red deer cohorts

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SUMMARY

The variability of two fitness-related phenotypic traits (body weight and a mandibular skeletal ratio) was analysed among cohorts and age-classes of red deer in Norway. Phenotypic variation among cohorts was pronounced for calves, yearlings and reproductively mature adults. Fluctuations in cohort-specific mean body weights and skeletal ratios of adults correlated with global climatic variation in winter conditions influenced by the North Atlantic Oscillation while cohorts were *in utero*. Red deer born following warm winters were smaller than those born after cold winters, and this inter-cohort variability persisted into adulthood. Phenotypic variation among cohorts of red deer influenced by climate change may pose consequences for fitness of cohorts since body size and condition contribute to reproductive success and survival in male and female red deer. In particular, the recent trend of increasingly warm winters in northern Europe and Scandinavia may lead to reduced body size and fecundity of red deer, and perhaps other ungulates, in those areas.

1. INTRODUCTION

Latitudinal, seasonal, and interannual variation in climatic regimes are known to influence reproduction (Picton 1984; Rachlow & Bowyer 1991), physical growth (Albon *et al*. 1983*a*; Clutton-Brock & Albon 1983; Langvatn & Albon 1986; Klein *et al*. 1987) and demography (Albon & Clutton-Brock 1988; Forchhammer & Boertmann 1993) of large mammalian herbivores in a variety of ecosystems, through effects on temporal and spatial quality and quantity of forage plants (Klein *et al*. 1987; Guthrie 1984; Langvatn *et al*. 1996). Among Cervidae, geographical and temporal variation in climate influences skeletal development (Klein 1964; Klein & Strandgaard 1972), body weight (Sæther 1985; Langvatn & Albon 1986; Reimers *et al*. 1983), and age-specific reproductive rates within and among cohorts (Sæther & Heim 1993; Sæther & Haagenrud 1983). In red deer (*Cervus elaphus* Linnaeus 1758), phenotypic variation within cohorts induced by climatic variation influences individual fitness (Clutton-Brock *et al*. 1988; Langvatn *et al*. 1996) because reproductive success is related in males to body size and weight (Clutton-Brock *et al*. 1982) and in females to body weight (Albon et al. 1983*b*; Langvatn *et al*. 1996) and condition (Clutton-Brock *et al*. 1982, 1988). Furthermore, birth weights of red deer vary with climatic conditions during their first spring (Albon *et al*. 1983*a*), and cohorts of low birth weight in turn produce low-weight calves that suffer poor survival (Albon *et al*. 1987; Clutton-Brock *et al*. 1988). Ultimately, climatic variation may influence population dynamics of red deer through effects on survival during winter (Watson 1971; Clutton-Brock & Albon 1982; Albon & Clutton-Brock 1988), and growth *in utero* which later affects survival and fecundity of cohorts (Albon *et al*. 1987).

Although previous studies have focused on effects of local climate on development and reproductive success of large herbivores, studies of the potential influences of global climatic fluctuation on extant ungulates have been lacking. In northern Europe and Scandinavia, climatic conditions during winter are strongly determined by a global-scale alternation of atmospheric mass, the North Atlantic Oscillation (NAO) (Rogers 1984; Hurrell 1995). Because the NAO drives interannual fluctuations in winter temperatures and precipitation, it also has the potential to determine interannual variation in snow depth, duration of snow lie, degree-days and, consequently, timing of plant growth in spring. The NAO index is therefore a single integrative measure of winter severity which, by incorporating several environmental variables that have important consequences for the ecology of northern ungulates, provides a useful overall quantification of general climatic conditions during winter. Effects of winter temperatures and depth and persistence of snow on performance of red deer and

