Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier valley, Norway

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The growth of individuals and populations can be affected by both density-dependent and density-independent factors. Severe environmental conditions typically affect young and very old individuals more than prime-aged individuals, so that limiting factors such as climate and density frequently interact with the sex- and age-structure of the population. For roe deer *Capreolus capreolus* explicit analyses of growth rates of individuals and populations at northern latitudes are rare. In this article, we present the first analysis of a 17-year record of body weight data (N = 286) and harvest statistics (a proxy for population size) from the Lier valley, Norway. We tested whether climate (winter and spring) and population density affected individual body weight in autumn and the growth rate of the population as indicated by harvest statistics. We found that population growth rate in the Lier valley was negatively affected by increasing snow depth during winter. There was also a tendency for body weight to be lower after snowy than after less snowy winters. We found no significant effect of spring temperature or population density, though parameter estimates of both were negative. Our findings provide quantitative data supporting the 'common knowledge' that winter is the critical period for roe deer at northern latitudes, and that population density is unlikely to be a regulating factor in most inland areas of Norway with today's low population densities.

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Large herbivores in the strongly seasonal environments at northern latitudes use the summer season for the most energy-demanding parts of reproduction (last part of gestation and the lactation period) as well as for growth and for building up the body reserves needed to survive the coming winter (e.g. Mautz 1978). Climate may thus affect northern ungulates through winter conditions affecting weight loss and survival directly, and/or indirectly through foraging quality during the summer season (Klein 1965, review in Weladji et al. 2002). Density-dependent processes often affect ungulate populations, and may interact with the climatic effect. Typically, high density may

increase the effect of severe winter conditions (Sauer & Boyce 1983, Portier et al. 1998, Coulson et al. 2001).

The proximate mechanisms by which climate affects ungulate populations vary between regions and species (review in Mysterud et al. 2003). For the Soay sheep *Ovis aries* in the St. Kilda archipelago, Scotland, wetting of the pelage due to cold winter rain causes chilling, and increased thermoregulatory costs induces high levels of mortality (Catchpole et al. 2000, Coulson et al. 2001). In areas with colder climate, snowy winters leading to increased costs of locomotion (Parker et al. 1984) and also restricting access to the field layer are regarded as the most severe conditions. This coincides with a period of generally low availability and quality of forage (Mautz 1978, Parker et al. 1984), and cold temperatures also increase the risk of hypothermia (Moen 1973, Moen 1976, Mautz 1978, Schmitz 1991). Such conditions are most severe for small cervids, such as white-tailed deer *Odocoileus virginianus* in North America and roe deer *Capreolus capreolus* in Scandinavia (Holand et al. 1998), since they are not well adapted to snow (Telfer & Kelsall 1984), lose relatively more energy due to a large surface area to volume ratio and are not able to utilise very coarse food (Demment & Van Soest 1985). Despite its negative effect on winter survival, increased snow depth may increase spatial variability in plant phenology in summer. Since newly emergent plants are of higher quality, this may lead to a longer period of access to high-quality forage and, thus, higher individual body weight the next autumn (Langvatn 1994, Mysterud et al. 2001).

Roe deer are distributed over most of Europe and reach the northernmost point of their range in Norway (Andersen et al. 1998). Variation in life history and population dynamics has been reported from a number of studies in areas with mild climate (e.g. Gaillard et al. 1993, 1996, Hewison et al. 1996, Focardi et al. 2002, reviewed in Andersen et al. 1998). Theory suggests that climate is expected to play a more important role in population limitation at distribution edges, and studies of roe deer performance at northern latitudes with severe climate are needed. Snow depth is an important determinant for roe deer diet (Cederlund et al. 1980) and habitat use (Mysterud et al. 1997, Mysterud et al. 1999). Increased red fox *Vulpes vulpes* predation on roe deer was found during a severe winter compared to a mild one (Cederlund & Lindström 1983). However, there has been no formal statistical testing of an effect of winter severity on population growth rate. In order to fill this gap, we present analyses of new data on body weight of 286 roe deer and on population growth rates as indicated by harvest statistics for the period 1985-2001 in the Lier valley, Norway. We tested the following hypotheses:

H_1; the winter severity hypothesis: We predict a negative effect of winter severity (snow depth) on growth rates of both individuals (Cederlund et al. 1991) and populations (Cederlund & Liberg 1995). Clearly, a negative effect of snow depth on individual weight may provide a link to the population-level responses.

