>
<td>1.0</td>
<td>0.01</td>
</tr>
<tr>
<td>NAO$_t$</td>
<td>0.0208 (0.0423)</td>
<td>0.24</td>
<td>&lt;1</td>
<td>0.62</td>
</tr>
<tr>
<td>(d) Age of first reproduction$^b$</td>
<td>0.0027 (0.0004)</td>
<td>16.5</td>
<td>21.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$N_t$</td>
<td>0.0058 (0.0017)</td>
<td>3.8</td>
<td>4.9</td>
<td>0.03</td>
</tr>
</tbody>
</table>

$^a$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). $^b$The full model included the following independent variables: [mother’s age, mother’s birth weight, litter size, NAO$_t$, $N_t$] for birth weight ($n = 769$) and birth date ($n = 543$), [mother’s age, mother’s birth weight, NAO$_t$, $N_t$] for Pr(twin) ($n = 567$) and [mother’s age, mother’s birth weight, litter size, birth weight, NAO$_t$, $N_t$, $N_3$] for age of first reproduction ($n = 361$).

Similarly, cohorts experiencing high population densities while in utero ($N_t$) 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 $N_t$, on age of maturity, but high population densities during the postnatal period ($N_t$) delayed the age of maturity (Table 1d).

Combined, NAO$_t$, and $N_t$ explained 14% and 28% of the intercohort variation in birth weight and birth date, respectively, and NAO$_t$, 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$_t$) had reduced neonatal and yearling survivorship as compared to cohorts born after cold dry and calm winters (low NAO$_t$) (Table 2a–b). In contrast, cohorts born after high NAO$_t$ displayed significantly increased survival to 2–4 years of age (Table 2c–d). High population density while in utero ($N_t$) 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$_t$) 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 ($N_t$) 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, lighter-born ewes had higher juvenile and adult survivorship than heavier-born ewes and explained between 8 and 27% of intercohort variation in survivorship (Table 2).

Fecundity

Cohorts born after high NAO$_t$, winters produced more offspring as adults (2–4 years) than cohorts born following low NAO$_t$, 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 ($N_t$), 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).
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
Cohort variations in Soay ewes

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; Oris canadensis L.: Fest-a-Bianchet, Gaillard & Jorgenson 1998; Portier et al. 1998; Tragelaphus strepsigerus 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 (Cotman 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 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 foetuses.

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) \( (r_{\text{adj}} \text{ survival} 2-4\text{ years} < 0.12, n = 9, P > 0.75) \). Secondly, as would be expected through a 'weeding out' mechanism, increased density-dependent stress around birth (high \( N_{\text{le}} \), \( N_{\text{f}} \)) 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 faster (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.

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