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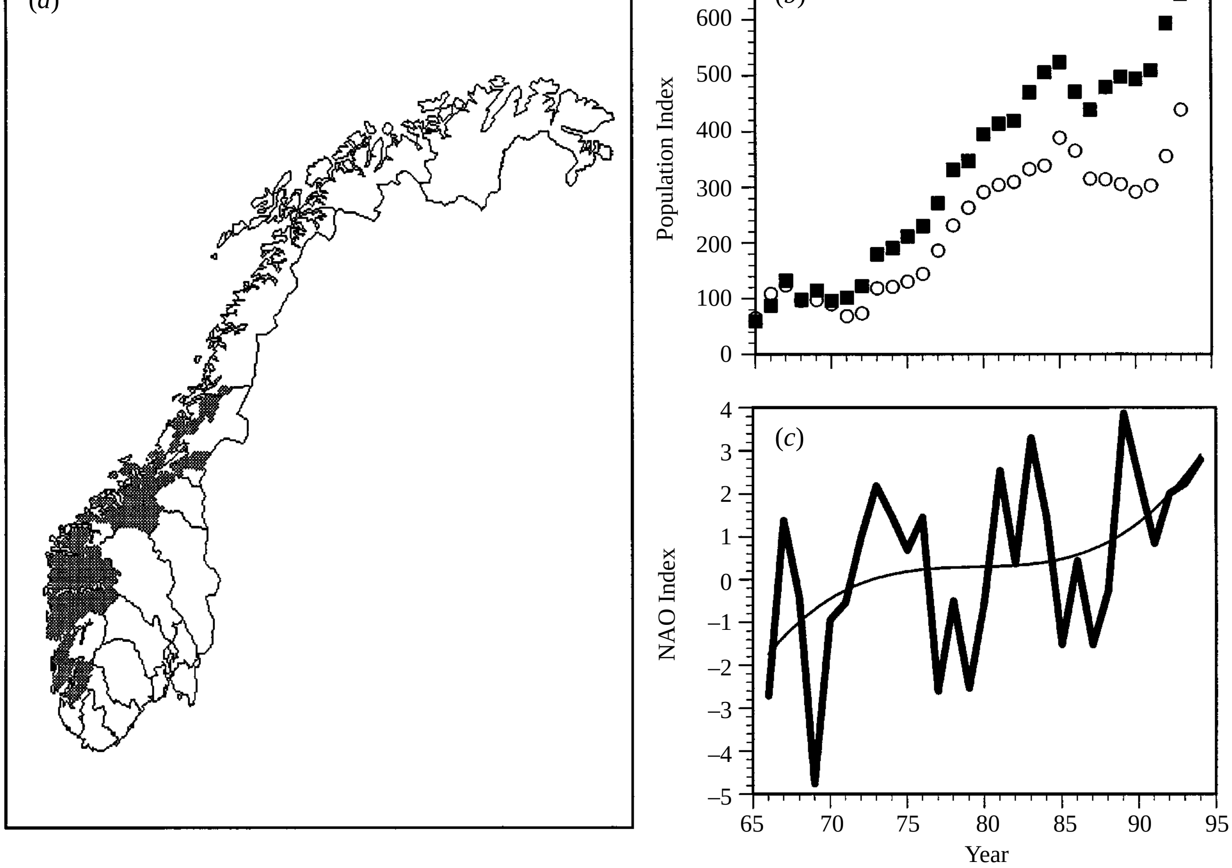

Figure 1. (*a*) Distribution of red deer throughout Norway (after Langvatn *et al.* 1996). (*b*) Index of abundance of red deer in Norway (1965–1994; ■ = males, ○ = females). (*c*) The NAO index (1966–1994) is a single measure of winter severity in the northern Atlantic based on large-scale fluctuation of atmospheric pressure due to differences between sub-tropical and sub-polar surface pressures measured at Ponta Delgadas (Azores) and Akureyri (Iceland), respectively, during winter (December through March). The magnitude and direction (positive or negative) of the NAO index quantify the strength and orientation of mid-latitude westerlies across the Atlantic ocean. The trend in the NAO index was estimated by third-order polynomial least squares regression ($R^2 = 0.41$, $p < 0.01$).

quality of their forage have been well documented (Watson 1971; Clutton-Brock & Albon 1982; Langvatn & Albon 1986; Albon & Langvatn 1992). Hence, in this paper we investigate the potential effects of the NAO on phenotypic variation among cohorts of red deer in Norway, and document consequences of global climatic fluctuation for fecundity of cohorts of red deer on the Isle of Rum, Scotland.