H_2; the early summer climate hypothesis: Based on studies of moose *Alces alces*, a warm early summer is expected to give low forage quality and hence lower autumn body weight in southeastern Norway (Sæther 1985, Bø & Hjeljord 1991).

H_3; the density hypothesis: We predict reduced individual and population growth rates at high density (Fowler 1987, Gaillard et al. 2000), as has earlier been found for roe deer in Sweden (Kjellander 2000).

H_4; the interaction hypothesis: The effect of winter severity is expected to be (H_{4a}) higher at high population density (e.g. Coulson et al. 2001). Severe environmental conditions, either due to severe climate or high density, are predicted to affect (H_{4b}) younger (and very old) individuals more strongly, and (H_{4c}) males more than females (e.g. Coulson et al. 2001).

Material and methods

Study area

The main study area (near Sylling) is located in the Lier valley in the municipality of Lier in the county of Buskerud, southern Norway (between 59°45'-60°00'N and 10°05'-10°20'E). Most of the area is forested and situated within the boreonemoral region (Abrahamsen et al. 1977). Vegetation is varied and dominated by Norway spruce *Picea abies* mixed with Scots pine *Pinus sylvestris* on the drier and poorer locations. The forest has been commercially managed, and there are several clearcuts of varying sizes within the study area. Along the valley bottom on richer soil, deciduous forest is dominant, fragmented by small, cultivated fields (Kjøstvedt et al. 1998). The topography is extremely hilly. On a coarse scale it rises from lake Holsfjorden at 63 m a.s.l. to > 500-600 m a.s.l. within a few kilometres, and is also variable at a more local scale (see Mysterud & Østbye 1995a, Mysterud 1999, Mysterud et al. 1999 for a further description of the study area).

Roe deer data

Data on sex, body weight and date of harvesting were collected by Eivind Østbye during the period 1985-2001 for roe deer harvested in the hunting area of a large hunting team (Vestre Sylling og Øverskogen Rådyrlag). The main hunting season is 25 September-23 December (1

Table 1. Sample size and age composition of roe deer from the Lier valley, Norway, collected during 1985-2001.

Age category	0	1	2	3	4	5	6	7	8	9	10	12	Total
Females	57	45	20	10	7	2	2	2		1	1	1	148
Males	52	44	16	14	13	6	1		1	1			148

October-23 December during the first part of the time series). A few males are shot during the special buck season (16 August -23 December; 21 August-23 December during the first part of the time series). In this article, we only report carcass weight (i.e. live weight minus head, skin, viscera, bendable blood and metapodials). Dressed weight is about 58% of live weight and correlates closely with total weight (E. Østbye, unpubl. data; see Wallin et al. 1996 for moose). Sample sizes split by age and sex are given in Table 1. Fawns were aged based on tooth eruption patterns (i.e. only four or five cheek teeth; Cederlund & Liberg 1995). The Matson laboratory in the USA aged individuals older than fawns by counting annuli in the cementum of the first incisor (e. g. Hamlin et al. 2000), but do note that this method has not yet been formally tested on roe deer from Scandinavia. In addition, data on harvest size, hunter effort (number of hunters, hunter days and hours) and number of 'observed deer' (adjusted for effort, including contact with deer by the dog, but not always seen) were collected for all years.

Data on harvest at the scale of the Lier municipality, termed population scale here, were also retrieved from the local wildlife authorities ('viltnemnda') for the years 1984-2000. In the following, we use harvest size as an index of population size, thus making the critical assumption that harvest size provides a fair proxy of changes in the population size of roe deer. It is important to know that the general hunting success for roe deer in Norway has been very low. Actual harvest relative to quota has been ~ 20%, in clear contrast to moose for which the success rate has been ~ 80% (Statistics Norway 2002). For Lier, the success rate was on average 40.5% for the years 1984-2000. Quotas for roe deer are set quite arbitrarily (no population census), are changed rather infrequently, and in many ways roe deer are currently not properly managed in Norway. To further substantiate the use of total harvest as a proxy for population size, we will also assess the correlation between year-to-year changes in harvest quotas and actual harvest, and also assess whether environmental factors affect changes in quota (scale of Lier municipality) and/or hunter effort (scale of detailed study area, where body weight is collected). We separate hunter effort in a numerical response (number of hunters) and a functional response (time effort devoted by individual hunters). The data on hunter effort form

the basis for sharing the meat in this particular hunting team. There is a strong social control, since most hunting occurs in groups, and it is easy to check if someone tries to cheat by adding more hours. This was done each year in all years by Eivind Østbye, who also participated in well above 95% of the hunts. We therefore regard these data as highly reliable.