2. MATERIALS AND METHODS

(*a*) *Red deer data*

We analysed two phenotypic traits of red deer that are indicative of growth and development: body weight (in kg), and the ratio of anterior mandible length to total mandible length (Langvatn 1977) (hereafter referred to as 'skeletal ratio'). The anterior portion of the mandible in red deer has growth priority over the posterior portion during growth *in utero* and the first year *post-partum* (Langvatn 1977). Thus, an individual animal experiencing poor conditions during foetal development and early growth will produce a short mandible, but, because investment was made in growth of the anterior portion, it will also display a high anterior to total ratio if growth conditions do not improve later in life. In contrast, if conditions for growth improve after growth priority has shifted to the posterior portion of the mandible, the anterior to total ratio will decrease as mandible length increases. Nonetheless, despite the potential for this skeletal ratio to change in response to variable environmental conditions at different ages, when the effect of age is controlled for, cohort mean skeletal ratios display consistent significant negative correlations with total mandible length and body weight in calves, yearlings and adults of both sexes (E. Post *et al.*, unpublished data). Thus, high skeletal ratios tend to correspond with low body weights and short mandibles indicative of compromised growth.

Data on body weights (minus head, skin, internal organs and blood) and skeletal ratios, as well as age (determined from dental cementum annuli (Reimers & Nordby 1968)), sex, and date and location of shooting were collected systematically by municipal wildlife boards throughout the range of red deer in Norway since 1971 (Langvatn *et al.* 1996) (figure 1*a*). We used analysis of covariance (ANCOVA) in a general linear model to calculate predicted values of both phenotypic traits of individual male and female calves, yearlings, and adults two years old and older, and then estimated cohort-specific means of each trait on the basis of predicted values. For calves and yearlings, ANCOVA was performed with cohort as the categorical independent variable, and predicted values from which means were estimated were statistically corrected for variation due to potentially significant covariates: date of

($\log_e$-transformed). In models for which skeletal ratio was the dependent variable, we used arcsine-transformed ratios of anterior : total mandible length. Date of shooting was treated as a continuous variable, and quantified as the day on which an animal was recorded as shot, starting with 'one' for 1 September and counting consecutively forward to 31 December, which was numbered as day 122. Location of shooting was coded numerically according to six geographic regions along north–intermediate–south and coastal–inland gradients as in Langvatn *et al.* (1996). The index of population abundance (figure 1*b*) was based on annual harvests relative to forested area in local regions reported by wildlife boards (distributed throughout the range of red deer in Norway) to the Norwegian Institute for Nature Research. Yearly values of abundance of red deer were derived by ANCOVA of total harvest by year, with location as a categorical covariate. These values therefore represent trends in abundance throughout Norway adjusted for regional differences in absolute abundance. Although abundance indices are displayed separately for males and females in figure 1*b*, we used a single index of total annual harvest in the ANCOVA in which cohort-specific mean body weights and skeletal ratios were estimated. We considered covariates significant when $p \leqslant 0.05$, based on stepwise ANCOVA in a general linear model in which the assumption of homogeneity of slopes of independent variables was confirmed by testing significance of interaction terms between independent variables. We compared inter-cohort variability in mean body weights and skeletal ratios of all three age classes of male and female red deer using *F*-tests of differences between coefficients of variation among means estimated from predicted values calculated in the general linear models (Zar 1984).

(*b*) *Climate data*

The NAO is a large-scale fluctuation in atmospheric mass between the sub-tropical North Atlantic region (centred on the Azores) and the sub-polar North Atlantic region (centred on Iceland) (Lamb & Peppler 1987). The state of the NAO determines the speed and direction of westerlies across the North Atlantic, as well as winter temperatures and precipitation in Atlantic coastal Europe, Scandinavia, and North America (Lamb & Peppler 1987; Hurrell 1995). The NAO is quantified annually for the months December through March by the NAO index (figure 1*c*). High, positive values of the NAO index are associated with relatively warm, moist winters in northern Atlantic coastal Europe, whereas low, negative values of the index are associated with unusually cold, dry winters in that region (Rogers 1984). Fluctuations in the NAO explain approximately 55% of the interannual variation in global temperatures (Schlesinger & Ramankutty 1994), and, over the past 75 years, the NAO accounts for 30–50% of the interannual variation in wintertime precipitation in Norway (Hurrell 1995).

We tested for correlations between cohort mean body weights and skeletal ratios of adult male and female red deer and the NAO index using Pearson product–moment correlation. We did not test for correlations between the NAO index and phenotypic traits of calves and yearlings because lack of systematic collection of data on body weights and skeletal ratios during years 1976–77, 1979–80, 1982 and 1987–88 led to low sample sizes ($n < 30$) in many cohorts. In testing for correlations between adult phenotypic traits and the NAO index, we used only cohorts for which mean estimates were based on 30 or more samples: cohort years 1966–1993. Because our time series on both phenotypic traits and the coefficients according to Bartlett (1946; see also Priestley 1981): $\mathcal{N}' = \mathcal{N}[(1 - a_1 a_2)/(1 + a_1 a_2)]$, in which $\mathcal{N}'$ is the corrected degrees of freedom, $\mathcal{N}$ is the number of paired observations in the two series, and a_1 and a_2 are the autocorrelation coefficients for the two series. This correction can result in a number of degrees of freedom greater than the number of paired observations if one series is negatively autocorrelated. Although this is statistically valid (Bartlett 1946), we constrained our estimates to ensure that $\mathcal{N}' \leqslant \mathcal{N}$ (see, for example, Myers *et al.* 1995). All statistical analyses were performed with Systat for Windows (Systat, Inc. 1992).

3. RESULTS

Body weights (table 1*a*) and skeletal ratios (table 1*b*) of males and females of all three age classes varied significantly among cohorts. Covariates for which estimates of cohort-specific mean body weights and skeletal ratios were corrected included month, location, and, for adults, age (table 1). In no case was population index a significant covariate of body weights or skeletal ratios ($p > 0.05$ in all instances); i.e., no density-dependence was indicated. For males, variation in body weight among cohorts was more pronounced in calves than in yearlings ($F_{(17,17)} = 5.27$, $p < 0.001$) (table 2). Body weights of male adults were, however, just as variable between cohorts as were those of male calves ($F_{(17,27)} = 1.53$, $p > 0.25$) and male yearlings ($F_{(17,27)} = 0.29$, $p > 0.25$) (table 2). For females, inter-cohort variation in body weight declined as animals aged (table 2). Female calves were more variable than female yearlings ($F_{(17,17)} = 7.0$, $p < 0.001$) and female adults ($F_{(17,27)} = 10.0$, $p < 0.0005$), although yearlings were not more variable than adults ($F_{(17,27)} = 1.57$, $p > 0.10$). In contrast, skeletal ratios of both males and females displayed consistent inter-cohort variability at all age classes ($p > 0.25$ in all instances) (table 2).

Observed inter-cohort variability of phenotypes of adult male and female red deer matched closely interannual fluctuations in the NAO index (figure 2). Body weights and skeletal ratios of adults of both sexes were correlated with the NAO index of the winter cohorts were *in utero* (figure 3) (males: $r_{\text{body weight}} = -0.32$, d.f. $= 24$, $p = 0.06$; $r_{\text{skeletal ratio}} = 0.46$, d.f. $= 28$, $p < 0.005$; females: $r_{\text{body weight}} = -0.36$, d.f. $= 24$, $p < 0.05$; $r_{\text{skeletal ratio}} = 0.39$, d.f. $= 23$, $p = 0.03$). For both males and females, however, skeletal ratios were more highly correlated with the NAO index than were body weights.

4. DISCUSSION

(*a*) *Climatic fluctuation and red deer phenotypes*

Phenotypic variability among cohorts of adult red deer documented in this study was related to climatic conditions encountered by their mothers during pregnancy. These climatic conditions were local to regions of Norway from which samples of red deer were taken, but were, in turn, governed by global atmospheric dynamics. Indeed, up to 50% of the interannual variability in winter precipitation in Norway during

(Sample sizes and test statistics for dependent variables (*a*) body weight, and (*b*) skeletal ratios of male and female red deer aged as calves, yearlings, and adults two years old and older. * $p<0.05$; ** $p<0.001$; *** $p<0.0001$.)