Climate data

Data on monthly averages of precipitation, temperature and snow depth were obtained from a nearby meteorological station (DNMI 18700 Blindern, 94 m a.s.l.). We also retrieved data on the North Atlantic Oscillation (NAO), both the commonly used station-based winter (December-March) index (Hurrell 1995) as well as the Principal Component Based seasonal indices (Hurrell et al. 2003, Stenseth et al. 2003). As we were mainly interested in winter vs spring conditions, we used the NAO for spring in addition to the winter NAO.

Statistical analyses

The relationships between climatic variables and the different seasonal NAO indices were explored using simple Pearson correlations. We analysed the growth rates $(\ln[N_{t+1}/N_t])$ of the harvest at the scale of the Lier municipality with linear models (Crawley 2003).

Variation in body weight was analysed with a combination of models. We first used generalised additive models with smoothing splines to explore possible non-linear relationships graphically (Hastie & Tibshirani 1990; see application in e.g. Mysterud et al. 2001). Initial modelling with additive models showed that weight was fairly stable from three years of age and older. As data on older individuals were scarce, we used fawns, yearlings, two-year olds and ≥ 3-year olds as age categories in further (linear) modelling. A logarithmic transformation [ln(weight)] of body weight was used to obtain residuals with constant variance. To help us select an appropriate model to test our hypotheses, we used the Akaike Information Criterion (AIC; Burnham & Anderson 1998, Johnson & Omland 2004). The model with the lowest AIC value is the most parsimonious model, i.e. the best compromise between explaining the maximum possible of the variation and using as few parameters as possible. We used linear models until this stage. We also ran the chosen model as a linear mixed-effects

model including 'year' as a random effect (Lindsey 1999, see details in Milner et al. 1999). Since all data derive from autumn, we used climatic covariates from the preceding winter and spring.

All analyses were performed in S-Plus version 6.2 (Venables & Ripley 1994, Crawley 2003).

Results

Correlation among explanatory variables

The winter NAO was positively correlated with temperature (for 1985-2001: N = 17; January: r = 0.618, P = 0.008; February: r = 0.608, P = 0.010; March: r = 0.691, P = 0.002), while there was a weak, non-significant negative correlation with snow depth (January: r = -0.099, P = 0.706; February: r = -0.217, P = 0.404; March: r = -0.304, P = 0.236) and a weak, non-significant positive correlation with precipitation (January: r = 0.043, P = 0.868; February: r = 0.272, P = 0.290; March: r = 0.150, P = 0.564).

The spring NAO was also very weakly, non-significantly positively correlated with temperature (April: r = 0.182, P = 0.485; May: r = 0.336, P = 0.187), but not consistently with precipitation (April: r = 0.216, P = 0.406; May: r = -0.331, P = 0.195).

The number of 'observed deer' was not correlated with winter NAO index (r = 0.150, P = 0.553), spring NAO index (r = 0.222, P = 0.376), snow depth (January: r = -0.351, P = 0.167; February: r = -0.139, P = 0.595; March: r = -0.124, P = 0.636), temperature (January: r = 0.302, P = 0.238; February: r = -0.071, P = 0.785; March: r = 0.365, P = 0.150; April: r = -0.189, P = 0.468) or precipitation (January: r < 0.001, P ~ 1.000; February: r = 0.077, P = 0.769; March: r = -0.157, P = 0.548; April: r = 0.446, P = 0.073; May: r = 0.131, P = 0.616), except for temperature in May which was positively correlated with the number of 'observed deer' (r = 0.558, P = 0.020).