sex/age class	n	independent variable	significant covariates	F-ratio	d.f.	significance level
(*a*)						
males						
calves	1462	cohort		4.8	17	***
			date	213.9	1	***
			location	27.2	5	***
yearlings	3581	cohort		10.3	17	***
			date	4.3	1	*
			location	374.6	5	***
adults	5460	cohort		19.5	35	***
			date	124.6	1	***
			location	199.1	5	***
			age	2598	1	***
females						
calves	1113	cohort		3.8	17	***
			date	100.1	1	***
			location	8.7	5	**
yearlings	1449	cohort		4.0	17	***
			date	10.4	1	**
			location	135.3	5	***
adults	4370	cohort		5.1	40	***
			location	352.6	5	***
			age	411	1	***
(*b*)						
males						
calves	1520	cohort		2.3	17	**
			date	483.6	1	***
			location	64.7	5	***
yearlings	3664	cohort		8.8	17	***
			date	100.1	1	***
			location	247.8	5	***
adults	5512	cohort		12.1	35	***
			date	23.5	1	***
			age	1248	1	***
females						
calves	1140	cohort		4.1	17	***
			date	274	1	***
			location	13.8	5	***
yearlings	1488	cohort		4.8	17	***
			date	73.1	1	***
			location	99	5	***
adults	4586	cohort		11.5	39	***
			date	7.5	1	*
			location	40.3	5	***
			age	844.2	1	***

the years red deer cohorts were *in utero* is attributable to fluctuations in the NAO (Hurrell 1995). Furthermore, approximately 55% of the interannual variability in winter temperatures in Atlantic coastal Europe, including Norway, is due to the NAO (Schlesinger & Ramankutty 1994). Such abiotic factors as winter precipitation and temperature are likely to act on the development of red deer phenotypes *in utero* through influences of snow depth and thermal stress on the energy balance and nutrient allocation of pregnant females (Albon & Clutton-Brock 1988; Hobbs 1989). Additionally, in red deer, foetal development in the critical third trimester of gestation as well as growth *post-partum* are influenced by late winter/early spring snow melt and its effects on the timing of onset of plant growth (Langvatn & Albon 1986), duration of the plant growth season (Langvatn *et al*. 1996), and hence temporal and spatial availability and quality of forage plants (Albon & Langvatn 1992; Shaver & Kummerow 1992). Although the NAO index extends only through March, it is conceivable that conditions during extreme NAO years influence climatic conditions through the end of gestation and beyond parturition. Thus, the NAO may influence foetal development through abiotic factors affecting pregnant females, as well as early growth of calves through *calves, yearlings and adults*

(Within columns and sexes, values with the same letter, i.e. ^{a} or ^{b}, are not significantly different (F-test, $p > 0.05$).)

	body weight	skeletal ratio
males		
calves	2.2^{a}	4.1^{a}
yearlings	0.8^{b}	2.2^{a}
adults	$1.4^{a,b}$	1.6^{a}
females		
calves	2.5^{a}	2.7^{a}
yearlings	0.9^{b}	2.4^{a}
adults	0.7^{b}	1.9^{a}

environmental conditions such as persistent snow cover encountered after birth.

Red deer body weights were negatively correlated with the NAO index, and red deer skeletal ratios were positively correlated with it, for the winter preceding their birth (figure 3). Thus, warm, wet winters compro-

may indicate a lack of density-dependent effects on growth of red deer in Norway. Because it was based on hunter harvests compiled throughout Norway, however, the population index we used may not accurately reflect actual local densities of red deer. Hence, the lack of a significant density-dependent effect on growth of red deer in Norway must be interpreted with caution, especially given the strong density-dependent effects demonstrated for growth and reproduction of red deer in Scotland (Clutton-Brock *et al.* 1982; Albon *et al.* 1983*b*).

Although our analysis did not address the potential for compensatory growth in body weights and skeletal ratios under variable climatic conditions during the first summer *post-partum*, developmental disadvantages manifest during winter that affected growth *in utero* and immediately *post-partum* apparently persisted into adulthood (figure 2; table 2). In northern latitudes, warm winters with deep snow increase costs to pregnant females of foraging and locomotion, and thereby compromise the allocation of energy and nutrients to foetal development (Sæther 1985; Hobbs 1989;

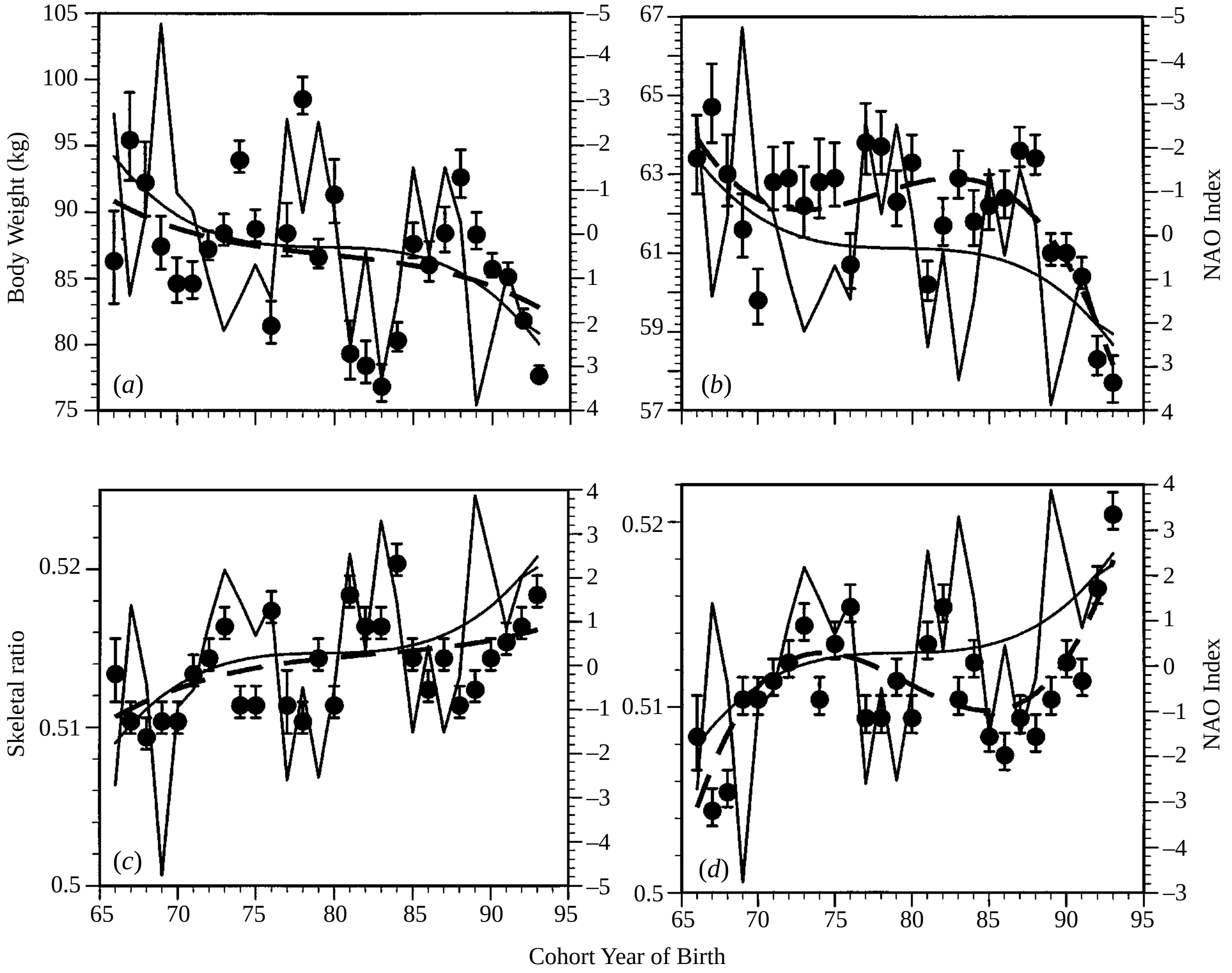

Figure 2. Adjusted least-squares means (±1 s.e.) by cohort of body weights (kg) (*a*,*b*) and skeletal ratios (anterior mandible to total mandible length) (*c*,*d*) of adult (two years old and older) red deer shot in Norway between the years 1971–1995. The NAO index is superimposed on each panel. Trends of the NAO (solid curves) and cohort-specific means (dashed curves) were estimated with third-order polynomial regression.