Individual level

Body weight of roe deer increased until about three years of age in both sexes (Fig. 1); after that it remained fairly stable and roe deer three years old and older were subsequently pooled in further analyses. There was a remarkably large variation in carcass weight of fawns the first autumn; it varied from 4.7 kg to 14.5 kg with a global average of 10.7 kg. The carcass weight of yearlings varied between 12.3 and 20.3 kg with a global average of 15.8 kg, of 2-year olds from 12.9 to 19.5 with a global average of 16.0, and of ≥ 3-year olds from 13.8 to 22.3 kg with a global average of 17.6 kg (see Fig. 1). Sexual

differences were minor. The most parsimonious model included in addition to age category and sex (and their interaction), both snow depth in March, winter NAO, temperature in May and population density (i.e. the number of 'observed deer') and explained 74.1% of the variation. However, in a linear model, only the effects of snow depth and NAO were significant, and both factors negatively affected body weight. The effect of May temperature and population density was not significant (but the parameter estimates were negative for both; Table 2). As these factors were positively correlated (see above), we also ran models without including these two factors. Removing the density factor made the effect of May significant (T = -2.046, P = 0.042), but density did not become significant (T = -0.794, P = 0.427) when excluding May temperature. When using a more conservative linear mixed effects model (controlling for dependency of observations from the same year), snow depth (l.s. estimate = -0.0015, SE = 0.00060, df = 13, T = -2.492, P = 0.027) and NAO (l.s. estimate = -0.0135, SE = 0.00470, df = 13, T = -2.873, P = 0.013) remained significant, but were not significant if the effect of May temperature and population density were retained in the
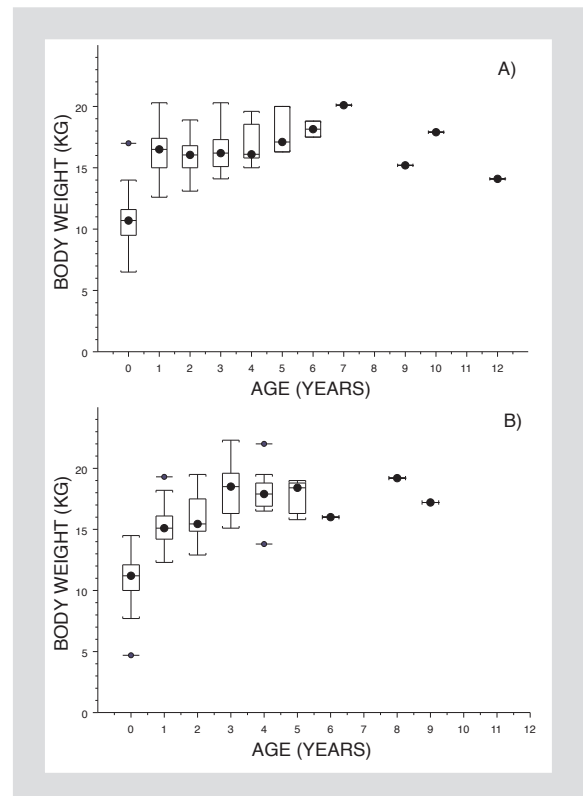

Figure 1. Box plot of body weight as a function of age in female (A) and male (B) roe deer in the Lier valley, Buskerud, Norway.

Table 2. Parameter estimates from the most parsimonious model of body weight from linear models. Note that effect of NAO and snow depth did not remain significant in a linear mixed effects model (see text).

Parameter	L.s. estimate	SE	T	P
Intercept	2.5376	0.0806	31.498	0.000
Age 1 year vs 0 years	0.4032	0.0268	15.026	0.000
Age 2 years vs 0 years	0.3952	0.0357	11.072	0.000
Age 3-12 years vs 0 years	0.4605	0.0319	14.457	0.000
Sex	0.0340	0.0252	1.349	0.179
Snow depth - March	-0.0013	0.0006	-2.243	0.026
NAO winter	-0.0099	0.0048	-2.077	0.039
Temperature - May	-0.0115	0.0077	-1.484	0.139
Density ('observed deer')	-0.1723	0.9175	-0.188	0.851
(Age 1 year vs 0 years)*sex	-0.0723	0.0376	-1.923	0.056
(Age 2 years vs 0 years)*sex	-0.0456	0.0511	-0.894	0.372
(Age 3-12 years vs 0 years)*sex	0.0160	0.0440	0.363	0.717

model as well (snow depth: T = -1.585, P = 0.144; NAO: T = -1.704, P = 0.119). Taken together, we found at least some evidence in favour of H_1, as increasing winter snow depth was negatively correlated with body weight. Parameter estimates for May temperature were not significant, and it therefore does not provide strong support for H_2, but since the parameter estimates were negative, our results are at least consistent with H_2. We can reject H_3 and H_4, as density was not significant and as no interaction term entered the most parsimonious model.

Population level

The most parsimonious model included only snow depth and April temperature and explained 58.6% of the variation, but several models differed by < 2 AIC units and hence were almost as good (Table 3). Consistently in all models, population growth of roe deer in Lier, as indicated by the harvest record, decreased significantly with increasing snow depth, thus supporting H_1 (see Table 3 and Fig. 2). April temperature was also included in the most parsimonious model, and tended to have a negative effect on population growth rates (see Table 3) and was thus consistent with H_3. Adding a year term to the model led to a slightly less parsimonious model, and the year term was not significant (l.s. estimate = -0.0162, SE = 0.0145, T = -1.119, P = 0.285). When including year, the effect of snow depth remained significant (l.s. estimate = -0.0141, SE = 0.0032, T = -4.403, P < 0.001), whereas the effect of April temperature was reduced and no longer close to being significant (l.s. estimate = -0.0587, SE = 0.0491, T = -1.196, P = 0.255). Density was not included in the most parsimonious model, so we rejected H_3.

There was no correlation between change in harvest

Table 3. Parameter estimates from the most parsimonious model of harvest size growth rate (A; $\ln[N_{t+1}/N_t]$ as a proxy for population size) for roe deer in the Lier valley during 1984-2000. For comparison, we also ran a similar model with the quota size at the scale of the Lier municipality (B), number of hunters (C) and time effort per hunter at the scale of the smaller study area (from where data on body weight derive; D), to show that the result was not a result of changes in these potential confounding factors.

| Parameter	L.s. estimate	SE	T	P
A) Harvest size				
Intercept	0.7127	0.2458	2.900	0.012
Snow depth - March	-0.0128	0.0030	-4.248	0.001
Temperature - April	-0.0840	0.0440	-1.911	0.078
B) Quota size				
Intercept	0.1499	0.1562	0.959	0.355
Snow depth - March	-0.0012	0.0019	-0.639	0.534
Temperature - April	-0.0167	0.0279	-0.599	0.560
C) Number of hunters				
Intercept	-0.1173	0.2101	-0.559	0.588
Snow depth - March	-0.0041	0.0031	-1.328	0.211
Temperature - April	0.0449	0.0399	1.123	0.286
D) Time effort per hunter				
Intercept	0.2867	0.2295	1.249	0.238
Snow depth - March	-0.0019	0.0034	-0.553	0.591
Temperature - April	-0.0541	0.0436	-1.239	0.241
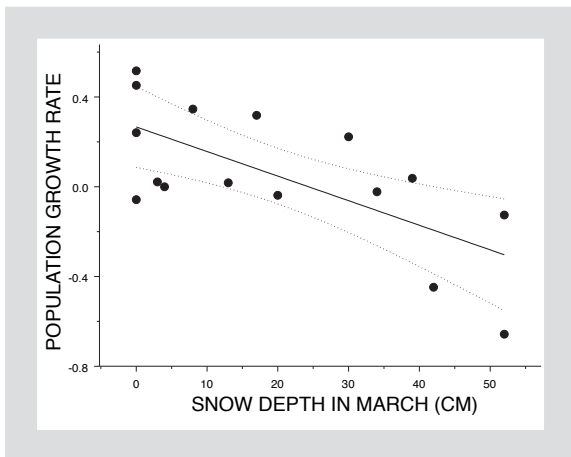
Figure 2. Population growth of roe deer in the Lier valley during 1984-2000 as a function of snow depth in March.

quota and actual harvest (r = 0.172, P = 0.523, N = 17). Furthermore, the annual change in quota or hunter effort was not related to snow depth or temperature in April (see Table 3). Managers thus did not respond to the severity of the previous winter when setting quotas for the coming autumn. We can also conclude that hunter effort was not the cause of the negative relationship between change in harvest size and snow depth. Together, this indicates that harvest size most likely reflects changes in population size.

Discussion

Our study documented that snow depth is limiting the growth rate in a roe deer population in the Lier valley, Norway. This may be regarded as 'common knowledge' among ecologists in Scandinavia (Cederlund & Liberg 1995). There was also a negative effect of snow depth on body weight, but whether a significance level of P = 0.05 was reached was somewhat dependent on other factors included when running a conservative linear mixed effects model controlling for dependency of observations from the same year. Even though more data clearly would reveal more details about the relative role of the different limiting factors, our study at least documents that winter conditions are among the most important for roe deer in inland habitats of Norway.

Body weight of continental roe deer varied considerably among cohorts (Pettorelli et al. 2002). Frequently, such variation is related to spring conditions (Pettorelli et al. 2003). Spring is considered an important time since females are in late gestation and will soon enter the energetically costly period of lactation (Clutton-Brock et al.