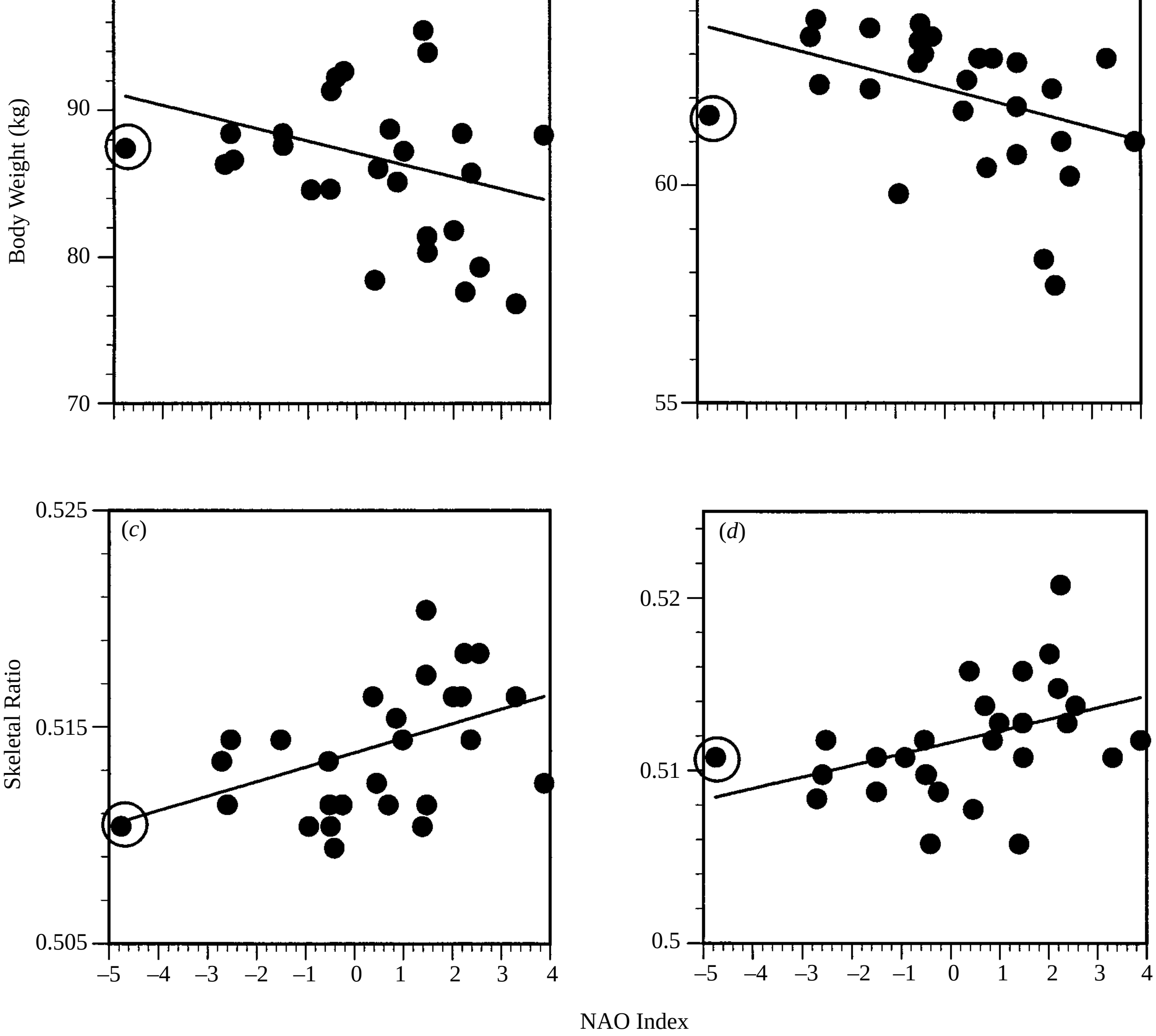

Figure 3. Relationships between the NAO index and body weights (kg) (*a*,*b*) and skeletal ratios (*c*,*d*) of adult (two years old and older) male (*a*, *c*) and female (*b*, *d*) red deer shot in Norway between the years 1971–1995. Cohort-specific mean body weights and skeletal ratios are plotted against the NAO index of the winter cohorts were *in utero*, for cohorts born in years 1966–1993. The circled point on each plot corresponds to the NAO index for 1969, which is the lowest value of the entire 133-year series, and which appears in most cases to be an outlier. Station data upon which the 1969 value is based are, however, reliable (J. Hurrell, personal communication).