1989). However, there was no significant effect of spring conditions in our study, but for both body weight and population growth rate the not quite significant effect of spring temperature was negative. At least we cannot reject the hypothesis that a slow phenological development in spring is favourable in inland populations (H$_3$), as has been found for moose (Sæther 1985, Bø & Hjeljord 1991).

The roe deer population in Norway and Sweden went through an increase phase during the mid-1980s and then a decrease phase after 1994 (Statistics Norway 2002). This was partly due to the eradication of the red fox population by a sarcoptic mange epidemic (Lindström et al. 1994, Kjellander & Nordström 2003). Weak density dependence in body weights has been documented from Norway (Andersen & Linnell 2000), but only in the island population on Storfosna, Sør-Trøndelag, reaching about 50 deer/km^2, some 5-10 times the density most common for inland populations in southeast Norway. In Sweden, where inland densities are generally higher than in Norway, density dependence was evident in both reproduction and mortality (Kjellander 2000). Prior to our study, no study has evaluated whether there was significant density dependence in inland roe deer populations in Norway. Even though we found no effect of density on body weight or population growth rates, it has been shown during the same period that the relatively high roe deer density during 1985-1993 led to no recruitment of the endangered yew *Taxus baccata* within nature reserves in Lier (Mysterud & Østbye 2004) due to very heavy browsing by roe deer (Mysterud & Østbye 1995b). Therefore, the absence of strong density dependence in body weight is no guarantee that negative impact on plants can be avoided. Monitoring the body weight of roe deer may thus not be sufficient to evaluate the impact of roe deer population on biodiversity.

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Appendix I

As recommended by Burnham & Anderson (1998), we present the exact model selection procedure that was used. The model with the lowest AIC values was then chosen for the parameter estimation used for testing the hypotheses.

Appendix Table I. Model selection procedure for the analysis of (ln) body weight. x = term included in model.

Age category	Sex	Julian date	Snow depth - March	NAO-winter	NAO-spring	Temperature - April	Precipitation - April	Temperature - May	Precipitation - May	Population density	Year	Age*Sex	Age*Julian date	Age*snow depth	Sex*snow depth	Age*NAO-winter	Sex*NAO-winter	Age*NAO-spring	Age*Density	Sex*Density	AIC	ΔAIC
x	x											x									-287.542	48.764
x	x	x										x									-270.802	65.504
x	x	x										x	x								-273.255	63.050
x	x		x									x									-292.777	43.528
x	x		x									x		x							-295.671	40.635
x	x		x									x		x	x						-299.426	36.880
x	x		x	x								x		x	x						-311.279	25.026
x	x		x	x								x		x	x	x					-310.478	25.828
x	x		x	x								x		x	x		x				-309.481	26.824
x	x		x	x	x							x		x	x						-309.339	26.967
x	x		x	x	x							x		x	x			x			-304.712	31.594
x	x		x	x		x						x		x	x						-310.578	25.727
x	x		x	x				x				x		x	x						-309.312	26.993
x	x		x	x					x			x		x	x						-313.938	22.367
x	x		x	x				x	x			x		x	x						-312.250	24.055
x	x		x	x				x	x	x		x		x	x						-330.432	5.873
x	x		x	x				x	x	x	x	x		x	x						-328.586	7.719
x	x		x	x				x	x	x	x	x		x	x				x		-327.469	8.836
x	x		x	x				x	x	x		x		x	x					x	-328.611	7.695
x	x		x	x				x	x	x				x							-335.210	1.095
x	x		x	x				x	x	x											-336.305	0.000
x	x		x					x	x	x											-333.086	3.219
x	x	x						x	x	x											-333.826	2.480

Appendix Table II. Model selection procedure for the analysis of population (harvest) growth rates. x = term included in model.

Snow depth-March	NAO-winter	NAO-spring	Temperature - April	Precipitation - April	Temperature - May	Precipitation - May	Population density	Year	AIC	Δ AIC
x									2.427	1.961
x	x								4.320	3.854
		x							11.889	11.423
x		x							4.260	3.795
x			x						0.466	0.000
x			x	x					2.458	1.992
x			x		x				2.146	1.680
x			x			x			2.162	1.696
x			x				x		2.419	1.953
x			x					x	0.878	0.412
			x					x	14.259	13.793