Langvatn *et al.* 1996). Additionally, warm winters lead to early and rapid snow melt, and, consequently, to early onset and rapid progression of the plant growing season (Albon & Langvatn 1992; Shaver & Kummerow 1992). Such conditions present red deer with a curtailed period of access to highly nutritious and digestible forage compared to colder years when plant growth is prolonged (Langvatn *et al.* 1996; Merrill & Boyce 1991). This in turn could adversely affect energetically expensive lactation and hence post-natal growth of calves.

(*b*) *Consequences of global climate change for fitness of red deer*

Climate-induced variation in phenotypes of cohorts poses consequences for fitness of individuals born into cohorts characterized by conditions in preceding winters. For female red deer at age two years in Norway and three years on the Isle of Rum, the probability of calving was negatively related to spring temperatures in the year of their birth (Langvatn *et al.* 1996). Furthermore, in red deer, body size and weight of rutting males determine access to females (Clutton-Brock *et al.* 1982), and female body weight (Langvatn *et al.* 1996) and condition (Clutton-Brock *et al.* 1982) directly influence age-specific probability of ovulation. Hence, cohorts of males carried *in utero* during, and born following, winters characterized by a high value of the NAO index suffered compromised growth for which they were unable to compensate because inter-cohort variability in body weights did not decrease as calves matured (figure 2, table 1). As a result, such males are likely to suffer depressed lifetime reproductive success due to their inability to outcompete larger, heavier males born into cohorts winters may suffer delayed sexual maturity as they are compelled to grow over more seasons before attaining a reproductively critical body weight (Langvatn *et al.* 1996), and, subsequently, contribute less to future generations because of an abbreviated reproductive life span (McCullough 1979). Moreover, offspring born to females of physically light-weight cohorts also exhibit low birth weights (Albon & Clutton-Brock 1988; Albon *et al.* 1987; Clutton-Brock *et al.* 1988) and reduced fitness (Albon *et al.* 1987), in addition to suffering from depressed maternal care (Bowyer 1991). Ultimately, abiotic factors such as winter severity during 'high' NAO years may act as population limiting factors through their effects on over-winter survival and offspring viability (Watson 1971; Clutton-Brock & Albon 1982; Mech *et al.* 1987; McRoberts *et al.* 1995).

Implications for the influence of prevailing climatic regimes on cohort fitness are apparent from the observation that fecundity of female red deer in Norway was negatively related to winter precipitation while they were *in utero* (Albon *et al.* 1992). Indeed, our analysis of published data on cohort-specific calving rates by female red deer at age of first reproduction (Langvatn *et al.* 1996) and as milk hinds (Albon *et al.* 1987) on the Isle of Rum indicates that fecundity of cohorts was negatively correlated with the NAO index for the winter these females were *in utero* (3-year-olds: $r = -0.34$, d.f. $= 20$, $p = 0.07$; milk hinds: $r = -0.61$, d.f. $= 12$, $p = 0.01$). Thus, global climatic variation has pronounced long-term effects on phenotypic variation, survival and reproductive success of large herbivores such as red deer. Furthermore, climatic fluctuation influences growth and development *in utero* to produce persistent cohort variability among adults (figure 2). The persistence of phenotypic variability among cohorts suggests that global climate change may induce fluctuations in populations of northern ungulates (see Albon *et al.* 1991).

5. CONCLUSIONS

Growth, development, and fecundity of ungulates in north-temperate regions are influenced by climatic conditions experienced by their mothers during pregnancy. Local conditions during winter in northern Europe and Scandinavia are, in turn, related to global atmospheric processes of the NAO. Hence, large-scale climatic dynamics have a documented effect on the biology of local populations of terrestial mammals. The recent trend of increasingly warm winters in northern Europe and Scandinavia (Hurrell 1995; figure 1*c*), may therefore elicit a phenotypic shift of reduced body size of red deer, and perhaps other ungulates, in those regions. Furthermore, because fecundity is related to body size in red deer (Clutton-Brock *et al.* 1982; Langvatn *et al.* 1996), climate change may also lead to declines in reproductive success of red deer in northern latitudes, and, through effects on offspring survival (*sensu* Albon & Clutton-Brock 1988; Albon *et al.* 1987), may ultimately lead to population declines.

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